Przemysław Busse

Results of ringing of European *Corvidae*

Wyniki obrączkowania ptaków krukowatych, *Corvidae* Europy

Итоги кольцевания вороновых, *Corvidae* в Европе

[With 36 maps, 13 tables and 4 diagrams in text]

INTRODUCTION

Over sixty years of bird-ringing in Europe has supplied us with an enormous scientific material in the form of tens of thousands of recoveries. A lot of material discussing the data obtained has been published. However, a considerable part of such publications contains material collected in limited areas, usually one country, and sometimes from one geographical region (e.g. Scandinavia — Rendahl, 1960; British Isles — Goodacre, 1959). Analytical publications covering the whole area of Europe have not been, so far, numerous and they have been mainly concerned with individual species (Stechov, 1938; Verheyen and Grelle, 1950; Verheyen, 1951; Rydzewski, 1956), and only exceptionally with whole families (Ashmole, 1962). The analysis of migratory habits of closely related species enables us to carry out comparative investigations which would yield more general biological regularities. A wide analysis concerned with the migratory habits of *Corvidae*, seems to be particularly interesting, as this family shows considerable differences in this respect, well demonstrated by the results obtained by ringing in Poland (Busse, 1963.)

METHODS

An initial preparation of the material consisted in collecting of all the available recoveries from European literature. Each recovery was given a separate card which later facilitated the task of filing them in the most suitable way. After completing all the data and putting them down on a card (co-ordinates of the ringing and recapture places, length of life) the recoveries were filed, separately for each species, according to the geographical data of the ringing place. In order to do that, I divided the whole area of Europe into sectors, in the majority of cases into rectangles whose sides were: 10° longitude and 5° latitude (Map 1). To avoid an artificial division, inevitable when rigorously following the principle mentioned above, I had to depart
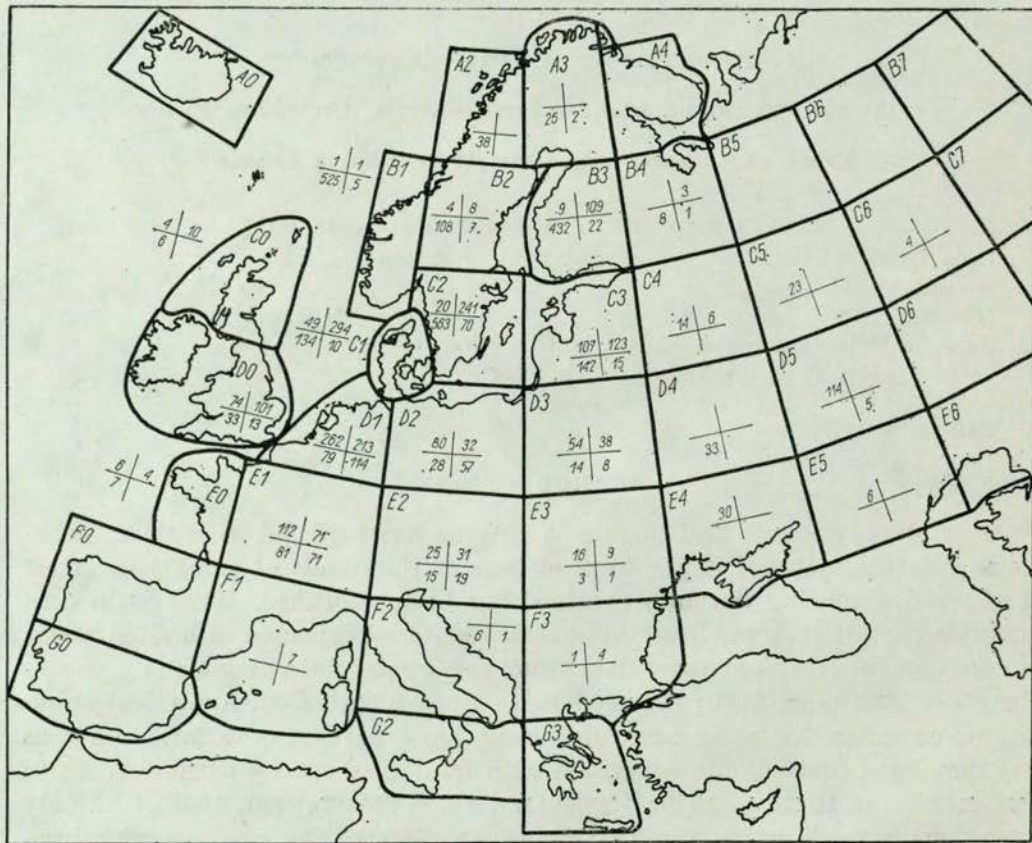
Map 1. Working division of Europe into sectors, according to which the material was analysed. In the cross-figures the number of recoveries of birds ringed in the sector is given:

C. frugilegus L.	*C. monedula* L.
C. corone L.	*G. glandarius* (L.)

from it in certain cases taking into account the separateness (e.g. Denmark) or unity (e.g. southern Norway) of individual areas. Each sector was marked by a combination of letters (stripes running parallely) and figures (columns placed meridionally). Within a species recoveries of birds ringed were worked out separately in each sector. The initial work consisted in drawing maps on which only recoveries recorded at distances longer than 100 kms and during the periods of migration and wintering were plotted. Only recoveries of birds ringed in the breeding season were taken into account for the purpose of plotting them on the maps. Separate maps were drawn on the basis of recoveries of birds ringed in the course of their migration. Besides, a number of recoveries concerning birds, from each sector, were tabulated: 1) the average date of ringing in the sector — the average of all dates of bird-ringing in nests; this characterizes the distribution of breeding of the species during the season in the given sector; 2) the distribution of mortality in the course of the annual cycle; 3) length of life; 4) how far the birds departed from the place of birth in the first and subsequent summer periods; 5) how far the birds departed from the place of birth in the winter period; 6) how far all the birds that were recaptured departed from the place of birth in the period of migration and wintering; I have taken here into account the age of each of the birds (young — old) and the distance that it had covered.

The period from the beginning of December to the end of February was taken to be the period of wintering. The period of migration includes the following months: October–November, and March–the middle of April. The division into "young" and "old" birds was carried out according to the criteria which have already been published (BUSSE, 1963) — as "old" birds I treated all such individuals which died after a period longer than 0–11–29 (11 months, 29 days) from the day when they had been ringed in the nest.

The analysis of the migratory habits of each species was carried out in the following stages:

1) The preliminary data on the winter quartes of European birds were plotted on a general map according to working maps of all the sectors. Separate groupings or evident crowding of recoveries enabled to mark out the more important winter quarters. Such winter quarters were allotted capital letters of the Latin alphabet.

2) The next operation was to define clearly the breeding ranges of all the birds wintering in given winter-quarters. After marking on the map the place of birth of the birds I added an arrow (sometimes with a description) indicating the area where the bird wintered. Consequently, if birds coming from the same breeding range wintered in different areas, the arrows on the map pointed in various directions from one spot. A map drawn up in this way showed areas from which all birds migrated to the same winter quarters, and such areas from which their inhabitants migrated in various directions. Areas from which birds migrated to more than one winter quarters are treated in

the present paper as zones where two or more populations mixed (i.e. populations from the point of view of migrations), and not as transitional zones between the populations. The point of view accepted turned out to be more in accordance with the relations prevailing within the family *Corvidae*, than the opposite one. On the basis of a map drawn up in such a way, the range of the species was divided into areas inhabited by separate migratory populations (or groups of populations), later on marked by letters according to the symbol of the winter quarters occupied.

3) After determining the areas occupied by individual migratory populations I checked the migrational uniformity of the populations so marked out: the whole range inhabited by the populations was divided into smaller sections and then I determined more precisely the winter quarters of birds coming from those areas. It turned out in certain cases that there existed even more subtle intrapopulational differentiation than it seemed at the beginning. As far as certain areas were concerned the analysis was complicated by the fact that there occurred migrational barriers (e.g. sea).

4) The method of determining tendencies in the evolutional changes of migration habits shown by a population, turned out to be useful when I wanted to clear up certain problems.

This method embraces the well known law of biogenesis by HAECKEL wherein he postulated that the individual development is a shortened reflection of the phylogenetic development of species. This law is usually applied when discussing anatomorphological changes of an animal, particularly when embrionic development is concerned. However, the way in which we determine the age of certain species of birds according to the size of their primaries (CORNWALLIS, 1963)* makes it possible to widen the law so that it embraced post-embrional development. Simultaneously it should be stressed that the well known theories that migration routes of certain birds are a replica of the ways in which the species was distributed, constitute in fact (although the fact has never been particularly emphasised) an application of HAECKEL'S law in the field of migration. In the method discussed, when concluding about former migratory habits of a population, I took into account the existing differences in the tendencies to migrate of one-year-old and older birds. It is possible here to come across the following three contingencies: a) young birds cover longer distances than old birds; b) young birds cover shorter distances than old birds; c) migratory tendencies do not depend on the age. The tables presented below illustrate the cases mentioned (examples taken from the material of the present paper) (Tab. 1). It is possible to assume, in the first case, that there occurs a considerable shortening of the migration routes (young birds migrate

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* First primaries of young birds are considerably longer than those of older birds, and this reflects the history of development of birds (as it is well known that in the course of phylogenetic development first primaries get shorter).

Table 1. Percentage distribution of recoveries according to distance and age.

Age of birds	Number of recoveries	Distances (km) (7)			over 1 000
		to 100	101–500	501–1000	
(1)	(2)	(3)	(4)	(5)	(6)
Garrulus glandarius (L) — entire Europe (8)					
imm.	89	75	18	5	2
ad.	52	96	4	—	—
Corvus corone cornix L. — Finland* (9)					
imm.	139	—	14	56	30
ad.	56	—	16	34	50
Corvus corax L. — entire Europe (8)					
imm.	47	74	26	—	—
ad.	12	75	25	—	—

* Resident birds (distance shorter than 100 km) were not taken into consideration in view of the existance of two independent processes (tendency to become resident and to change the route of migrations).

to distant, later on abandened winter areas), while in the second case the reverse seems to be true (old birds "favour" more distant winter areas and in this way they express new tendencies of the population). The third variant would characterize a population stabilized so far as migratory habits are concerned.

The method presented, although it seems quite correct for the species discussed, requires further conscientious testing on a number of species belonging to other systematical units.

5) On the basis of all the data obtained, and information on the dispersion of subspecies, I carried out an analysis concerned with the distribution of winter quartes and habitats of individual populations taking into account primary and secondary winter quarters from the point of view of the evolution of the population.

Among the not too numerous papers discussing the results of bird-ringing mentioned earlier, there can be noticed a conspicuous lack of uniformity in the way of dividing the continent. There were put forward divisions based on political or administrative frontiers (among others; HOLGERSEN, 1953; VOLLERT, 1959; SCHELDE, 1960), as well as attempts in geographical divisions (RENDAHL, 1960). Both these types of dividing may result in artificial cutting through biological units and consequently in blurring the existing migrational differences. It seems to me that the only way to avoid such distortions is to accept the rule that artificial political and administrative or geographical divisions can only be applied as working divisions and used exclusively by

the author, while for publication only the term "the area of a population" (or a group populations) seems acceptable. Similarly the classificiation of recoveries into "internal" and "external", used, among others, in a number of English publications, is purely a formal classification and should be substituted by a system based exclusively on the distance separating the place of recapture from the spot where the bird was ringed. It seems to me that we can accept for the majority of terrestrial birds a radius of a hundred kms as a maximum range of nomadic movements, and recoveries recorded at longer distances should be treated as results of migration.

The analysis of bird migration, when only one method is taken into account, as for example only visual observations or only bird-ringing results, may carry with it the threat of committing a number of mistakes in the interpretation of the facts obtained, Such a threat is particularly cogent for authors interpreting the results of bird-ringing. This statement, however, should not be understood as a vote of non-confidence in the method of bird--ringing. But, awareness as to where the potential possibilities of making mistakes come from and adopting a cautious approach to the results obtained, are necessary. In the first place it must be clearly realized that any information obtained about ringed birds is not, as a rule, a random sample from the population. The factor mainly contributing to the deformation of the real state of things is not the specific behaviour of birds ringed but the effect of man's influence on the entire population. And so:

1) Sometimes an enormous crowding of recoveries in certain winter quarters is not the result of wintering in the area of the majority of the population but is caused by hunting or fowling. As examples we may quote here mass capture of small birds in Spain or of hunting thrushes (*Turdus philomelos* BREHM and *T. merula* L.) in France. The effect of this factor on the results of bird--ringing was also recorded by GROMADZKI (1964).

2) A selective shooting of birds with rings which can be spotted from long distances can also play a significant role in certain areas.

3) Maps which give the distribution of recoveries clearly show the places of mass capture of birds for scientific purposes. For example at one of the camps of the Baltic Operation up to 50 birds with foreign rings were captured in the course of the season. On a number of maps attached to the present paper the same phenomenon can also be detected, e.g. Stavanger in Norway, Mjöhult in Sweden, or Ribatchi (Rossitten) on Kurische Nehrung.

4) In all the places where long-term bird-ringing is carried out there occurs a considerable crowding of local recaptures of birds ringed locally. This fact may distort, to a considerable extent, the results of investigation on the percentage of birds remaining during winter within the breeding range.

5) Beside these, easier to detect, causes of the distortion of results there is one more factor. Although it is difficult to asses it can be of a considerable importance — that is: do people realize what to do with bird-ring when it is

found. We do not know what per cent of rings, in a given country, obtained in an accidental way (coming upon the ring, non-selective shooting), reach the authorities concerned with bird-ringing. The existence of such differences can be demonstrated by the occurrence of considerable differences in the per cent of returns obtained in various countries, e.g .*Corvus frugilegus* L. — Great Britain 5–10% of the recoveries (E. and O. E., 1958), Poland 3,0% (BUSSE, 1963), USSR 0,6% (RIABOV, ŠEVAREVA, 1955).

It follows from the considerations mentioned above, that a great deal of caution must be applied when dealing with quantitative reasoning. Because it is impossible to calculate the percentage distribution of birds migrating in the direction of various winter quarters or the density with which those winter quarters are inhabited. Also, the results of calculations, with the aim to find the relation of the number of resident birds to the number of migrants in a given population, or per cent of birds changing the breeding colony, can only be treated as tentative data. In spite of all these reservations I would like to stress the enormous value of the material obtained by the method of bird--ringing for the considerations of qualitative nature (e.g. populational problems), and it may help solve certain quantitative problems (e.g. the determination of the rate of migration, some aspects of mortality). In such cases bird-ringing may consitute the sole method of solving these problems.

In the second part of the paper I discuss the problem of mortality of *Corvidae*. When determining the average life expectancy of individuals from a given species I took into account individuals from the whole area of Europe, as the calculations carried out within the sectors did not show any considerable or systematic differences. The sole exception here was the exclusion from our considerations of a large group of Rooks ringed in the Soviet Union, in view of the fact that the data were published only three years after the mass ringing had been carried out, and birds older than three years could not be included in the infromation published. In the case of birds ringed as adults in the breeding season or in the course of their migrations and wintering, and as "young birds" when they had already left the nest, I did not determine their age and such birds were not taken into consideration.

The length of life was determined by two methods. One of them has already been used in my previous paper and it consists in the calculation of the average life expectancy of those individuals which survived their first year. Results obtained in this way are comparable, if the rate of mortality (percentage of birds perishing in a given year of life in relation to the number of individuals starting this year of life) was constant in successive years for the species compared. In view of the fact, however, that this rate of mortality is changeable, the length of life of a species was also determined indirectly, taking as its exponent the data obtained from the curves of survival (LACK, 1954), and showing how many birds of a given species stand the chance of surviving five years (conventional period). The figure obtained indicates the number of individuals

surviving this period, taking here as the basis a thousand of young birds leaving the nest.

The distribution of mortality in the course of the year was determined in a way analogous to the determination of the rate of mortality in successive years. I calculated the percentage of birds perishing in a given month. I took as a total number of birds the number of recoveries obtained in the course of all the years of life. The way in which the calculations were carried out is illustrated by the example of the Rook (*Corvus frugilegus* L.) — the calculation of mortality in June and July of the first year of life: the total number of recoveries investigated amounted to 525; 50 individuals perished in June, which is $9,5^0/_0$ of 525; $525 - 50 = 475$ individuals were alive at the beginning of July; 35 birds perished in July, which is $7,4^0/_0$ of 475.

When investigating the problem of mortality one is faced with certain difficulties of methodical and statistical nature. Calculating the length of life on the basis of all the recoveries recorded, unusually low average results are obtained (sometimes the average length of life did not even reach the age in which birds were sexually mature). This phenomenon was caused by a very high mortality of birds in their first year of life reaching $60-70^0/_0$. In order to eliminate mortality in the first period of life, whose rate may be treated as a separate parameter characterizing the mortality of the species, I applied in my previous paper (BUSSE, 1963) the calculation of the average length of life of those birds which had already survived the critical first year of life. The figure obtained gives a better idea of the length of life of the species than the average of all the recoveries, but it still contains the error of being the result of the possibility of various courses of the curves presenting mortality. Because of that, in order to characterize the mortality of the species, I used two parameters in the present paper: percentage of birds perishing in the first year of their life and the number of birds standing the chance of surviving five years. However, it must be evident, that also these parameters may contain errors caused by different ways in which recoveries are published by individual birdringing centres. For there may be danger in certain cases that authors publishing their reports exclude some uninteresting shortterm and short-distance returns without indicating them in the introduction of the publication. Such practice would result in an underestimation of the results obtained for the rate of mortality in the first year of life and a respective overestimation in the successive years. Fortunately in reports published at present such operations are clearly signalized, and that helps to avoid errors. However, the custom, that short-term returns are not published, makes it impossible to carry out investigations on the distribution of mortality in the course of the first year of life. For it remains unknown how many birds perished, for example, in June and July, and consequently it is also impossible to calculate the mortality for other months of the first year of life by methods used so far (the calculation of the percentage of birds perishing in a given month

in relation to the number of birds perishing in a given year — e.g. MOHR, 1962; SWIRSKI, 1956). These difficulties are avoided by the use of the method applied for the purpose of the present paper (cf. description of the method). To its assets, beside the fact that it avoids the difficulties of short-term returns mentioned above (by simply treating the results from the first two months of life as uncertain), there also belongs the fact that it gives a more statistically true picture of the real state of things. Differences between the diagrams obtained by the application of the two methods mentioned are illustrated by Diagram 1. However, the method applied has also its shortcomings: 1) a very copious material is required; 2) the mortality analysis of old birds is usually limited to 2–3 years (for further years the number of recoveries is insufficient), while there may occur differences in the mortality of two-three-year-old-birds and upwards; 3) the method is extremely time consuming. However, in spite of these difficulties I consider the method described as suitable for application in all cases where it is possible, and all results obtained by the classical method should be treated as tentative.

MATERIAL

Recoveries concerning the area of Europe and published in reports of the bird-ringing centres or in analytical papers, from the onset of bird-ringing to the middle of 1964, were used for analyses in the present paper. In view of the difficulties connected with obtaining certain publications from the beginning of the 20th century, I have been unable to collect all the materials containing published recoveries. However, the gaps are insignificant. The list of publications containing recoveries of *Corvidae* is given at the end of the paper. The material collected contains the following numbers of recoveries:

Raven, *Corvus corax* L.	—	125
Carrion and Hooded Crow, *Corvus corone* L.	—	2243
Rook, *Corvus frugilegus* L.	—	1048
Jackdaw, *Corvus monedula* L.	—	1304
Magpie, *Pica pica* (L.)	—	560
Nutcracker, *Nucifraga caryocatactes* (L.)	—	13
Jay, *Garrulus glandarius* (L.)	—	421
Chough, *Pyrrhocorax pyrrhocorax* (L.)	—	10
Alpine Chough, *Pyrrhocorax graculus* (L.)	—	14
Total		5738

There were no recoveries of the two remaining European species — the Siberian Jay, *Perisoreus infaustus* (L.) and the Azure-winged Magpie, *Cyanopica cyana* BP. Recoveries of birds transported for experimental studies were not considered at all.

For the analysis of various problems different amounts of recoveries were used. Some of them had no precise date of finding, for some it was impossible

to find out the co-ordinates of localities. The basic material used for the analysis of population problems were recoveries of young birds ringed in their nests. A serious obstacle in my work was the fact that birds were ringed in various countries irregularly and with changing intensity, and that some bird-ringing centres did not publish their reports. Because of these reasons recoveries from the greater part of southern and eastern Europe were fragmentary and incomplete.

ANALYSIS OF THE MIGRATIONS OF INDIVIDUAL SPECIES

Rook, *Corvus frugilegus* L.

The Rook lives in Europe southwards of the 60–63° of the northern latitude; the southern boundary of its range runs through central France, the foot of the Alps in Italy and the Balkans (VAURIE, 1959). Only the nominate subspecies *Corvus frugilegus frugilegus* L. occurs in this area.

Table 2. Recoveries used to analyse migrations of *Corvus frugilegus* L.

Areas	Receveries from winter period (2)			Recoveries from migration (3)			Grand total
	shorter than 100 km	longer than 100 km	total	shorter than 100 km	longer than 100 km	total	
(1)	(4)	(5)	(6)	(4)	(5)	(6)	(7)
Great Britain (8)	7	1	8	3	—	3	11
Sectors D1, EO–1							
Holland, France (9)	45	17	62	74	19	93	155
Scandinavia (10)	3	8	11	18	11	29	40
Sectors D2–3 E2							
Central Europe (11)	11	26	37	14	21	35	72
Sectors C3–4							
Baltic Lands (12)	—	17	17	3	15	18	35
Sectors C5– D4–5							
Russian Plain (13)	—	85	85	32	60	92	177
Sectors E3–5							
Southern Russia (14)	2	32	36	3	9	12	48
Total (6)	68	186	254	147	135	282	536

As I mentioned in the previous chapter the material used contains 1048 recoveries. However, quite a number of these recoveries refers to birds ringed in a relatively small area of Europe (Map 1). Out of this number only 536 could be used for the analysis of the migrations of the species, and only 525 were suitable for considerations on the problems of mortality. Table 2 also contains basic data on the rate of migration of Rooks occurring in various areas of Europe. The species discussed shows in Europe considerable changeabi-

lity of its migratory tendencies (Map 2), from nearly resident populations (Great Britain — 12% of birds migratory distances longer than 100 km) to populations entirely leaving their breeding ranges in winter (north-eastern Europe)*. Also the average distance flown by birds from their breeding colonies oscillates within the following range: from 374 km for French Rooks to 1970 km for birds from the Russian Plain.
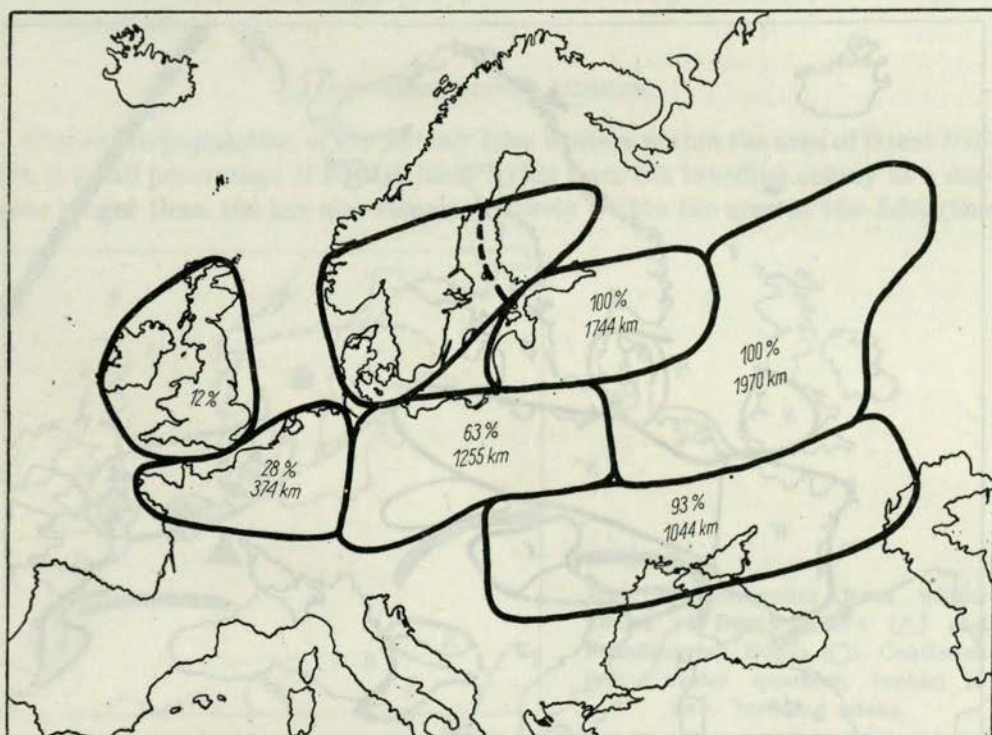

Map 2. Migratory habits of *Corvus frugilegus* L. The per cent of migrating birds and the mean length of migration are given.

Analysing the distribution of the winter quarters of European Rooks on the basis of the distribution of recoveries from the winter period (from the beginning of December to the end of February) it becomes evident that these birds avoid mountains and highlands. The frequency of occurrence of winter recoveries from plateaux higher than 250 meters above the sea level is, in the case of Rooks, five times lower than for the respective figure concerning lowlands. This relation, although not in such a clear form, remains true in the course of migrations when recoveries from higher lying areas make up

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* In parts of the areas marked as entirely left by birds in winter individuals remain irregularly in some years (DEMENTIEV et al., 1954).

only 70% of the number of recoveries from the lower lying areas. The effect of highlands on the occurrence and migrations of Rooks was also stressed by other authors (GIBAN, 1947; WATERHOUSE, 1949). GIBAN (1947) described the density of the stream of migrating Rooks in the "gate of Belfort". The crowding of recoveries at the foot of mountains sealing any lowland is also characteristic, e.g. Brno in the northern part of the Hungarian Plain, or the
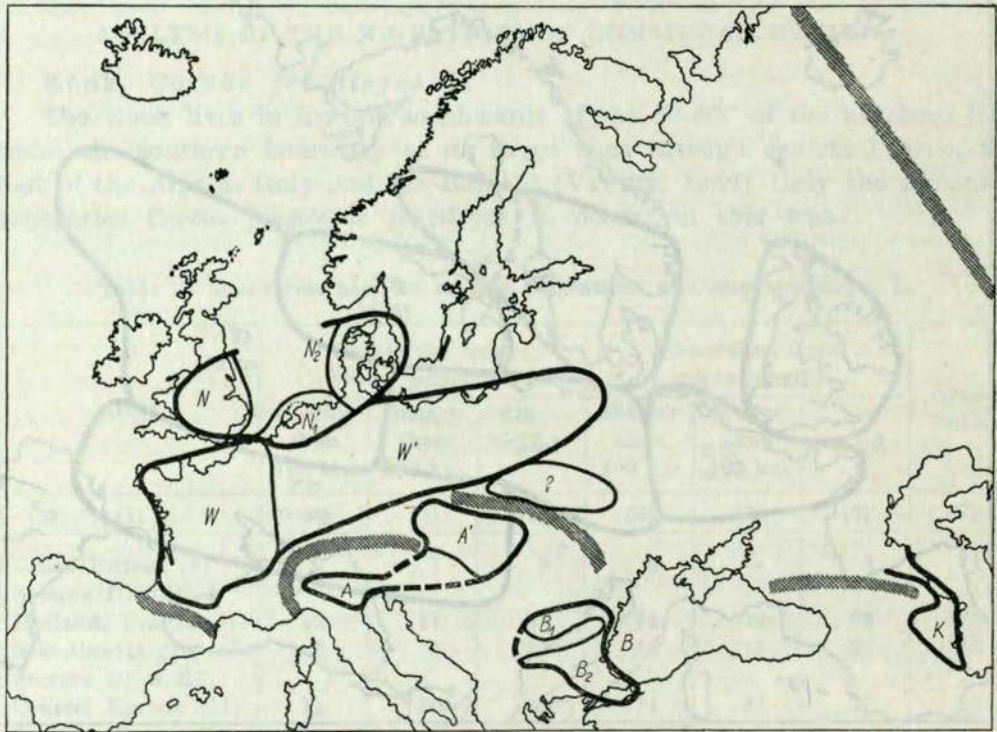

Map 3. Winter quarters of *Corvus frugilegus*. Crossed line — main mountain ridges; heavy line — boundaries of winter quarters; thin line — division within the group of winter quarters. Capital letters — basic winter quarters; letters with apostrophe (N', W', A') — secondary winter quarters developed by way of shortening migration routes.

foothills of the Sudetes in Poland. This phenomenon results in a clear-cut division of Europe into separate winter quarters (Map 3). The following are the main winter ranges: 1) the south-eastern part of Great Britain — "northern" winter quarters marked "N"; 2) almost entire France (with the exception of the Mediterranean part) and going further eastwards, this winter quarter covers Germany and reaches Poland — "western" winter quarter "W"; 3) the Lombardy Plain and the Hungarian Plain — "subalpine" winter quarter "A"; 4) Woloska Plain and the lowland part of Bulgaria — "Balkan" winter quarter "B"; 5) southwestern shores of the Caspian Sea — "Caucasian" winter

quarter "K". It is obvious that because European winter ranges are so widely spaced and because they contain such differing areas there are bound to occur differences in the direction of migrations, and that birds coming from various areas may become attached to individual winter quarters. And so we can expect that there will be clearly distinguishable migrational populations. Undertaking the attempt to single out the populations expected I shall discuss now the range of the breeding areas of birds wintering within the winter quarters mentioned.

NORTHERN WINTER QUARTER

The entire population of the British Isles winters within the area of Great Britain. A small percentage of British birds flying from the breeding colony at a distance longer than 100 km also remains entirely within the area of the Isles (the
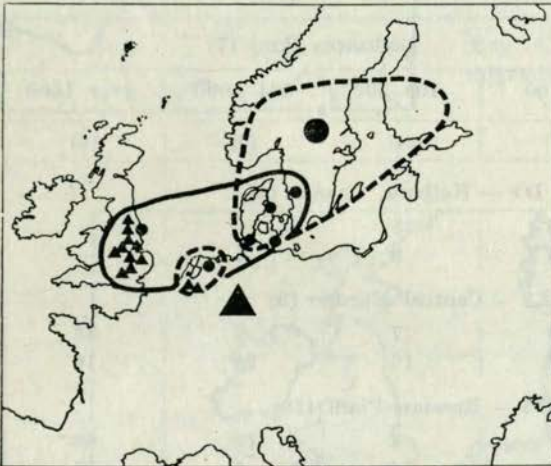
Map 4. Recoveries from winter period of Dutch Rooks (△) and Scandinavian Rooks (○). Continous line — winter quarters, broken line — breeding areas.

Map 5. Recoveries from winter period and migration of Baltic Rooks. Solid signs — recoveries from winter period, open signs — recoveries from migration; continous line — boundaries of winter quarters, broken line — breeding areas.
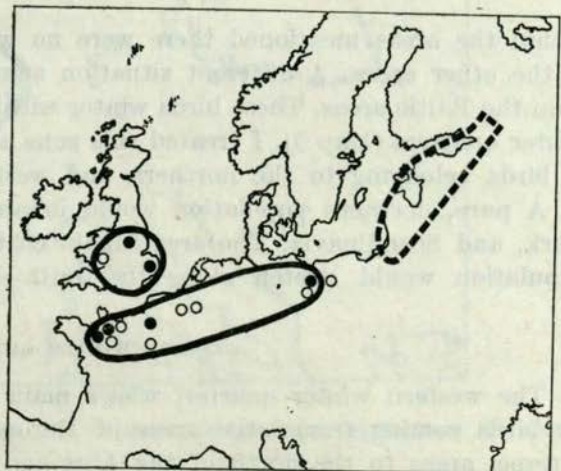
longest flight — 250 km SW). Besides this nearly all migrating Dutch birds (Map 4), a part of Danish birds, some birds from the south-eastern shores of the Baltic Sea, and, possibly, a part of birds from Scandinavia winter in Great Britain. One winter recovery of a Danish bird comes from Holland, while all recoveries of Scandinavian birds are crowded in the area of Denmark and south-eastern Scandinavia. Danish and Scandinavian birds could, however, be treated as belonging to the northern population, taking here into account the fact that there were no recoveries of birds, inhabiting this area, coming from the typical western winter quarters. Consequently the area of Holland, Denmark and southern Scandinavia should be treated as a part of the northern winter quarter which came into being by way of an evolutional shortening of the migration route (Tab. 3). This thesis is easier to accept because

Table 3. Percentage distribution of recoveries according to distance and age *C. frugilegus* L.

Age of birds	Number of recoveries	Distances (km) (7)			
		to 100	101–500	501–1000	over 1000
(1)	(2)	(3)	(4)	(5)	(6)
Sectors EO, E1, D1 — Holland, France (8)					
imm.	87	65	35	—	—
ad.	71	90	9	1	—
Sectors D2, D3, E2 — Central Europe (9)					
imm.	45	33	7	7	53
ad.	19	42	16	25	16
Sectors C5, D4, D5 — Russian Plain (10)					
imm.	156	17	4	10	69
ad.	21	23	14	5	57

within the areas mentioned there were no wintering birds coming from any of the other areas. A different situation arises in the case of Rooks coming from the Baltic areas. These birds winter within both the northern and western winter quarters (Map 5). I treated this zone as an area occupied by a mixture of birds belonging to the northern and western populations.

A pure, northern population would inhabit Great Britain, Holland, Denmark, and Scandinavia. The area inhabited together with a part of Western population would stretch along the south-eastern shores of the Baltic Sea.

WESTERN WINTER QUARTERS

The western winter quarter, whose main part lies in France, is occupied by birds coming from large areas of Europe: France, Central and Eastern Europe, areas to the north of the Alps and Carpathians, and further on to

the north of the line: Czerniowce — Kharkov — Voronezh, and nearly the entire Russian Plain. Because of the size of the area subpopulational differences may appear, and therefore I shall carry out an analysis singling out, provisionally, smaller units within the area of the western population. They are:

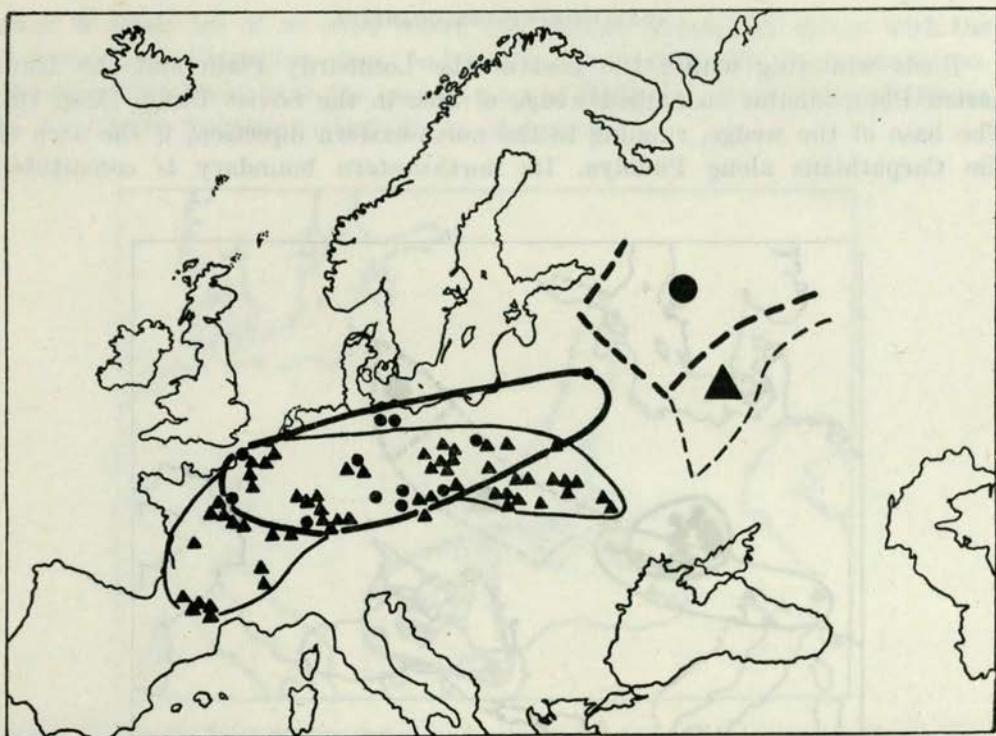Map 6. Recoveries from winter period and migration of French Rooks. Descriptions — see Map 5.
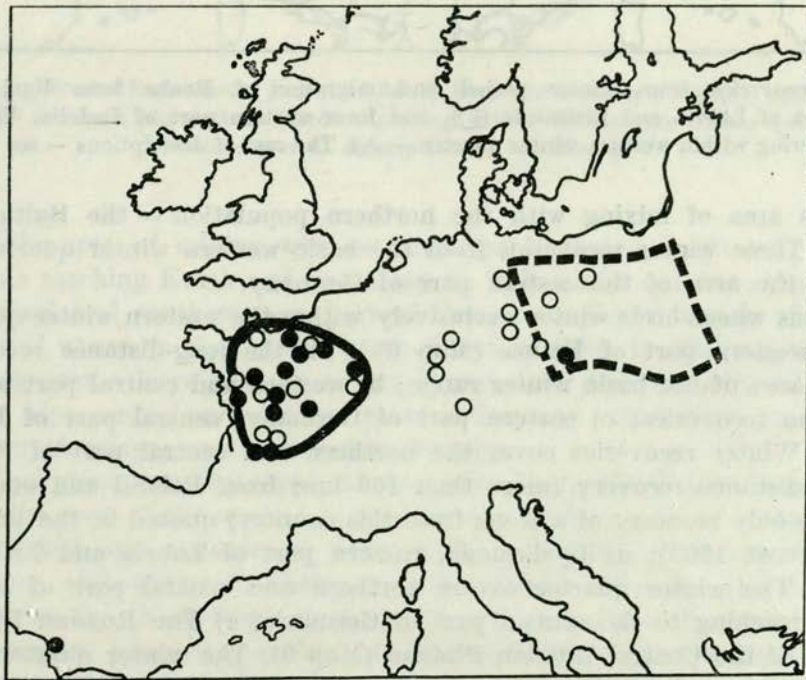
Map 7. Recoveries from winter period and migration of Rooks from Eastern Germany and Central Poland. Descriptions — see Map 5.
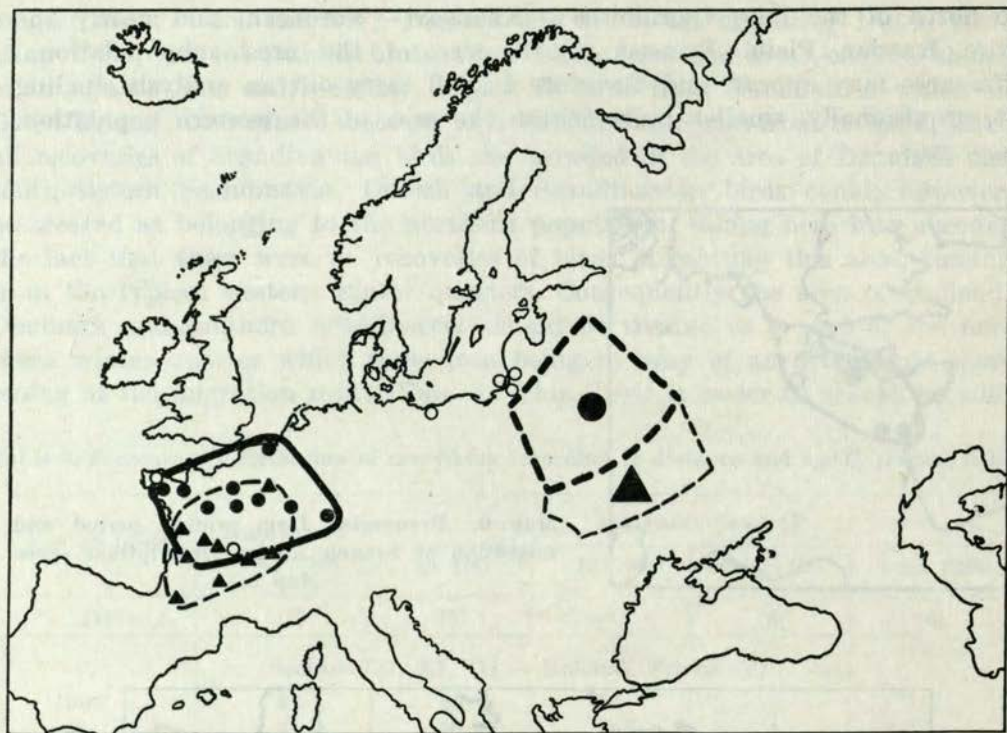
Map 8. Recoveries from winter period and migration of Rooks from Byelorussia, eastern part of Latvia and Lithuania (◯), and from western part of Podolia, Volhynia (birds wintering within western winter quarter — △). The rest of descriptions — see Map 5.

1) The area of mixing with the northern population — the Baltic zone (Map 5). Three winter recoveries from the basic western winter quarter and one from the area of the eastern part of Germany.

2) Areas whose birds winter exclusively within the western winter quarter: a) north-western part of France (Map 6) — all the long-distance recoveries from the area of the basic winter range; b) western and central part of Germany — no recoveries; c) eastern part of Germany, central part of Poland (Map 7). Winter recoveries cover the northern and central part of France. One long-distance recovery (more than 100 km) from Poland and one from Spain (the only recovery of a Rook from this country) quoted in the previous paper (Busse, 1963); d) Byelorussia, eastern part of Latvia and Lithuania (Map 8). The winter quarter covers northern and central part of France, Belgium, reaching to the central part of Germany; e) The Russian Plain to the north of the Central Russian Plateau (Map 9). The winter quarter stretches from the north-eastern part of France to the central part of Poland; one winter recovery from the north of Byelorussia.
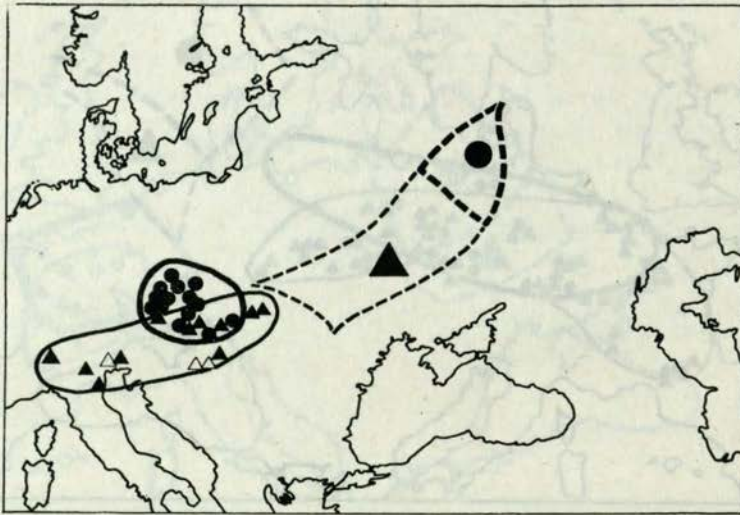
Map 9. Recoveries from winter period of Rooks from the Russian Plain (○) and the mixed belt with southern populations (birds wintering within the western winter quarter — △). The rest of descriptions — see Map 5.

3) The area of mixing with southern populations: a) Western Podolya, Volhynia reaching Kursk and Orel (Map 8). This winter quarter covers mainly the central and south-western part of France. b) the extension of the zone mentioned above in the south-eastern direction (Map 9). The winter quarter stretches over a large area: it covers France with the exception of Brittany and the Alps, central and southern parts of Germany and Poland. An additional crowding of returns was recorded in Podolya.

It is evident that birds from all the areas distinguished provisionally meet within the area of the central part of France. Only a part of birds from the northernmost and easternmost parts of the population area, cut short their migrations and winter in Germany and Poland. Generally one can detect a regularity that birds living in the southernmost parts of the area have their winter ranges somewhat shifted to the south in relation to their northern neighbours (Maps 8, 9). This, however, does not affect adversely the uniformity of the western population.

SUBALPINE WINTER QUARTERS

Birds wintering within the area of the Lombardy Plain and the Hungarian Plain inhabit an arched wedge of area in the Soviet Union (Map 10). The base of the wedge, running in the north-eastern direction, is the arch of the Carpathians along Podolya. Its northwestern boundary is constituted

Map 10. Recoveries from the winter period and migration of Rooks belonging to the Subalpine population. Recoveries from the period of migration of birds coming from the sector ○ are here neglected. The rest of descriptions — see Map 5.

approximately by the line Lvov — Gomel — Kaluga — Vladimir, white its southern boundary is the northern frontier of Moldavian Soviet Republic, Cherkasy, Voronezh, Riazsk. The pure alpine population does not occur in this area. Birds from the areas mentioned here migrate in the direction of two, three, and sometimes even four winter quarters. The pure Subalpine population occurs most probably (however, there is a complete lack of recoveries) only on the Hungarian Plain. Besides, Map 10 indicates internal differences of the population discussed: birds which live south-westwards to the line Orel — Voronezh, also winter on the Lombardy Plain and on the Hungarian Plain, while birds from the north-eastern part of the population area turn up only in Hungary, and do not reach Italy.
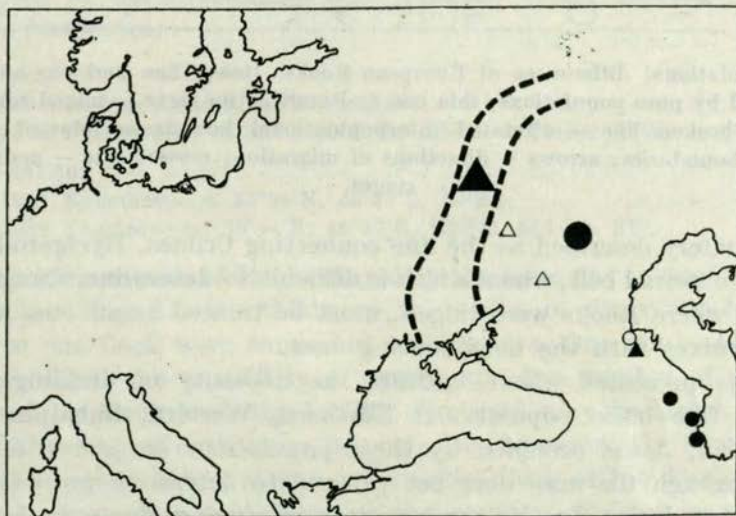
BALKAN WINTER QUARTERS

Birds inhabiting the rapidly narrowing wedge of area stretching from Moldavia and the Sea of Azov shores to the vicinity of Ryazan in the north (Map 11) winter within the Balkan winter quarters. A greater part of this

wedge is made up of an area where the Balkan population mixes with the Subalpine and Caucasian ones, and in the north also with the western, populations. Only birds from the eastern part of Moldavia, the vicinity of Odessa and Nikolayev migrate exclusively to Bulgaria.


Map 11. Recoveries from winter period and migration of Rooks belonging to the Balkan population. Recoveries from the period of migration from the breeding area are here neglected. Descriptions see — Map 5.

Map 12. Recoveries from winter period and migration of Rooks belonging to the Caucasian population. Descriptions see — Map 5.

CAUCASIAN WINTER QUARTERS

Birds migrating to this winter range live in the south-easternmost parts
of Europe (Map 12). The north-western boundary of their occurrence may
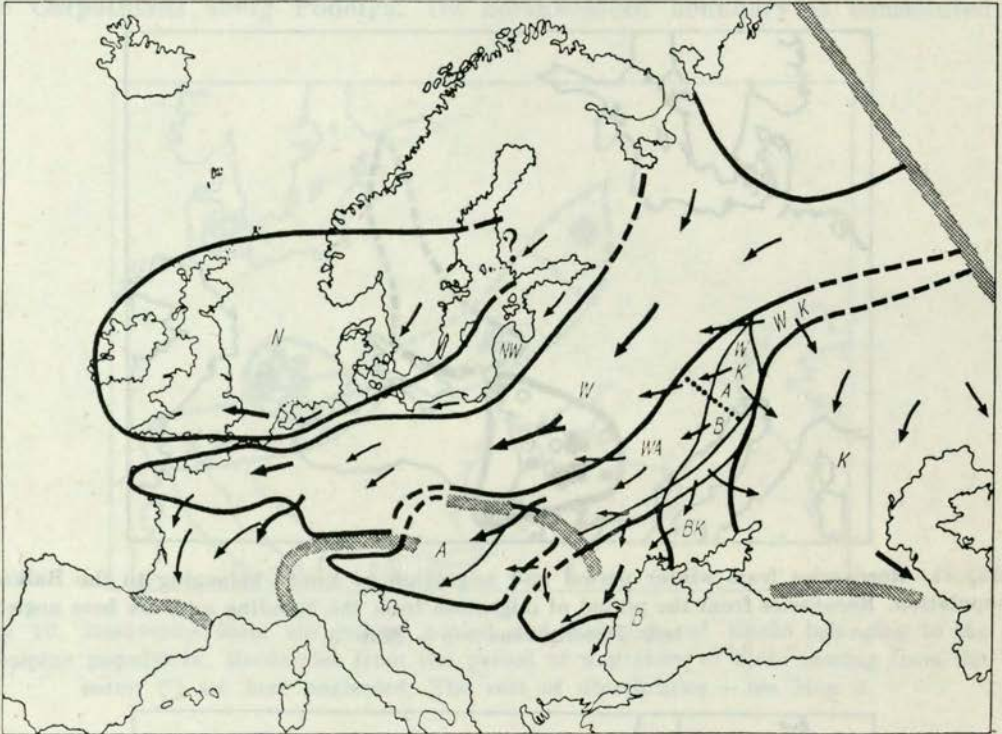
Map 13. Populational differences of European Rooks. Heavy line and one-letter signs —
areas occupied by pure populations; thin line and multi-letter signs — mixed zones between
populations; broken line — estimated interpopulational boundaries; dotted line — sub-
populational boundaries; arrows — directions of migration; crossed line — main mountain
ridges.

be approximately described as the line connecting Crimea, Byelgorod, Ryazan,
Gorkiy. The external belt, whose width is difficult to determine, a small number
of localities where Rooks were ringed, must be treated as an area where this
population mixes with the neighbouring ones.

The facts presented above indicate the necessity of dividing European
Rooks into five basic populations: Northern, Western, Subalpine, Balkan,
and Caucasian. Areas occupied by these populations are shown on Map 13.
Obviously enough the map does not pretend to determine precisely interpo-
pulational boundaries. In the present state of ringing Rooks in Europe (the
same also applies to other species) there is no possibility of determining accu-
rately these boundaries. The main obstacle here is not only the small number

of long-distance recoveries, but first of all the fact that places where birds are ringed are scarce and irregularly distributed. The most complicated popula-tional relations occur within the area of the Central Russian Plain. Birds living
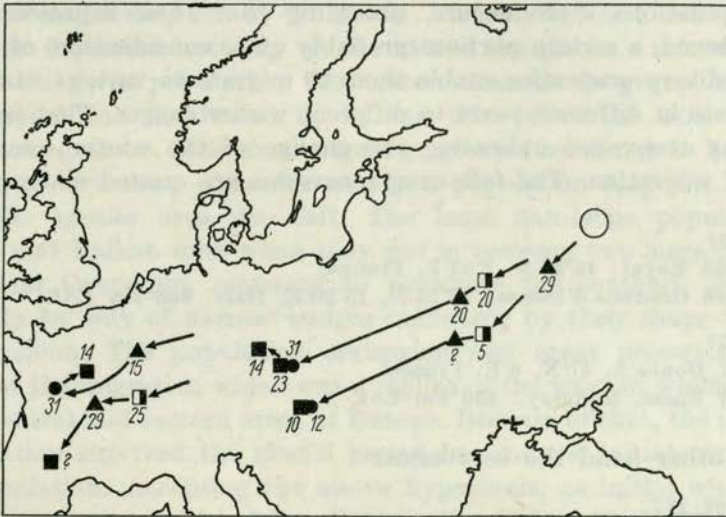
Map 14. Recoveries from the first year of life of Rooks ringed on 25. 05. 1959 in Shelu-chov: 54°20′N, 40°56′E, USSR. ○ — place of ringing, [▪ — October, ▲ — November, ● — December, ▪ — January. Figures give the data of the recovery. Arrows indicate the assumed migration routes of flocks.

there migrate in the direction of four different winter quarters. This is illu-strated by recoveries:

Moskwa E 467 779
o   04.06.1957 Iberdus: 54°55′N, 41°25′E, USSR.
(?) 14. 09. 1958 Byelayevsk: 46°30′N, 30°46′E, USSR. 1190 km SSW.

Moskwa E 467 562
o   05. 06. 1957 Romanovo: c. 55°08′N, 40°35′E, USSR.
(?) 06. 09. 1959 Neustroyevo: 50°44′N, 40°27′E, USSR. 460 km SW.

and a series of recoveries of Rooks ringed on the same day in one locality which are shown on Map 14. On this map recoveries of birds which may have belonged to one flock were connected with arrows. One must obviously take into consideration the possibility of errors, and the number of flocks which were formed by birds from the locality discussed may be larger than it was shown on the map (five flocks) In any case, however, the example quoted illustrates the possibility of splitting the initial flock of the Rook colony into several flocks migrating to different winter quarters. This exposes the errone-ousness of the assumption accepted for the purpose of my previous paper (BUSSE, 1963) that a long migration can only be undertaken by birds from

one colony which form one flock. Consequently the suggestion, put forward there, that Ukrainian Rooks migrate through Italy to France is also incorrect. It is possible to undertake migrations in one flock only in the areas inhabited by any of the "pure" populations. In the areas inhabited simultaneously by various populations there occurs, providing that their representatives can freely crossbreed, a certain portion (probably quite considerable) of individuals (whose hereditary properties enable them to migrate to various winter ranges) which migrate in different years to different winter ranges. That is why there are so many recoveries indicating the change of the winter quarter or the direction of migration. The following recoveries are quoted as examples:

Paris FA 8051
* 29. 02. 1956 Royat: 45°45′N, 3°03′E, France.
( ) 04. 11. 1956 Gradisca-d'Isonzo: 43°53′N, 13°30′E, Italy. 800 km ESE.

Versailles 1757
* 10. 11. 1927 Doubs c. 47°N, 6°E, France.
† 11. 02. 1931 Enese, Hungary. 830 km ESE

On the other hand the recoveries:

Moskwa E 467 287
o 05. 06. 1957 Romanovo: c. 55°08′N, 40°35′E, USSR.
* 30. 10. 1958 Wittenberg: 48°30′N, 9°00′E, Germany.

Moskwa E 467 526
o 05. 06. 1957 Alekseyevo: c. 55°10′N, 40°35′E, USSR.
† 08. 02 .1959 Wittenberg: 48°30′N, 9°00′E, Germany.

Moskwa E 467 538
o 05. 06. 1957 Alekseyevo: c. 55°10′N, 40°35′E, USSR.
* 07. 12. 1957 Wittenberg: 48°30′N, 9°00′E, Germany.

indicate a regular appearance of the flock of Rooks from a given locality within the same winter quarters.

The existence of the populations mentioned above and their distribution in Europe show the necessity of attempts to explain the differences recorded. The existing populational boundaries do not coincide, as a rule, with any natural barriers which would foster isolation resulting in the differentiation. The hypothesis of GIBAN (1947) that woodlands may be such a barrier is unapplicable to the majority of existing boundaries. Also putting forward the idea that the existing migrational barriers are the cause of populational divisions (BUSSE, 1963) can in no respect be the right solution, as it leaves unexplained differences in the migrations of Rooks in Holland and France, and the south--eastern direction of Caucasian populations. The shape of the areas of individual populations suggests the possibility of solving the problem by discussing the history of the spreading of Rooks in Europe. In the period of glacial movements Rooks, together with other birds, were forced to withdraw from the

areas of the entire central and north-eastern part of Europe. Individual groups of withdrawing birds became isolated from each other within separate areas: Great Britain*, southwestern part of France, Italy, the Balkans, and the western part of Asia. When the glacier retreated birds began to spread over those five areas, already left by the glacier. The rate at which individual populations spread depended not only on the rate of the glacier's retreat but also on the size of the given population. The more numerous the group, the larger the areas occupied and dominated by it, and this prevented other populations from spreading there. The most vigorous group turned out to be birds from the south-western area — for the northern population only the northermost part of the species area was left. The least numerous populations — the Subalpine and Balkan ones when they got in between two large groups — the Western and Caucasian, managed to penetrate the southern areas of East Russia only by way of narrow wedges indicating by their shape the direction of the invasion. The population occupying new areas preserved the initial direction of the migration which was a replica of the ways in which they spread over the central and eastern areas of Europe. Because of that, the area in which the population survived the glacial period became the initial winter quarters of the population. Accepting the above hypothesis, as initial winter quarters we must treat: the British Isles, France, the Italian Peninsula, the eastern part of the Balkan Peninsula, and Western Asia (or the foothills of the Caucasus). As time went by Rooks started to show tendencies to cut short the route of the migration and to become resident. This tendency remains up to now — old birds from all groups in Europe display a decreased migratory tendency (Tab. 3). This tendency to cut short the migration route resulted in the formation of secondary winter quarters (see Map 3). Holland, Denmark, and the southern part of Scandinavia would be secondary winter quarters of the Northern population, the area of Germany and Poland for the Western population, the Hungary Plain for the Subalpine population. The Balkan population had no secondary winter quarters. In the case of the Caucasian population the situation is not clear — it is possible that the present winter quarter in the Caucasus is already a secondary one formed by birds which came up against a barrier (the Caspian Sea), when migrating in the south--eastern direction towards Western Asia. It seems more probable that the present winter quarters were unsuitable for the *Corvidae* (MOREAU, 1955).

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* The present reasoning is concerned with a somewhat later period than when the glacier in Europe advanced to its farthest point, and when the areas of Great Britain were not suitable for *Corvidae* (MOREAU 1955). In the period of the most extensive glaciations birds considered here as "British" must have occurred in the area of France, isolated from the "Western" population, then inhabiting the Iberian Peninsula, by the glacier in the Pyrenees. The remaining groups were also isolated from each other by areas totaly unsuitable for raising broods by *Corvidae*.

Jackdaw, *Corvus monedula* L.

The Jackdaw occupies the whole area of Europe with the exception of its northernmost region: the northern part of the Scandinavian Peninsula and the Timan region (VAURIE, 1959). Three subspecies can be distinguished in Europe: *C.m. monedula* L. — Scandinavia to the 64° of northern latitude, Denmark to the vicinity of Esbjerg and Haderslev, and most probably the southern part of Finland; *C.m. soemmerringii* FISHER — the north-eastern part

Table 4. Recoveries used to the analysis of migrations of *Corvus monedula* L.

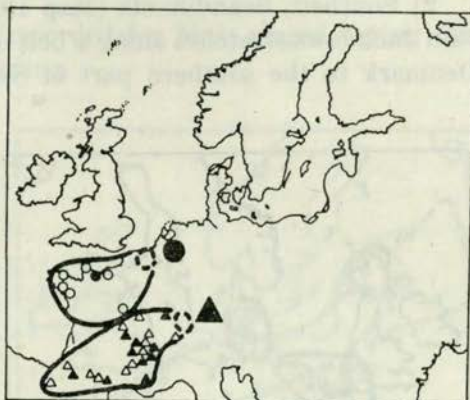| Areas	Recoveries from winter period (2)			Recoveries from migration (3)			Total
	shorter than 100 km	longer than 100 km	total	shorter than 100 km	longer than 100 km	total	
(1)	(4)	(5)	(6)	(4)	(5)	(6)	(7)
Great Britain (8) Sectors D1–2	11	2	13	13		13	26
Holland, Germany (9) Sectors EO–2, F1	27	5	32	56	8	64	96
France, Switzerland (10) Sector C1	7	13	20	24	13	37	57
Denmark (11)	15	6	21	45	15	60	81
Scandinavia (12) Sectors B3–4	14	20	34	75	20	95	129
Finland (13) Sectors C3, D3	7	9	16	28	16	44	60
Baltic Lands (14)	7	14	21	13	5	18	39
Total (6)	88	69	157	254	77	331	488

of Europe, westwards to the central part of Poland, Transylvania and Yugoslavia; *C.m. spermologus* VIEILL. — the remaining area westwards and southwards.

Material concerning the Jackdaw (1304 recoveries) comes from an even smaller part of Europe than in the case of the Rook and is also unevenly spread (Map 1), and this, to a certain degree makes it more difficult to analyse the material. I made use of 488 recoveries to investigate the migrational problems (Tab. 4). The Jackdaw, similarly as in the case of the Rook, is only a partial migrant (Map 15). A total desertion of breeding ranges in winter can be observed only in the north-eastern part of Europe (DEMENTIEV et al., 1954). The European winter quarters of the Jackdaw stretch along vast areas covering, as a rule, common areas with the Rook. However, so far there has been only one recovery received from Italy. The lack of data on bird-ringing

in the Soviet Union makes it impossible to analyse the migratory habits of Jackdaws migrating southwards and eastwards to the Hungarian Plain. In view of the fact that the picture of the distribution and migratory habits of the European populations of the Jackdaw is quite complicated, the way of
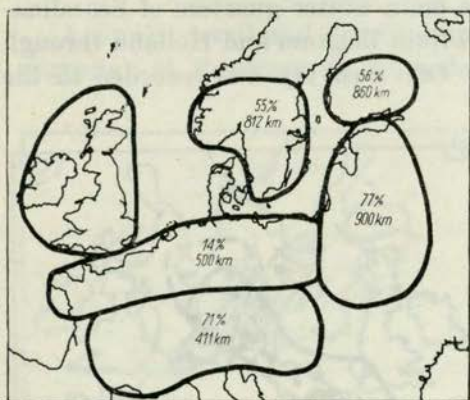
Map 15. Migratory habits of *Corvus mo-nedula* L. Descriptions see — map 2.

Map 16. Recoveries from winter period and migration of Jackdaws from the north of France, Belgium (○), and Switzerland (△). Descriptions see — Map 5.

presenting the material will be somewhat different than the one used in the case of the Rook. Because the boundaries of the populations cannot exceed beyond the area occupied by a subspecies, I shall discuss successively the taxons distinguished in Europe.

Corvus monedula spermologus VIEILL.

1) Great Britain. Birds living in this area do not move about intensively: out of 13 winter recoveries only two were recorded at a distance longer than 100 km (240 km SW, 170 km W).

2) Northern France, Belgium (Map 16). Jackdaws from these areas migrate in directions WSW to SW, and they reach the French shores of the Atlantic Ocean.

3) Switzerland (Map 16). Swiss Jackdaws leave in great numbers their breeding ranges in winter, because of the harsher mountain climate as compared with the lower lying regions. Such birds usually migrate in SW direction and winter in the Rhône Valley or at the foot of the Pyrenees. One recovery was reported from Spain:

Sempach 926 444
○ 27. 05. 1952 Ufenau: 37°15′N, 8°45′E, Switzerland.
* 23. 11. 1952 Milagro: 42°15′N, 1°47′W, Spain. 990 km SW.

4) A few recoveries from Czechoslovakia and the south-western part of Poland will be discussed later on.

Corvus monedula monedula L.

1) Denmark (Map 17). Jackdaws living in Denmark winter in the south-
-eastern part of England, northern France, Belgium, and Holland. One reco-
very was recorded in the northern part of Scotland.

2) Southern Scandinavia (Map 18). The main winter quarters of Scandina-
vian Jackdaws stretches along a belt of land from Belgium and Holland through
Denmark to the southern part of Sweden. One recovery was recorded in the
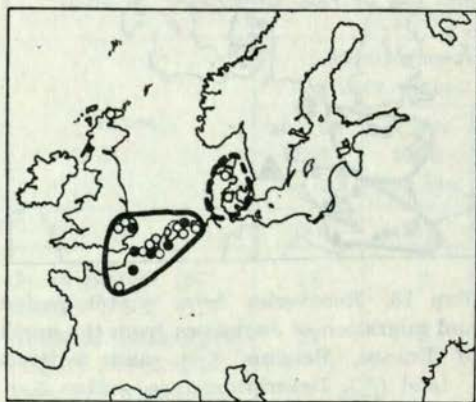
Map 17. Recoveries from winter period
and migration of Jackdaws from Denmark.
Descriptions see — Map 5.
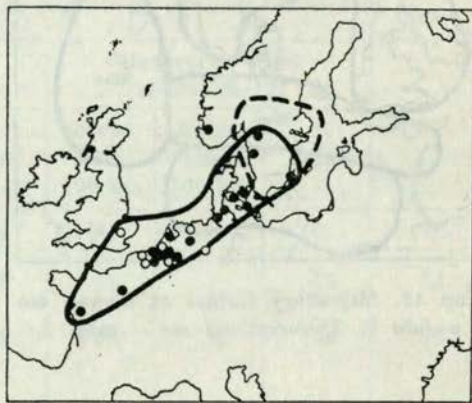
Map 18. Recoveries from winter period
and migration of Jackdaws from southern
part of Scandinavia. Recoveries from the
period of migration neglected within the
area of Denmark and breeding range.
Descriptions — see Map 5.

south-eastern part of England, two in the north-western part of France, and
one in Norway. The latter concerns a bird which had also been ringed in
Norway; that Jackdaw wintered in a typical winter quarter of Norwegian
Hooded Crows:

Stavanger 515 773
o 16. 06. 1955 Daelin: 60°45.N, 11°08′E, Norway.
() 23. 12. 1955 Tjora: 58°54′N, 5°36′E, Norway.

3) Finland (Map 19). All the long-distance returns of Finnish Jackdaws
were recorded within a narrow belt of land running from Holland through
Denmark to the vicinity of Stockholm. This is somewhat shifted, in the north-
-eastern direction, winter quarters of birds from the south of Scandinavia.

Corvus monedula soemmerringii FISHER

1) Baltic countries, north-eastern part of Poland (Map 20). Winter quar-
ters of this group are spread over a vast area: from the central part of France,

through Belgium, Germany, and the northern part of Poland, to their own breeding areas. One recovery was recorded on Oland:
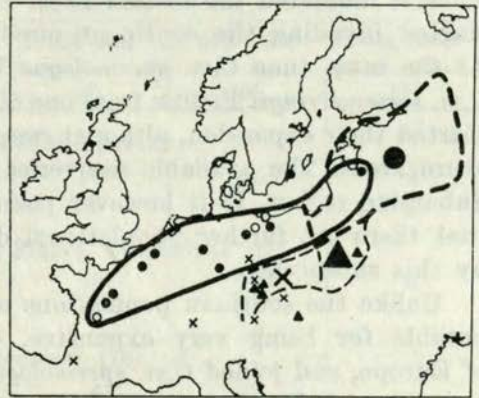
Moskwa E 281 746
o 07. 06. 1955 Puhtu: 58°33′N, 23°34′N, USSR.
* 01. 02. 1956 Rootsi: 56°30′N, 16°30′E, Sweden. 500 km SW.

A similar territorial distribution was recorded for birds ringed during their migration at Rossitten on Kurische Nehrung.

Map 19. Recoveries from winter period and migration of Jackdaws from Finland. Descriptions — see Map 5.

Map 20. Recoveries from winter period and migration of Jackdaws from the Baltic countries (◯), south-eastern part of Poland (△), and south-western part of Poland and north-western part of Czechoslovakia (X). The rest of descriptions — see Map 5.

2) South-eastern part of Poland, the Ukraine (Map 20). Jackdaws living within this small area migrate in two directions: WSW to the north-western part of Czechoslovakia — southern part of Germany, and SW — SSW to the Hungarian Plain.

There is no information on Jackdaws inhabiting the areas to the east and there are no recoveries published. A group of birds from the south-western part of Poland and north-western part of Czechoslovakia, taxonomically belonging to the subspecies *C.m. spermologus* VIEILL., migrates similarly to the Jackdaws from Ukraine that is in two directions: SW (even to France) and S to SE (to the Hungarian Plain).

Considering the problem of the occurrence of migrant Jackdaw populations in Europe we must take into account the distribution of subspecies over this area. The migration of the representatives of two subspecies in the same direction, to the same winter quarters (*C.m. spermologus* VIEILL. and *C.m. soemmerringii* FISHER from the Baltic countries) seems to contradict the hypothesis, which I put forward when discussing the Rook, and which says that migrating

birds repeat the ways in which the population spread. It is quite evident that the two subspecies mentioned did not originate within the same area in the glacial period. Where do they come from then? And there is one more question: where did the Scandinavian subspecies, migrating in winter to areas occupied by another subspecies live in the glacial period. In spite of the apparent contradictions, the facts presented so far may be explained by the hypothesis elucidating the occurrence of migratory populations of the Rook.

C.m. monedula L. separated as a subspecies at the end of the glacial period, when it inhabited the British Isles. When the glacier retreated the subspecies started invading the continent moving along the shores of the North Sea. At the same time *C.m. spermologus* VIEILL from the south-western area and *C.m. soemmerringii* FISHER from one of the southern areas (Subalpine or Balkan) started their expansion, although we do not know yet from which of the southern areas. The available recoveries from the Hungarian Plain point to the Subalpine region. It is however possible, that in the future it will turn out that there are further populational differentiations within the area occupied by this subspecies.

Unlike the southern populations of the Rook, *C.m. soemmerringii* FISHER, notable for being very expansive, occupied the entire south-eastern part of Europe, and joined *C.m. spermologus* VIEILL. in the areas to the north-west forming in Poland a mixed belt between these two subspecies. *C.m. spermologus* VIEILL. checked in its expansion eastwards by an equally strong subspecies, *C.m. soemmerringii* FISHER, started invading areas previously occupied by *C.m. monedula* L. This subspecies, most probably weaker numerously, was ousted from its original breeding range in the British Isles but being more resistant to a harsh climate retained its position in Scandinavia. After crossing the Gulf of Bothnia this subspecies came upon the representatives of *C.m. soemmerringii* FISHER and that limited its spreading over the continent to the southern part of Finland.

Migratory habits of *C.m. spermologus* VIEILL. and *C.m. monedula* L. support the hypothesis presented here. *C.m. spermologus* VIEILL. migrates in the SW direction of the original Western winter quarters (W), and it coincides with the Western population of the Rook. At present the two groups of Jackdaws of this subspecies are in the middle of cutting short their migration routes (Tab. 5 — Sectors D1–2, EO–2, F1). A part of the representatives of *C.m. monedula* L. migrate to their original winter quarters (Great Britain), from where the subspecies comes, while a part of them occurs within the secondary winter ranges which were formed when the migration route became shorter (Holland, Denmark, southern part of Scandinavia). Groups belonging to this subspecies cut short the route of migration (Tab. 5 — Sectors B2–3, C1–2). The occurrence of old birds at distances longer than 1000 km and not recorded anywhere else (except the south-eastern shores of the Baltic Sea) can give rise to doubt only in the case of the southern part of Sweden. A possible cause here might

be a secondary occupation of the winter quarters in France (see Map 18). The main problem remaining to be solved is the behaviour of *C.m. soemmerringii* FISHER living in the Baltic countries. These birds instead of migrating directly southwards, in the direction of the original winter quarter, fly exclusively in the SW direction to the areas occupied by a different subspecies.

Table 5. Percentage distribution of recoveries according to distance and age *C. monedula* L.

| Age of birds	Number of recoveries	Distances (km) (7)			
		to 100	101–500	501–1000	over 1000
(1)	(2)	(3)	(4)	(5)	(6)
Sectors D1, D2 — Holland, Germany (8)					
imm.	28	68	14	14	4
ad.	35	95	5	—	—
Sectors EO–E2, F1 — France, Switzerland (9)					
imm.	34	44	30	21	6
ad.	19	85	15	—	
Sectors C1 — Denmark (10)					
imm.	22	50	5	45	—
ad.	29	87	10	3	
Sectors B2, C2 — Scandinavia (11)					
imm.	55	55	18	18	9
ad.	64	81	6	6	3
Sectors B3 — Finland (12)					
imm.	33	51	12	15	21
ad.	26	70	15	15	—
Sectors C3, D3 — Baltic Lands (13)					
imm.	23	48	18	26	9
ad.	11	45	18	18	18

The distribution of recoveries supplying information about young and old birds shows that old birds migrate more intensively (Tab. 5 — Sectors C3, D3), and that may indicate that migration routes become longer in this direction. Independently the migratory habits investigated on the Kurische Nehrung yield approximately the same results. Consequently it can be accepted that these Jackdaws completely abandoned the original direction of their migration and "encouraged" by flocks of Rooks migrating westwards along the belt of lowlands reach winter ranges proper to Rooks. The westward migration enables to choose the route along the belt of lowlands where food is easily available for Jackdaws which join Rooks and form mixed flocks. It is interesting that the winter ranges of all the three subspecies of the Jackdaw may coincide

(Map 21) which is impossible only in the case of populational differences (e.g. in the Rook).

Groups of Jackdaws of the subspecies *C.m. soemmerringii* FISHER, inhabiting areas in the vicinity of the Carpathians, preserved the original direction of their migration and quite clearly cut short the route of the migration It is difficult to decide on the basis of the data available the populational composition of Czechoslovak birds. They are either a mixed group from the *C.m. spermologus* VIEILL. and *C.m. soemmerringii* FISHER, or a part of individuals belonging to *C.m. soemmerringii* FISHER, inhabiting these areas, repea-
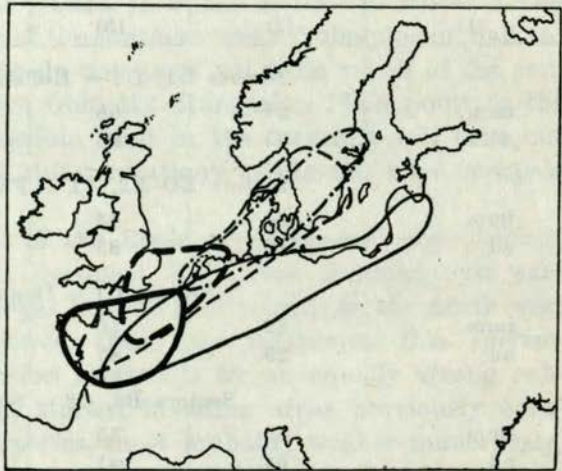
Map 21. Winter quarters of the described groups of Jackdaws. Heavy lines: continous — the birds from the north of France and Belgium, broken — from Denmark; thin lines: continous the birds from the Baltic countries, broken — from the south of Sweden, dotted — from Finland.
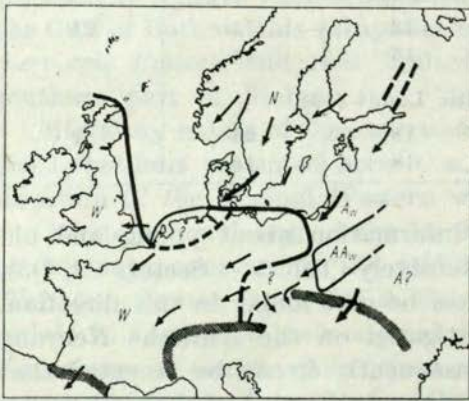
Map 22. Populational differences of European Jackdaws. A$_w$ — population with an altered direction of migration. The rest of descriptions — see Map 13.
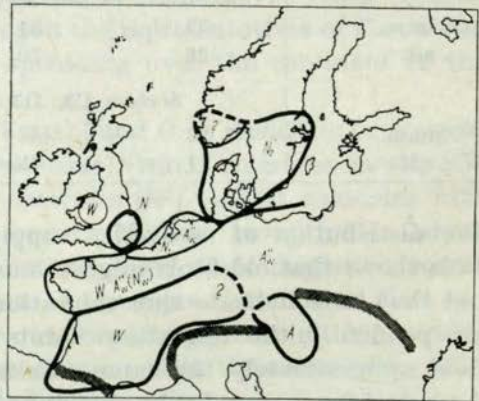
Map 23. Winter quarters of Jackdaws. Letter in a circle — resident populations; letters with double apostrophe (A″, N″) — secondary winter quarters developed by way of lenghtening migration routes. The rest of descriptions — see Map 3.

tedly chose the shortest route to a convenient winter quarter in the Hungarian Plain (when migrating both westwards and south-eastwards birds must fly over highland regions).

We can accept the existance of three migrational populations, corresponding to the Jackdaw subspecies, within the area of Western, Northern and Central Europe (Map 22), Among *C.m. soemmerringii* FISHER there appeared a subpopulation whose main characteristics is a repeatedly changed direction of its migration. The distribution of the European winter quarters of the Jackdaw is shown on Map 23.

### Carrion and Hooded Crow, *Corvus corone* L.

Corvus corone L. occurs in three subspecies all over Europe (VAURIE, 1959). Carrion Crow, *C.c. corone* L. occurs in Western Europe as far as the southern part of Scotland and Schleswig-Holstein in the north, the Elbe and western

Table 6. Recoveries used to the analysis of migrations of *Corvus corone* L.

Areas	Recoveries from winter period (2)			Recoveries from migration (3)			Grand total
	shorter than 100 km	longer than 100 km	total	shorter than 100 km	longer than 100 km	total	
(1)	(4)	(5)	(6)	(4)	(5)	(6)	(7)
Great Britain (8) Sectors EO–1	5	—	5	12	—	12	17
France (9) Sector D1	13	5	18	18	2	20	38
Holland (10) Sector C1	12	1	13	17	—	17	30
Denmark (11) Sector B1	8	3	11	17	—	17	28
Norway (12) Sector C2	37	39	76	74	31	105	181
S Scandinavia (13) Sector C2	23	25	48	94	32	126	174
Central Scandinavia (14) Sector A	1	19	20	25	47	72	92
N Scandinavia (15) Sector E2	3	10	13	25	11	36	49
Switzerland (16) Sectors D2–3	2	—	2	3	—	3	5
Germany, Poland (17) Sectors B3–4, C3	5	5	10	8	1	9	19
Baltic Lands (18)	25	86	11	75	155	230	341
Total (6)	134	193	327	368	279	647	974

part of Czechoslovakia in the east, and the Alps in the south. *C.c. sardonius* Kleinschmidt occurs in Italy (with the exception of the northernmost parts), Yugoslavia, and the southern part of the Balkans; Hooded Crow, *C.c. cornix* L. lives in Ireland, the northern part of Scotland and the remaining area of Europe northwards and eastwards to the subspecies mentioned earlier.

Among the European recoveries of *Corvidae* the Crow is represented by he highest number 2243 recoveries. These recoveries, however, refer mainly
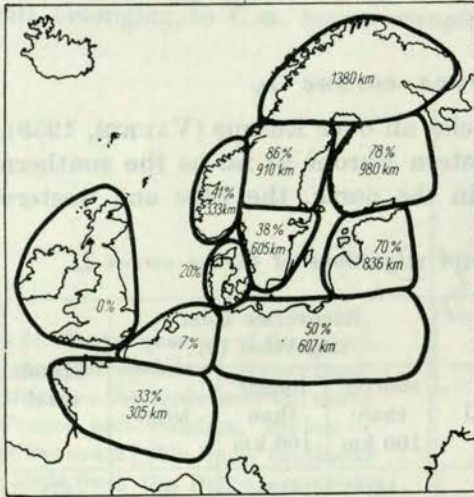
Map 24. Migratory habits of *Corvus corone* L. Descriptions see — Map 2.

Map 25. Recoveries from winter period and migration of Crows from the south of Sweden and Denmark (○), and from Switzerland (△). Neglected recoveries from the period of migration within the breeding area. Descriptions see — Map 5.

to birds ringed in the Scandinavia (1627 recoveries — Map 1), whereas there are practically no recoveries of birds from Central and Eastern Europe. 974 recoveries were used to investigate the migrations (Tab. 6). Similarly as in the case of the species discussed earlier, birds inhabiting Western Europe migrate less intensively than other European birds (Map 24). Towards the east and north more intensive migration is encountered.

Corvus corone corone L.

1) Great Britain. Carrion Crows living in Great Britain may be treated as resident — all the 17 recoveries from the autumn-winter period were recorded at distances shorter than 100 km from the ringing place.

2) Northern part of France, Belgium, Holland. Out of 30 autumn-winter recoveries of birds ringed in this region only one was recorded at a distance longer than 100 km from the place where the bird had been born.

3) Switzerland (Map 25). Similarly as in the case of the Jackdaw, Alpine Carrion Crows migrate in winter in the SW direction and display more intensive migratory habits then their neighbours from lower regions. The harsh mountain climate should be treated as a main reason for that.

Generally the Carrion Crow is a bird which has lost, to a considerable extent, its migratory urge. Among the part of birds which still undertake migrations the tendency is also quite evident (Tab. 7 — Sectors D1, EO–1).

Table 7. Percentage distribution of recoveries according to distance and age *C. corone* L.

Age of birds	Number of recoveries	Distances (km) (7)			
		to 100	101–500	501–1000	over 1000
(1)	(2)	(3)	(4)	(5)	(6)
Sectors D1, EO, E1 — Holland, France (8)					
imm.	36	81	17	6	—
ad.	32	97	3	—	—
Sectors C1, C2 — Denmark, S Scandinavia (9)					
imm.	124	69	18	12	1
ad.	67	85	10	5	—
Sector B1 — SW Norway (10)					
imm.	96	57	38	3	1
ad.	34	77	18	3	3
Sector B2 — Central Scandinavia (11)					
imm.	60	23	30	40	8
ad.	21	58	14	14	14
Sector A — N Scandinavia (12)					
imm.	29	65	7	17	10
ad.	14	50	21	7	21
Sector B3 — Finland (13)					
imm.	194	31	9	39	20
ad.	94	41	10	20	29
Sector C3 — Baltic Lands					
imm.	30	50	3	40	7
ad.	24	46	8	33	12

Corvus corone sardonius KLEINSCHMIDT

No recoveries.

Corvus corone cornix L.

1) Ireland, Scotland. There are no winter recoveries of birds from these areas; according to WITHERBY (1920) these Crows do not migrate.

2) Denmark, southern part of Sweden (Map 32). The winter quarters of Crows inhabiting these areas stretche from the eastern part of England through Belgium, Holland, to Denmark. The distribution of recoveries of young and old birds shows clearly that the routes of migration get shorter (Tab. 7 — Sectors C1–2).

3) Norway and mountainous areas of Western Sweden to the 65° line of northern latitude (Map 26). Hooded Crows occurring in the mountainous south-western parts of Scandinavia have distant winter quarters which coincide with the

Map 26. Recoveries from winter period and migration of Hooded Crows from Norway. Descriptions see — Map 25.

Map 27. Recoveries from winter period and migration of Hooded Crows from Central Sweden. Descriptions see — Map 25.

winter quarters of the previous group (from England by way of Holland to Denmark). Besides this there is an additional winter quarter in the south-western point of Norway, the vicinity of Stavanger. Mass wintering in this area must be caused by a strong reluctance of birds to cross the sea. The following recovery deserves attention:

Oslo 3880
o juv. 13. 07. 1934 Dovre: 62°05′N, 9°07′E, Norway.
*   06. 11. 1934 Kinbrace: 58°15.N, 3°56′W, Great Britain.

The early date of killing the bird gives ground for assumption that it migrated directly from Norway to Scotland (a possible case of drift). The distribution of recoveries of young and old birds gives information as to whether the route gets shorter or longer (Tab. 7 — Sector B1). However it is difficult to accept that the group is a stabilized population unlike all the neighbouring ones. It seems more probable that it is a mixture of birds displaying contradicting migratory tendencies.

4) Central Sweden (Map 27). The area of the winter occurrence of migrants from this group coincides with the winter ranges of birds from the southern part of Sweden, but the north-eastern boundary is shifted to the 60° line of latitude. In spite of these similarities groups inhabiting these areas differ in the distribution of recoveries (Tab. 7 — Sector B2). In as much as birds from the southern part of Sweden shorten the range of migration, birds from the central part of Sweden have a tendency to lengthen their migration routes, and they form an intermediary group between the southern one (lowlying regions of the southern part of Sweden) and birds inhabiting the entire northern part of Scandinavia.

5) Northern part of Scandinavia (Map 28). Crows from this area disperse over vast areas of winter quarters which coincide with the winter ranges of the groups discussed above — they occur in winter in the area from Belgium and Holland, through Denmark to the central and western part of Scandinavia. The distribution of recoveries indicates a strongly elongated range of their migration (Tab. 7 — Sector A).

Map 28. Recoveries from winter period and migration of Hooded Crows from the north of Scandinavia. Descriptions see — Map 5.

Map 29. Recoveries from winter period and migration of Hooded Crows from western part of Finland. Descriptions see — Map 5.

6) Finland and the Baltic countries: a) western part of Finland (Map 29) — the winter quarters of these Hooded Crows can be accurately determined by their numerous recoveries. They cover a relatively narrow belt from Belgium, through Holland, Denmark, to the vicinity of Stockholm. Birds from this region quite clearly lengthen the route of their migration (Tab. 7 — Sector B3). b) "Mixed zone" ("Mischgebiet" according to RENDAHL, 1960) — Map 30.

Birds inhabiting the narrow belt accurately determined by RENDAHL (1960) migrate along two routes: over Aland Islands (as birds from the western part of Finland) over Sweden, Denmark and along the eastern and southern shores of the Baltic Sea. In effect they occur in winter quarters characteristic for both birds from the western part of Finland (and from Gotland Island), and for Hooded Crows from the more southern Baltic countries. Most probably birds sometimes migrating along the eastern shores of the Baltic Sea, and sometimes along the western shores, come from the zone discussed. For example:

Rossitten D 35 608
o 15. 10. 1926 Rossitten: 55°11′N, 20°49′E, USSR.
* 28. 11. 1927 Oland: c. 56°30′N, 16°30′E, Sweden.

Stockholm U 39 824
* 09. 04. 1951 Mjöhult: 57°19′N, 14°13′E, Sweden.
(?) 03. 04. 1955 Sabile: 57°00′N, 22°28′E, USSR.

c) South-eastern part of Finland, Estonia, Latvia, Lithuania (Map 31) — winter quarters of Hooded Crows from these countries are quite precisely determined and they cover the north-eastern part of Germany, the northern

Map 30. Recoveries from winter period and migration of Hooded Crows from the "transitional belt" in Finland. Descriptions see — Map 5.

Map 31. Recoveries from winter period of Hooded Crows from the Baltic countries (○) and a part of Central Europe (△). One recovery added (from Holland) from the period of migration. Descriptions — see Map 5.

part of Poland, and then in a narrow belt they reach the Gulf of Finland. Only a small part of this winter quarter, at the foot of the Jutland Peninsula, is common with the Scandinavian birds. One recovery was recorded in Holland.

Similarly as in the case of Finnish birds the distribution of recoveries indicates the lengthening of the route of migrations (Tab. 7 — Sector 63).

7) Poland (with the exception of the north-western area), (Map 31). There is only a small number of winter recoveries of Polish birds. They all imply that the general direction of their migrations is WSW, while the most distant recovery was recorded in the western part of Central France. The insufficient number of recoveries made it impossible to investigate the migratory tendencies of this group of birds.

From the remaining areas of Europe there are only single, scattered recoveries.

In spite of the fact that there are three subspecies of Crows in Europe the analysis of populational differences is not simple. The problem of the origin of *C.c. corone* L. seems to be quite evident. The distribution of this subspecies as compared with the area of the Hooded Crow (taking into account, among other things, the latter's occurence on the British Isles) suggests that the former comes from the south-western region, and so the same as the western population of the Rook and subspecies *C.m. spermologus* VIEILL., *C.c. corone* L. is only a partial migrant population and is in the middle of the process of cutting short its migration routes. The Carrion Crow occupying the continent when the glacier retreated came upon two populations, differing as far as their origin was concerned, of the Hooded Crow: British (the counterpart of the northern population of the Rook and subspecies *C.m. monedula* L. of the Jackdaw), and a strong Balkan population in Central Europe (or any other south-eastern population).

The correlation between the populations is analogous to the situation that prevails with the Jackdaw — the northern population (British) was ousted to the north of the British Isles, where they now form a sort of an oasis there, and to the Scandinavian Peninsula. It should be mentioned here that the spreading of the Hooded Crow in Scandinavia must have come up against obstacles. The Hooded Crow, as one of the most resistent to low temperatures *Corvidae* birds (see their geographical distribution), must have moved just behind the retreating glacier. When it started invading the Scandinavian Peninsula, in the mountainous regions prevailed conditions which for a long time rendered life there impossible. As a result of this the first wave of invasion, coming from the British Isles, could occupy only the lowland part of Southern Sweden. Simultaneously, on the other side of the Baltic Sea, which had been freed from the glacier, Hooded Crows, from the southern populations migrated to the north. These birds occupied the entire northern part of Scandinavia and in the mountainous regions of Sweden and Norway they came upon the representatives of a less dynamic northern population. In Central Scandinavia an area was formed where northern and southern populations mixed with each other. Hooded Crows coming from the southern regions, after they had occupied Scandinavia, were forced by the local conditions to migrate along

the route natural for northern populations. And as Hooded Crows display a pronounced reluctance to cross the sea, migrations to the original winter quarters became impossible. Hence the winter ranges of the two populations inhabiting the Scandinavian Peninsula are almost identical, disregarding a specific winter quarter in the southern part of Norway. Birds from the western part of Finland, for which the most economic route across the sea was the flight over Aland Islands, accepted the same migration route as Swedish birds. It may be considered here whether the hypothesis of the secondary migration route of Scandinavian birds disposes of the assumption concerned with the double invasion of the peninsula. This assumption is based on the analysis of migratory tendencies of Hooded Crows from Denmark and various localities of Scandinavia. Birds from Denmark and the southern part of Sweden (the lowlands — hypothetical regions occupied mainly by the northern population) are in the middle of the process of shortening their migration routes. Crows from the areas where the mixing of populations is supposed to occur do not display their tendencies strongly (Norway, Central Sweden), while Hooded Crows from Finland and the north of Scandinavia quite clearly lengthen the route of their migrations. Common winter quarters in Holland or in Denmark are for some of them (the northern population) secondary winter ranges which were formed by way of cutting short the migration routes (original winter ranges within the British Isles), while for others they are the result of lengthening their routes (the southern population). Hooded Crows from Poland and the Baltic Countries migrating to the west, and not to the south as their hypothetical origin might indicate, should display tendencies to lengthen the migration routes which was in fact recorded.

And so we can accept for the investigated area of Europe the existence of four basic Carrion Crow populations (Map 32): 1) Western population (W) covering the entire area within which subspecies $C.c.$ $corone$ occurs; 2) Subalpine population covering the area within which subspecies $C.c.$ $sardonius$ occurs; 3) northern population (N) whose area is scattered — Ireland, Scotland, Denmark, and the south of Sweden; 4) southern population (S) which includes at least three subpopulations: a) Norwegian (Sr) covering the western part of Scandinavia, b) pseudo-northern (Sn) occurring in the central and northern part of Scandinavia and in the western part of Finland, c) pseudo-western (Sw) population inhabiting the eastern and southern shores of the Baltic Sea. The winter quarters of the populations mentioned are presented on Map 33. There remains still the problem of subpopulational boundaries within the southern population. The frontier belt between birds migrating to the southern point of Norway and birds flying to Denmark by way of Kattegat runs approximately along the valley of the Glommy river and further on along the main ridges of the Scandinavian mountains forming a sort of continuation of Skagerrak. This division was most probably caused by the specific topographical features, as the existence of a similar boundary for Jackdaws and Rooks is implied

by, unfortunately occasional, recoveries. The "mixed belt", as understood by RENDAHL (1960), running within the area of Finland, seems to me to be a "transitional belt" between the subpopulations. A deciding factor in the division of the migrational directions of Finnish Hooded Crows are the topographical features. For Crows from the west of Finland the route ensuring
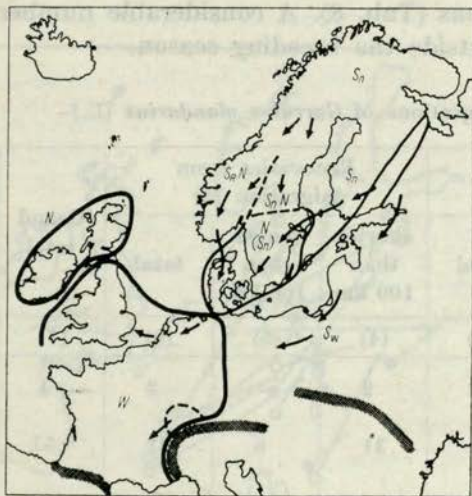
Map 32. Populational differences of Crows. Description of symbols in the text; description of signs — see Map 13.
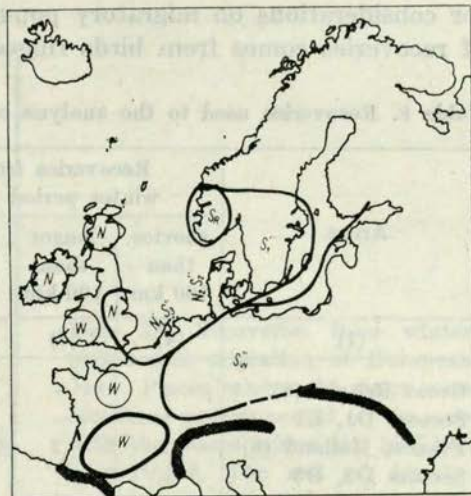
Map 33. Winter quarters of Crows. Descriptions see — Map 23

the safest flight over the sea is the belt of Aland Islands. Crows from the eastern part of Finland fly over the Gulf of Finland which is only a small area of open water. For birds inhabiting the above mentioned transitional belt both these routes are similarly gruelling and the decision as to the choice of the route of migration may depend on the actual state of atmospheric conditions (winds, visibility, etc.), and the same birds may sometimes choose different routes in successive years. This seems to be supported by recoveries of birds ringed on the Kurische Nehrung.

Jay, *Garrulus glandarius* (L.)

The Jay inhabits the entire area of Europe, northwards to the 65° line of northern latitude in Scandinavia, and to the 61° line of northern latitude in the north-eastern part of the Soviet Union. Within this area the Jay occurs in many subspecies *G.g. hibernicus* WITHERBY and HARTERT — Ireland, Scotland, *G.g. rufitergum* HARTERT — the remaining area of the British Isles, *G.g. fasciatus* (BREHM) — the Iberian Peninsula, *G.g. ichnusse* KLEINSCHMIDT — Sardinia, *G.g. corsicanus* LAUBMANN — Corsica, *G.g. albipectus* KLEINSCHMIDT —

Italy, Sicily, Yugoslavia, *G.g. cretorum* MEINERTZHAGEN — Greece, Crete, *G.g. inphigenia* SUSHKIN and PTUSCHENKO — the Crimea, southeastern part of Ukraine, *G.g. sewertzowii* BOGDANOV — north-eastern part of the Soviet Union, *G.g. glandarius* (L.) the remaining part of Europe (VAURIE, 1959). The Jay belongs to the species of which we have a considerable number of recoveries (421 — Map 1). However, out of this number only 151 recoveries are useful for considerations on migratory populations (Tab. 8). A considerable number of recoveries comes from birds ringed outside the breeding season.

Table 8. Recoveries used to the analysis of migrations of *Garrulus glandarius* (L.)

Areas	Recoveries from winter period (2)			Recoveries from migration (3)			Grand total
	shorter than 100 km	longer than 100 km	total	shorter than 100 km	longer than 100 km	total	
(1)	(4)	(5)	(6)	(4)	(5)	(6)	(7)
Great Britain (8) Sectors D1, E1	2	—	2	2	—	2	4
France, Holland (9) Sectors D2, D3	12	2	14	31	6	37	51
Germany, Poland (10) Sectors B3, B4,	17	6	23	15	10	25	48
Baltic Lands (11)	3	1	4	12	1	13	17
Scandinavia (12)	11	—	11	17	3	20	31
Total (6)	45	9	54	77	20	97	151

Some authors consider the Jay as an invading bird (e.g. DORST, 1962) which does not undertake any migrations except in the years of invasion. Recoveries do not seem to support this opinion: long distance recoveries come from different years relatively regularly and they do not show any crowding in the years of invasion as given by PUTZIG (1938), and BERNDT and DANCKER (1960). Also ULFSTRAND (1963) has doubts whether the Jay is an invading bird. A considerable number of recoveries come from the sector within directions from S to W which would not occur if Jays carried out only nomadic flights. This indicates the existence of a determined direction of migration (Map 34).

European Jays, displaying a tendency to cut short the routes of their migrations (Tab. 1), are at the same time only partial migrants so that in normal years only a small per cent of birds leave their breeding grounds. Migrations of a small number of Jays often remain unnoticed by many observers. But the occurrence of this phenomenon is proved by the fact that the observation stations along the Polish coast of the Baltic Sea (Operation Baltic) continually record passages of this species although sometimes of quite

small numbers. The occurrence of an annual migration of a small number of Jays was also recorded by BERNDT and DANCKER (1960). In some years, when there occurs a considerable increase in Jay populations possibly with a simultaneous shortage of food, an intensive migration of young Jays in the direction of normal migrations follows. A mass flight of birds in then easily noticeable and is recorded as an invasion. Such an invasion is a mass migration
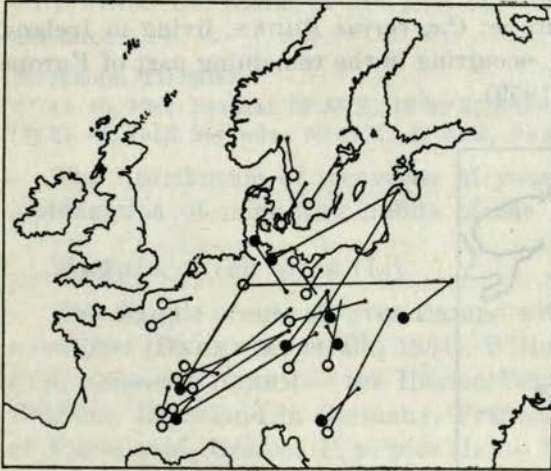
Map 34. Recoveries from winter period and migration of European Jays. Places where the rings were recovered are connected on the map with the places where the bird had been ringed. The rest of descriptions — see Map 5.

of a population of birds whose instinct of migration has declined. For a majority of birds from such a population a strong ultimate factor is needed, to induce to migration (e.g. lack of food) — (THOMSON, 1949), while indirect stimuli, connected with the seasons and stimulating migrations of typical migrants, are insufficient. This tendency to invasions should be considered as the lowest degree of migratory habits of a population. Only those populations of birds whose instinct to seasonal migrations has declined completely can not react with a directional invasion to such a strong stimulus as the lack of food (or symptoms which indicate it, like the overcrowding of the population). A similar opinion was expressed by BERNDT and DANCKER (1960) mentioned above. However, they consider that the effect of the lack of food must be excluded in the case of the Jay, and they assume the occurrence of the over-crowding of the population to be a basic stimulus releasing the inclination to migrate. However, it must be taken into consideration that the concept of overcrowding is a relative one — we are here not so much concerned with an absolute density of bird occurrence per unit of area, as with the relation of birds to the amount of available food in the environment. The state of things in which there occurs a premature exhaustion of food reserves is such an overcrowding of an area and releases the impulse to migrate. And so migration turns out to be a sort of reaction to the possibility of a food shortage

which is one of the original stimuli to seasonal migrations of birds living in cold and temperate zones (THOMSON, 1949).

A small number of long-distance recoveries of European Jays, as well as a complicated pattern of the distribution of subspecies within this area give no grounds for considerations on the occurrence of migratory populations in Europe.

Raven, *Corvus corax* L.

Only two subspecies occur in Europe: *C.c. varius* BRUNN. living in Iceland and Faeroe Islands, and *C.c. corax* L. occurring in the remaining part of Europe including the Far North (VAURIE, 1959).

Map 35. Recoveries from the autumn, winter and spring periods of Europeans Ravens. Descriptions see — Map 34.

Table 9. Recoveries used to the analysis of migrations of *Corvus corax* L.

Areas	Rocoveries from winter period (2)			Recoveries from migration (3)			Grand total
	shorter than 100 km	longer than 100 km	total	shorter than 100 km	longer than 100 km	total	
(1)	(4)	(5)	(6)	(4)	(5)	(6)	(7)
Great Britain (8)	3	1	4	4	—	4	8
Scandinavia (9)	7	4	11	11	6	17	28
NE Europe (10)	4	2	6	10	1	11	17
Rest of Europe (11)	2	1	3	4	—	4	7
Total (6)	16	8	24	29	7	36	60

There is a relatively small number of recoveries of European Ravens (125), and out of this number 60 recoveries concern birds captured in the autumn--winter period (Tab. 9). It is evident, on the basis of the table, that 15 recoveries out of the total number concern Ravens which migrated at least 100 km from the place where they had been born. This shows that there is no pronounced direction of migrations and that we can treat the Raven as a mainly resident bird. In the autumn-winter period Ravens undertake nomadic movements but only within the radius of 200 km; only one recovery was recorded at a longer distance:

Stockholm TB 5037
o 18. 05. 1952 Bjorna: 63°33′N, 18°36′E, Sweden.
(?) 21. 09. 1952 Sorunda: 59°00′N, 17°48′E, Sweden. 500 km S.

The distribution of recoveries of young and old birds indicates a definite stabilization of migratory habits of the Raven (Tab. 1).

Magpie, *Pica pica* (L.)

The Magpie occurs all over Europe with the exception of its north-easternmost part (DEMENTEV et all., 1964). Within this area there are five subspecies: *P. p. melanotos* BREHM — the Iberian Peninsula; *P. p. galliae* KLEINSCHMIDT — Belgium, Rhineland in Germany, France, Switzerland, Italy with Sicily, part of Yugoslavia, Greece; *P. p. pica* (L.) — the British Isles, Holland, Denmark,
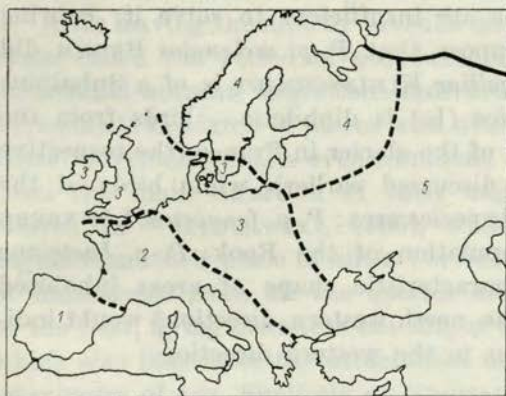
Map 36. Distribution of Magpie in Europe. Subspecies: 1—*P. p. melanotos* A. E. BREHM, 2 — *P. p. galliae* KLEINSCHMIDT, 3 — *P. p. pica* (L.), 4 — *P. p. fennorum* LÖNBERG, 5 — *P. p. bactariana* BONAP. Continous line — north boundary of breeding area, broken line — boundaries of subspecies.

the southern part of Sweden, Germany, Poland, south-eastern Europe to Roumania and Bulgaria; *P. p. fennorum* LÖNNBERG — Scandinavia with the exception of the southern part of Sweden, Finland, the Baltic countries, the Soviet Union to Moscow; *P. p. bactriana* BONAPARTE — the remaining part of Europe as far as the Ural (VAURIE, 1959).

There is a relatively considerable number of recoveries concerning European Magpies (560). However, this material does not supply many possibilities for populational considerations. Out of 274 recoveries recorded in the autumn-

-winter period only two were recorded at distances longer than 100 km; the material contains only 7 long-distance recoveries of birds ringed in their nests — 210 km S, 275 km NE, 450 km SW, — of birds ringed in the course of the year as adult birds — 110 km ENE, 145 km S, 153 km S, 150 km S (the last three birds had been ringed in spring in Denmark). The distribution of recoveries of young and old birds is quite identical (Tab. 10). These data indicate that the Magpie is a resident bird, and it is impossible to discern any migratory

Table 10. Percentage distribution of recoveries according to distance and age *P. pica* (L.)

Age of birds	Number of recoveries	Distances (km) (7)			
		to 100	101–500	501–1000	over 1000
(1)	(2)	(3)	(4)	(5)	(6)
imm.	176	99.5	0.5	—	—
ad.	81	99	1	—	—

populations. And so the origin of individual subspecies can be deduced by drawing an analogy between the present distribution of Magpie subspecies and the *Corvidae* species discussed in greater detail. An attempt to apportion subspecies to separate glacial areas should however be treated only as a suggestion which might help to solve this problem. At present the methods of taxonomic and zoogeographic investigations are insufficient to solve it. Bearing in mind this reservation we might suppose that *P. p. melanotos* BREHM did not abandon the area occupied; *P. p. galliae* KLEINSCHMIDT is of a Subalpine origin (the Italian Peninsula); *P. p. pica* (L.) is diphiletic — birds from the British Isles survived the farthest reach of the glacier in France (the respective northern populations of the *Corvidae* discussed earlier), while birds of the Balkan origin occupy the rest of the subspecies area; *P. p. fennorum* LÖNNBERG is a counterpart to the Caucasian population of the Rook; *P. p. bactriana* BONAPARTEIS of Asian origin. The characteristic shape of areas inhabited by European subspecies (pointing in the north-western direction) would indicate a strong drive of Asian populations in the western direction.

Nutcracker, *Nucifraga caryocatactes* (L.); Chough, *Pyrrhocorax pyrrhocorax* (L.); Alpine Chough, *Pyrrhocorax graculus* (L.)

These species can not be discussed in greater detail because of the lack of material. 13 recoveries of Nutcrackers ringed (8 local, 50, 80 km) were recorded, the three remaining recoveries (one of them only probably) concern the invasion of *N. c. macrorhynchos* BREHM:

Helsinki B 18 166
* 03.09. 1954 Signilskar: 60°12′N, 19°22′E, Finland.
x skeleton 14. 10. 1955 Dorrod: 55°35′N, 13°22′E, Sweden.

Helsinki B 18 173
* 13. 09. 1954 Signilskar: 60°12′N, 19°22′E, Finland.
x 03. 11. 1954 Brastad: 58°20′N, 11°25′E, Sweden.

Göteborg C 48 425
* 10. 02. 1954 Falun: c. 61°N, 15°E, Sweden.
(?) 19. 08. 1955 Troitzk-Petyorsk: 62°40′N, 56°15′E, USSR.

Out of ten recoveries of the Chough 5 are retraps, 4 short-distance recoveries (25 km NNW, 40 km S, 50 km ENE, 60 km ESE), and one recovery recorded at a distance longer than 130 km SSW (a bird from Switzerland). Out of 14 recoveries of the Alpine Chough 11 are retraps, three from distances: 35 km ESE, 35 km ESE, 85 km NNE.

CERTAIN PROBLEMS OF THE BIOLOGY OF *CORVIDAE*

The disposition in the time of European *Corvidae* breeding season is illustrated in Table 11. We can assume, generally, that the well known regularity in the delay of the breeding season as we move to the north and east is evident from the table. A permanent succession in which birds start their broods is, as a rule, preserved within individual areas. Some insignificant deviations from this rule were observed only in the case of species starting their broods late (Jackdaw, Magpie, Jay). However, it seems possible that they are only accidental deviations being the result of the paucity of material.

After leaving the nest by juvenile birds there commences in their life a period often called the period of post-breeding dispersion. In the period preceeding directional autumn migrations individual birds and flocks undertake nomadic movements in search of places with available food. In the case of certain species these movements reach even hundreds of kilometres in directions which differ from the main direction of their migrations (e.g. the Grey Heron, *Ardea cinerea* L. — RYDZEWSKI, 1956), while other species carry out only short flights from their place of birth. *Corvidae* belong to the latter group: a majority of individuals from all the species discussed remain in the nearest vicinity of the nest, flying distances not longer than 10 km. This is shown in Table 12 which also illustrates the attachment of *Corvidae* to the place of birth in their later years of age. Similarly as GROMADZKI (1964) I consider it more accurate to use the phrase "attachment to the locality of birth" than "…. the place of birth" when considering the problem of young birds' return to their broods. The latter phrase is acceptable in the case of colonial birds when they return to the same colony. However, it should be remarked that a Rook killed a few kilometers away from its place of birth could have nested in its natal colony which it had left flying to the feeding ground. And so, without dividing the species discussed into colonial and solitary, I assumed for all *Corvidae* that a bird recorded within the radius of 10 km from the place of breeding returned to the place of birth. This conventional distance turned out to be

Table 11. Phenology (average dates) of the breeding season of *Corvidae* in Europe (in brackets number of recoveries which were taken as a basis for calculating average data; boundaries of sectors were taken only approximately).

Areas (1)	Corvus corax L.	C. corone L.	C. frugilegus L.	C. monedula L.	Pica pica L.	Garrulus glandarius (L.)
CO, DO Great Britain (2)	24 IV (25)	28 V (30)	29 IV (37)	30 V (46)	28 V (15)	
C1 Denmark (3)		22 V (39)		3 VI (90)	23 V (44)	
C2 S Scandinavia (4)		30 V (214)		4 VI (108)	1 VI (71)	
B1 SW Norway (5)	23 V (38)	3 VI (171)	27 V (37)		2 VI (64)	9 VI (43)
B2 Central Scandinavia (6)		8 VI (90)			9 VI (15)	
A N Scandinavia (7)		18 VI (65)			17 VI (16)	
B3–4 Finland (8)	14 V (22)	6 VI (424)		9 VI (105)	13 VI (138)	8 VI (23)
C3–4 Baltic Lands (9)		3 VI (93)	25 V (59)	4 VI (63)	12 VI (13)	
D3 S Poland, Byelorussia (10)	12 V (19)	28 V (36)	24 V (118)		4 VI (35)	7 VI (49)
D2 W Poland, E Germany (11)						
D1 Holland (12)		26 V (53)		28 V (126)		7 VI (43)
EO Brittany (13)			4 V (283)		31 V (29)	
E1 France (14)		25 V (46)		29 V (89)		4 VI (18)
E2 Austria (15)	*	25 V	*		*	
E3–5 Southern Russia (16)			27 V (49)			
C5, D4–5 Russian Plain (17)			31 V (270)			

* calculated together with sectors D2, D3.

Table 12. Post-breeding dispersion and the abandonment of the locality of birth (percentage of birds given was recorded at a distance longer than 10 km from the place of birth; in brackets number of recoveries considered).

Species	First post-breeding period	Later breeding periods
(1)	(2)	(3)
Garrulus glandarius (L.)	0 (21)	12 (24)
Pica pica (L.)	3 (98)	12 (65)
Corvus corone L.	8 (191)	43 (169)
Corvus monedula L.	14 (57)	23 (216)
Corvus frugilegus L.	28 (123)	48 (113)
Corvus corax L.	— (7)	89 (37)

suitable for all the species with the exception of the Raven whose normal hunting range exceeds the radius of 10 km from the nest. It seems that tendencies to abandon the locality of birth are correlated with the size of the post-breeding dispersion of young birds. An exceptionally high per cent of Rooks nesting outside the locality of birth indicates that the connection of young birds with the flock of the natal colony is not stronger than connections within the flock of Crows.

Birds abandoning the locality of birth sometimes fly very long distances:

Corvus frugilegus L.

Riga 115 240
o   28. 05. 1939 Rezeknensk: 56°06′N, 27°31′E, USSR.
(?) 02. 06. 1941 Brudzew: 51°55′N, 18°00′E, Poland. 810 km SW.

Corvus corone cornix L.

Stockholm TA 7608
o 03. 06. 1947 Sundsgruvan: 56°40′N, 14°40′E, Sweden.
x 22. 05. 1948 Apeldoorn: 52°20′N, 6°10′E, Holland. 670 km SW.

and even contrary to GROMADZKI's suppositions (1964) they abandon the area inhabited by their own subspecies:

Corvus monedula L.

Copenhagen 698 226
* ad. 11. 05. 1957 Utterslev Mose: 55°43′N, 12°30′E, Denmark.
x   28. 05. 1959 Wieluń: 51°05′N, 18°30′E, Poland.

This last case, however, is quite exceptional. Also exceptional and difficult to explain are recoveries recording migrations of single individuals in an opposite direction to the one expected:

Corvus monedula L.

Bruxelles 4 E 9996
* 26. 04. 1958 Knokke: 51°21′N, 3°19′E, Belgium.
(?) 12.06. 1958 High Halstow: 51°27′N, 0°34′E, Great Britain.

Corvus monedula L.

Rossitten Nr ?
* 25. 04. 1932 Rossitten: 55°11′N, 20°49′E, USSR.
(?) 15.05. 1932 Steegen: 52°02′N, 6°04′E, Holland.

Rossitten Nr ?
* 22. 10. 1937 Rossitten: 55°11′N, 20°49′E, USSR.
(?) 07. 12. 1937 Bene: 56°28′N, 23°05′E, USSR.

The next problem which can be solved on the basis of recaptures of ringed birds is the problem of mortality. Table 13 characterizes the length of life of the species discussed. In order to present better differences between individual species the table contains various parametres determining the process of mortality. As it can be seen the comparison of the length of life of representatives of various species, with the indices applied, is not unequivocal. It is

Table 13. Mortality and survival of *Corvidae* in Europe (in brackets number of recoveries considered).

Species	Mortality in the first year of life %	Average length of life of individuals which survived their first year of life	Maximum length of life*	Chances of surviving five years %o
(1)	(2)	(3)	(4)	(5)
Pica pica (L.)	69.0 (425)	2–8–24 (125)	14–11–25	31
Corvus corax L.	63.5 (104)	2–2–21 (33)	–	–
Corvus corone L.	62.4 (1254)	2–9–15 (427)	14–8–12	40
Garrulus glandarius (L.)	60.7 (181)	3–3–16 (69)	17–11–4	71
Corvus frugilegus L.	54.0 (525)	3–5–28 (235)	19–11–6	79
Corvus monedula L.	45.5 (745)	2–7–14 (428)	14–3–8	53

* on the basis of ringing — according to RYDZEWSKI (1962).

mainly caused by differences in the mortality curves for individual species (Diagram 2). The curve for the Jackdaw differs particularly significantly from the other curves, as its mortality in the first year of life is very low. This phenomenon, already mentioned in the previous paper (BUSSE, 1963) seems

to be beyond any doubt (745 recoveries considered). The course of the curve
for the Rook is also very interesting: it shows a clear drop in the mortality
of birds older than five years.

The mortality of *Corvidae* in individual months of the first few years of
life is presented on Diagrams 2–4. In spite of a considerable number of data
used these diagrams show uneven courses caused by accidental deviations.
To give a better picture of mortality in different seasons the same data were
used for the construction of simplified curves (Diagram 4). High mortality
occurs mainly in the two basic periods — in autumn and in the breeding season.
High mortality in autumn is most often observed in young birds, while in
spring — in old birds.
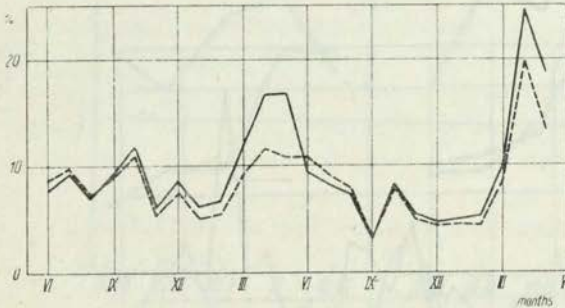
Diagram 1. Comparison of mortality
curves of the Jackdaw, obtained
with the help of the classical me-
thod — broken line, and with the
help of the method used in the pre-
sent paper — continous line.
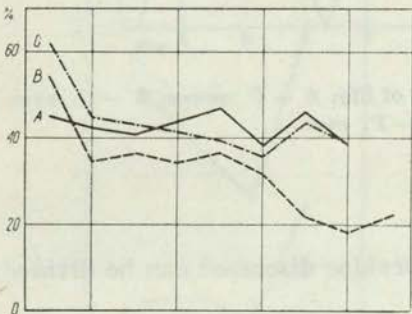
Diagram 2. Mortality curves of *Corvidae* birds.
A — *C. monedula*; B — *C. frugilegus*; C — *C. corone*;
D — *Pica pica*; E — *G. glandarius*.
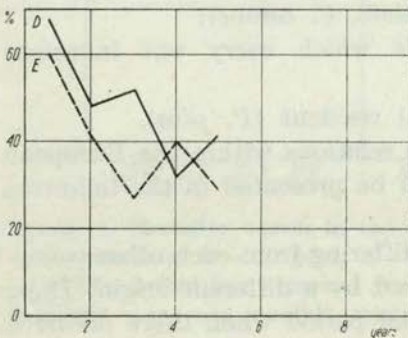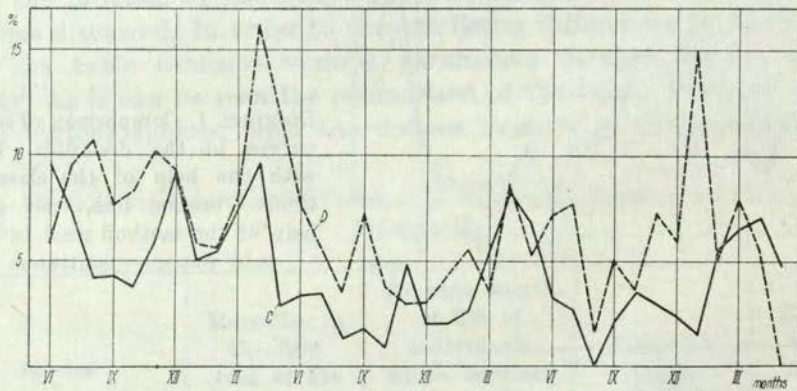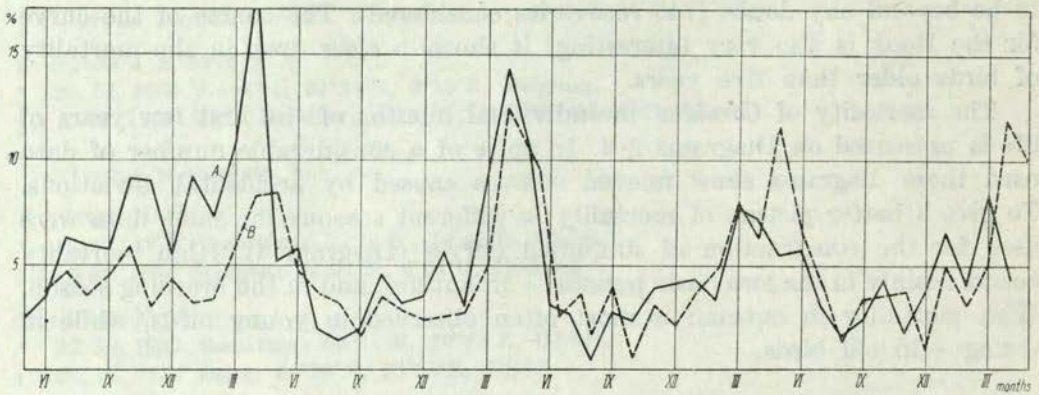
Diagram 3. Mortality curves in the first few years of life: A — *C. corone*; B — *C. mone-dula*; C — *C. frugilegus*; D — *P. pica*.

CONCLUSIONS

From the point of view of migrations the Corvidae discussed can be divided into:

1) typical migrants (*C. frugilegus*, *C. monedula*, *C. corone*);

2) partial migrants — bordering with birds which carry out invasions (*G. glandarius*);

3) non-migrants: a) nomadic (*C. corax*), b) resident (*P. pica*).

It seems that the present ornithogeographic relations within the European part of the area of the *Corvidae* mentioned can be presented in the following way:

In Europe there are migratory populations differing from each other (sometimes equivalent to subspecies), and characterized by a different origin. These populations became distinguishable in the glacial period when there occurred

an isolation of individual groups of birds within separate areas. The present habits are the result of the distribution of birds in the period following the retreat of the last glacier. We can discern five home areas of individual populations for Europe: Great Britain ("Northern" population), south-western
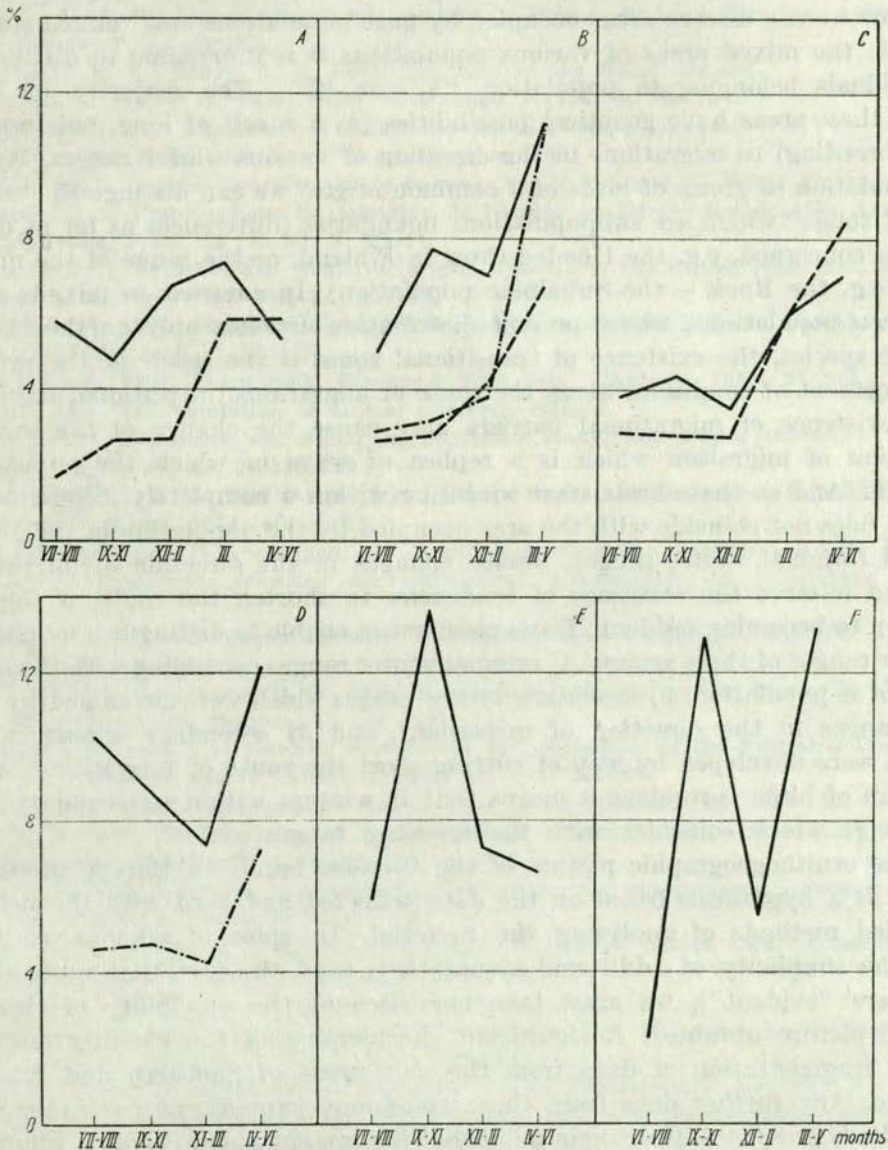
Diagram 4. Mortality curves in the course of the year: A — *C. frugilegus*, B — *C. corone*, C — *C. monedula*, D — *P. pica*, E — *G. glandarius*, F — *C. corax*. Continuous line — first year of life, dotted line — second year of life, broken line — next years of life. On vertical axis — average monthly mortality from periods plotted on horizontal axis.

part of France ("Western" population), the Italian Peninsula ("Subalpine" population), the Balkan Peninsula ("Balkan" population), and Central Asia ("Caucasian" population).

Populations, even those not showing morphological differences, did not mix together completely within the European area occupied at present, but by now we can discern areas occupied by pure populations and "mixed zones". Within the mixed areas of various populations it is impossible to distinguish individuals belonging to population "X" or "Y". The majority of birds from these areas have genetical possibilities (as a result of long, unhampered crossbreeding) to migrations in the direction of various winter ranges. Within a population (a group of birds of a common origin) we can distinguish "transitional zones" which are subpopulations boundaries (differences as far as direction is concerned, e.g. the Hooded Crow in Finland, or the range of the migration, e.g. the Rook — the Subalpine population). In contrast to mixed zones between populations, whose present distribution depends only on the history of the species, the existence of transitional zones is the result of the present arrangement of conditions along the route of migrations (migrational barriers). The existence of migrational barriers may cause the change of the original direction of migration which is a replica of ways in which the population spreads. And so these birds start wintering within a completely different area which does not coincide with the area occupied by the population in the glacial period (original winter range). Beside changes in the direction of migrations we can observe the existence of tendencies to shorten the route of the migration to becoming resident. These phenomena enable to distinguish in existing winter ranges of three groups: 1) original winter ranges coinciding with the home area of a population, 2) secondary winter ranges which were developed by way of changes in the direction of migrations, and 3) secondary winter ranges which were developed by way of cutting short the route of migrations. When a group of birds is resident it means that it winters within a secondary winter range which coincides with the breeding ranges.

The ornithogeographic picture of the *Corvidae* family in Europe presented above is a hypothesis based on the data collected and used with the help of specified methods of analysing the material. In spite of copious material and the simplicity of additional assumptions (and the fact that quite often they are "evident"), we must take into account the possibility of changes in the picture obtained. A significant shortcoming of the existing material is the fragmentation of data from the vast areas of Southern and Eastern Europe. Any further data from these areas may support, or contradict, the hypothesis presented. Bearing in mind that the present paper is only a summary of a certain stage of investigations on the migrations of *Corvidae*, I trust that it will give a stimulus to further efforts in ringing this group of birds, in particularly interesting areas.

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STRESZCZENIE

W pracy zostały wykorzystane wiadomości powrotne dotyczące ptaków krukowatych, *Corvidae* w Europie, od początku obrączkowania ptaków do połowy r. 1964. Materiały te były opublikowane w sprawozdaniach central ornitologicznych i biur obrączkowania oraz w pracach analitycznych. Ogółem analizowany materiał obejmuje 5738 wiadomości dotyczących następujących gatunków: kruk, wrona, gawron, kawka, sroka, orzechówka, sójka, wrończyk i wieszczek. Na mapach zaznaczono wiadomości o ptakach obrączkowanych w okresie lęgowym, pochodzące z okresu wędrówek (X–XI, III– połowa IV) i zimowiska (XII–II), z odległości ponad 100 km od miejsca zaobrączkowania. Na podstawie tych map została przeprowadzona analiza zwyczajów wędrówkowych poszczególnych gatunków z różnych terenów Europy z uwzględnieniem zróżnicowania populacyjnego. Do wyjaśnienia niektórych zagadnień została wprowadzona metoda określania tendencji ewolucyjnych zmian zwyczajów wędrówkowych populacji, oparta na rozszerzeniu znanego prawa biogenetycznego HAECKLA. W metodzie tej na podstawie obecnie istniejących różnic między skłonnościami do wędrówki ptaków jednorocznych i ptaków starszych wnosi się o dawniejszych zwyczajach wędrówkowych populacji.

W części poświęconej zagadnieniom biologii krukowatych zostały zastosowane nowe sposoby przedstawiania śmiertelności. Do określania długowieczności ptaków użyto trzech parametrów: a) śmiertelność w pierwszym roku życia, b) średnia długość życia ptaków, które przeżyły pierwszy rok i c) szansa przeżycia przez ptaka danego gatunku pięciu lat (wyrażona w promilach). Rozkład śmiertelności w poszczególnych miesiącach był ustalany przez obliczenie procentu ptaków ginących w danym miesiącu w stosunku do ilości ptaków rozpoczynających dany miesiąc życia.

Podstawowe wyniki pracy przedstawiają się następująco:

1) Z punktu widzenia wędrówek, omówione gatunki krukowatych można podzielić na: a) typowo wędrowne (gawron, kawka, wrona); b) słabo wędrowne — na pograniczu z inwazyjnymi (sójka); c) niewędrowne; c′) koczujące (kruk), c″) osiadłe (sroka).

2) Wydaje się, że obecne stosunki ornitogeograficzne w obrębie europejskiej części areałów wymienionych krukowatych wyglądają następująco: Na

terenie Europy istnieją zróżnicowane populacje wędrówkowe (czasem równoznaczne podgatunkom), charakteryzujące się różnym pochodzeniem. Populacje te wyłoniły się w epoce lodowcowej, w czasie izolacji poszczególnych grup ptaków na terenie odrębnych ostoi. Na obecne zwyczaje decydujący wpływ miało rozmieszczenie ptaków w okresie po rozpoczęciu regresji ostatniego lodowca. Dla Europy autor wyróżnia pięć obszarów macierzystych poszczególnych populacji: Wyspy Brytyjskie (populacja „północna"), południowo-zachodnia część Francji (populacja „zachodnia"), Półwysep Apeniński (populacja „subalpejska"), Półwysep Bałkański (populacja „bałkańska") i Azja Środkowa (populacja „kaukaska").

3) Populacje, nawet nie zróżnicowane morfologicznie, nie uległy całkowitemu wymieszaniu na obecnie zajmowanych obszarach Europy, lecz do chwili obecnej można wyróżnić tereny zajmowane przez czyste populacje i strefy mieszane. W strefach mieszania się różnych populacji nie można obecnie wyróżnić osobników należących do populacji „X" czy „Y". Większość ptaków z tych obszarów posiada bowiem genetyczne przesłanki (skutkiem długiego, swobodnego krzyżowania się) do wędrówki w kierunku różnych zimowisk. W obrębie wyróżnionych przez autora populacji (grupy ptaków o wspólnym pochodzeniu) można wykryć „strefy przejściowe" będące granicami subpopulacyjnymi (zróżnicowanie pod względem kierunku — np. wrona w Finlandii, lub zasięgu wędrówki — np. gawron z populacji subalpejskiej). W przeciwieństwie do stref mieszanych między populacjami, których obecne rozmieszczenie zależy, według autora, jedynie od historii gatunku, istnienie stref przejściowych jest wynikiem obecnego układu warunków na trasie wędrówki (bariery wędrówkowe). Istnienie barier wędrówkowych może spowodować zmianę pierwotnego kierunku wędrówki, będącego powtórzeniem dróg rozprzestrzeniania się populacji. W tej sytuacji ptaki rozpoczną zimowanie na zupełnie nowym terenie, nie pokrywającym się geograficznie z terenem zajmowanym przez populację w epoce lodowcowej (zimowiskiem pierwotnym). Prócz zmian kierunku wędrówki, daje się zaobserwować istnienie tendencji do skracania drogi wędrówki i osiadłości. Zjawiska te pozwalają zróżnicować obecnie istniejące zimowiska na trzy kategorie: 1) zimowiska pierwotne (odpowiadające terenom macierzystym populacji), 2) zimowiska wtórne, powstałe drogą zmiany kierunku wędrówki, 3) zimowiska wtórne, powstałe drogą skracania wędrówki. Osiadłość określonej grupy ptaków jest więc zimowaniem na zimowisku wtórnym, pokrywającym się z terenem lęgowiska.

Objaśnienia do map, tabel i wykresów:

Mapa 1. Podział roboczy Europy na sektory, według których analizowano materiał. W znakach w formie krzyża podana jest ilość wiadomości powrotnych o ptakach zaobrączkowanych w danym sektorze, w układzie:

C. frugilegus L.	*C. monedula* L.
C. corone L.	*G. glandarius* (L.)

Mapa 2. Wędrowność *Corvus frugilegus* L. Podano procent ptaków odlatujących i średnią odległość przelotu.

Mapa 3. Zimowiska *Corvus frugilegus* L. Linia kratkowana — główne grzbiety górskie; linia gruba — granice zimowisk; linia cienka — podział w obrębie grup zimowisk. Duże litery — zimowiska zasadnicze; litery małe z apostrofem (N', W', A') — zimowiska wtórne, powstałe drogą skrócenia wędrówki.

Mapa 4. Wiadomości powrotne z okresu zimowiska gawronów holenderskich (△) i skandynawskich (○). Linia ciągła — zasięg zimowiska, linia przerywana — tereny lęgowe.

Mapa 5. Wiadomości powrotne z okresu zimowiska i wędrówek gawronów z krajów nadbałtyckich. Znaki pełne — wiadomości z okresu zimowego, znaki puste — wiadomości z okresu wędrówek; linia ciągła — granice zimowisk, linia przerywana — tereny lęgowe.

Mapa 6. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów francuskich. Objaśnienia — patrz mapa 5.

Mapa 7. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów ze wschodnich Niemiec i środkowej Polski. Objaśnienia — patrz mapa 5.

Mapa 8. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów z Białorusi, wschodniej Łotwy i Litwy (○) i zachodniego Podola, Wołynia (ptaki zimujące na zimowisku zachodnim — △). Reszta objaśnień — patrz mapa 5.

Mapa 9. Wiadomości powrotne z okresu zimowisk gawronów z Niziny Rosyjskiej (○) i pasa mieszanego z populacjami południowymi (ptaki zimujące na zimowisku zachodnim — △). Reszta objaśnień — patrz mapa 5.

Mapa 10. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów należących do populacji subalpejskiej. Wiadomości z okresu przelotów ptaków pochodzących z sektora ○ zostały pominięte. Objaśnienia — patrz mapa 5.

Mapa 11. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów należących do populacji bałkańskiej. Pominięte są tu wiadomości z okresu przelotów na terenach lęgowych. Objaśnienia — patrz mapa 5.

Mapa 12. Wiadomości powrotne z okresu zimowisk i wędrówek gawronów należących do populacji kaukaskiej. Objaśnienia — patrz mapa 5.

Mapa 13. Zróżnicowanie populacyjne europejskich gawronów. Linia gruba i oznaczenia jednoliterowe — tereny zajmowane przez czyste populacje; linia cienka i oznaczenia wieloliterowe — strefy mieszane między populacjami; linia przerywana — przypuszczalny przebieg granic międzypopulacyjnych; linia kropkowana — granice subpopulacyjne; strzałki — kierunki wędrówki; linia kratkowana — główne grzbiety górskie.

Mapa 14. Wiadomości powrotne z pierwszego roku życia o gawronach zaobrączkowanych dnia 25 V 1959 w Szełuchowie: 54°20′N, 40°56′E, ZSSR. ○ — miejsce obrączkowania, ▮ — październik, ▲ — listopad, ● — grudzień, ■ — styczeń. Liczby oznaczają datę wiadomości powrotnej; strzałki wyznaczają przypuszczalne trasy wędrówki stad.

Mapa 15. Wędrowność kawki. Objaśnienia — patrz mapa 2.

Mapa 16. Wiadomości powrotne z okresu zimowisk i wędrówki kawek z północnej Francji, Belgii (○) i Szwajcarii (△). Objaśnienia — patrz mapa 5.

Mapa 17. Wiadomości powrotne z okresu zimowisk i wędrówki kawek z Danii. Objaśnienia — patrz mapa 5.

Mapa 18. Wiadomości powrotne z okresu zimowisk i wędrówki kawek z południowej Skandynawii. Wiadomości z okresu przelotu pominięte na terenie Danii i lęgowisk. Objaśnienia — patrz mapa 5.

Mapa 19. Wiadomości powrotne z okresu zimowisk i wędrówek kawek z Finlandii. Objaśnienia — patrz mapa 5.

Mapa 20. Wiadomości powrotne z okresu zimowisk i wędrówki kawek z krajów nadbałtyckich (○), południowo-wschodniej Polski (△) oraz południowo-zachodniej Polski i północno-zachodniej Czechosłowacji (X). Reszta oznaczeń — patrz mapa 5.

Mapa 21. Zasięg zimowisk omawianych grup kawek. Linia gruba: ciągła — ptaki francusko--belgijskie, przerywana — ptaki duńskie; linia cienka: ciągła — z krajów nadbałtyckich, przerywana — południowo-szwedzkie, kropkowana — fińskie.

Mapa 22. Zróżnicowanie populacyjne europejskich kawek. A_W — populacje ze zmienionym kierunkiem wędrówki. Pozostałe oznaczenia — patrz mapa 13.

Mapa 23. Zimowiska kawek. Litera w kole — zimowanie populacji na miejscu; litery z wtórem (A'', N'') — zimowiska wtórne, powstałe drogą wydłużenia wędrówki. Pozostałe oznaczenia — patrz mapa 3.

Mapa 24. Wędrowność wron. Objaśnienia — patrz mapa 2.

Mapa 25. Wiadomości powrotne z okresu zimowisk i wędrówki wron z południowej Szwecji i Danii (○) oraz Szwajcarii (△). Pominięto wiadomości z okresu przelotów na terenie lęgowisk. Objaśnienia — patrz mapa 5.

Mapa 26. Wiadomości powrotne z okresu zimowisk i wędrówek wron z Norwegii. Objaśnienia — patrz mapa 25.

Mapa 27. Wiadomości powrotne z okresu zimowisk i wędrówek wron ze środkowej Szwecji. Objaśnienia — patrz mapa 25.

Mapa 28. Wiadomości powrotne z okresu zimowisk i wędrówek wron z północnej Skandynawii. Objaśnienia — patrz mapa 5.

Mapa 29. Wiadomości powrotne z okresu zimowisk i wędrówek wron z zachodniej Finlandii. Objaśnienia — patrz mapa 5.

Mapa 30. Wiadomości powrotne z okresu zimowisk i wędrówek wron z „pasa przejściowego" w Finlandii. Objaśnienia — patrz mapa 5.

Mapa 31. Wiadomości powrotne z okresu zimowisk wron z krajów nadbałtyckich (○) i części Europy środkowej (△). Dołączona jedna wiadomość z Holandii z okresu wędrówek. Objaśnienia — patrz mapa 5.

Mapa 32. Zróżnicowanie populacyjne wron. Objaśnienie symboli w tekście; objaśnienie znaków — patrz mapa 13.

Mapa 33. Zimowiska wron. Objaśnienia — patrz mapa 23.

Mapa 34. Wiadomości powrotne z okresu zimowisk i wędrówek europejskich sójek. Miejsca znalezienia obrączek połączono liniami z miejscami obrączkowania. Pozostałe objaśnienia — patrz mapa 5.

Mapa 35. Wiadomości powrotne z okresu jesieni, zimy i wiosny europejskich kruków. Objaśnienia — patrz mapa 34.

Mapa 36. Występowanie sroki w Europie. Podgatunki: 1 — *P. p. melanotos* A. E. BREHM, 2 — *P. p. galliae* KLEINSCHMIDT, 3 — *P. p. pica* (L.), 4, — *P. p. fennorum* LÖNBERG, 5 — *P. p. bactariana* BONAP.

Wykres 1. Porównanie krzywych śmiertelności kawki uzyskanych metodą klasyczną — linia przerywana i stosowaną w niniejszej pracy — linia ciągła.

Wykres 2. Krzywe śmiertelności ptaków krukowatych. A — *C. monedula*; B — *C. frugilegus*; C — *C. corone*; D — *P. pica*; E — *G. glandarius*.

Wykres 3. Krzywe śmiertelności w pierwszych latach życia. A — *C. corone*; B — *C. monedula*; C — *C. frugilegus*; D — *P. pica*.

Wykres 4. Uproszczone krzywe śmiertelności w ciągu roku. A — *C. frugilegus*; B — *C. corone*; C — *C. monedula*; D — *P. pica*; E — *G. glandarius*; F — *C. corax*; linia ciągła — pierwszy rok życia; linia kropkowana — drugi rok życia; linia przerywana — następne lata życia. Na osi pionowej odłożona jest średnia śmiertelność miesięczna z okresów zaznaczonych na osi poziomej.

Tabela 1. Procentowe rozkłady wiadomości powrotnych z uwzględnieniem odległości przelotu i wieku ptaków. (1) wiek ptaków, (2) ilość wiadomości powrotnych, (3) do, (6) ponad, (7) odległości, (8) cała Europa, (9) Finlandia; *nie uwzględniono ptaków osiadłych (poniżej 100 km oddalenia od miejsca zaobrączkowania) ze względu na istnienie dwóch niezależnych procesów (tendencje do osiadłości i zmiana trasy wędrówki).

Tabela 2. Wiadomości powrotne wykorzystane do analizy wędrówek *Corvus frugilegus* L. (1) tereny, (2) wiadomości z okresu zimowisk, (3) wiadomości z wędrówek, (4) poniżej, (5) powyżej, (6) razem, (7) suma, (8) Wielka Brytania, (9) Sektory D1, EO–1 Holandia, Francja, (10) Skandynawia, (11) Sektory D2–3, E2 Europa Środkowa, (12) sektory C3–4 kraje nadbałtyckie, (13) sektory C5, D4–5 Nizina Rosyjska, (14) sektory E3–5 południowa Rosja.

Tabela 3. Procentowe rozkłady wiadomości powrotnych z uwzględnieniem odległości przelotu i wieku ptaków u *Corvus frugilegus* L. Objaśnienia od (1) do (7) — patrz tab. 1; (8) sektory EO, E1, D1 — Holandia, Francja, (9) sektory D2, D3, E2 — Europa Środkowa, (10) sektory C5, D4, D5 — Nizina Rosyjska.

Tabela 4. Wiadomości powrotne wykorzystane do analizy wędrówek *Corvus monedula* L. Objaśnienia od (1) do (8) — patrz tab. 2; (9) sektory D1–2 — Holandia, Niemcy, (10) sektory EO–2, F1 — Francja, Szwajcaria, (11) sektor C1 — Dania, (12) Skandynawia, (13) sektory B3–4 — Finlandia, (14) sektory C3, D3 — kraje nadbałtyckie.

Tabela 5. Procentowe rozkłady wiadomości powrotnych z uwzględnieniem odległości przelotu i wieku ptaków u *Corvus monedula* L. Objaśnienia od (1) do (7) — patrz tab. 1; (8) sektory D1, D2 — Holandia, Niemcy, (9) sektory EO–2, F1 — Francja, Szwajcaria, (10) sektor C1 — Dania, (11) sektory B2, C2 — Skandynawia, (12) sektor B3 — Finlandia, (13) sektory C3, D3 — kraje nadbałtyckie.

Tabela 6. Wiadomości powrotne wykorzystane do analizy wędrówek *Corvus corone* L. Objaśnienia od (1) do (8) — patrz tab. 2; (9) sektory EO–1 — Francja, (10) sektor D1 — Holandia, (11) sektor C1 — Dania, (12) sektor B1 — SW Norwegia, (13) sektor C2 — S Skandynawia, (14) sektor B2 — środkowa Skandynawia, (15) sektory A — N Skandynawia, (16) sektor E2 — Szwajcaria, (17) sektory D2–3 — Niemcy, Polska, (18) sektory B3–4, C3 — kraje nadbałtyckie.

Tabela 7. Procentowe rozkłady wiadomości powrotnych z uwzględnieniem odległości przelotu i wieku ptaków u *Corvus corone* L. Objaśnienia od (1) do (7) — patrz tab. 1; (8) sektory D1, EO, E1 — Holandia, Francja, (9) sektory C1, C2 — Dania, Skandynawia, (10) sektor B1 — SW Norwegia, (11) sektor B2 — środkowa Skandynawia, (12) sektory A — N Skandynawia, (13) sektor B3 — Finlandia, (14) sektor C3 — kraje nadbałtyckie.

Tabela 8. Wiadomości powrotne wykorzystane do analizy wędrówek *Garrulus glandarius* (L.). Objaśnienia od (1) do (8) — patrz tab. 2; (9) sektory D1, E1 — Francja, Holandia, (10) sektory D2, D3 — Niemcy, Polska, (11) sektory B3, B4 — kraje nadbałtyckie, (12) Skandynawia.

Tabela 9. Wiadomości powrotne wykorzystane do analizy wędrówek *Corvus corax* L. Objaśnienia od (1) do (8) — patrz tab. 2; (9) Skandynawia, (10) NE Europa, (11) reszta Europy.

Tabela 10. Procentowy rozkład wiadomości powrotnych z uwzględnieniem odległości przelotu i wieku ptaków u *Pica pica* (L.). Objaśnienia — patrz tab. 1.

Tabela 11. Fenologia (średnie daty okresu lęgowego) *Corvidae* w Europie. W nawiasach podano ilość wiadomości, na podstawie których obliczono średnie; granice sektorów brane były w przybliżeniu. (1) tereny, (2) Wielka Brytania, (3) Dania, (4) S Skandynawia, (5) SW Norwegia, (6) środkowa Skandynawia, (7) N Skandynawia, (8) Finlandia, (9) kraje nadbałtyckie, (10) S Polska, Białoruś, (11) W Polska, E Niemcy, (12) Holandia, (13) Bretonia, (14) Francja, (15) Austria, (16) południowa Rosja, (17) Nizina Rosyjska; * liczone razem z sektorami D2, D3.

Tabela 12. Dyspersja polęgowa i porzucanie okolicy urodzenia (podany jest procent ptaków stwierdzonych w odległości większej, niż 10 km od miejsca urodzenia; w nawiasach ilość rozpatrywanych wiadomości powrotnych). (1) gatunek, (2) pierwszy okres polęgowy, (3) późniejsze okresy lęgowe.

Tabela 13. Śmiertelność i przeżywalność *Corvidae* w Europie (w nawiasach podano ilość rozpatrywanych wiadomości powrotnych). (1) gatunek, (2) śmiertelność w pierwszym roku życia, (3) średnia długość życia osobników, które przeżyły 1 rok, (4) maksymalna długość życia, (5) szanse przeżycia 5 lat; *) na podstawie obrączkowania — wg RYDZEWSKIEGO (1962).

РЕЗЮМЕ

Настоящая работа основывается на анализе возвратных сведений о вороновых, *Corvidae* окольцованных в Европе от начала кольцевания по I половину 1964 года. Автор воспользовался тут материалами из различных отчетов, аналитических статьей опубликованных орнитологическими центрами и бюро кольцевания соответственных стран. В общем, материал охватывает 5738 возвратных сведений касающихся следующих видов: ворона, вороны, грача, галки, сороки, кедровки, сойки, клушицы и альпийской галки. На картах обозначены сведения о птицах окольцованных в течение гнездового периода и найденных во время миграционного периода (X–XI, III–половина IV) и зимовок (XII–II) в дистанциях свыше 100 км от места окольцевания. Принимая за основу упомянутые карты, автором был произведен подробный анализ миграционных путей и некоторых связанных с миграциами вопросов биологии каждого из видов, причем учитывалась популяционная дифференцировка и происхождение из соответственных районов Европы. Для выяснения некоторых других проблем автор воспользовался методом определяющим тенденции эволюционных изменений миграционных обычаев основывающимся на более широкой трактовке известного биогенетического закона Геккеля. Судя по существующим в настоящее время разницам в наклонности к миграциам молодых одногодичных особей и старых птиц, по этому методу можно полагать о более древних миграционных обычаях соответственной популяции.

В части касающейся биологии вороновых, автор применяет новые способы представления смертности. Для определения продолжительности жизни воспользовался он следующими параметрами: а) смертность на первом году жизни, б) продолжительность жизни в среднем птиц, которые успешно прожили первый год и в) вероятные шансы жизни в последующих 5-ти годах (выраженные в промилле). Распределение смертности на протяжение соответственных месяцев определялось путем приравнивания процента погибших птиц к числу живых особей, начинающих

каждый новый месяц жизни. Основные выводы сделанные автором представляются следующим образом:

1) Принимая во внимание миграции врановых, можно подразделить отдельные виды на: а) типичных мигрантов (грач, галка, ворона); б) слабо выраженных мигрантов с тенденцией к инвазионности (сойка); виды неперелетные подразделяющиеся на: в') совершающие кочевки (ворон), в") оседлые (сорока).

2) Существующие в настоящее время в пределах европейских частей ареала рассматриваемых видов орнитогеографические отношения можно, по мнению автора, представить следующим образом: Европу заселяют весьма дифференцированные по отношению к миграциям популяции (иногда равноценные с подвидами) характеризующиеся различным происхождением. Одни их них формировались в ледниковом периоде, когда отдельные скопления птиц в своих убежищах были изолированы друг от друга. На нынешнем характере миграций решительным образом отразилось распределение птиц после начала регрессии последнего оледенения. Автор выделил для Европы 5 районов, являющихся родиной отдельных популяций: Британские о-ва для „северной" популяции, юго-западная часть Франции для „западной" популяции, Аппенинский п-ов — „субальпийской" популяции, Балканский п-ов — „балканской" популяции и Средняя Азия — „кавказской" популяции.

3) Популяции занимающие в Европе современные ареалы и даже не отличающиеся друг от друга морфологически, не смешались полностью. До настоящего времени можно выделить „чистые" популяции и зоны „смешанных" популяций. Определить, принадлежат ли заселяющие эти зоны птицы к популяции „Х" или „У" почти не представляется возможным. Большинство из них имеет генетические предпосылки мигрировать по направлению к различным зимовкам (возможность длительного свободного скрещивания). В пределах ареалов выделенных автором популяций (группировки характеризующиеся общностью происхождения) можно выделить „переходные зоны", где проходят субпопуляционные границы (субпопуляции отличающиеся по отношению к основным направлениям миграции — например, ворона из Финляндии, или же пределом мигрирования — например, субальпийская популяция грача). В противоположность к зонам смешанных популяций, современные границы которых обусловлены, по мнению автора, историей вида, на очертания переходных зон сложились ныне действующие вдоль миграционных путей условия (миграционные барьеры). Наличие барьеров препятствующих миграциям может быть причиной изменения первичного направления перелетов, которое по автору является повторением путей распространения данной популяции. В таких случаях птицы вынуждены зимовать на новой территории, не покрывающейся географически с ареалом занимаемым популяцией в ледниковом периоде, то-есть местом первичных зимовок. Кроме изменений направленности миграционных маршрутов, можно также констатировать тенденцию к сокращению их длины и переходу к оседлому образу жизни. Автор, на основании выше упомянутых фактов, современные зимовки птиц подразделяет на три категории: 1) первичные зимовки (соответствующие родине данной популяции), 2) вторичные зимовки, сформировавшиеся

путем изменений миграционного маршрута, 3) вторичные зимовки, возникшие путем сокращения первичных путей и пределов перелета. По отношению к седентарному образу жизни данной группы птиц, автор считает их зимовку вторичной, покрывающейся с гнездовым ареалом.

Объяснения к картам, графикам и таблицам:

Карта 1. Рабочее подразделение Европы на зоны, по которым был анализирован материал. В графах в виде креста приведено количество возвратных сведений о птицах окольцованных в данной зоне по схеме:

C. frugileus	C. monedula
C. corone	G. glandarius

Карта 2. Миграции *Corvus frugilegus* L. Приводятся процент мигрирующих птиц и средние дистанции перелета.

Карта 3. Зимовки грача. Прямоугольная штриховка — главные горные хребты; жирной линией обозначены границы зимовок; тонкой линией отмечены внутренние подразделения зимовок. Большие буквы — основные зимовки; более мелкие буквы с апострофом (N', W', A') — вторичные зимовки, возникшие путем сокращения миграционного пути.

Карта 4. Возвратные сведения касающиеся грачей из Дании (△) и Скандинавского п-ва (○). Сплошная линия — границы зимовок, прерывистая линия — гнездовой ареал.

Карта 5. Возвратные сведения из зимовок грачей, происходящих из прибалтийских стран. Сплошные черные значки — возвратные сведения охватывающие зимний период; светлые значки — возвратные сведения из миграционного периода; сплошная линия — границы зимовок; прерывистая линия — гнездовые территории.

Карта 6. Возвратные сведения французских грачей из периода зимовок. Объяснения — см. карту 5.

Карта 7. Возвратные сведения касающиеся зимовок и миграционного периода грачей, происходящих из восточных районов Германии и центральной Польши. Объяснения — см. карту 5.

Карта 8. Возвратные сведения грачей из Белорусской ССР, восточных частей Латышской и Литовской ССР (○), западных частей Подольской и Волынской областей ,касающиеся миграционного периода и зимовок (△ — птицы на западных зимовках). Остальные обозначения — см. карту 5.

Карта 9. Возвратные сведения касающиеся грачей из Русской низменности (○) и пояса смешивания с южными популяциями (△ — птицы пребывающие на западных зимовках). Остальные обозначения — см. карту 5.

Карта 10. Возвратные сведения касающиеся грачей субальпийской популяции из миграционного периода и зимовок. Не учитываются тут сведения касающиеся миграционного периода птиц из зоны обозначенной „О". Обозначения, как на карте 5.

Карта 11. Возвратные сведения балканской популяции грача из зимовок и периода миграции. Не учитываются тут сведения охватывающие период перелетов на гнездовых территориях. Обозначения — см. карту 5.

Карта 12. Возвратные сведения кавказской популяции грача, охватывающие период зимовок и миграции. Обозначения — см. карту 5.

Карта 13. Популяционная дифференцировка грачей заселяющих Европу. Жирной линией и буквами обозначены территории заселенные чистыми популяциями; тонкой линией и символами состоящими из нескольких букв обозначены зоны смешивания отдельных популяций; прерывистой линией обозначено предполагаемое прохождение границы между популяциями; пункти-

ром обозначены субпопуляционные границы; стрелками указывается направление миграции; широкой штрихованной линией отмечены горные хребты.

Карта 14. Возвратные сведения касающиеся грачей на первом году жизни, окольцованных 25 V 1956 в Шелухове: 54°20'N, 40°56'E (СССР). ◯ — места кольцевания, ▯▮ — октябрь, ▲ — ноябрь, ● — декабрь, ▮ — январь. Числами обозначены даты находки окольцованной птицы; стрелки указывают предполагаемый миграционный путь отдельных стад.

Карта 15. Миграции галки, *Coloeus monedula* (L.). Обозначения — см. карту 2.

Карта 16. Возвратные сведения о галке из северной части Франции, Бельгии (О) и Швейцарии (△) касающиеся зимовок и периода перелетов. Обозначения — см. карту 5.

Карта 17. Возвратные сведения галки из Дании охватывающие период зимовок и перелетов. Обозначения — см. карту 5.

Карта 18. Возвратные сведения о галке из южной части Скандинавского п-ва охватывающие период зимовок и миграции. Не учитываются тут сведения из Дании и гнездовых территорий. Обозначения — см. карту 5.

Карта 19. Возвратные сведения о галке из Финляндии охватывающие период зимовок и миграции. Обозначения — см. карту 5.

Карта 20. Возвратные сведения о галке из прибалтийских стран (О), юго-восточной части Польши (△), юго-западных районов Польши и северо-западных частей Чехословакии (X). Остальные обозначения — см. карту 5.

Карта 21. Распределение зимовок рассматриваемых группировок галки. Жирной сплошной линией обозначены зимовки птиц из Бельгии и Франции; прерывистой линией обозначены зимовки птиц из Дании и тонкой сплошной линией — зимовки птиц из прибалтийских стран; прерывистая линия — южношведские; пунктир — финляндские.

Карта 22. Популяционная дифференцировка галки заселяющей Европу. A_w — популяции характеризующиеся измененным направлением миграций. Остальные обозначения — см. карту 13.

Карта 23. Зимовки галки. Кружочки с буквой — популяция зимует на месте; буквы обозначенны двойным апострофом (A", N") — вторичные зимовки, возникшие путем вытягивания в длину миграционного пути. Остальные обозначения — см. карту 3.

Карта 24. Миграции вороны, *Corvus cornix* L. Обозначения — см. карту 2.

Карта 25. Возвратные сведения из периода зимовок и перелета о вороне из южной Швеции и Дании (О), а также Швейцарии (△). Не учитываются тут сведения охватывающие перелеты над гнездовыми территориями. Обозначения — см. карту 5.

Карта 26. Возвратные сведения о вороне из Норвегии касающиеся периода зимовок и перелетов. Обозначения — см. карту 25.

Карта 27. Возвратные сведения о вороне из центральной Швеции касающиеся периода перелетов и зимовок. Обозначения — см. карту 25.

Карта 28. Возвратные сведения о вороне из северных частей Скандинавского п-ва касающиеся зимовок и периода перелетов. Обозначения — см. карту 5.

Карта 29. Возвратные сведения о вороне их западной Финляндии охватывающие период зимовок и перелетов. Обозначения — см. карту 5.

Карта 30. Возвратные сведения о вороне из „промежуточного пояса" в Финляндии охватывающие период зимовок и перелетов. Обозначения — см. карту 5.

Карта 31. Возвратные сведения о вороне из прибалтийских стран (О) и части центральной Европы (△) охватывающие период зимовок. Добавочно отмечено одно сведение из Голландии из периода миграции. Обозначения — см. карту 5.

Карта 32. Популяционная дифференцировка вороны. Объяснение символов приведено в тексте; остальные обозначения — см. карту 13.

часть Скандинавии, (14) — зона В2 центральная часть Скандинавии, (15) — Зона А северная Скандинавия, (16) — зона Е2 Швейцария, (17) — зоны: D2-3 Германия, Польша, (18) — зоны В3-4, С3 прибалтийские страны.

Таблица 7. Процентные распределения возвратных сведений о вороне, *C. corone* с учетом дисстанции перелета и возраста птиц. Объяснения от (1) по (7) — см. таб. 1; (8) — зоны: D1, ЕО, Е1, Голландия, Франция, (9) — зоны: С1, С2, Дания, Скандинавия, (10) — зона В1 юго-западная Норвегия, (11) — зона В2 — центр. Скандинавия, (12) — зоны: А, сев. Скандинавия, (13) — зона В3 Финляндия, (14) — зона С3 прибалтийские страны.

Таблица 8. Возвратные сведения, которые послужили для анализа миграции сойки, *G. glandarius*. Объяснения от (1) по (8) — см. таб. 2; (9) — зоны: D1, Е1 Франция, Голландия, (10) — зоны: D2, D3 Германия, Польша, (11) — зоны: В3, В4 прибалтийские страны, (12) — Скандинавия.