THE PATTERN OF WINTER-QUARTERS OF ROBINS (*Erithacus rubecula*) MIGRATING IN AUTUMN THROUGH THE SOUTHERN BALTIC COAST

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ABSTRACT

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In the study, 225 long-distance winter recoveries of Robins ringed during autumn migration (15 August-2 November) of years 1961-1997 at three stations of the Polish Operation Baltic: Mierzeja Wiślana (54°21'N, 19°19'E), Hel (54°46'N, 18°28'E) and Bukowo (54°21'N, 16°17'E/54°28'N, 16°25'E) were analysed in order to distinguish winter-quarters of the species. Hypothetical delimitation of winter-quarters, assumed according to the course of geographical barriers and localisation of winter-quarters of related species, was verified using an iterative combination of different methods of analysing ringing recoveries. They were as follows: correlating angle and geographical longitude of recoveries with the ringing date, analysing maps of recoveries of birds ringed in different parts of migration season (15 August-20 September, 21 September-10 October, 11 October-2 November), comparison of mean migration distance in these three periods for all the records jointly, and separately within each quarter. As a result, the presumed existence of four winter-quarters of the species: the Western, the Mediterranean, the Apennine and the Balkan quarter, occupied by separate wintering populations, was confirmed. Borders of the first three quarters were defined. It was also stated that the shortening of the distance to the wintering area took place in the course of the season, which was clearly demonstrated for all the records jointly and within the Western quarter.

The proposed distribution of winter-quarters seems to consist well with the localisation of bird refuges in the last glacial period presented by Harrisson (1982). The phenomenon of shortening the distance to the wintering place probably reflects the history of re-colonisation of Europe by the species and creation of secondary winter-quarters northeast to the initial refuges (Busse 2000).

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Key words: Robin, *Erithacus rubecula*, ringing recoveries, winter-quarters, wintering populations.

INTRODUCTION

The Robin is one of the most numerously ringed passerine species in Europe. The existing material from ringing recoveries enabled many authors to provide a solid, but general description of the migratory distribution and wintering range of Robins ringed in the majority of European countries (*e.g.* Nordström 1963, Busse and Gromadzki 1966, Erard 1966, Rendahl 1966, Payevsky 1971, Saurola 1983, Pettersson and Lindhölm 1983). However, for more detailed studies on migration flyways and wintering distribution of different populations, wide and homogenous material is needed (Busse 1987). Therefore, only several attempts of this deeper approach were made (Adriaensen 1987, Jenni 1987, Pettersson *et al*. 1990, Remisiewicz *et al*. 1997). This disproportion derives from the fact that in studies based on the material coming from birds ringed on migration, large samples are needed to meet methodological requirements (Perdeck 1977) and to allow for any division of records into sub-groups. Therefore, studies of that kind come only from recent two decades, as only after many years of effort of long-term ringing schemes it was possible to collect the suitable number of records.

This kind of material was provided by 40-year activity of the Polish Operation Baltic ringing stations, as Robin is one of dominant species caught there on migration. Earlier papers on recoveries of Robins caught on the Polish Baltic coast gave only a very general idea on their migrations and wintering (Gromadzki 1964, Busse and Gromadzki 1964). The recent paper of Remisiewicz *et al*. (1997) begun new, more detailed investigations on the pattern of movements of these Robin populations, and the present paper is its logical continuation.

From the last mentioned study, it is known by ringing recoveries that Robins that cross the southern Baltic coast originate from Fenno-Scandia, the Baltic countries, the northern and the central parts of the European Russia, and from Belarus. All these populations belong to the nominative subspecies and are entirely migratory, in contrast to populations of Robin breeding in Western and Southern Europe, which are partially migratory or sedentary (Cramp 1988). The wintering area of Robins ringed on the Polish coast covers the majority of the known wintering range of the species – from Spain and Morocco at the West to the Balkans and Turkey at the East (Remisiewicz *et al*. 1997).

The presented study is aimed to define separate winter-quarters within this wide wintering area and to show that they are used by separate migratory populations. The study has also a methodical aspect, presenting an iterative method of analysing ringing recoveries, based on combination of different approaches to the analysed material.

MATERIAL

Recoveries used in the study came from Robins ringed in the autumn migration period (15 August-2 November) in years 1961-1997 at three stations of the Polish

Operation Baltic (Fig. 1): Mierzeja Wiślana (54°21'N, 19°19'E), Hel (54°46'N, 18°28'E) and Bukowo (54°21'N, 16°17'E / 54°28'N, 16°25'E). In the analyses there were used 225 long-distance (over 10 km from the place of ringing) recoveries of Robin recorded elsewhere in the period of wintering, established after literature (Erard 1966, Rendahl 1966, Adriaensen 1987) on 1 December-28 February. The analysed sample met methodical requirements, postulated by Perdeck (1977). The postulate of the homogeneity of the site and term was met by the close localisation of the stations (*ca* 200 km at the most) on the same coastline and in similar habitats (Busse and Kania 1970). The sample size allowed to perform statistical analyses with dividing the records into the expected populational groups, except for the three records from the Balkan direction, which were excluded from the detailed analyses because they were too few for any internal division. Knowing the limitations of the material, coming from different sources (both from Robins found and shot), mainly the qualitative (regarding the localisation of records) analyses were performed and the only quantitative comparisons among geographical groups of records referred to the date of ringing.

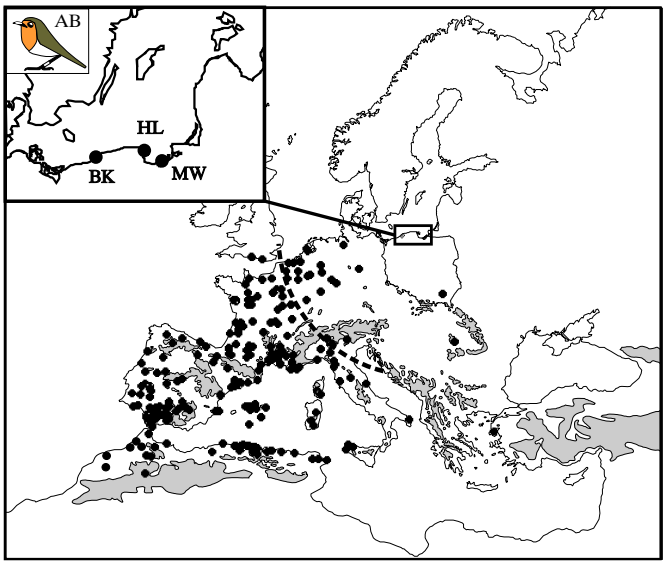

Fig. 1. Localisation of ringing stations (*BK* – Bukowo, *HL* – Hel, *MW* – Mierzeja Wiślana) and distribution of recoveries of Robins ringed on autumn migration (15 Aug.-2 Nov.) in years 1961-1997 at these stations and recaptured elsewhere in the winter season (1 Dec.-28 Feb.) – $N = 225$. Dashed line marks the 1600 km distance form the sites of ringing; records northeast to this line were excluded from some correlation analyses (see the text). Grey area – mountain ridges over 1000 a.s.l.

METHODS

The results of the earlier analysis of Robin recoveries (Remisiewicz *et al*. 1997) showed that neither between direct (from the season of ringing or from the follo-

wing winter) and indirect (from further seasons) recoveries nor between records of Robins ringed as immatures and as adults there occurred any remarkable differences in distribution. Therefore, in the present study all the records of Robins recovered in the wintering season were treated jointly. However, from all calculations, the three ringing recoveries coming form the Balkan direction were excluded (see Fig. 1), and only 222 winter records from western and southwestern Europe and from northern Africa were analysed in detail.

For these recoveries, recovery angle (the azimuth of recovery) and geographical longitude of the place of recovery were correlated with the date of ringing, as suggested by Jenni (1987). The recovery angle was calculated for each record according to the loxodrome formula (Imboden and Imboden 1992). The date of ringing within the season was described by the day and month of ringing, excluding the year. In the case of both correlations, Spearman rank correlation coefficients and their statistical significance were calculated, as distributions of both variables did not fitted the normal distribution (Zar 1996).

Calculations of recovery angle and maps of distribution of records were prepared with the use of the RECRING software by P. Busse. The maps present only the localisation of records – the number of recoveries coming from the same place is not indicated. Separate maps were drawn for records of Robins ringed in different parts of the autumn migration season. For that purpose, the ringing season was divided into three parts: 15 August-20 September, 21 September-10 October, 11 October-2 November. The first term included 35 days, but in fact throughout all the fourty analysed years only three recoveries were produced by Robins ringed between 15 and 31 August as the migration of Robins actually starts in the studied region at the beginning of September. Thus, the first defined period contained in fact only *ca* 20 days of „effective" catching, similarly to the two remaining periods. On the basis of visual comparison of distribution of records at these maps, the hypothetical delimitation of winter-quarters was verified and records were assigned to each of the defined quarters. In the paper there was used the nomenclature of winter-quarters following Busse and Maksalon (1986). In the case of 12 records, the qualification to one of the neighbouring quarters was questionable and therefore they were not included to any of them and thus not used in these of further analyses in which records were divided into winter-quarters.

The mean distance of recoveries of Robins ringed in different periods of the autumn migration season was compared for the whole sample ($N = 222$), except for records for the Balkan direction (which could bias the results), by ANOVA and post-hoc Tukey's test. Then, the same comparison was performed separately for the Western and the Mediterranean quarters – in the case of the Apennine quarter the sample was too small.

RESULTS

General distribution of winter records

The map of distribution of all the analysed winter records (Fig. 1) gives an overview of wintering area of Robins caught at the Polish coast, which is very wide. Such a wide range of the recovery angle (162-298°) suggests that this pattern could be the effect of passage through the Polish coast of several migratory populations (Busse 2000).

Correlation between the date of ringing and the localisation of recoveries

In order to check the above assumption, the geographical longitude of recovery and the recovery angle were correlated with the date of ringing (excluding the few records from the Balkans). Both relations were weak, although statistically significant (geographical longitude – $R_s = 0.32$, $p \ll 0.0001$; recovery angle – $R_s = 0.18$, $p < 0.01$; $N = 222$). This would support the presumption that in different terms, different Robin populations cross the southern Baltic coast. However, the results of correlations were contradictory, with the geographical longitude becoming more eastern, but the angle of recovery – more western, in the course of the season. Presuming that this ambiguousness could be the effect of records from central and northern France and from Germany coming from late-migrating Robins that stay closer to their breeding grounds (Remisiewicz *et al*. 1997), the next comparison was performed excluding these records. They had relatively high values of recovery angle but the geographical longitude – the same as, for example, recoveries coming from the Balearic Islands or from the Apennine Peninsula. For this reason, only 155 recoveries coming from the more distant part of wintering grounds (over 1600 km from the ringing stations – see Figure 1) were used in this analysis. In such case, the correlation coefficient for the relation between the date of ringing and the geographical latitude changed only slightly in comparison with the previous correlation ($R_s = 0.31, p < 0.0001$). However, the relation between the recovery angle and the date of ringing became insignificant. This confirmed the assumption that it was the records from the northern part of the wintering area, which were responsible for the inconsistency of results of the previous analysis, as they were responsible for the westwards shift of the recovery angle in the course of the autumn season. It can be also seen clearly that while speaking about more distant parts of the wintering range, Robins crossing the southern Baltic coast with the course of the season prefer the most eastern wintering grounds.

Hypothetical winter-quarters

Analyses of distribution of recoveries of the Robin (Jenni 1987, Remisiewicz *et al.* 1997), and of the species from the same family – the Song Thrush *Turdus philo-*

melos (Busse and Maksalon 1986), suggest that well-pronounced geographical barriers, such as seas and mountain ridges, can separate migration flyways or winter-quarters of the species. Therefore, the wintering range of Robin, indicated by the recoveries, was divided into four hypothetical winter-quarters: the Western, the Mediterranean, the Apennine and the Balkan (Fig. 2), according to the land configuration and the division of wintering grounds for the Song Thrush (Busse and Maksalon 1986). In the course of analyses, the legitimacy and delimitation of these hypothetical quarters was checked. However, in the case of the Balkans, the few records from this direction allowed only to state that Robins ringed at the Polish Baltic coast use this region as a winter-quarter.

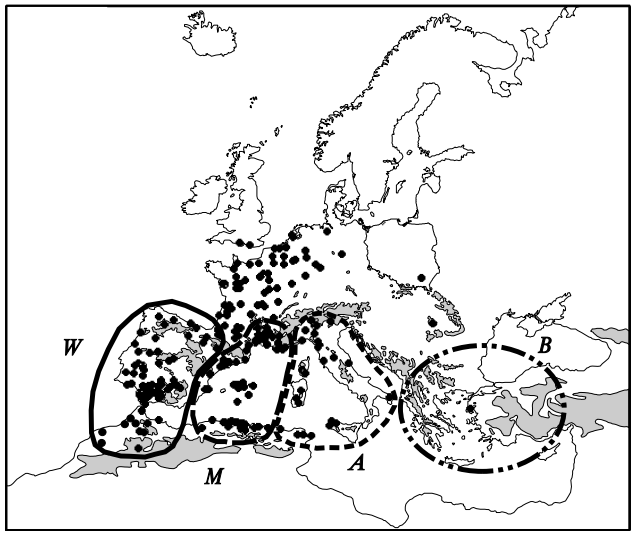

Fig. 2. Hypothetical localisation of Robin wintering quarters, verified in the paper (see the text). *W* – Western winter-quarter, *M* – Mediterranean winter-quarter, *A* – Apennine winter-quarter, *B* – Balkan winter-quarter.

Delimitation of winter-quarters

Knowing that there is a relation between the date of ringing and the localisation of records, another approach to the data was undertaken. Maps presenting distribution of recoveries of Robins ringed in three subsequent parts of the migration season (Fig. 3-5) were compared and on this basis, the postulated winter-quarters were verified and their limits were adjusted.

Apennine winter-quarter

Delimitation of this quarter by this method was the most evident. Records of Robins ringed in the period 15 August-20 September (Fig. 3) came almost exclusively from the areas of the postulated Western and the Mediterranean quarters,

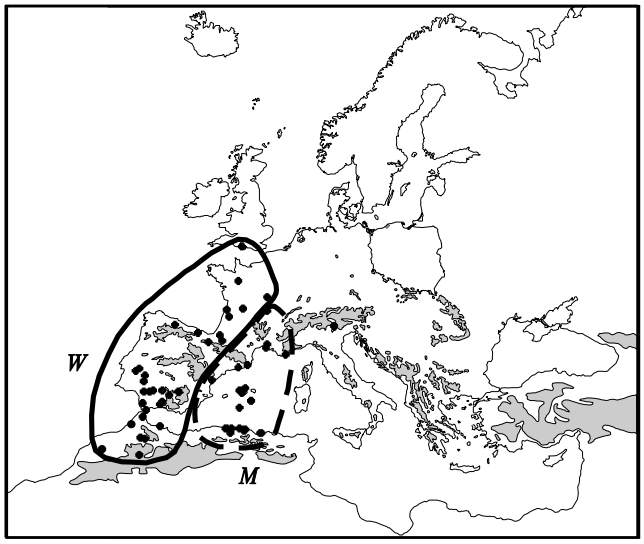

Fig. 3. Recoveries of Robins ringed at the studied stations in period 15 Aug.-20 Sept. and delimitation of winter-quarters according to their distribution. Symbols of winter-quarters as in Fig. 2.

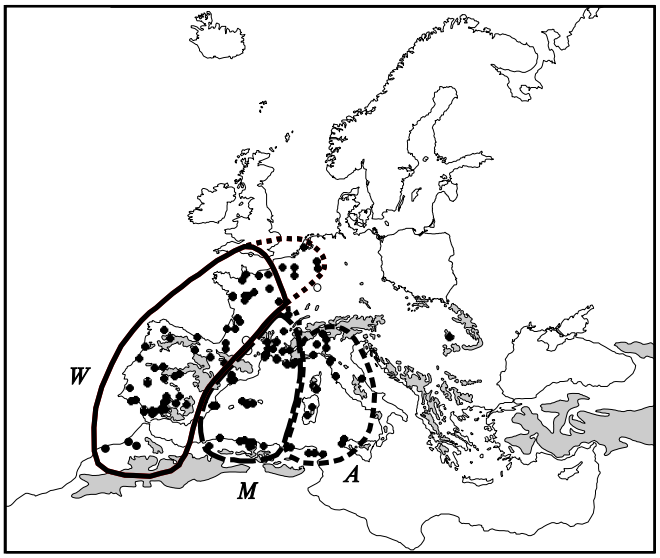

Fig. 4. Recoveries of Robins ringed at the studied stations in period 21 Sept.-10 Oct. and delimitation of winter-quarters according to their distribution. Symbols of winter-quarters as in Fig. 2.

with only one record falling in the area regarded as a part of the Apennine winter-quarter. However, among recoveries of Robins ringed in the next term (21 September-10 October), records from this area were well represented (Fig. 4).

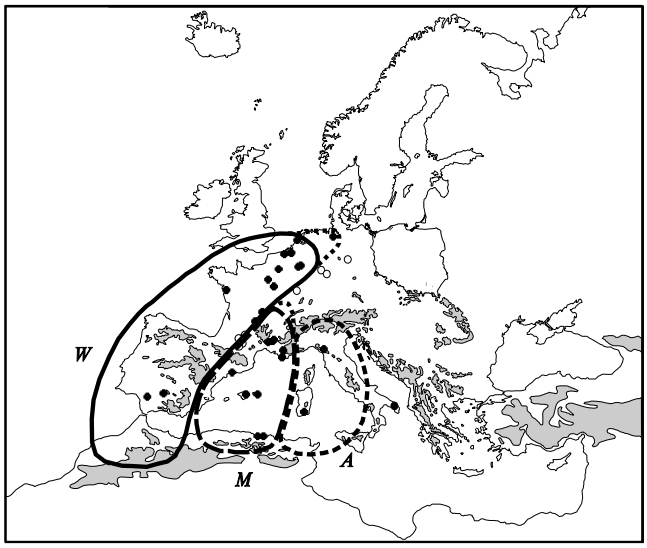

Fig. 5. Recoveries of Robins ringed at the studied stations in period 11 Oct.-2 Nov. and delimitation of winter-quarters according to their distribution. Symbols of winter-quarters as in Fig. 2.

Therefore, by comparison of Figures 3 and 4, borders between the complex of the Western + the Mediterranean quarters and the Apennine quarter could be drawn quite precisely. Especially, a clear delimitation of the southernmost parts of these quarters, which can be done in such way, is worth attention. Looking at the map of distribution of all winter records (Fig. 1), a rather continuous stripe of Robin recoveries along the Algerian and Tunisian coast can be seen. However, by the above comparison (compare Figures 3 and 4), a very clear border between the group of recoveries from the Tunisian coast, regarded as the southernmost part of the Apennine quarter, and the group of records from the Algerian coast, belonging to the Mediterranean quarter, can be drawn. Further north, the suspected western borders of the Apennine quarter – the open area of the Mediterranean Sea and the southwestern ridges of Alps, are also confirmed by the applied comparison of records' distribution maps.

Separation of the Western and the Mediterranean winter-quarters

The delimitation of these two quarters was much more difficult than in the previous case. Records from both these regions come from Robins ringed on the Polish coast in all the distinguished terms. However, there are some clues, which could help in distinction of these quarters. Looking at maps of distribution of recoveries of Robins ringed in the first two parts of the season (Fig. 3 and 4), and even at the overall distribution of winter recoveries (Fig. 1), some areas lacking records and localised at the junction of the postulated quarters could be seen. In the African part of the wintering range, a several-hundred kilometres section of the coast, where no

Robins were recaptured, separates groups of records from Morocco and from Algeria. On the opposite Spanish Mediterranean coast, again a „gap" in the occurrence of records, corresponding geographically with the above one, can be seen. Its continuation could be an area lacking recoveries within the Iberian Peninsula, which seems to separate records concentrated in the eastern part of the Spanish Mediterranean coast from those localised closer to the Atlantic coast. Further northeast, the division is not so evident, thus several records were difficult to unambiguously qualify to one of the quarters. However, records of birds ringed at the beginning of the migration season (Fig. 3) seem to be well separated in the area of western France and this distinction is blurred by the much more numerous and more spread records of birds ringed in the subsequent period of the highest migration intensity of Robins on the Polish coast (Fig. 4).

In the case of the Western quarter, its proposed exceeding towards the northeast (Fig. 4, 5) seems to be the logical implication of the localisation of records of birds ringed in subsequent terms along the Atlantic and then – the North Sea coast. In the case of the Mediterranean quarter, it was exceeded in northeastern direction only slightly (Fig. 4, 5), as it was difficult to decide, which of the two quarters the several records marked at Figure 5 as circles could belong to. However, it should be borne in mind that if these records, or even some of them, were included to the quarter, this would give a similar pattern of elongation of the quarter to the northeast, as in the case of the Western quarter.

Shortening of the distance of wintering in the course of the season

Comparing the maps of recoveries of Robins ringed in subsequent parts of the migration season (Fig. 3-5), it can be seen that the later term of ringing, the more records come from areas closer to the place of ringing. To verify this observation, the recovery distance was compared among records of birds ringed in the three subsequent parts of the migration season. The results, presented in Table 1, proved that a significant shortening of the distance to the place of wintering occurred in the course of the season (ANOVA: $F_{2, 219} = 14.4$, $p \ll 0.0001$).

In order to find how this phenomenon was reflected within each winter-quarter, Figures 3-5 were visually compared focussing on this aspect. Within the Western quarter the shortening of the migration distance could be observed most clearly. Firstly, a major part of Robins ringed in the period 15 Aug.-20 Sept. were recovered in the most distant part of the wintering area – in Morocco and in the southern part of the Iberian Peninsula (Fig. 3). Secondly, all the African records from this quarter come exclusively from birds ringed before 10 Oct. (Figs. 3, 4); in the last period even records from the Iberian Peninsula were scarce (Fig. 5). Finally, considering the northern limits of this winter-quarter, subsequent maps suggest its enlargement towards the north-east (Fig. 3-5). These observations were confirmed by the comparison of the mean recovery distance among Robins ringed in the three parts of the autumn season, conducted only for records belonging to this quarter, as delimited at Fig. 6. Differences of the mean recovery distances (Table 1) among these three groups were highly significant (ANOVA: $F_{2, 110} = 14.2$, $p < 0.0001$). The values

of the mean recovery distance, declining in subsequent periods (Table 1), indicate that in the course of the season more north-eastern (closer to the ringing site) parts of the wintering range are occupied. The fact that the difference between the first and the second period was non-significant seems to be the effect of both a small sample and a high variance for the first group.

Table 1
Comparison of recovery distances for Robins ringed in subsequent parts of the migration season and statistical significance of differences (*post-hoc* Tukey's test), for all the records treated jointly, and for Iberian and Balearic winter-quarters.
ns – $p > 0.05$

Period of ringing	All records			Iberian quarter			Balearic quarter		
	N	Mean distance in km (min-max)	*p*	*N*	Mean distance in km (min-max)	*p*	*N*	Mean distance in km (min-max)	*p*
15 Aug.-20 Sept.	59	2221 (1088-3266)	**0.02**	35	2344 (1195-3266)	*ns*	23	2081 (1431-2382)	*ns*
21 Sept.-10 Oct.	127	1933 (888-3196)		64	2102 (888-3196)		39	1859 (1266-2537)	
11 Oct.-2 Nov.	36	1562 (438-5363)	**$2.6 \cdot 10^{-5}$**	14	1345 (631-2566)	**0.003**	11	2075 (1401-5363)	*ns*

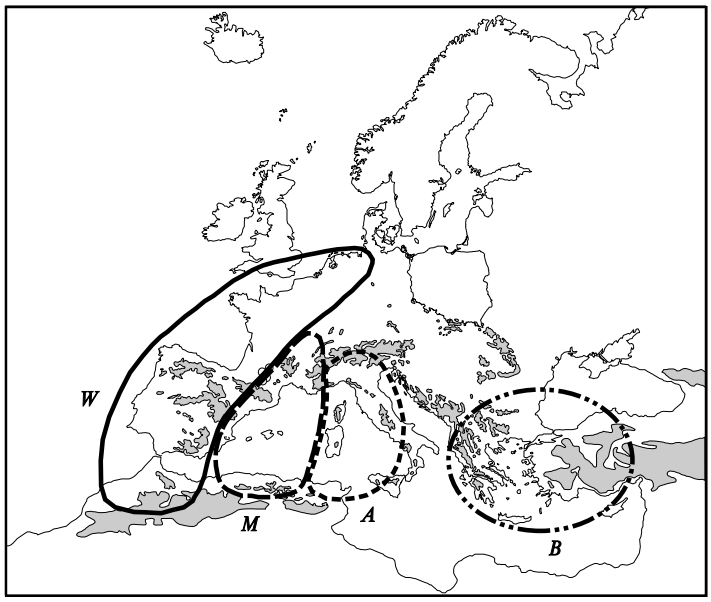

Fig. 6. The pattern of Robin winter-quarters obtained in the study. The delimitation of the Balkan winter-quarter is an assumption. Symbols of the quarters as in the Fig. 1.

In the case of the Mediterranean quarter, shortening of the wintering distance was not so evident. African records come from birds ringed throughout the whole season. However, some distinct differences can be seen in distribution of recoveries between Figures 3 and 4 – among birds ringed in the term 15 August-20 September there were only few records from the French Mediterranean coast, while among those ringed in the subsequent period – the major concentration of records came from this region. This was reflected to some extent by the mean recovery distance, which was shorter for birds ringed in the second term than in the first one, however this difference is statistically non-significant, probably for the same reasons as in the previous analysis. Records of Robins ringed in the third part of the migration season were scarce and distributed within whole of this winter-quarter, thus the value is intermediate. However, in the case of this quarter it should be borne in mind that the results could show the shortening of the migration distance much weaker than it actually is, due to the unclear northeastern limitation of this quarter.

In the case of Robins wintering in the Apennine winter-quarter, the interpretation of time-dependent changes of distribution is difficult. It can be seen that all the African records come exclusively from birds ringed in the earlier of the two terms, in which recoveries from this quarter occur (compare Figures 4 and 5). However, it might be an artefact derived from generally a very low number of records from this quarter of Robins ringed in the last period of migration. Any statistical verification of these notices was impossible, due to the small sample not allowing for internal division of the group.

DISCUSSION

Methods of analysis

In the study, a combination of different methods was used as each of the methods usually used in analyses of recovery data has its own shortcomings. From the two coordinates describing the localisation of records, I chose the geographical longitude for analyses, as it seemed to differentiate the range of the breeding grounds most. This variable has a wider range of values than the recovery angle, which is also commonly used in this type of analyses (*e.g.* Perdeck 1977, Pettersson and Lindholm 1983, Jenni 1987), thus using it was more sensible to the changes in distribution of records. This was confirmed by the results of performed correlations. However, as bird migration routes are curved, which is enforced in Europe by the curvature of the Atlantic coast and by the course of mountain ridges (Remisiewicz *et al*. 1997), in subsequent parts of the wintering range the same values of the recovery longitude or angle can refer to different winter-quarters or migration routes. Therefore, it was necessary to exclude from some correlations the part of records from the northern part of the wintering range (Fig. 1), in order to eliminate this methodical problem and explain empirically the obtained inconsistency of results of correlations of these two variables with the ringing date.

For the above reasons, simple statistical methods were not sufficient to analyse the internal differentiation of the localisation of wintering records and I had to divide *a priori* the recoveries into geographical groups by a traditional method of interpreting maps of recoveries, and to verify the accuracy of this division by the statistical methods. However, the applied geographical division of records, and thus – the produced hypotheses on the delimitation of the winter-quarters, were based on biological premises considering the evolution of the migration routes, the migration pattern of related species and the present knowledge of pattern of Robin's movements, which will be discussed below.

The subsequent method – comparisons of maps of distribution of records coming from birds ringed in different parts of migrating season, was also commonly used in other papers (Rendahl 1966, Saurola 1983, Pettersson *et al*. 1990, Remisiewicz *et al*. 1997), leading to the conclusions, which are verified in the present work. In this case, more detailed division of the ringing period than in the cited studies allowed to find more subtle differences in localisation of records and to correct the borders of the postulated winter-quarters.

While drawing at a map any borders between populations it should be remembered that, except for the cases when clear geographical barriers distinguish them, the limits are only approximate, as birds can mix in the junction zone (Busse 2000). Thus, the lines dividing the winter-quarters are probably few-hundred-kilometre wide zones of mixing of wintering populations. In the case of Robin, some short-distance movements can be performed during the wintering season (Cramp 1988). For these reasons, the lines between the quarters were drawn rather cautiously and it was decided rather not to qualify the records localised in the border areas (especially between the Western and the Mediterranean) than to assign them without any clear premises. The course of borders was also compared in detail with the earlier delimitation of migration flyways (Remisiewicz *et al*. 1997) performed by separation of records according to a clear criterion of their recovery angles. It occurred that the records, which were doubtful in the present study as to their assignation to the winter-quarter, were localised in the zone of the overlap of distributions of records qualified to different (the Atlantic and the Alpine) migration routes in the earlier paper. Thus, excluding these 12 records from a part of statistical analyses seems to be justified.

In the described way, iteratively using objective methods and those sometimes regarded as more subjective, I attempted to eliminate the methodical limitations of the first and the bias of the latter ones.

Subsequent migration of different populations

The wintering range of Robins ringed at the Polish coast (Fig. 1) corresponds well to the area of wintering of Robins originating from Sweden, Finland and Russia (Erard 1966, Rendahl 1966, Pettersson and Lindholm 1983, Saurola 1983, Pettersson *et al*. 1990). In addition, the clear relation between the date of passage and localisation of recoveries presented hereby was found in other studies. Similarly as

stated here, the shift of the occupied wintering areas towards east in the course of the season was stated for Robins ringed on migration in Finland (Saurola 1983) as well as in Ottenby (Pettersson and Lindholm 1983, Pettersson *et al*. 1990). The same was found with respect to recoveries coming from the period of autumn migration of Robins ringed in the above areas (*op. cit.*) as on the Polish coast (Remisiewicz *et al*. 1997). Thus, all the studies present the same general rule for Robins migrating in autumn southwards through the Baltic basin. This shift in direction undoubtedly results from subsequent passage through the southern Baltic coast of populations, which differ with respect to breeding origin, migration direction and term, and winter distribution, as proved by the cited authors (Pettersson and Lindholm 1983, Pettersson *et al*. 1990, Remisiewicz *et al*. 1997) and the present paper. The same phenomenon was stated on the Baltic coast also in species closely related to Robin – such as the Song Thrush (Busse and Maksalon 1986) and in other passerines – like for example the Goldcrest *Regulus regulus* (Remisiewicz and Baumanis 1996).

Correspondence of the division of wintering grounds with the literature data

Having stated such a phenomenon, it was tempting not only to state the passage of different populations, but also to define them and to describe the sequence of their passage. It was difficult with regard to the breeding origin, due to a limited material (Remisiewicz *et al*. 1997), however the numerous recoveries from the wintering season allowed to delimit within the wintering range separate winter-quarters – *i.e.* areas occupied by different wintering populations, according to the definition of Busse (1986).

Western winter-quarter

This quarter, clearly distinctive by exclusiveness of its occupation by Robins migrating at the beginning of the season, is also clearly indicated by records of Robins breeding in Norway, which spend winter only in this area (Rendahl 1966, Erard 1966). Their distribution not only justifies the distinction of the area as a separate winter-quarter, but also approves the limits of the Western quarter presented hereby, especially the approximate border between this quarter and the Mediterranean one. The recoveries of Robins hatched in southern Sweden come also in majority from this quarter (a few records from the Mediterranean quarter). Also recoveries of Robins ringed in Belgium (Adriaensen 1987), confirm the delimitation of this quarter, as a distinct majority of them wintered there, mainly in the southern part of this area, however also some of these birds stayed for winter in Belgium. The cited paper also confirms the duration of passage of this wintering population observed hereby – Robins using the Western winter-quarter ground were recovered in Belgium on route from the very beginning and pass by till the end of the migration season, similarly as shown in the present study.

Apennine winter-quarter

The literature data supporting distinguishing this region as a winter-quarter are not so evident as in the case of the previous one. However, more detailed analysis of

recovery maps of Robins ringed in different countries allows to find some evidence in favour of such delimitation. The most solid one is lack or accidentality of recoveries from this area of Robins originating from Norway (Rendahl 1966) and southern Sweden (Pettersson and Lindholm 1983) or ringed on migration in the latter region (ringing station Falsterbo – Roos 1984) and in Belgium (Adriaensen 1987), thus these numerously represented in the Western quarter.

Distinguishing of the Mediterranean winter-quarter

The presented distinction of this region as a separate winter-quarter can be more questionable than in the case of the previous two. The eastern border of this quarter seems to be well distinguished thanks to the difference in terms of passage of birds occurring in this region and in the neighbouring Apennine quarter. However, the western border is discursive and it could be questioned whether the Mediterranean region should be separated from the Western quarter at all, or it is one winter-quarter.

On Figure 3, clearly showing winter distribution of early migrants, beside the Western quarter records, also recoveries from the Mediterranean one occur. In addition, the majority of recovery maps of Robins ringed in different regions of Europe present these records usually accompanied by these from the two neighbouring winter-quarters (Erard 1966, Rendahl 1966, Adriaensen 1987, Pettersson *et al*. 1990). However, if one takes a closer look at the two maps presenting most clearly the delimitation of the Western part of the migratory system (records of Norwegian-breeding Robins – Rendahl 1966, and Belgium-ringed Robins recovered in September – Adriaensen 1987), not a single record from the Mediterranean region can be found. Even the postulated hereby border between these two quarters, cutting the Mediterranean coast of Spain out of the Western quarter, seems to be fully confirmed by distribution of the cited records. The division of this quarter from the Western one can be also supported by the course of the two different, clearly separated flyways – the Atlantic and the Alpine ones, defined in the earlier study for the same populations of Robins (Remisiewicz *et al*. 1997). The distribution of records belonging to the Atlantic flyway corresponds very well to that of the northeastern part of the Western winter-quarter, while that of records from the Alpine flyway – to this from the northern part of the Mediterranean quarters, which would be evidence that these areas are occupied by different migratory and wintering populations.

The Balkan winter-quarter

The delimitation of the Balkan winter-quarter in such detail as in the case of the other quarters was impossible, although its existence is undoubted. The existence of this quarter is supported by records of Robins ringed in other countries of the Baltic basin (Erard 1966, Rendahl 1966, Saurola 1983, Pettersson *et al*. 1990) as well as the existence of the migration route leading to this wintering area (Remisiewicz *et al*. 1997). The question remains whether it covers only the Balkan Peninsula, or in-

cludes also Cyprus and Turkey, from where some winter records of Robins also come (Nordström 1963, Erard 1966, Rendahl 1966, Payevsky 1971, Saurola 1983, Pettersson *et al*. 1990).

Relation of the proposed pattern of wintering to the history of the species

Many of the above literature evidence found to support the obtained results, are based on the assumption that the defined migratory-wintering populations differ also with respect to the breeding distribution. This can be understood while accepting the idea of „looking from the south" (Busse 1987) on the pattern of bird migrations with regard to the history of re-colonisation of Europe from north-African refuges following the retreat of the ice cover after the last glacial period (Moreau 1972, Harrison 1982). The mountain ridges, accepted hereby as borders between winter-quarters, although today not so critical for migrants, were at these times a clear geographical barriers – the ice covering mountain ranges of Alps and Pyrenees. The distinction of bird refuges at the southern edge of Europe in the last glacial period presented by Harrison (1982) corresponds well with the pattern of winter-quarters presented hereby – areas of the Iberian Peninsula, the Western Mediterranean Islands, the Adriatic and the Aegean are regarded as separate refuges. If, as a result of isolation, evolution of different subspecies or even species was possible in separated refuges, then it is even more evident that separated populations diverged. Such populations, in the result of the genetic drift, can differ morphologically like it was presented by many species, not only of passerines, by Harrison (1982). Knowing that also migratory behaviour undergoes genetic control (Berthold 1993) and that migrations reflect the history of the species (Busse 1969, Moreau 1972, Harrison 1982), we may expect that different pattern of re-colonisation of Europe presented by birds from different refuges (Moreau 1972, Harrison 1982) is reflected by their different genetic heritage. Following the retreating front of the glacial ice, breeding ranges of these populations advancing northwards met and partially overlapped, resulting in a complicated pattern of migrations while tracing movements of birds breeding in some geographical area. In the case of Robin, different patterns of migration flyways and winter-quarters seem to be retained in different populations. However, the question of distribution of these populations at breeding grounds and the extent of overlap of these areas needs further investigations in order to reconstruct the history of the species and to understand entire pattern of its movements.

The stated phenomenon of shortening of the distance to the wintering grounds in the course of the season can reflect the history of the species and establishment of the secondary winter-quarters by shortening the migration route (Busse 1969). The southernmost parts of the winter-quarters defined hereby seem to correspond to the localisation of the ice-age refuges (Moreau 1972, Harrisson 1982). However, as climate warmed, birds probably stayed for wintering along the migration route, in places where winters were mild enough to survive. In this way, there could evolve winter-quarters in their present range, exceeded northeastwards. This could be seen

to some extent in the results presented hereby, especially for the Western winter-quarter, when migrants stayed successively closer to the place of ringing.

A pattern of expansion of the primary winter-quarters, very similar to that of Robin, was found in the Song Thrush (Busse and Maksalon 1986). The stated pattern of occupation of subsequently more northern parts of winter-quarters would suggest an occurrence in the Robin of a model of the „leap-frog migration" more than of the sequential migration (Busse 2000), however more data would be needed on breeding origin of the wintering populations to confirm this hypothesis.

CONCLUSIONS

1. Through the Polish Baltic coast there migrate the Robin populations flying towards different wintering grounds (different wintering populations).
2. There are clear phenological differences in migration terms among these populations of the Robin: populations migrating to the south-western wintering grounds occur in the studied region through the whole migration season, while these migrating to southern and south-eastern winter-quarters occur on the Polish coast only after *ca* 20 September. This results in the shift of the general direction of migration.
3. According to the phenological differences, the Western, the Apennine and the Mediterranean winter-quarters (defined as areas occupied by different populations) can be clearly distinguished and delimited. The existence of the Balkan winter-quarter was also stated.
4. Dates of passage though a certain area are not the definitive criteria of dividing birds into separate migratory populations, however can be a useful tool in delimiting their migration flyways and winter-quarters.
5. Birds migrating later in the season stay for winter in the more northern regions of the quarter, which can be seen in particular in the Western quarter. This phenomenon probably reflects the pattern of re-colonisation of Europe after the glacial period from the primary refuges and creation of secondary winter-quarters by shortening migration routes.

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