EUROPEAN PASSERINE MIGRATION SYSTEM – WHAT IS KNOWN AND WHAT IS LACKING

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ABSTRACT

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European passerines show an impressive variety of migration strategies and migration patterns. Despite a long history of bird migration studies in Europe (100 years of bird ringing, nearly 100 years of the oldest bird stations), it must be stated that knowledge of the passerine migration system is far from being complete. Although tens of millions birds were ringed throughout Europe and hundreds of thousands recoveries were collected, these data still have not been scientifically used as much as necessary. We have only single analytical papers using data from the whole of Europe. Bird ringing atlases (Schüz and Weigold 1931, Zink 1973-1985) are the most known to a wide ornithological audience. They show ringing results in the same convention – dots representing recovery places connected by lines with ringing places. This kind of presentation gives a clear picture but first impression from it is very misleading as most of people believe that almost all European passerines migrate in the SW direction, to or through south-western Europe. This impression is false as a number of recoveries depends more on the hunting pressure and the level of education of people living in the area than on the relative number of ringed birds migrating or wintering there. Detectability of rings is close to null in eastern and southeastern parts of Europe, moreover bird ringing in this area is negligible in comparison to the western Europe. Results of other than bird ringing studies suggest that most of birds from central and eastern Europe migrate in southeastern direction. This shows that the knowledge of bird migration in these areas should be based on the complex bird migration studies carried out within a wide net of bird stations working with more modern methods (biometric studies, orientation experiments) rather than on the ringing results. The area of central and eastern Europe is larger and richer in passerines population than the rest of Europe and it could be stated, without a risk to be wrong, that more European passerines migrate SE than SW. Thus, it is impossible to understand passerine migration system over Europe without drawing the real picture of bird migration within eastern part of the continent.

Taking into consideration the migration in SE direction and the results of Europe-wide analyses of ringing recoveries it is possible to build up a general model of the European passerine migration system. Generally, European breeding grounds of the species consist of migratory populations areas that can overlap in some parts of Europe. Population members migrate to (for wintering) or through (directing to African winter-quarters) the late ice-age refuges, from which the population expanded to central and northern Europe after the ice cap had disappeared. Individuals living on the territories, where population areas overlap, could be inter-population hybrids and they could have inherited more than one navigation programme. Thus, some cases of wide-angle migration (birds from a limited area migrate to very wide wintering grounds) can be explained without assumptions that they have lost navigation abilities or that they avoid actual ecological barriers (*e.g.* Alps – that are not a real barrier for any passerine migrant). Differentiation of population patterns of passerine species depends on the ecological preferences of the species and the development of suitable habitats after regression of the ice cap and, possibly, on the inter-population competition that can be continued nowadays.

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INTRODUCTION

Birds' migration patterns have always been of interest to man, because, from the earliest times, bird migration was a conspicuous event in spring and autumn. Where do the birds go? Where do they come from? These are questions posed by the inhabitants of different areas at different times of the year. The general answer to these questions is simple: birds move from the cold regions of the North to the warmer countries of the South. During the nineteenth century, this simple, but only partly correct, picture was more precisely drawn due to the giant development of birds' systematics, faunistics and zoogeography. Observations of huge concentrations of migrants at some areas, *e.g.* Courish Spit, Gibraltar or Bosporus Strait allowed to develop the idea of bird migration flyways and even such inconspicuous landmarks as rivers were thought to be guiding lines for passerines. However, since the beginning of the twentieth century, it has been possible to mark birds individually using rings, and that event has changed many of the earlier theories about bird migration.

Bird ringing atlases (Schütz and Weigold 1931, Zink 1973-1985) are the most known to a wide ornithological audience. They show ringing results in the same convention – dots representing recovery places connected by lines with ringing places. This kind of presentation gives a clear picture but first impression from it is very misleading as most of people believe that almost all European passerines migrate in SW direction, to or through south-western Europe. This impression is false as a number of recoveries depends more on the hunting pressure and the level of education of people living in the area than on the relative number of ringed birds migrating or wintering there. Nevertheless, this fact was found and discussed much later (Payevsky 1973, Busse and Kania 1977, Perdeck 1977, Busse 1981, Kania and Busse 1987). The earliest, classic papers summarizing the results of ringing were so impressive (because of their spectacular maps) that such picture of bird migration was deeply imprinted in the brains of many ornithologists. Unfortunately, this imprinting is really blocking the recent studies of bird migration and it has even forced some ornithologists to urge that bird ringing should stop – arguing that migration patterns of most European birds are now well known and nothing else can be discovered. A summary of common believes was presented in an atlas of ringing recoveries published quite recently (Zink 1973): „Many of land birds do not migrate by „flyways" as it was assumed earlier, but by „broad front" from breeding grounds to winter-quarters" (Fig. 1). Fortunately, there are new methods of analysis and the first results develop our knowledge both about the general picture and the fine details of migration.

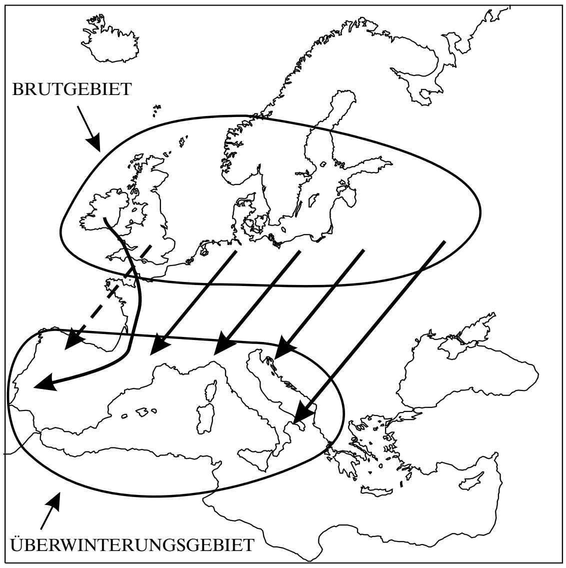

Fig. 1. European bird migration system as seen by Zink 1973. *Brutgebiet* – breeding area, *Überwinterungsgebiet* – wintering area.

DISTRIBUTION PATTERNS

From a zoogeographical viewpoint, bird migration generally is composed only of three elements: the breeding range of the species, its passage routes and its winter range. This is shown schematically on Figure 2. If on the distribution map we can see all three elements, *i.e.* winter range separated from the breeding range by areas where the species is observed on migration, *e.g.* Fig. 3 – the Sedge Warbler (*Acrocephalus schoenobaenus*), then we can speak about the long-distance migration. Such pattern is relatively common among European passerines and involves 63 species, of which 49 are African and 14 – Asian migrants.

A large group of European passerines (69 species) has their winter range very close to or overlapping the breeding range, *e.g.* Fig. 3 – the Song Thrush (*Turdus philomelos*) and the Blue Tit (*Parus caeruleus*). Such zoogeographical pattern does not tell us whether all individuals of the species are migrants. It is possible that they

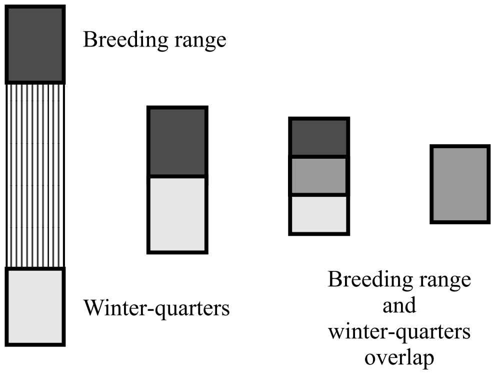

Fig. 2. Diagram of distribution patterns of birds. From left to right: long distance migrants, two patterns of short distance migrants and the pattern of a sedentary species. Dark – breeding area, light – winter-quarters, grey – overlapping breeding and wintering ranges, vertical hatching – area of migration. After Busse 1987, modified.

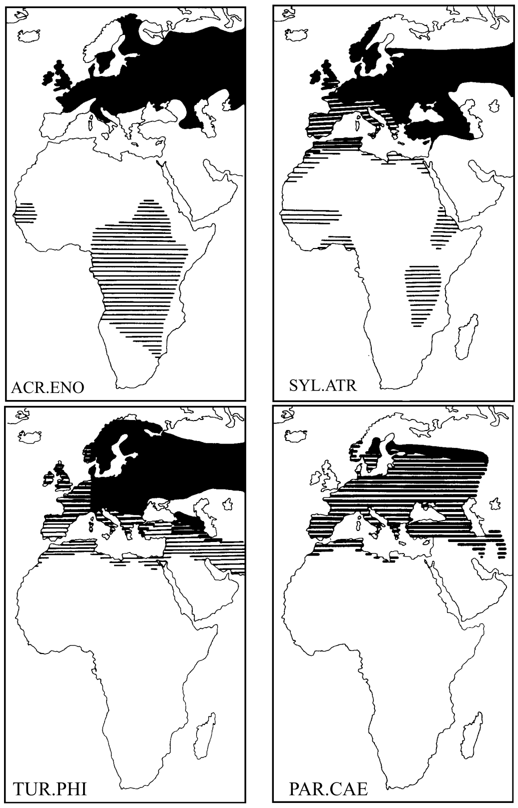

Fig. 3. Distribution patterns of the Sedge Warbler (ACR.ENO – *A. schoenobaenus*), Blackcap (SYL.ATR – *S. atricapilla*), Song Thrush (TUR.PHI – *T. philomelos*) and Blue Tit (PAR.CAE – *P. caeruleus*). After Busse 1987.

are sequential migrants, *i.e.* southern groups of birds migrate to the southern part of the wintering range, while northern ones winter within the southern part of the breeding range. The other possibility is a „leap-frog" migration, in which the southern groups are sedentary and the northern ones migrate south of the breeding range „jumping" over the sedentary birds. For many of these species it is not known, which strategy is used, but the problem can be solved (if subspecies occur) by means of faunistic methods.

Two European passerines show very special distribution patterns in between these two groups – the Blackcap (*Sylvia atricapilla*) (Fig. 3) and the Sardinian Warbler (*Sylvia melanocephala*) have wintering areas both far away (in Africa) and close to the breeding range (Mediterranean or purely European areas).

The opposite group to the clearly long-distance migrants is 35 species of passerines, in which the winter range completely covers the breeding range. The migratory status of these birds is not clear from distribution maps alone. There is still the possibility of partial migration, irruptive movements as well as the case, in which all birds of the populations remain resident all the year.

This short review of distribution patterns shows clearly that such simplification of bird migration is insufficient and one should conduct more detailed studies.

RESULTS OF RINGING – CLASSIC STUDIES

Bird ringing, the method used for migration studies since the beginning of this century, documents the data on the displacement of an individual bird from the place where it has been ringed to a place where it has been met again (caught, shot, found). To plot the movements of group of birds the classic ringing studies have mapped together the ringing and recovery places of individuals grouped by area of ringing, sex and/or age. As ringing was developing over the years most vigorously in northern and central Europe, the first and most important question posed by the scientist was „Where do our local breeding birds go to winter?" This brought about many papers presenting the collected recoveries from local studies. Logically, the idea is very simple – map the recovery place of the birds ringed at delimited breeding area (most of the birds ringed at the beginning of ringing were nestlings and breeding adults) and their movements will be shown. Since the early studies of Mortensen, and regrettably even today, this sort of analysis has contained mainly the maps of recoveries collected some time after the birds were ringed. Frequently, the maps include lines connecting ringing and recovery places, which may obscure the real migration pattern and force a false association about migration routes on the reader. Such studies are usually very descriptive in character, with particular attention being paid to the listing and discussion of „curious" recoveries – singular recoveries of individuals found far from concentrations of other birds. These often consist of comments about unusual deviations from „normal" wintering areas for the population. In this case, the word „population" means simply the group of birds from the study area. Typically, such study area contains birds ringed only in the part of their breeding range delimited by administrative or political boundaries. Even the analyses of all European recoveries of a species are often split up in this manner or by other formal regions as discussed many years ago in „*The Ring*” (Rydzewski 1959, 1966; Busse 1967) and adopted in the newest rules of recovery coding (Spencer 1979).

Such classic analytical techniques can, however, give a good picture of migration patterns of the native population of an area, where birds inhabiting the area are homogeneous in their migration habits. In such case, the picture of migration can be clear and the wintering grounds and/or migration routes precisely delineated (Fig. 4). One can easily speak about distinct migrational population and even of narrow-angle migration (Fig. 5A).

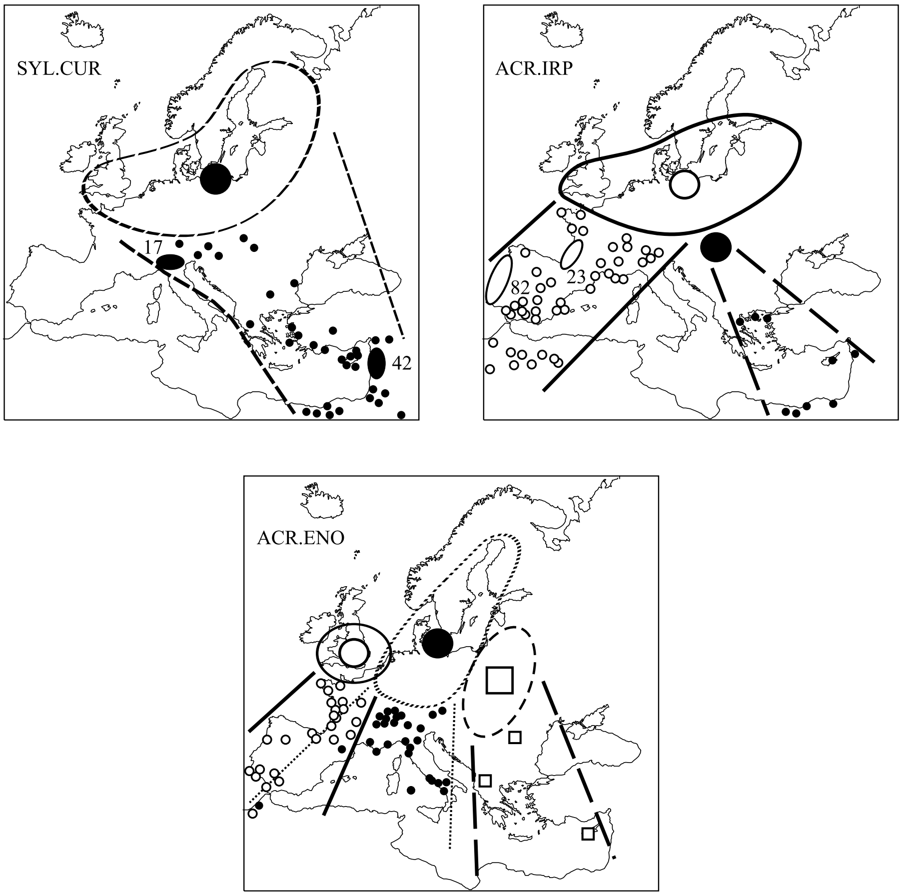

Fig. 4. Recovery patterns of Lesser Whitethroat (SYL.CUR – *S. curruca*), Reed Warbler (ACR.IRP – *A. scirpaceus*) and Sedge Warbler (ACR.ENO – *A. schoenobaenus*). Each small symbol shows the recovery place of the bird ringed at the area designated by the bigger symbol. The number shows the number of recoveries from a pointed area. After Busse 1987, modified.

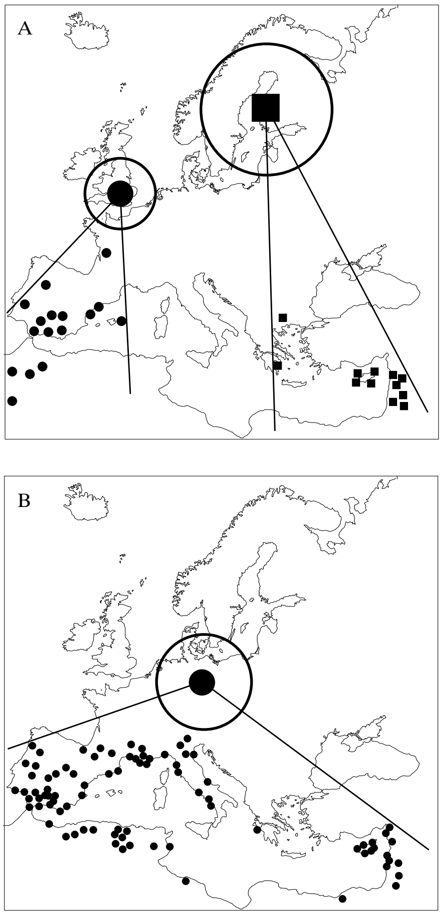

Fig. 5. A. Recoveries of Blackcaps ringed in Britain and Scandinavia as an example of narrow-angle migration patterns; B. Recoveries of Central European Blackcap as an example of wide-angle migration pattern. Explanations as in Fig. 4. After Busse 1987, modified.

However, some other classical local analyses have met serious problems in the interpretation of the picture obtained in such way – birds from a limited breeding area can migrate to an astonishingly wide winter range (Zink 1973, Gromadzki and Kania 1976). An excellent example is the recovery pattern shown by the Blackcap ringed in central Europe (Fig. 5B). Such pattern must be further investigated. Explanations put forth such as „transitional populations" (Gromadzki and Kania 1976) or the assumption of the massive influence of the Alps (Klein *et al.* 1973) on migration seem doubtful.

The recovery analysis of the birds ringed as migrants is generally much more difficult than that of birds ringed as natives within an area. Heterogeneous migrants show, in most cases, a very wide angle of further migration and often a changing recovery distribution when subsequent groups of migrants are compared (*e.g.* Robin

Erithacus rubecula – Pettersson and Lindholm 1983). Detailed explanation of such patterns is not easy and it can lead to very controversial conclusions. Most cases of a wide-angle migration cannot be explained satisfactorily, if only the recovery pattern is considered.

When one finds, in the course of research, a complicated pattern of migration composed of groups with both narrow- and wide-angle migration (Fig. 5 and 6), as in case of the European Blackcap or the Garden Warbler (*Sylvia borin*), one is forced to look for new and much more efficient methods of study.

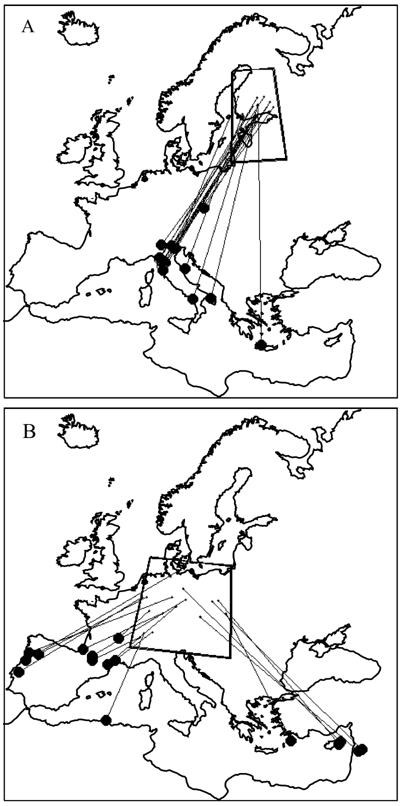

Fig. 6. A. Recoveries of Garden Warblers (*S. borin*) ringed in Finland as an example of narrow-angle migration pattern; B. Recoveries of Central European Garden Warblers as an example of wide-angle migration pattern. Ringing (small dots) and recovery (bigger dots) are connected by lines.

THEORETICAL MODELS IN AN INTERPRETATION OF RECOVERY PATTERNS

After one hundred years of ringing and collecting of recovery data and after the publication of number of papers evaluating spatial distribution of recoveries, migration pattern is treated by some ornithologists as already known for most species. More careful analysis of contemporary works shows, however, that they are still methodically rather simple and traditional, closely resembling the old papers devoted to this problem. The assumptions underlying the interpretation of patterns are not clearly stated. Methods of interpretation of recovery patterns are discussed here and they are a generalization of conclusions of some earlier publications (Busse 1969, 1986a, 1986b, 1987; Busse and Maksalon 1986).

Types of recovery patterns

A starting point for any evaluation of the spatial distribution of ringing data is a map with ringing and recovery localities shown, with additional information on the time enabling to separate subsequent parts of the bird life-cycle (especially migration and wintering periods). In evaluation of ringing results, two main kinds of data are used: (1) recoveries of birds ringed in their native areas (*pulli* and breeding individuals), and (2) recoveries of birds both ringed as migrants at permanent ringing stations and caught by individual ringers accidentally. This last group of recoveries is hardly applicable to evaluations and in many cases should be omitted. Evaluations of recoveries of birds ringed during wintertime are rather scarce.

The first step in the evaluation of spatial distribution in winter is the presentation of the recovery pattern of birds ringed in a specified ringing area (breeding ground or a bird station). Usually these ringing areas are delimited by political or administrative borders and constitute formal units without any biological significance. Generally, in European migrants, two rather clearly separated recovery patterns can be found (Fig. 7): (1) narrow-angle recovery pattern (with the angle between the furthest western and eastern recoveries being under 60°), and (2) wide-angle recovery pattern (with the angle above 90°). They are the simplest patterns to be interpreted in local ringing evaluations (for a relatively small breeding area or a single ringing station).

More complicated recovery patterns can be found, if a study contains analysis of birds ringed within a wide breeding area or at number of bird stations. In such case, results of the analysis frequently depend on hidden assumption underlying the interpretation but not explicitly discussed. The most common assumption, though usually not stated, is that of the homogeneity of the sample under study. This assumption is a basis for one of the models of migration discussed later, while if heterogeneity is suspected, it may result in a quite different interpretation.

Models of migration

Different pictures of migration idealized from recovery evaluations can be reduced to two essential models defined by the assumptions, which are the basics of the model construction.

Cline model

Assumptions:

1. The breeding and the wintering area are occupied by a homogenous bird population, within which all its features (both morphological and behavioural) are changing gradually;

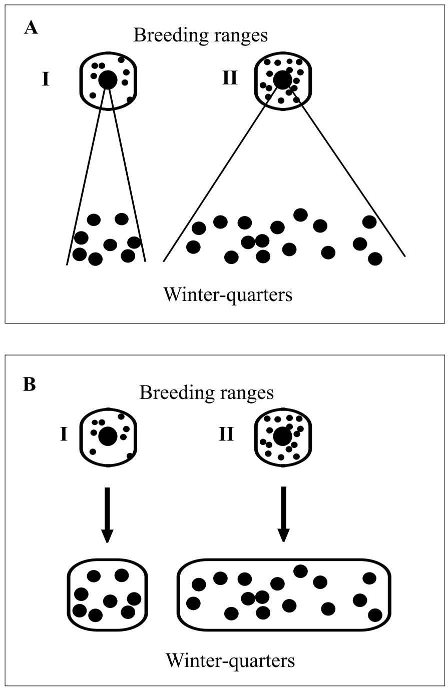

Fig. 7. Scheme of elementary recovery patterns (*A*) and their interpretation by means of the cline model (*B*). *I* – narrow-angle recovery pattern, *II* – wide-angle recovery pattern. Ringing and recovery localities shown by dots. After Busse 1986, modified.

2. The birds are forced into seasonal movements by existing environmental circumstances, which define destination area, route and timing of migration;
3. The problem of inheritance in orientation and navigation is ignored.

Conclusions:
1. The word „population" used in the context of this model can be treated as a shortened form of an expression: „a group of individuals inhabiting a defined study area". It does not imply that any genetic difference between such „populations" exists;
2. The winter recovery pattern shows the wintering area not differentiated into separable winter-quarters;
3. Any differences in recovery patterns of birds originating from neighbouring areas are due to the clinal change of environment at the breeding or wintering areas or result from the presence of migratory barriers;
4. Any differences in recovery patterns of birds migrating through a bird station in subsequent parts of migration period are due to clinal change of migration time of birds originating from a number of sub-areas localized side by side at the breeding grounds.

Methodical consequences:

1. Migration patterns can be sufficiently presented as maps of recovery places of birds originating from breeding sub-areas, ringed at some bird stations or migrating during different parts of migration period;
2. The migration pattern of birds originating from one study area or migration period can be described by an average direction of migration (the mean direction being calculated from all data from the period defined), and by average coordinates of recoveries;
3. Wide-angle recovery patterns should be explained additionally by the occurrence of contemporary ecological barriers or instability of orientation mechanisms of migrants, as such patterns are not explained by the model itself;
4. Curved migration routes found in some species are an effect of presently operating circumstances of migration (*e.g.* prevailing winds).

Population model

Assumptions:

1. The wintering area of European migrants can be divided into separate winter-quarters localized in the late ice-period refuges of the species (Fig. 8) or created from them by shortening the migration route (secondary winter-quarters – Busse 1969); for long-distance migrants these areas are the first parts of Europe occupied in the past by the populations invading the continent from the south, what determines the present-day pattern of migration;
2. Winter-quarters are occupied in wintertime by a defined population, members of which are genetic descendants of birds that started their expansion from this area to central and northern Europe in the period after the Ice Age;

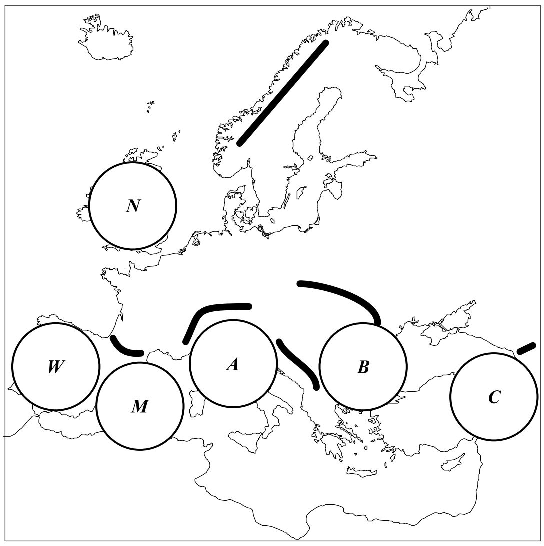

Fig. 8. Distribution of primary winter-quarters in Europe as accepted in the population model (after Moreau 1955, simplified). Main European mountain ridges shown.

3. Wintering in the defined winter-quarters is genetically encoded; individuals that are hybrids from parents of different population origin have inherited tendency to migrate towards different winter-quarters;
4. Present-day migration routes are inherited and reflect the history of expansion of populations from refuges to central and northern Europe; they can be modified continuously by a selection pressure of natural or human origin;
5. If a population winters at secondary winter-quarters or migrates by a modified migration route, the recovery pattern of first-year birds reflects older migration customs of the population, while the recovery pattern of adults shows the most recent wintering area.

Conclusions:
1. The word „population" in the context of this model has a defined genetic meaning: „A group of individuals, which are descendants of birds originating from a specified ice-age refuge and having inherited migratory behaviour involving wintering at the same winter-quarter and migration by a historically evolved route". Population members can breed in separated areas or in mixed zones (these are inter-population hybrids). As membership of the population is defined by genetic characteristic of an individual, hybrids can demonstrate features of two or even more populations;
2. Winter-quarters are homogenous regarding the population of wintering birds, while breeding areas can be occupied by a pure population or by individuals of mixed-population origin;
3. The shape and localization of pure population areas and/or mixed zones as well as present-day migration routes can be a basis for hypotheses explaining the post-glacial history of the species;
4. Differences in recovery patterns of migrants ringed at a bird station in subsequent parts of migration period are due to the differentiated population composition of migrants in these parts. Trespassing individuals can originate from pure population areas, from mixed zones or at the bird station there can be an intersection of migratory routes of populations originating from quite different breeding areas;
5. It is not necessary to explain curved migration routes by present-day environmental constraints.

Methodical consequences:
1. The migration pattern presented in a paper should describe winter-quarters, migration routes and breeding areas of populations;
2. After a preliminary analysis of the distribution of winter-quarters, it is necessary to map in the breeding grounds the ringing localities of the birds wintering within specified winter-quarters; they will create a basis for the delimitation of pure population areas and mixed zones;
3. A wide-angle recovery pattern means that the breeding area lies at a mixed zone of two or more populations, so calculation of mean direction and/or co-ordinates is not acceptable;

4. A curved migration route can be explained by the history of population expansion, if there are no other clear causes;
5. A shift of recovery patterns of birds ringed at a station in subsequent parts of migration period means that there is a population mixture and that the calculation of average directions and/or co-ordinates is not allowed; the population structure of migrant waves can be reconstructed from the changing relations between numbers of recoveries at defined winter-quarters;
6. If there is a suggestion that the studied sample comprises members of a number of different populations (because of a shift in the recovery patterns of the migrants), then it is necessary to use special methods of analysis for elaboration of biometric data.

Interpretation of recovery patterns

Elementary recovery patterns

Elementary recovery patterns occur when recovery data from a relatively small breeding area or just one ringing station are studied. After the cline model theory, these patterns are interpreted as denoting the winter area of local population or migrants passing through the station. The population model suggests that a narrow-angle recovery pattern means that the studied area lies at the pure population breeding area, while a wide-angle pattern occurs because the area under study lies, at least partly, within a mixed zone between populations. In the case of bird station recoveries, the first pattern implies that migrants are recruited from one population, while the second – that they are a mixture of members of different populations. The latter statement makes it necessary to study further the migrants, and to take under consideration at least time-dependent differentiation of recovery patterns.

Complex recovery patterns

Complex recovery patterns occur when the ringing area is wide (Fig. 9 and 10) and can be divided into several sub-areas, or when ringing data from several ringing stations are evaluated, or when ringing data from one station are divided into time-dependent sub-samples of migrants (Fig. 11).

While working with recoveries of native birds, a situation may occur, in which all component elementary patterns display a narrow-angle recovery pattern (Fig. 9A). Interpretation by means of the cline model gives a simple picture (Fig. 9B) of homogeneous breeding area, from which the birds migrate on a broad front to a wide wintering area of the species. The population model interpretation (Fig. 9C) suggests that there are population differences within the breeding area (since the winter area contains several winter-quarters) but the borders chosen by an analyst agree with population borders at breeding grounds. Mixed zones between populations are so narrow that the studied sample of birds does not show their existence. Figure 10 depicts the most common situation, when a complex recovery pattern

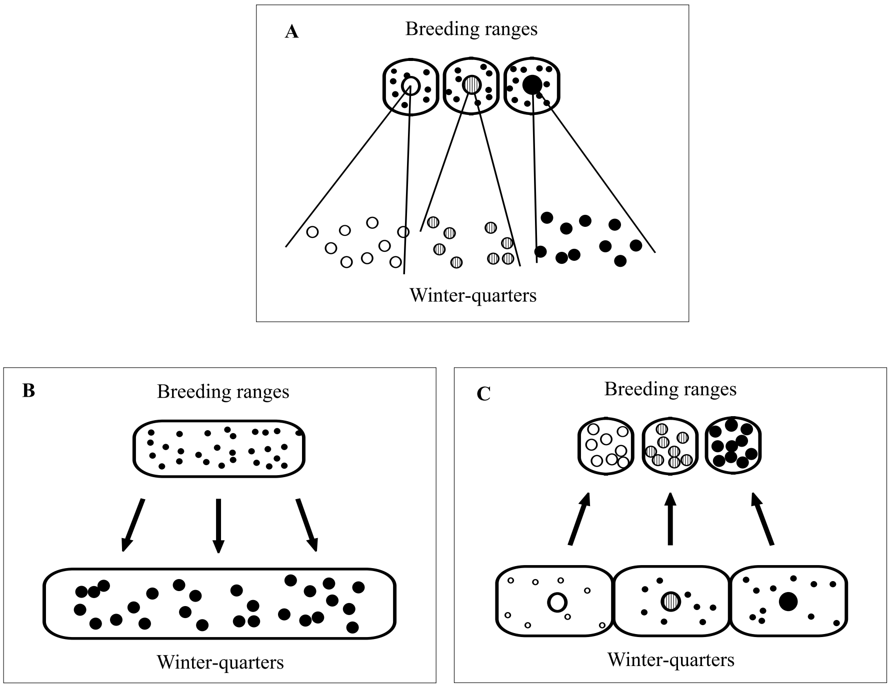

Fig. 9. Scheme of a complex recovery pattern of native birds and its interpretations: components are exclusively narrow-angle patterns, *A* – not interpreted recovery pattern; *B* – interpretation of the pattern *A* according to the cline model; *C* – interpretation of the pattern *A* according to the population model. Ringing and recovery localities symbolised by dots. After Busse 1986, modified.

contains both narrow- and wide-angle patterns. The cline model explains this type of pattern (*e.g.* Fig. 5 and 6) only with difficulty – it assumes homogeneity of both breeding and winter areas, suggesting the same explanation as in case of narrow-angle patterns. Additional hypotheses about environmental conditions having forced the birds originating from central sub-areas to migrate in different directions become necessary. However, such interpretation contradicts the assumption of inheritance of orientation mechanisms and has to be supplemented by additional assumptions. Interpretation using the population model (Fig. 10C) shows two winter-quarters and two population areas at breeding grounds overlapping in their central part. Migration of birds from this territory in the direction of two winter-quarters produces a wide-angle recovery pattern. Individuals living in the overlapping area are inter-population hybrids and they may be genetically able to choose different directions of migration. This choice can depend on actual weather conditions (when the individual starts to migrate) or may be accidental. In both cases, the migrant individual is steered by one of inborn programs of navigation.

Working with recoveries of birds ringed at a bird station during migration time one can consider additional data. Such additional information can be used in migration dynamics (time and/or waves of migration) evaluation, which allows one to find

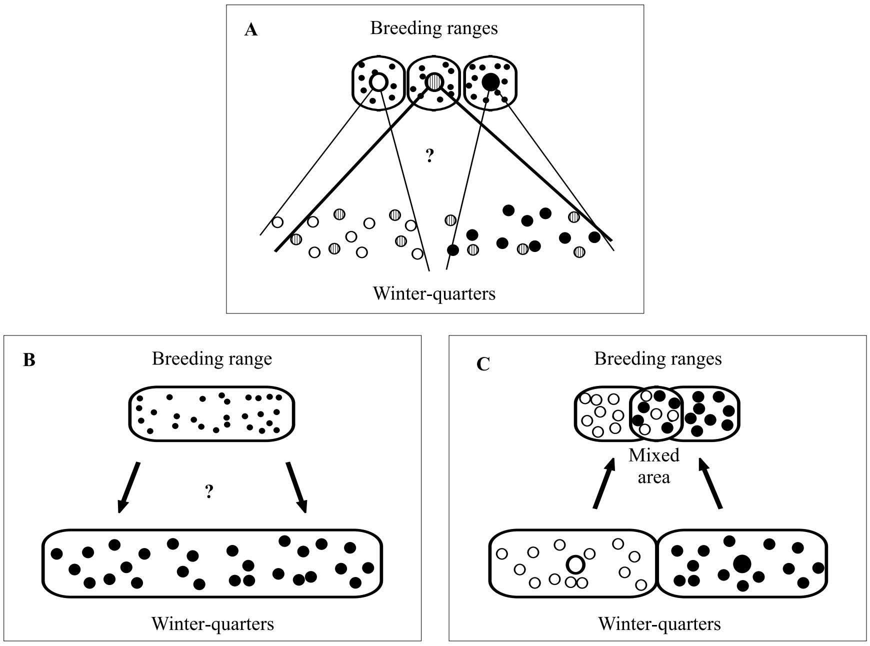

Fig. 10. Scheme of a complex recovery pattern of native birds and its interpretation: components are both narrow- and wide-angle patterns. *A* – not interpreted recovery pattern; *B* – interpretation of the pattern *A* according to the cline model; C – interpretation of the pattern *A* according to the populational model. Ringing and recovery localities symbolised by dots. After Busse 1986, modified.

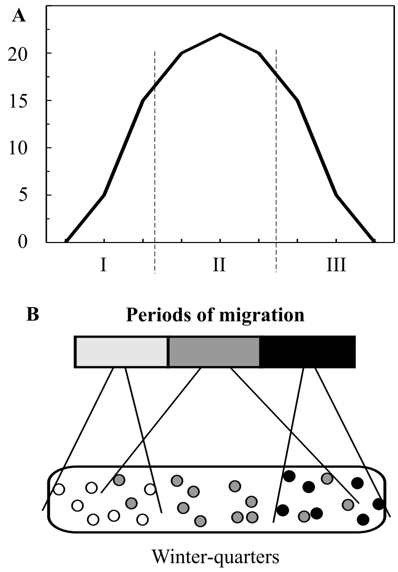

Fig. 11. Raw data in study of recovery pattern of birds ringed as migrants at a bird station. *A* – migration dynamics pattern: *I, II, III* – periods of migration; *B* – recovery patterns of birds ringed in subsequent periods. After Busse 1986, modified.

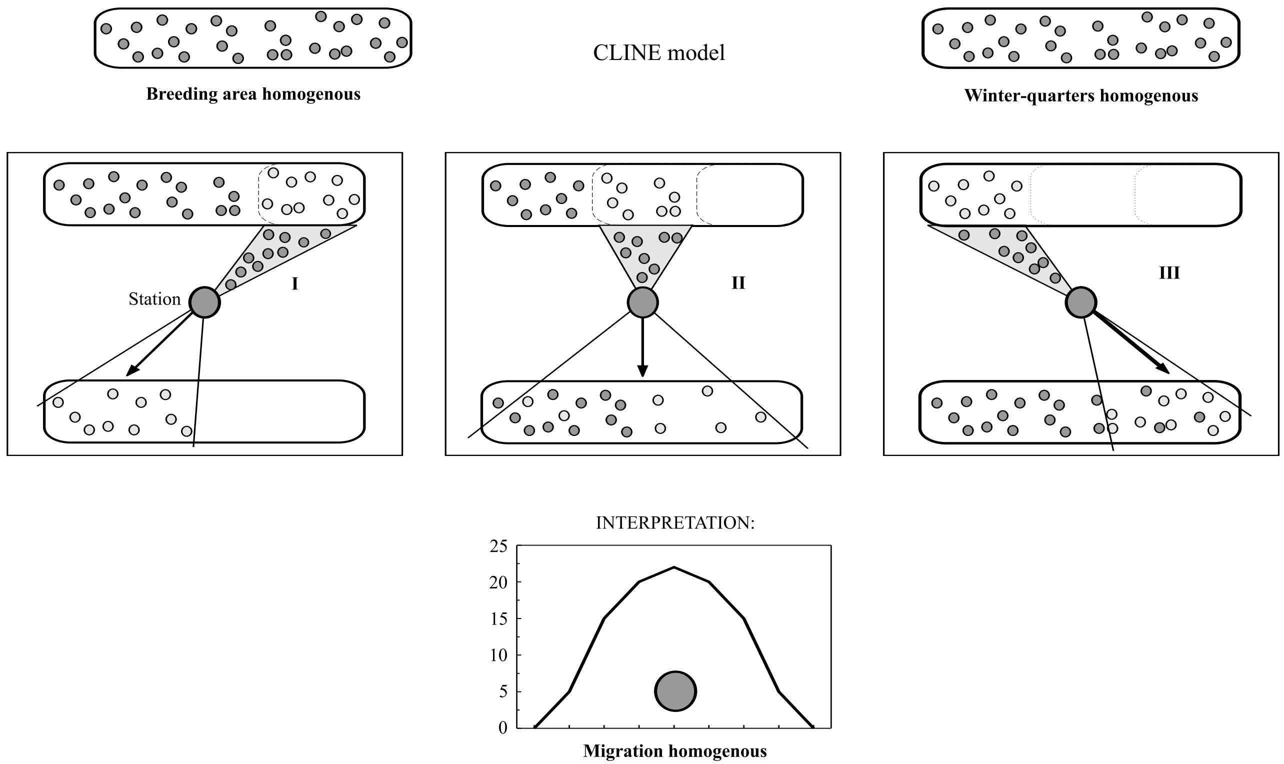

Fig. 12. Scheme of interpretation of a complex recovery pattern of migrants passing one station, according to the cline model. Above - assumed homogeneous structure of breeding area and winter-quarters. In the middle - concluded migration patterns of individuals passing the same station in subsequent periods of migration (*I, II, III*); large circles represent the same station in three periods of migration; arrows show routes of migration and point at mean longitude of recovery places. Below - resulting image of migration dynamics structure - one homogeneous group of migrants in passage is symbolised by one circle. After Busse 1986, modified.

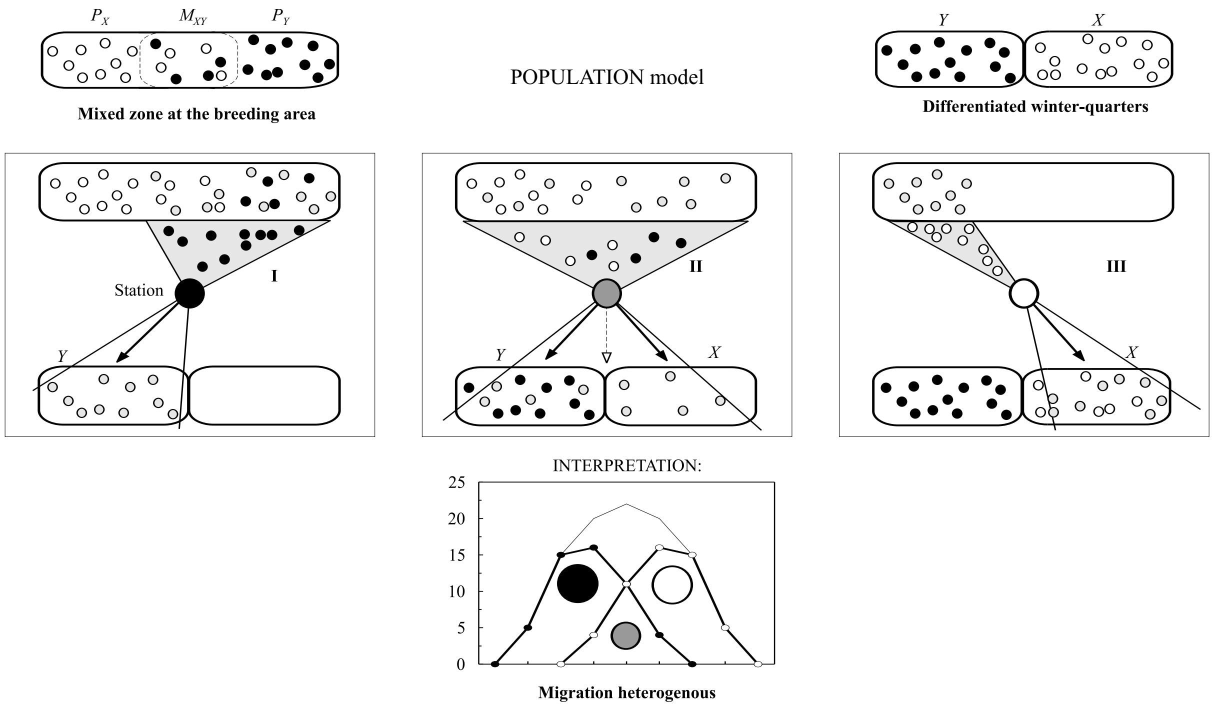

Fig. 13. Scheme of interpretation of complex recovery pattern of migrants passing one station according to the population model. Above – assumed heterogeneous structure of breeding area containing pure population areas (P_X, P_Y and mixed zone M_{XY}) and heterogeneous winter-quarters (*X* and *Y*). In the middle – concluded migration patterns in subsequent periods of migration (*I, II, III*) of individuals representing populations *X* and *Y* and passing one station: the circles representing the station are differentiated because during three subsequent periods population *X* (*I*), mixture of individuals belonging to populations *X* and *Y* (*II*) and population *Y* (*III*) migrate, black arrows – routes of migration of "*X*" and "*Y*" population members, in period *I* and *III* they show mean longitude of recovery places, but in period *II* they do not (mean recovery longitude is pointed by a white-headed arrow). Below – resulting image of migration dynamics at the station is composed of two elements (curve of migration dynamics of population *X* and that of population *Y*); circles symbolize population composition as station symbols above. After Busse 1986, modified.

time-dependent changes in recovery patterns (Fig. 11). The lack of time-dependent differentiation of recovery patterns reduces the problem to an analysis of the elementary pattern. More interesting is the case, in which recovery patterns change in subsequent parts of migration offering a combination of narrow- and wide-angle recovery patterns with a shift of concentration of recoveries within the wintering areas. Interpretation of such complicated patterns clearly depends on an accepted model of the structure of breeding bird population. Accepting the cline model assumption of the homogeneity of the breeding area (Fig. 12), the assumption of a continuously changing starting time for migration has to be agreed on, as well as the homogeneity of the wintering area. Consequently, there is a homogeneous interpretation of migration dynamics, which does not require further, *e.g.* biometrical, studies of the migrants.

The population model assumes dividing the breeding area into three sub-areas (Fig. 13) – pure population areas: P_X and P_Y, and a mixed zone *XY*. Populations *X* and *Y* have different average times of migration (in Figure 13 large difference in the timing of migration is assumed to make the explanation clearer). Only in this case, one can find shifting recovery patterns. In the first period of migration, only members of population *X* migrate, in the second one – members of both populations, while in the last period – only members of population *Y*. They all direct to their own winter-quarters. The population model easily explains curved migration routes. In conclusion, the structure of migration shows the differences between the migrants and suggests a further study of their origin, *e.g.* through biometrical differences in the samples.

Discussion of the models

The cline model of migration is a classic one, widely accepted by analysts of ringing recoveries, although never formulated as a set of assumptions constituting a base for interpretation of recovery patterns. It has dominated in published papers, helping to evaluate both local and Europe-wide ringing data. Interpretation by means of this model is simple and easy for discussion when local (one country or one station) data are analysed. Its assumptions allow to use statistical calculations for the presentation of data (mean direction and/or mean co-ordinates) that are thought to be a modern way of presenting migration patterns. There are, however, some weak points in the model:

1. Wide-angle recovery patterns and curved routes of migration must be explained additionally as they do not correspond with the current knowledge of navigation mechanisms;
2. Its assumptions obscure the picture of migration by neglecting internal differentiation of the sample and discourage students from more complex and deeper studies on migration dynamics and biometrical differentiation;
3. The final results of evaluation are descriptive in character and difficult to present in a synthetic form, in case a large breeding area is studied.

The population model limits the value of local studies (nation-wide or one-station data) by showing that they cannot solve problems of the distribution of populations. The full analysis based on this model should contain several steps:
(1) primary identification of winter-quarters by classic mapping of recovery locations,
(2) delimitation of populations breeding areas and mixed zones,
(3) evaluation of data describing migratory routes,
(4) control of differences in migration pattern between young and adults, and
(5) reconstruction of evolution of the species migration pattern.

The desired complexity of evaluation makes it more difficult for less advanced students and needs much more effort. The advantages of the model are, however, quite numerous:

1. The picture resulting from the evaluation – population pattern with mixed zones and more or less defined routes of migration – explains all elements of the migration pattern (wide-angle patterns and curved routes of migration);
2. Evaluation of age-dependent migration patterns reveals contemporary trends in the evolution of migratory habits of the species, which encourages studies of evolutionary causes (of climatic or anthropogenic character) of observed changes;
3. The model provides a theoretical basis for quantitative analysis of recovery distributions by means of probability methods;
4. The comparison of population patterns of ecologically different species allows to reconstruct the development of bird communities in different parts of Europe;
5. The model facilitates complex studies of migrants as it stresses the possibility of internal differentiation of samples.

The population model is logically more general than the cline model. The latter can be treated as a special case of the former: interpretations are identical if the birds from a pure population area migrate to one winter-quarter only.

A rough analysis of recovery patterns of about forty species presented in Zink's atlas of passerines ringing recoveries (Zink 1973-1981) and some more detailed studies (Busse 1969, Busse and Maksalon 1986, Remisiewicz 2000) adequately support the population model. The study of recovery pattern of the Blackcap (Fig. 5) using the population model assumption and „looking from the south" analysis procedure (Fig. 14) gives results clear and understandable without additional assumption that Blackcaps do not like to cross the Alps. Mapping of the breeding places of birds found at three destination areas (wintering and migration) gives breeding distributions of the individuals concerned, which have shown the differentiated migration. One can easily assume that they belong to populations exhibiting different migration urges and the apparently complicated recovery pattern becomes much simpler. Now, it shows areas inhabited by populations with a single migration route (here England and France and most of Scandinavia) and those occupied by a mixture of birds, which have inherited different directions of migration. Similar pattern, but with a little bit shifted population areas, is shown by the Garden Warbler (Fig. 15). Three examples (Fig. 16) demonstrate clearly that the Alps are not a real obstacle in migration of small passerines. The Icterine Warbler (*Hippolais icterina*)

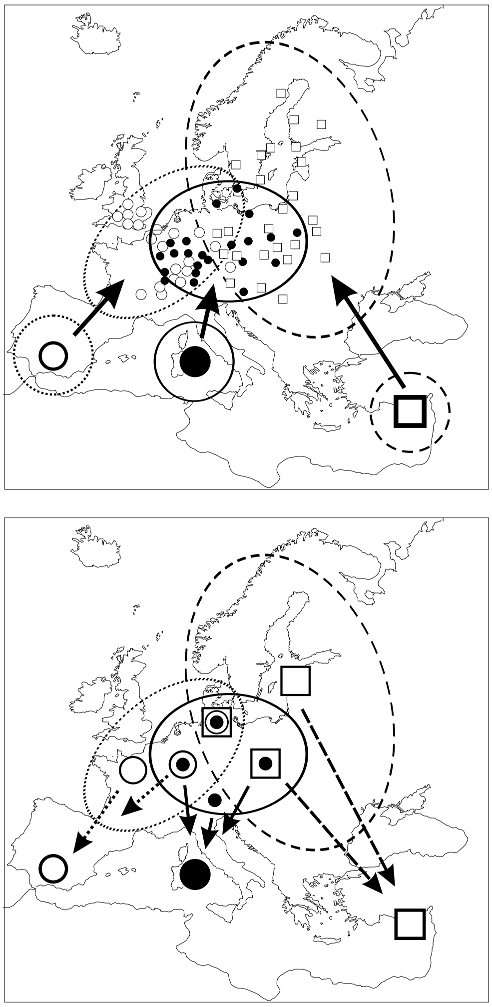

Fig. 14. A. Recovery pattern of the Blackcap drawn after „looking from the south" method. Small symbols show the ringing places of birds found in the wintering quarters designated by the big symbols. B. Population areas of the Blackcap from that shown in A. The simple symbols at the breeding grounds show areas occupied by pure populations, combined symbols show zones where there is a mixture of two or three populations. After Busse 1987, modified.

points at Apennine Peninsula as the refuge, through which it had been invaded Europe, and the Wood Warbler (*Phylloscopus sibilatrix*) shows, even more clearly, that not the azimuth of migration defines the population navigation behaviour but inherited repetition of the route of dissemination through central and northern Europe. The Meadow Pipit (*Anthus pratensis*) demonstrates that from one refuge, one population could invade different areas and set up two completely different migration tracks (these two subpopulations are isolated from each other by the area occupied for breeding by birds migrating toward Iberian Peninsula).

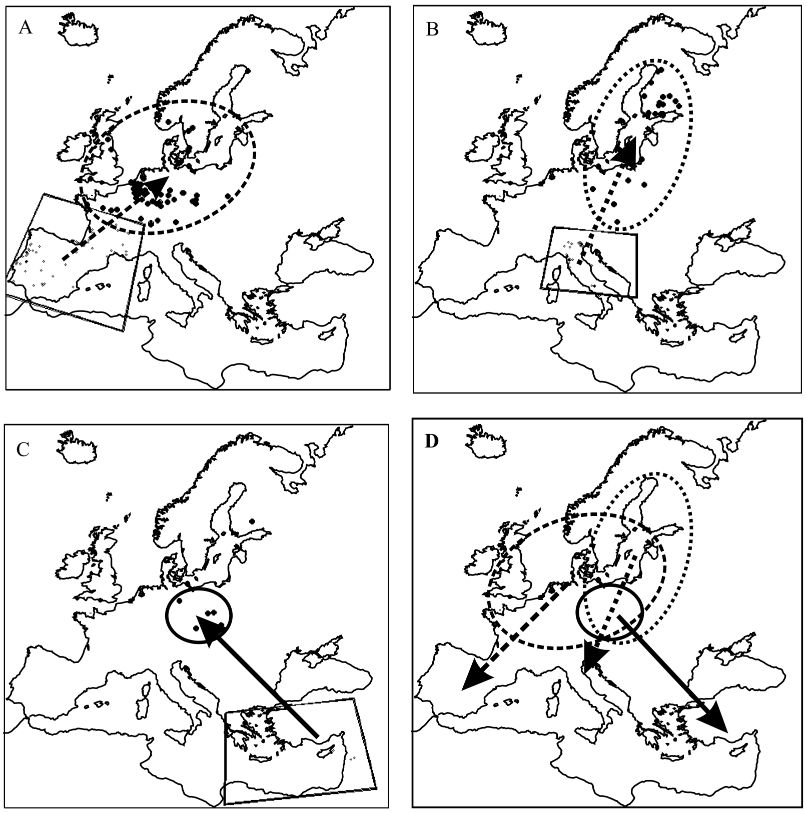

Fig. 15. Recovery pattern of the Garden Warbler drawn after „looking from the south" method. *A*. Breeding area of birds (ellipse with bigger dots) recovered within Iberian Peninsula and France (trapezium). *B*. Breeding area of birds recovered in Italy. *C*. Breeding area of birds recovered in eastern Mediterranean. *D*. Population and migration pattern of the Garden Warbler in Europe.

RECOVERY PATTERN AND DISTRIBUTION OF RINGED BIRDS

One of the most important tasks of ringing is to determine the distribution of the birds after migration (*e.g.* from breeding to wintering grounds). It is often done by showing the recoveries on the map, assuming that their distribution corresponds to that of the ringed birds. Such an assumption usually is not true (*e.g.* Busse and Kania 1977, Perdeck 1977), as the detection coefficient (ratio of number of the recoveries to the number of ringed birds present in the area – Busse and Kania 1977) is variable in time and space. Time changes can refer to years (*e.g.* in Robin; Fig. 17, Table 1 – Busse 2000), seasons or even shorter periods (for example, rings found on waterfowl are reported much more often during the hunting season than beyond it). It is also known (*e.g.* Payevsky 1973) that the detection coefficient varies from area to area. It can be null in an area uninhabited by man and close to 100% in case of

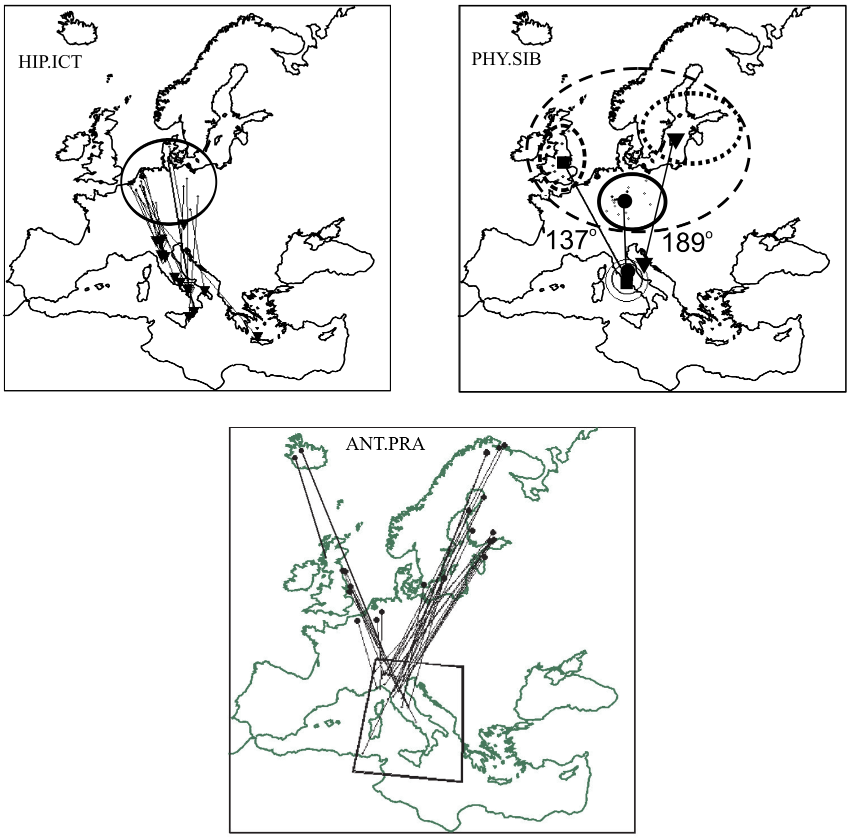

Fig. 16. Examples of recovery patterns of passerine species crossing Alps during migration. Icterine Warbler (HIP.ICT – *H. icterina*), Wood Warbler (PHY.SIB – *P. sibilatrix*) – azimuths of autumn migration of western and eastern groups are given, Meadow Pipit (ANT.PRA – *A. pratensis*) – example of sub-population diverge.

birds carrying rings readable by binoculars and staying for a longer time in the restricted area, which is densely populated by ornithologists (*e.g.* arctic geese and swans wintering in some parts of Western Europe).

Table 1
Recovery rate of Robins ringed at the Operation Baltic stations in subsequent decades. Linear regression slope b = -0,015 (p < 0.001).

Years	Ringed	Recovered	Recovery rate
1960-1969	71605	419	0.59
1970-1979	54974	286	0.52
1980-1989	44825	134	0.30
1990-1996	31085	97	0.18
Total	**202489**	**936**	**0.46**

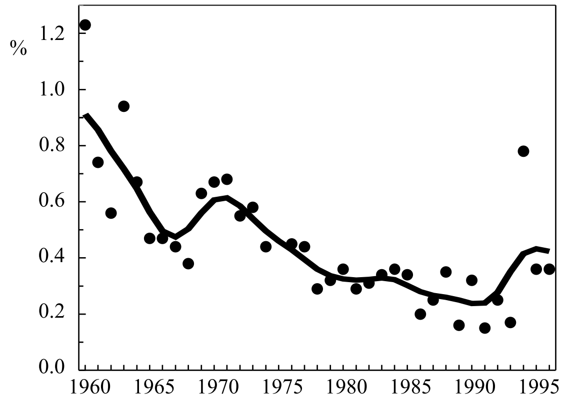

Fig. 17. Recovery rate of Robins ringed at the Operation Baltic in years 1960-1996. Dots – yearly rates, line – smoothed data (five-year moving average). After Busse 2000.

The detection coefficient depends on many factors, *e.g.* density, hunting customs and cultural level of people, place where the ring is put on – tibia or tarsus, kind of address written on it (Sales 1973), habitat, predator pressure, of which all are hard or impossible to quantify. Thus, the calculation of their influence seems to be impossible.

Ringers can observe influence of the detection coefficient on their work looking for number of recoveries obtained from ringed birds (recovery rate – number of recoveries per hundred ringed birds). In passerines recovery rate is usually low, as detection coefficient for these birds is low, too. However, it can be low, very low or very, very low. How low it is, depends in Europe mainly on migration pattern of the population. As an example, the recovery pattern of Robins ringed at the Operation Baltic stations could be given (Fig. 18). It suggests that nearly all Robins migrating through the south coast of the Baltic are moving SW-W, while only single individuals – SE. This is in clear contradiction with results of orientation tests performed at the Operation Baltic stations and elsewhere (Fig. 19). The situation at Figure 20 is similar to that at Figure 18, where only two recoveries of the Song Thrush ringed at the same area came from the Balkan Peninsula. In the last case, studying recovery rate of birds ringed at different bird stations could help to solve the problem of migration pattern in this area. We can use here values of the index of ringing efficiency (x) that is handier for presentation:

$$x \quad \frac{N}{V}$$

where:
N – number of ringed birds,
V – number of recoveries.

The index x gives the number of birds that have to be, in average, ringed to obtain one recovery.

In the discussed case, differentiation of x values is very well pronounced and distribution of the high values of x index (Fig. 21) suggests direction of migration of

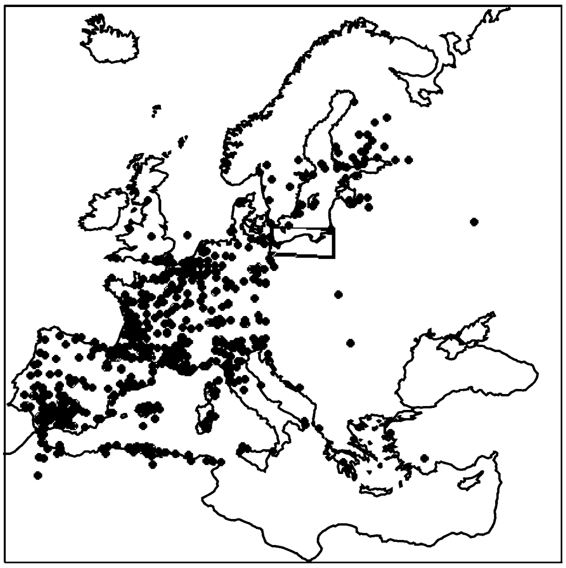

Fig. 18. Recovery places of Robins (*Erithacus rubecula*) ringed during the Operation Baltic work at the Polish Baltic coast (N = 557). A few recoveries SW of the map boundaries. After Remisiewicz *et al*. 1997.

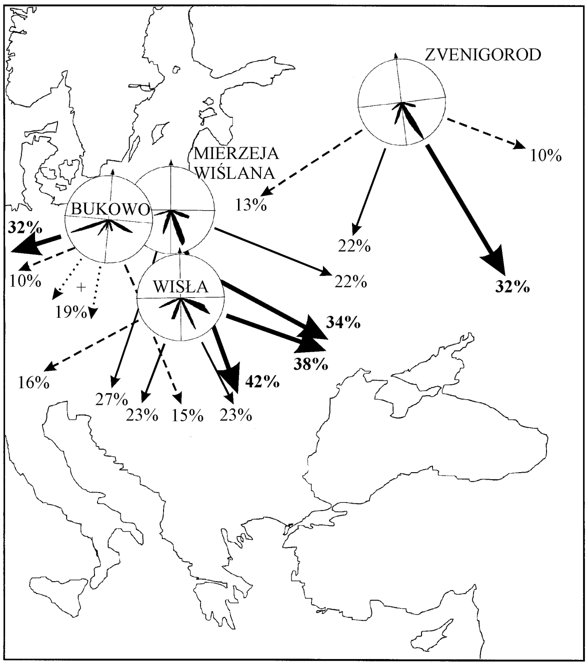

Fig. 19. Patterns of headings of Robins tested in Busse's orientation cages at different bird stations in Sept. 1998. After Busse *et al.* 2001.

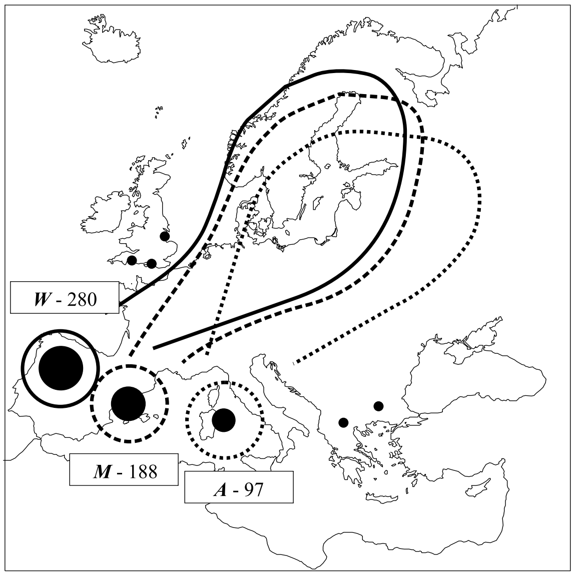

Fig. 20. Breeding grounds of the Song Thrush populations wintering on the main winter-quarters. Small black dots – recoveries outside main winter-quarters. Numbers of recoveries used are given. After Busse and Maksalon 1986, modified.

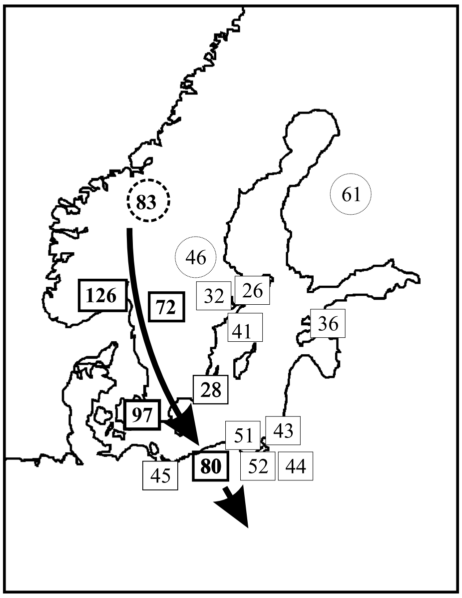

Fig. 21. *x* values for Song Thrushes ringed at different ringing stations (in squares) and at various areas (in circles). Estimated flyway of birds directed to Balkans is shown. After Busse and Maksalon 1986, modified.

some birds to the null reporting rate area somewhere in SE Europe. The stream of such birds is concentrated in the central part of the Polish Baltic coast (Bukowo station). The example shows that reporting rate can influence ringing recovery evaluations very much.

AUGMENTATION OF RECOVERY DATA BY ORIENTATION TESTS

As it was mentioned above (Fig. 19), testing the directions shown by nocturnal migrants could broaden knowledge about migration pattern of the species. A new field method of performing such tests was elaborated recently at the Operation Baltic stations (Busse 1995). It was scrutinized in a few countries and in very different locations.

The pilot study on directional preferences of night migrants in Eilat (Israel) was made on their spring migration in 1999 (Trocińska *et al*. in press). As a new method was applied, localisation of the study was very important. Located at the northern tip of the Gulf of Aquaba (the Red Sea), at the edge of almost 2000 km of continuous desert regions of the Sahara and Sinai Deserts, Eilat is the place, which is passed by thousands of birds migrating from Palearctic during both spring and autumn migration (Yom-Tov 1984, Morgan and Shirihai 1997, Yosef 1997). Number of passerine birds caught there is much higher in spring than in autumn for many species (Yom-Tov 1984, Frumkin *et al.* 1995). Birds migrating over Eilat in spring, heading to the breeding grounds, should be clearly orientated on their migration. Eilat is located on the Eastern Palearctic Flyway that is not well studied in comparison with the Western one, and there is a great need to study this direction of migration. The studied group was diverse – there were species breeding all over Palearctic like the Lesser Whitethroat (*Sylvia curruca*) or the Chiffchaff (*Phylloscopus collybita*), as well as species typical for Mediterranean, *e.g.* the Orphean Warbler (*Sylvia hortensis*) and the Sardinian Warbler (Harrison 1982, Hagemeijer and Blair 1997, Morgan and Shirihai 1997). The aim of the study in Eilat was to learn about the directional preferences of night migrants, in the place that was appropriate due to both a huge number of migrating birds and their assumed clear orientation to the breeding grounds.

For the Lesser Whitethroat, there is available a number of ringing recoveries, so the results of tests were compared with the data on localities the birds recovered/ringed at Eilat coming from the paper by Yosef (1997). Directions pointed by the vectors that birds have shown are very similar (Fig. 22). Contrary to most European passerine species, the Lesser Whitethroat migrates from Europe in the southeastern direction to its wintering grounds (Glutz and Bauer 1991, Hagemeijer and Blair 1997) and in spring flies northwest. According to Morgan and Shirihai (1997), the large spring passage of this species in Eilat results from the fact that the West European populations all pass through the Levant. The result of this comparison showing predominance of the western direction in the orientation cage also supports this.

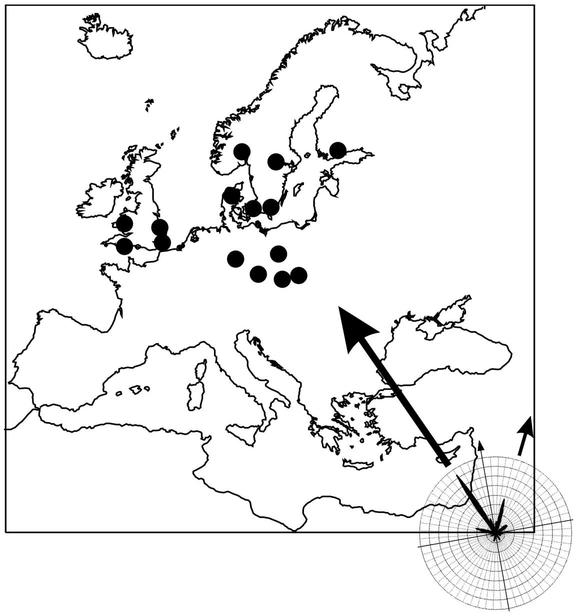

Fig. 22. Simplified distribution of headings of the Lesser Whitethroat ($N = 218$) tested in the field experiments in Eilat, Israel, spring 1999 and ringing/recovery localities of individuals recovered/ringed at Eilat ($N = 15$). After Trocińska *et al.* in press.

RESULTS OF RINGING – ADVANCED STUDIES

As it was stressed earlier, traditional imprinting of some point of view (stressing the breeding grounds) does not lead to an easy analysis. Fortunately, it is also possible to carry out the analysis conversely: from the recovery place, that is an area, where ringed birds have been found during winter and/or on migration (as it was explained above).

The population pattern was already found in the Rook (*Corvus frugilegus*), where the mixed zones of two or even four populations occur (Fig. 23), as well as in other corvids, *e.g.* the Hooded Crow (*Corvus corone cornix*) and the Jackdaw (*Corvus monedula*) (Busse 1969) and in a limited analysis of the Meadow Pipit (Petryna 1976).

In recent years, migration pattern of the European Song Thrush has been intensively studied (Busse and Maksalon 1978, 1986a, 1986b; Maksalon 1983). Hence, this species can be an example to demonstrate possibilities offered by the new concept of analysis of bird ringing and catching data. Recoveries of Song Thrushes ringed on breeding grounds in northern, eastern and central Europe suggest a pattern of population movements shown on Figure 20. Most of these areas are inhabited by a mixture of birds directing their migration to West Iberian Peninsula and Western France for the *W* population, East Spain and South France for the *M* popu-

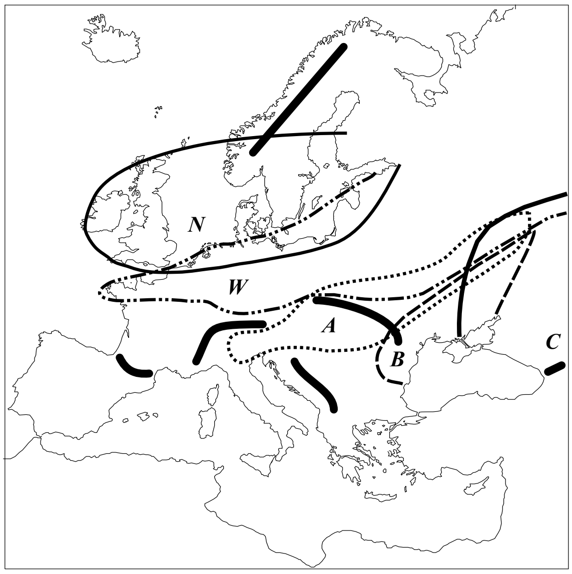

Fig. 23. Population pattern of the Rook (*Corvus frugilegus*). Letters – symbols of different populations, lines – borders of different population areas, black stripes – main mountain ridges. After Busse 1969.

lation and Italy and North Africa for the *A* population. There are a few recoveries from Great Britain and the Balkan Peninsula and a problem if they are exceptions to the rule. However, this problem can be solved, when a quantitative method of studying the recovery dispersal is applied to the data (Fig. 21). By studying both the recoveries distribution of the Song Thrush migrating through different parts of the Polish Baltic coast in different waves of migration, and the recovery rate of these birds, it has been found that they migrate to four winter areas (Fig. 24) instead of three, suggested by the preliminary analysis. The fourth wintering area (and its corresponding breeding zone) was discovered by using the migration pattern of the Song Thrush observed at the Polish Baltic coast (Maksalon 1983) and the recovery rates of this species ringed in different parts of the Baltic basin (Busse and Maksalon 1986b). In addition, by re-analysing Ashmoles (1962) data from the British Isles, the final migration pattern of European populations of the Song Thrush seems to be as shown in Figure 25.

GENERAL PICTURE OF PASSERINE MIGRATION IN EUROPE

The results obtained by means of „looking from the south" analysis suggest that, in general, it is correct and can help to explain the recovery patterns of a number of passerines.

The first and basic question, when considering the idea of „looking from the south", is „why does the species winter distribution seem to be more important than

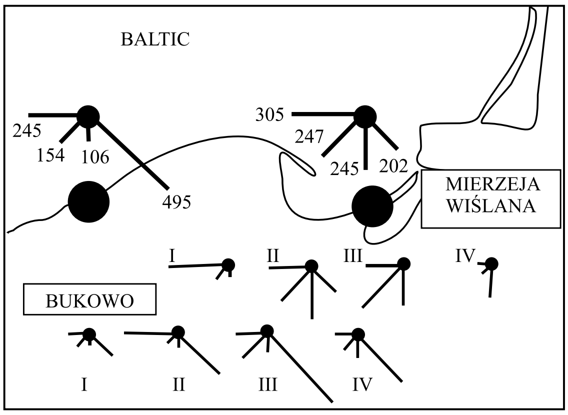

Fig. 24. Migration pattern of the Song Thrush at two Polish Operation Baltic ringing stations Bukowo and Mierzeja Wiślana. Numbers indicate the proportion of individuals (per 1000 migrants) directing to four winter quarters (three specified at Fig. 20 and the Balkan one). Two lower rows of sings show differentiation between subsequent waves of migrants. After Busse and Maksalon 1978, modified.

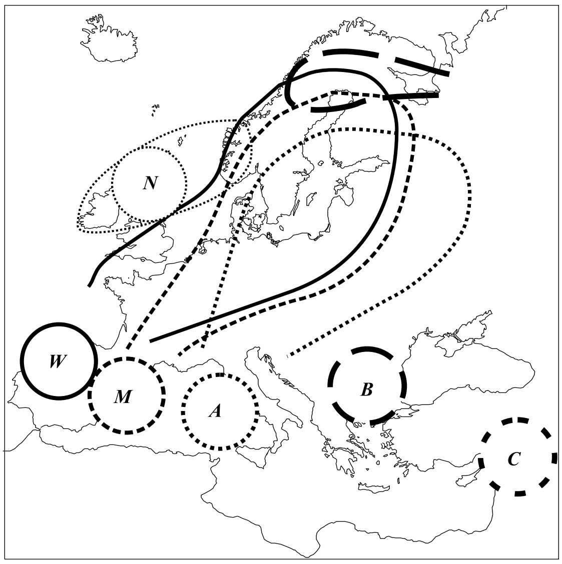

Fig. 25. Population pattern of the Song Thrush. After Busse and Maksalon 1986, modified.

the breeding one?" As population patterns and the inherited directions of migration of many species cannot be explained by any recent history, an answer to this question can only be found by studying the past distribution of birds. The influence of ice ages on animal and plant distribution in Europe is well known. It has been used to explain sub-specific and distribution patterns of some species of birds in various zoogeographical papers (Moreau 1955, 1972; Harrison 1982; Blondel 1997). These authors stressed the importance of the ice-free refuges during the glacial periods for sub-specific and even specific differentiation within the passerines. It is accepted that in the glacial periods, small and isolated populations of birds inhabited these refuges.

This situation contributed to genetic differentiation but in most cases, it did not reach sub-specific level, so descendants and the different refugees are inseparable now by conventional systematic methods. When climate became milder, the areas occupied by the different populations spread northwards and birds dispersed to new breeding grounds. Inhabitants of the newly occupied areas migrated generally to or through their earlier refuges and this instinct became fixed as an inherited direction of migration. The evolution of migration and population patterns depended on the ecology of each species (its habitat and temperature preferences) and it will depend upon the origin and numbers of individuals starting to invade the changing areas of central and northern Europe. It seems clear that the first northwards invasion routes were from the Iberian Peninsula to the British Isles and from the Balkans to Central Europe. They were isolated for a long time from each other by the tundra areas between the Alps and Scandinavia. Amelioration of the Atlantic climate was so intensive that the species, which had occupied the British Isles early, became resident and when they re-invaded the Continent to the east and north, they migrated to winter on the British Isles and created secondary winter-quarters. Taking an overview of the passerine migration in Europe, one is able to show winter-quarters distributed as shown at Figure 26 – the example of hypothetical develop-

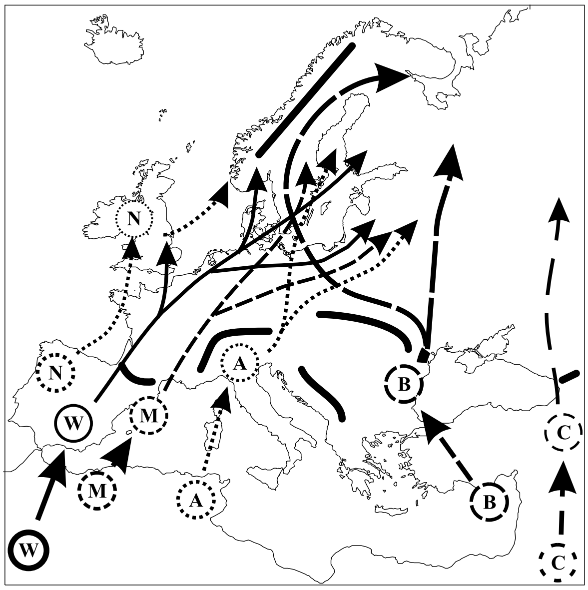

Fig. 26. Dispersion pattern of European populations of the Song Thrush as reconstructed from recent migration pattern. Letters in thin-line circles – actual winter-quarters, letters in heavy-line circles – primary winter-quarters during the last glaciation; arrows indicate directions of expansion. After Busse and Maksalon 1986, modified.

ment of recent population structure of the Song Thrush. These are, of course, main winter areas, but many species have secondary winter-quarters, which have been formed more recently. Still, the connections between contemporary migration flyways passing southern Europe and central/south African winter-quarters of many long-distance migrants are not known.

The colonizing birds from the different ice-free refuges met each other in various areas of central and northern Europe. Depending on the genetic differentiation and the density of population from the different areas, they could form mixed zones of a varying width, or birds from one area could drive out the weaker population. Such situations could create a differential migration pattern of some complexity. This explains an existence of apparently uneconomical migration routes found in several species (the Meadow Pipit – Petryna 1976, the Robin – Pettersson and Lindholm 1983, the Song Thrush – Busse and Maksalon 1986a).

To summarize, „looking from the south" method allows to look at migration processes with an insight from the historical occupation of Europe of the different ice-free refuges. Recent spring migration is a repetition of this process, whilst the autumn one forms the corollary of the basic pattern.

RECENT EVOLUTION OF MIGRATION PATTERNS

The schematic representation of invasion patterns, as shown in Figure 25, can be complicated by the recent evolution of migration routes. Populations are still dispersing, *e.g.* the Blackbird – *Turdus merula* (Spencer 1975), the Carrion Crow – *Corvus c. corone* (Cook 1975). Migration habits are changing by the shortening of a migration route and creation of the secondary winter-quarters. In such case, even residency can be treated as wintering on the secondary winter-quarters, which occurred to be identical with that of the breeding area. Even changes in the direction of migration can happen. This, for example, was suggested for the Hooded Crow and the Jackdaw (Busse 1969), in which the different subspecies are now wintering on the same areas. The most recent geographic changes can be found, if one compares recovery patterns over a series of decades in our century (Fig. 27), while some older ones can be studied by the distribution of young and adult birds in different parts of the winter-quarters (Busse 1969). The latter method assumes that young birds on their first migration follow the older customs of population and migrate longer distance than the adults do, if the process of shortening of migration took place. On the contrary, they migrate to areas closer to the breeding grounds if the migration route is extending.

The continuing evolution of migration patterns can have both natural and human origin, as it could be expected while interpreting unusual creation of a totally new winter-quarter that was found in the Blackcap and discussed extensively (Berthold and Terrill 1988, Busse 1992, Fransson and Stolt 1993). Long-term climatic changes have their effect on the distribution of birds and their migratory habits as, for example, on the distance travelled or the proportion of migrants in par-

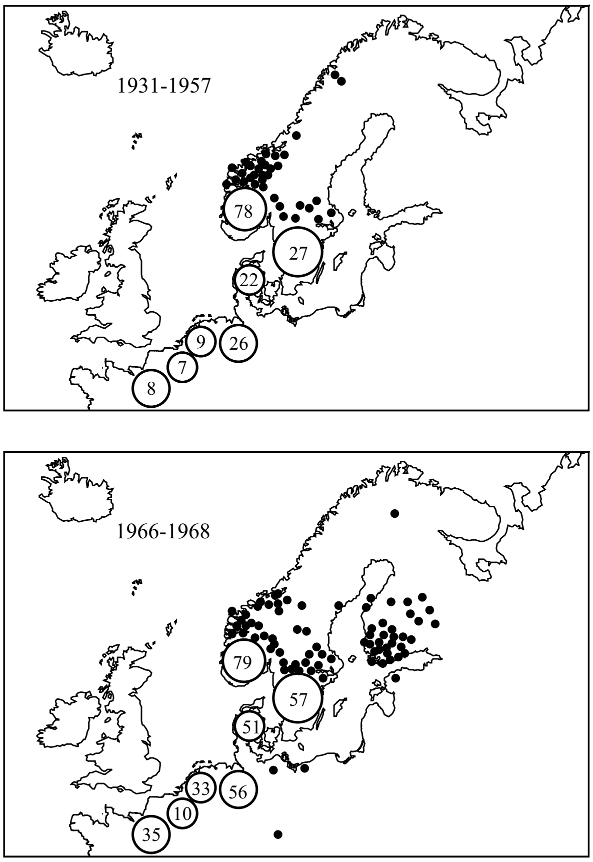

Fig. 27. Changes in distribution of recoveries of Blackbirds (*Turdus merula*) ringed in Great Britain and Ireland. After Spencer 1975.

tially migrating species. These are certainly out of human control. However, human activity, so far hardly studied is potentially very important for at least a few species. Change in habitats, both on breeding grounds and in winter-quarters, chemical contamination of the environment and hunting activities can have pronounced influence on the density of bird populations and even on their migratory habits. The selection pressure of these factors is not known so far, but very serious effects on population have been suggested by the first attempts of its evaluation (Rabøl 1978). This is clearly the important factor and is of great value for future studies and environmental management.

CONCLUSIONS

Although detailed studies on bird migration patterns have been carried out for a very long time, our knowledge is rather poor and superficial. It is certainly not sufficient for some practical decisions on population management and bird protection that need to be taken nowadays. Even the ringing, which has been carried out for so many years and has produced so much data that some scientists feel it should be stopped for many species, certainly has not run out of its possibilities. One can discover much more, using new methods of analysis of a huge file of recovery data, which are now available, than it was ever possible by the mapping of ringing and recovery places – so spectacular for dilettantes, but rather pointless for more demanding students of bird migration. In particular, the knowledge about birds that migrate by eastern flyway is urgently needed.

For a detailed analysis of bird migration patterns, one should use complicated analytical methods and a very wide ringing cooperation between researchers. The realization of these dreams is something we should strive for in the future.

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