

THE SPATIO-TEMPORAL PATTERN TO ROBIN *ERITHACUS RUBECULA* MIGRATION – EVIDENCE FROM RINGING RECOVERIES

MAGDALENA REMISIEWICZ

Remisiewicz M. 2002. The temporal pattern to Robin *Erithacus rubecula* migration: evidence from ringing recoveries. In: Both C. & T. Piersma (eds) The avian calendar: exploring biological hurdles in the annual cycle. Proc. 3rd Conf. European Orn. Union, Groningen, August 2001. Ardea 90(3) special issue: 489-502.



The pattern of the present migration routes and winter distribution of a species is the consequence of historical factors (re-colonisation from Ice-Age refugia), and of more recent evolutionary mechanisms superimposed upon this base. The present study discusses the balance between these factors as exemplified in the Robin *Erithacus rubecula*. The two hypotheses on the course of the species' autumn migration through the Baltic coastal area which were tested considered: (1) sequential passage of different populations, with early migrants migrating SW and later ones heading gradually more to the SE; (2) alternate passage of populations heading to the SW, SSW and SE during the season. Analysis of 1082 recoveries of Robins ringed in the autumn on the Baltic coast allowed to distinguish four main routes of passage across Europe, as used by allohiemic populations differing in timing of migration, and partly separated by migratory divides. The temporal sequence in which the routes are used by populations crossing the Baltic coastal area is in agreement with the second hypothesis. The revealed spatio-temporal segregation of Robins over the non-breeding range can provide a basis for further studies on the origin of this pattern within the species, and the mechanisms by which it is maintained.

Key words: *Erithacus rubecula* – ringing recoveries – migration routes – winter quarters – migratory divides – spatio-temporal segregation – migratory behaviour – allohiemic populations

M. Remisiewicz, Dept. of Vertebrate Ecology and Zoology, Univ. of Gdańsk, Al. Legionów 9, 80-441 Gdańsk, Poland; Bird Migration Research Station, Univ. of Gdańsk, 84-210 Choczewo, Poland, E-mail: biomr@univ.gda.pl

INTRODUCTION

The present distribution and migration patterns of bird species over the northern hemisphere are the result of two main factors – the history of the species' expansion and the influence of current environmental factors (Alerstam 1990; Burton 1995; Sutherland 1998). The history of colonisation after the last Pleistocene glaciation forms the background to species distributions (Mayr & Meise 1930; Moreau 1955; Busse 1969, 2001; Harrisson 1982; Alerstam 1990; Blondel 1997). However, the

evolution of bird migration systems is a dynamic process, and present migration routes are the result of more recent adaptations to environmental conditions superimposed upon the aforementioned base (Alerstam 1990; Burton 1995; Sutherland 1998). Sutherland (1998) gave examples of songbirds displaying both novel changes in migration pattern and sub-optimal routes probably reflecting historical expansion of species ranges. The heritable and population-specific character of migration directions and timing have also been demonstrated in passerines, including

the Robin (Berthold & Querner 1981, Biebach 1983; Helbig 1991; Berthold & Helbig 1992). Moreover, a high potential rate of evolution of migratory behaviour has been revealed, with a strong selection changing it rapidly in a relatively short period of time (Berthold *et al.* 1990; Berthold *et al.* 1992; Berthold & Pulido 1994; Pulido *et al.* 2001). There is thus a basis for the adjustment of migration timing and routes to environmental conditions (Berthold & Pulido 1994, Pulido *et al.* 2001). However, Sutherland (1998) points out that the potential for adaptation is species-specific and difficult to predict. Thus, with regard to each species, it is possible to address whether the ultimate cause of the present migration routes and wintering grounds are mainly determined by historical factors, or they are a recent adaptation to climatic changes?

Salomonsen (1955) discussed how evolutionary mechanisms acting at the wintering grounds could lead to intraspecific population differentiation in migration route and winter distribution resulting in interpopulational spatial segregation. At one extreme he proposed a model of synhiemic populations that mix over the whole wintering range (e.g. in the Coal Tit *Parus ater*), while at the other extreme there were allohiemic populations occupying separate winter quarters (e.g. in the Blackcap *Sylvia atricapilla*). A variety of transitional stages were also foreseen. As a consequence of allohiemy, selection would enforce the evolution of different adaptations to conditions in the winter quarters, and thence different migration routes and timing. In some species, populations heading to different winter quarters are separated (partly or completely) at breeding grounds so that migratory divides can be drawn between them (Berthold 1993; Bensch *et al.* 1999).

The populations of the Robin breeding in a limited northern part of the species' range – around the Baltic Sea – are known to winter throughout the Mediterranean region from Morocco to Turkey (Saurola 1983; Pettersson *et al.* 1990; Remisiewicz *et al.* 1997). Pettersson *et al.* (1990) discovered morphological variation in the Robins passing the Swedish station Ottenby

on the Baltic island of Öland, and a corresponding west-east cline of morphological characters within the wintering range. They pointed out that birds from the SE winter quarters differ significantly in these traits from those wintering in the SW part of the range. In an earlier study (Remisiewicz 2001) based on recoveries of Robins ringed at Polish Baltic stations, I revealed differences in migration timing among populations from different regions of the SW part of the wintering range. Both cited studies give evidence for some spatio-temporal segregation of Robin populations in the non-breeding season, though the degree and course of this over the whole wintering range is unclear. A corresponding variation could be expected among populations using migration routes that head to different regions of the wintering area.

Studies of Robin movements point to two main directions of autumn migration over Europe – to the SW and the SE (e.g. Rendahl 1966; Pettersson & Lindholm 1983). For Robins ringed at Baltic ringing stations, a gradual change in mean migration direction from SWW to SSW has been revealed as the season progresses (Högestedt & Persson 1971; Pettersson & Lindholm 1983; Remisiewicz 2001). This could be explained by two models for the passage of Robins along the Baltic coast: (1) Sequential passage of Robin populations, with the early migrating individuals heading to the SW and the later ones migrating more towards the SE (Högestedt & Persson 1971; Pettersson & Lindholm 1983; Pettersson *et al.* 1990); (2) Alternate passage of Robin populations with different migration timing and routes, heading to the SWW, SSW and SE (as suggested by the results of Remisiewicz 2001).

The consequence of both models would be variation in Robins within the non-breeding range (both on migration routes and in winter quarters) in terms of the timing of their migration through the Baltic coastal area – early migrants would end up to the SW and late ones to the SE. However, if the first model holds true, the predicted course of the variation would be clinal along a SW-SE axis. Alternatively, if the second hypothesis is true, then the migration dates of populations wintering

in different parts of the range should be arranged alternately along this axis. In this case, the gradual shift in the mean migration direction towards the SSW, found in the cited papers, could be a computational effect resulted from predomination of SWW-migrants at the beginning of the season and distinctly later occurrence of the SE-migrants. The aim of the study has thus been to propose a comprehensive spatio-temporal pattern to autumn migration of the Robin between the Baltic region and the winter quarters.

MATERIAL AND METHODS

In the study, 1082 long-distance ringing recoveries of Robins ringed on autumn migration were used (1 Sep-31 Oct), collected in 1961-99, at ten ringing stations located along different parts of the Baltic coast (Fig. 1), and recovered outside the Baltic region during autumn migration and in winter (1 Sep-28 Feb). Material from the Finnish stations Signildskär and Lägskär located closely together on the Åland Islands was treated jointly. The ringed Robins belonged to the entirely migratory populations of the nominative subspecies, originating from areas to the NW, N and NE of the Baltic region (Rendahl 1966; Pettersson & Lind-



Fig. 1. Locations of Baltic ringing stations which provided material for this study (squares) and the mean geographical location for these stations (triangle). Station names (in alphabetical order): BK – Bukowo, FA – Falsterbo, HL – Hel, MW – Mierzeja Wiślana, OT – Ottenby, PP – Pape, RB – Rybachy, SA – Säppi, SL – Signildskär and Lägskär.

Table 1. Numbers of recoveries of Robins used in the study from each station on the Baltic coast, years of work of stations referred to in the study and 'standard seasons' in which catching effort covered the entire period 1 Sep-31 Oct.

Station	All years	<i>n</i>	Standard seasons	<i>n</i>
Säppi	1962-99	49	1962-99	49
Signildskär + Lägskär	1961-99	127	1961-99	127
Pape	1967-99	34	1967-99	34
Rybachy	1961-99	83	1961-99	83
Mierzeja Wiślana	1961-99	189	1963-99	180
Hel	1961-81, 1983-86	118	–	–
Bukowo	1961-99	168	1972-99	89
Falsterbo	1961-99	140	1961-99	140
Ottenby	1961-99	174	1961-99	174
Total		1082		876

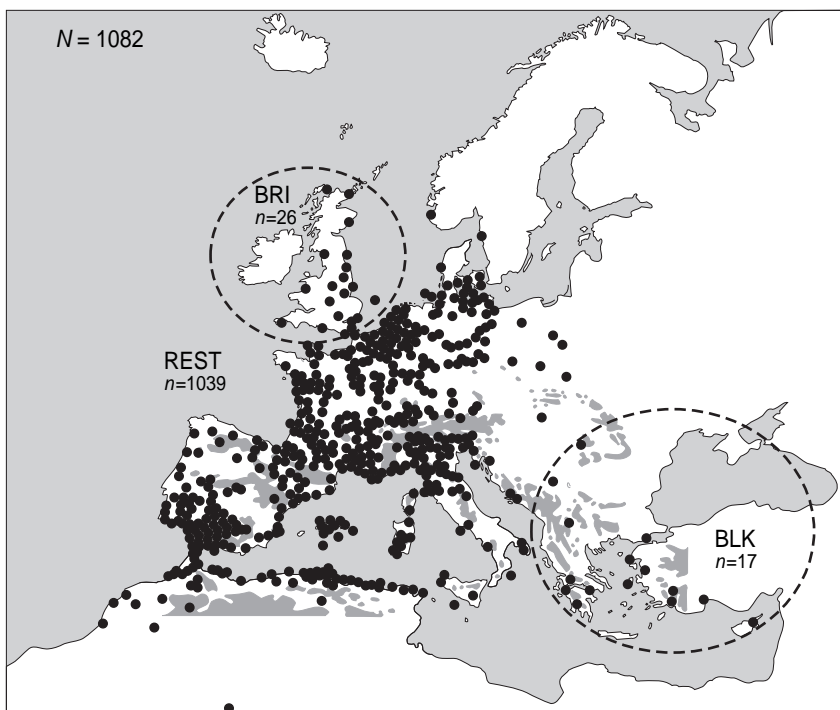


Fig. 2 Recoveries of Robins used in the study (solid dots) and delimitation of the 'Balkan' (BLK) and 'British' (BRI) groups. This and subsequent maps show only the distribution of records, not the number of records from the same locality; grey areas are mountain ranges over 1000 m a.s.l.

holm 1983; Saurola 1983; Remisiewicz *et al.* 1997). The distribution of the recoveries (Fig. 2) indicated that, in the non-breeding period, these populations spread out over the whole wintering range of the species.

Almost the entire autumn migration period of the Robin across the whole Baltic region falls within Sep and Oct (Högstedt & Persson 1971; Busse & Halastra 1981; Saurola 1983). The periods of autumn migration over the rest of Europe, and of wintering, are drawn from the literature (Erard 1966; Rendahl 1966; Adriaensen 1987). Robins were caught at the study stations using mist-nets and various modifications of Heligoland traps; the details of the catching routine at each station being described in other papers (Busse & Kania 1970; Hildén 1974; Roos 1984; Payevsky 1998). The numbers of recoveries of Robins from

each station, and the years they operated within the study period, are presented in Table 1. Analyses of the distribution of recoveries made use of all the available material, while those concerning migration dates included 876 of the recoveries (Table 1), coming from seasons in which the catching effort covered the entire Sep and Oct at a given station (henceforth referred to as the 'standard season'). Comparisons of the distribution of recoveries that were direct (from the autumn of ringing or the nearest winter) or indirect (from subsequent seasons) did not reveal any substantial differences, neither did comparisons between first-year and adult Robins ringed at the Polish stations (Remisiewicz *et al.* 1997). In consequence, the present study took all these cohorts together. About 43% of all recoveries came from birds shot or trapped (for a purpose other than

ringing), and 36% from Robins found accidentally, while recaptures gave 4% and recoveries of unknown fate 17%. The proportions among the material used in analyses of dates were very similar. For each record, the recovery angle (N referred to as 0°) and recovery distance (between place of ringing and recovery) were calculated according to the loxodrome formula (Imboden & Imboden 1972), from geographical coordinates. Samples for each station separately were too limited to allow for a very detailed study, so all were taken together. To enable joint analysis to be made for the whole sample, recovery angles and distances were re-calculated in relation to a mean point for the studied stations (the mean of their coordinates). Similar procedures were used by Pettersson & Lindholm (1983) and Mouritsen (2001) for unified records of different ringing sites. It should therefore be borne in mind that the re-calculated parameters do not exactly reflect the real directions and distances of bird migrations.

The third variable analysed in the study was the Julian date of ringing. I will refer to this variable as the 'migration date' through the Baltic coastal area. Calculations of recovery angles and distances and the presented maps of recoveries were made using RECRING software from P. Busse. In the course of analyses it proved possible to distinguish groups of recoveries. Firstly, the opposite edges of a fan-shaped distribution allowed the Balkan and British groups to be defined by reference to simple geographical criteria (Fig. 2). Mean migration dates were then compared among them, and all the remaining recoveries, using ANOVA (model I) and a *post-hoc* Duncan's test (the data met the assumptions of the tests; Zar 1996). The relatively isolated Balkan group was then excluded from further calculations, as its low sample size did not allow for any internal analyses. In contrast, the recoveries from the remaining part of the range were so abundant that, to allow for the distinguishing of any groups, the records were divided, in terms of recovery distance, into five 600-km sectors (Fig. 3). The choice of such a division represented a compromise between the highest aimed-at accuracy, and sam-

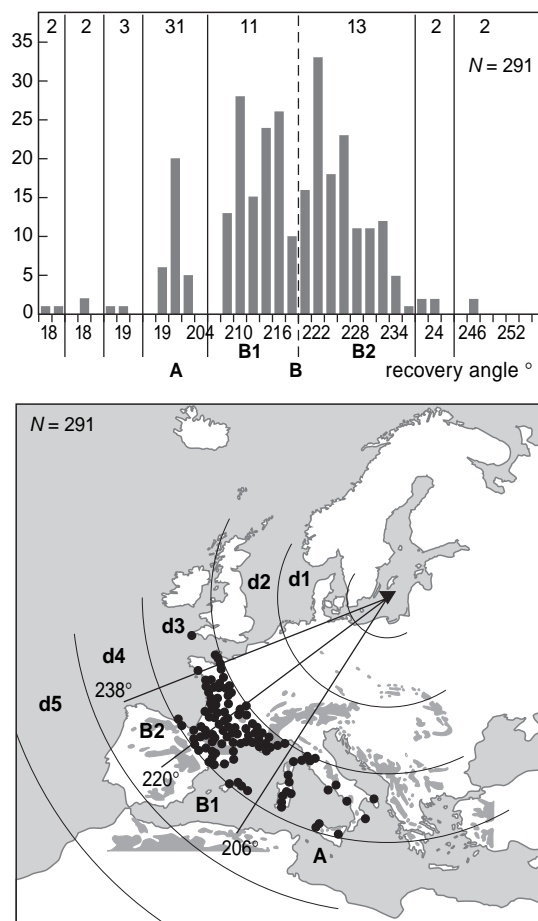


Fig. 3. Division of Robin recoveries from sector d3 of recovery distances 1201-1800 km. Top figure: frequency distribution for recovery angle – see text for how divisions were made; continuous line – first division, dashed line – secondary division, sample sizes at top of figure. Bottom figure – final division of recoveries from sector d3; continuous lines – divisions between groups verified by date criterion, groups B1 and B2 as on upper figure, group A enlarged to include adjacent low sample size groups. Marked in background are 600-km sectors (d1-d5) of recovery distances (dashed lines) and mean geographical location for the ringing stations (triangle). Other explanations as in Fig. 2.

ple sizes that had to be sufficient in each sector to allow analyses to be performed. Five scattered records from beyond the last sector were excluded.

Table 2. Numbers of Robins ringed at different stations on the Baltic coast in groups distinguished for recoveries within sector d3 of recovery distance (see Fig. 3). For comparison of all three groups (excluding the Robins ringed in Falsterbo, see the text): $G = 15.4$, $df = 12$, $0.1 < P < 0.25$; for comparison of full set of stations between groups B1 and B2: $G = 6.5$, $df = 7$, $0.25 < P < 0.5$.

Station/Group	A	B1	B2
Sappi	4	4	2
Signildskär + Lägskär	5	9	8
Pape	3	2	2
Rybachy	5	10	10
Mierzeja Wiślana	6	19	18
Bukowo	2	7	13
Falsterbo	0	13	24
Ottenby	3	25	19

ed, giving 1060 recoveries to be used in this part of the analysis. In exemplifying the further procedure, reference will be made to recoveries from sector d3 (recovery distance 1201-1800 km, see Fig. 3). The drawing of recovery angles for each sector revealed that distributions were not uni-modal, but rather revealed peaks corresponding to aggregations of recoveries, along with minima representing regions with no or fewer recoveries (sector d3 – Fig. 3). Thus, distribution aggregations were separated by minima, which were defined in that they held less than 10% of the number of records in the preceding peak (Fig. 3). Among the resultant groups, only those with more than 10 records were subject to further statistical procedures (on Fig. 3 – groups A and B); smaller groups at the edges of distributions were omitted at this stage.

Other papers (Jenni 1987; Pettersson & Lindholm 1983; Remisiewicz 2001) have demonstrated that a correlation can be expected between migration timing and variables describing the location of recoveries – like geographical coordinates, recovery angle or distance. I checked for any correlation between the date of ringing within each distinguished group (data from ‘standard seasons’ applied) and the recovery angle. In sector d3 (see

Fig. 3), there was no significant relation of this type within group A ($r_s = 0.23$, $P = 0.24$, $n_A = 28$), but a statistically significant correlation for group B ($r_s = -0.18$, $P = 0.02$, $n_B = 185$). This meant that the concentration of records in group B was not homogenous with respect to migration date. At the same time, the distribution of migration angle within this group was bi-modal, suggesting that further division in line with migration angle would generate groups more uniform with respect to migration date. The group in question was thus split subsequently by reference to the most distinct minimum. The homogeneity of migration dates in the resultant groups was then re-tested, again by checking for the occurrence of a correlation of the described type. In the described example (Fig. 3), group B was sub-divided into groups B1 and B2, and, since no significant correlation was noted within each of the two groups (for B1: $r_s = 0.09$, $P = 0.39$, $n_{B1} = 89$, for B2: $r_s = -0.06$, $P = 0.53$, $n_{B2} = 96$), this division was considered final. In fact it was almost the rule for the first subdivision to result in groups showing no significant internal correlation (in all cases $P > 0.2$); relatively large samples were held in most sub-groups (see Table 3). In only one case (that of sector d4) did this procedure of sub-dividing have to be repeated twice. It was only in this way that intra-sectoral concentrations of recoveries homogeneous with respect to migration date were obtained.

The correctness of the obtained spatial division was verified by a temporal criterion by comparing mean migration dates using ANOVA and the *post-hoc* Duncan's test. If the difference in migration dates between neighbouring groups was significant, the division was kept as a probable migratory divide, if it was non-significant – the division was not justified and the groups joined. In sector d3, groups A and B1, and groups B1 and B2 differed significantly in this respect (ANOVA: $F_{2, 210} = 4.83$, $P = 0.01$; for both comparisons $P < 0.05$; $n_A = 28$, $n_{B1} = 89$, $n_{B2} = 96$) so this division was maintained. In two cases – in sector d4, when $0.05 < P < 0.1$ but sample sizes were low ($n < 30$), the borders between groups

Table 3. Sample sizes and mean migration dates of Robin in the distinguished groups of recoveries, and level of statistical significance to differences between the neighbouring groups (for d2 – t-test, for d3 and d4 – *post-hoc* Duncan's test). Location of the groups in Fig. 5 is defined within each sector in the order from west to south by mean date (calculated from data from standard seasons). In sectors d1 and d2, the mean (in brackets) is calculated for low sample size groups ($n < 10$) combined.

Sector or group	Mean date	SD (d)	Robins ringed in stand. seasons	Robins ringed in all seasons	Level of significance
d1	5 Oct	10.1	79	91	
(d1+d2)	(1 Oct)	10.3	10	10	
d2	27 Sep	12.8	119	135	$P = 0.03$
	2 Oct	12.3	131	154	
d3	26 Sep	12.1	96	130	$P = 0.03$ $P = 0.02$
	1 Oct	8.9	89	116	
	27 Sep	11.8	34	39	
d4	25 Sep	10.6	27	38	$P = 0.07$ $P = 0.02$ $P = 0.09$ $P = 0.05$
	20 Sep	10.1	27	34	
	24 Sep	9.5	36	55	
	1 Oct	11.5	24	28	
	26 Sep	10.2	103	121	
d5	21 Sep	10.3	69	97	
Balkan	8 Oct	8.0	15	17	
Total			859	1065	

were also retained as suspected divides. In order to make this pattern complete, if the edge low sample size groups held jointly more than 5 recoveries, distributions of their migration dates were compared by Mann-Whitney U-test with the adjacent larger group. If the means were similar and no significant difference occurred, the small group was incorporated into the larger one. Sector d3 was augmented in this way by a few recoveries from the range 180° - 192° (see Fig. 3) included into the neighbouring group A. The final division of recoveries from sector d3 is mapped on Fig. 3.

At this point it was necessary to determine whether differences in migration dates among groups did not result from the individuals assigned to them having been ringed at different stations. Proportions of birds ringed at each station

were thus compared among the groups across each sector, by G-test (for sector d3 see Table 2). Stations with no recoveries from at least one group (in the described example – Falsterbo, see Table 2), had to be excluded from this calculation, in line with the assumptions of the test (Zar 1996). As no significant difference among groups was revealed within any of the sectors, the effect of the location of ringing stations could be excluded. Indeed, the idea of this influence of station location on the results being minor is supported by short-term monitoring showing Robins capable of crossing between the north-eastern and south-western coasts of the Baltic in 1-2 days (M. Remisiewicz – unpubl. data). The assignment of records within each of the five sectors was followed by a comparison of mean migration dates

among groups from subsequent sectors (by t-test or ANOVA and *post-hoc* Duncan's test). All the statistical procedures followed Zar (1996).

RESULTS

In order to verify the initial assumptions of both formulated hypotheses on the course of Robin migration, I checked if birds recovered in extreme parts of the non-breeding range differed in the timing of passage through the Baltic coastal area. At the western edge of the fan-shaped distribution, I distinguished a group of records from the British Isles (Fig. 2), and at the south-eastern edge, following the results of Pettersson *et al.* (1990), I delimited the 'Balkan' group. I then compared these groups and all remaining records with respect to mean migration date. The results showed that these groups differed in the timing of their crossing of the Baltic coast (ANOVA: $F_{2, 873} = 5.58$, $P = 0.004$, $n_{BRI} = 23$, $n_{REST} = 838$, $n_{BLK} = 15$). Robins heading to the Balkans migrated significantly later than those heading to other parts of the wintering range (*post-hoc* Duncan's test: for difference from the 'British' group – $P < 0.005$, from the 'rest' of the records – $P < 0.001$). However, the British group did not differ significantly from the intermediate ('rest') group of recoveries.

I excluded the outstanding Balkan group from further analyses, but the British group was treated jointly with the remaining ones, according to the results of the previous test. The described procedure then generated the spatio-temporal division of these recoveries, which was mapped alongside the Balkan group distinguished previously (Fig. 4). Sample sizes and mean migration dates of the distinguished groups are presented in Table 3. In sectors d2, d3 and d4, the groups distinguished by the described procedures differed significantly in mean migration dates (for d2 – t-test: $t_{248} = 3.02$, $P = 0.03$; for d3 – ANOVA: $F_{2, 213} = 4.92$, $P = 0.03$; for d4 – ANOVA: $F_{4, 212} = 3.75$, $P = 0.006$). The level of significance to differences between the neighbouring groups is given in Table 3 (t-test and *post-hoc* Duncan's test, respec-

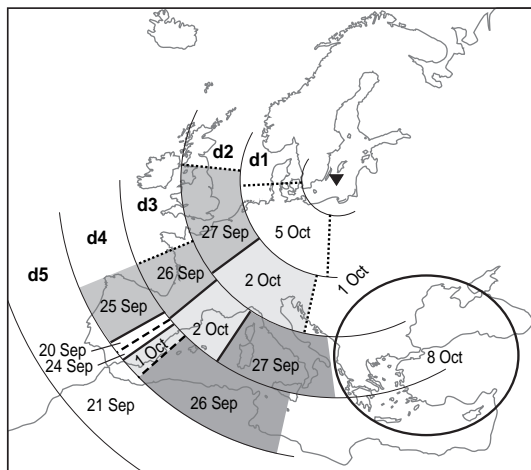


Fig. 4. Groups of recoveries distinguished in subsequent sectors and their mean dates (sample sizes in Table 3). Arches and symbols d1–d5 – sectors of recovery distance (see Fig. 2), thick line – divide between groups with mean migration date differing at $P < 0.05$, dashed line – divide between groups with mean differing at $0.05 < P < 0.1$, dotted lines – borders of low-size groups not confirmed by statistical test, ellipse – delimitation of 'Balkan' group (see Fig. 2). Groups joined in series marked with the same fill pattern.

tively). The key to the further interpretation of the obtained pattern are the presented mean migration dates of the groups.

While in the first distance sector (d1), no major internal differentiation was revealed, and while in the fifth sector (d5) all recoveries formed just one concentration, in the remaining three sectors clear divisions can be seen (Fig. 4). I discuss the division pattern from SW to SE. The western coasts of Europe have three groups in consecutive sectors (d2–d4) which hold recoveries of very similar mean migration dates (25–27 Sep; ANOVA: $F_{2, 239} = 0.31$, $P = 0.73$, sample sizes in Table 3, Fig. 4). These will be referred to below as the 'Western' series of groups. Their mean dates of migration are relatively early in comparison with neighbouring groups. In the region of the Alps and the French Mediterranean, sectors d2 and d3 have two groups of identical mean dates (2 Oct) that are later than in the adjacent 'Western'

groups. They will be referred to as the 'Mediterranean' series. At the Iberian Peninsula (d4) the pattern is more complicated. On the Mediterranean coast, a group of migrants 'late' in relation to the neighbouring groups (mean date 1 Oct) is again located along the axis of the 'Mediterranean' series of 'late' groups from preceding sectors. These three 'Mediterranean' groups (Fig. 4) did not differ significantly in their migration dates (ANOVA: $F_{2,241} = 0.16$, $P = 0.85$, sample sizes in Table 3). There was a highly significant difference in migration dates between the series of the three 'Western' groups taken together and the three 'Mediterranean' groups (t-test: $t_{484} = -4.63$, $P < 0.001$, $n_{West.} = 242$, $n_{Med.} = 244$). The division line between these groups runs for 1800 km with a surprising accuracy – in sectors d2-d4 (at 226° , 220° , and 218° - 222° , resp.). In d4, there is a group of very early migrants (mean date 20 Sep) between the 'Western' and 'Mediterranean' series. The mean migration date in this group corresponds with birds found in Morocco (21 Sep, sector d5) (t-test: $t_{94} = -0.74$, $P = 0.5$, sample sizes in Table 3), and so both groups will henceforth be called the 'Moroccan' series. This in turn draws attention to the fact that the Iberian Peninsula has a small group of intermediate mean date (24 Sep), which is located between these 'very early' migrants and the 'late' group included into the 'Mediterranean' series (see Fig 4).

To the south-east of the groups described so far – on the Apennine Peninsula and part of the opposite African coast, sectors d3 and d4 again include two groups of very similar mean dates (26-27 Sep) (t-test: $t_{135} = 0.39$, $P = 0.69$, sample sizes in Table 3). Both are earlier than in the neighbouring 'Mediterranean' and previously distinguished 'Balkan' groups. The October 1st mean date for the low sample size groups in sectors d1 and d2 taken together (see Fig. 4), and located along the axes leading to the 'Apennine' and the 'Balkan' series was intermediate in comparison with their mean dates (for comparison with each series, Mann-Whitney U-test: $P > 0.1$, $n_{d1+d2} = 10$, $n_{Ape.} = 137$, $n_{Blk.} = 15$).

Direct comparison of the three series of

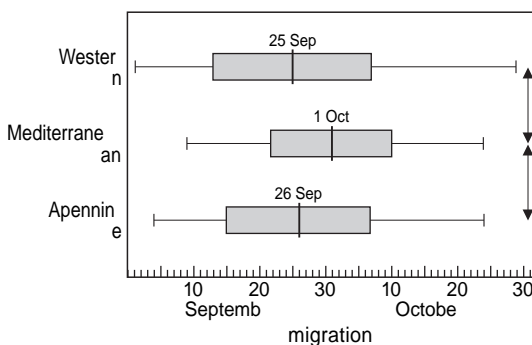


Fig. 5. Comparison of mean migration dates among three series distinguished in the SW part of the non-breeding range, for sectors d3 and d4 jointly. Vertical line and date above – mean migration date, box – \pm SD, horizontal line – range of migration dates (min-max); arrows – differences significant at level $P < 0.001$ (post-hoc Duncan's test).

groups distinguished in the SW part of the non-breeding range, i.e. the 'Western', 'Mediterranean' and 'Apennine' groups, was possible at the course of the joined sectors d3 and d4 (see Fig. 4). This confirmed that these series differed in the distribution of migration dates (ANOVA: $F_{2,397} = 11.28$, $P < 0.001$, results of post-hoc Duncan's test in Fig. 5). The same comparison confined to the birds from each series shot and trapped showed the same sequence of means and a significant difference (ANOVA: $F_{3,181} = 5.93$, $P = 0.003$, $n_{Wes.} = 40$, $n_{Med.} = 40$, $n_{Ape.} = 83$). For birds found accidentally, the sequence of means was the same, though the difference was not significant, probably on account of the smaller sample size (ANOVA: $F_{2,118} = 1.14$, $P = 0.3$, $n_{Wes.} = 47$, $n_{Med.} = 43$, $n_{Ape.} = 27$).

DISCUSSION

The proposed spatio-temporal pattern to Robin migrations

In this paper I showed that there was not a clear trend of later migrating individuals to head more towards SE Europe, and this contradicts the first of the presented hypotheses. Although mean

migration date of birds recovered in the western-most part of the range was the earliest, and of those stated in the south-eastern part was the latest, in between these groups the more easterly birds were earlier migrants (Fig. 5).

In the three cases of the 'Western', 'Mediterranean' and 'Apennine' series, the migration dates of groups located along the same axes in subsequent sectors were consistent (see Fig. 4). This suggests that each of the three distinguished series of groups include birds of similar migration timing. They probably reflect migration routes of different allohiemic populations, as they are located along lines leading to different winter quarters. The populational character of the presented divisions seems to be confirmed by the distribution of recoveries of Robins ringed in other regions of Europe. Robins ringed in Norway (Rendahl 1966) have been reported exclusively from the described 'Western route', while ca 95 and 90% respectively of those ringed in Belgium (Adriaensen 1987), and in Britain (Mead 1989) also take this route. Data from the two latter papers combined with the results of Adriaensen (1988) - describing the exchange of Robins between the British Isles and the continent during the migratory season - support the conclusion of the present paper that the British Isles are a part of the 'Western' route. Robin recoveries presented in these studies also come from the Moroccan coast, suggesting that the 'Moroccan' series of groups should be regarded as a continuation of the 'Western' route. The division between the 'Mediterranean' and 'Apennine' routes are in turn confirmed by results of Remisiewicz (2001), though the details of their delimitation differ slightly. The course of the latter route is supported by results from Scebba & Olivieri del Castillo (1983), describing the distribution of Robins ringed on the Apennine Peninsula. Finally, the existence of the 'Balkan' route and winter-quarters has been postulated in other papers (e.g. Högstedt & Persson 1971; Pettersson & Lindholm 1983; Pettersson *et al.* 1990).

Berthold (1993) stated that migratory divides usually run along geographical barriers such as seas or mountains. The division lines found to

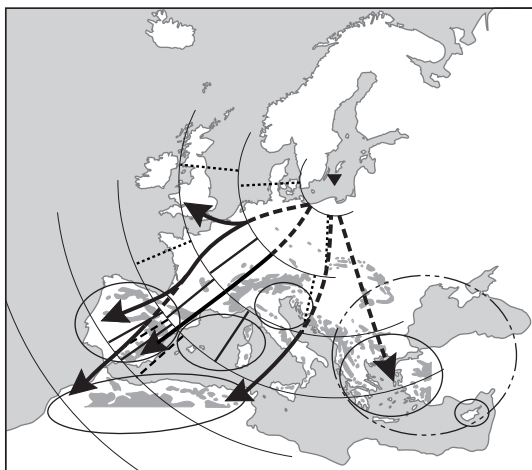


Fig. 6. Proposed course of migration routes against background of distinguished groups of recoveries (see Fig. 5) and glacial refugia. Thick continuous lines – course of migration routes documented by statistical tests (see text), thick dashed lines – hypothetical course, continuous line ellipses – ranges of glacial refugia (according to Harrison 1982, modified).

occur between the 'Mediterranean' and 'Apennine' routes are of that kind (Fig. 4). The well-pronounced border between the 'Western' and 'Mediterranean' routes mainly crosses lowland regions with no potential barriers. Nevertheless, its exact consistency with the south-eastern edge to the distribution of recoveries of Norwegian, and the majority of British and Belgian Robins' (op.cit.) would seem to confirm that it is a migratory divide. However, the distribution of recoveries indicates that the migratory divides are more zones of overlap of adjacent routes than sharp borderlines, with birds following the different routes mixing in at least some parts of the non-breeding range.

Based on these results, I suggest the course of migration routes as presented in Fig. 6. This pattern is surprisingly similar to that proposed for the Song Thrush *Turdus philomelos* by Busse & Maksimalon (1986). Robins using these routes differed in the timing of their passage through the Baltic coastal area. Going from the western to the south-eastern edge of the non-breeding distribution, a sequence of routes followed by early, late, early

and again late migrants can be determined (see Figs 4, 5). The results show that this sequence is not an effect of the different circumstances of recovery in different regions. Within each of the routes (except the hypothetical 'Balkan' one) birds migrating the furthest had the earliest migration dates. A similar phenomenon has been found in other migrants, e.g. in the Chaffinch *Fringilla coelebs* (Kania 1981) and the Great Tit *Parus major* (Nowakowski 2000). The described migration pattern of Robins seems to be very general, and probably represents main migration routes *sensu* Berthold (1993). It would undoubtedly be possible to discover internal differences within these routes, for example in the region of the Alps as suggested by results from Jenni (1987) and Remisiewicz *et al.* (1997). However, the method applied did not allow recoveries from this area to be investigated further.

From all the presented facts I conclude that the European continent is traversed each autumn by at least four allohiemic Robin populations differing in winter quarters and migration routes, partly split by migratory divides, and disparate in migration timing. The transient character of the migration divides suggests partial allohiemy (Salomonson 1955). The fact that an alternate pattern of 'early' and 'late' migration dates can be seen across the whole non-breeding range for Robins using subsequent migration routes is in contradiction with the predictions of the first hypothesis assuming the sequential migration of Robins to neighbouring wintering areas located along the SW-SE axis. It is however consistent with the second hypothesis describing the course of migrations by Robins through the Baltic coastal area.

The available material from the Baltic stations was too limited for the presented non-breeding distribution of allohiemic populations to be linked with their breeding origin. Pettersson & Lindholm (1983) suggested that Robins passing through the Ottenby station in late autumn are of north-eastern origin, while the results of Remisiewicz *et al.* (1997) indicate differences in the source areas of Robins passing through the Baltic coastal area in subsequent parts of the autumn season. Jenni

(1987) in turn showed partial difference in areas of origin between Robins caught on the two sides of the Alps. However, no consistent pattern in the migration sequence of individuals from different parts of the breeding range can be derived from the literature data. Indeed, the relation between breeding origin and migratory behaviour may prove very difficult to trace, as Robins breeding in the Baltic region – in Sweden (Rendahl 1966; Pettersson *et al.* 1990), Finland (Saurola 1983) and Poland (Remisiewicz *et al.* 1997), seem to use all the described routes.

The origin of the present migration pattern

Comparing the presented pattern of Robin migration routes with the location of Ice-Age refugia, it is possible to trace the historical background of these current routes (see Fig. 6). In studies on the Willow Warbler *Phylloscopus trochilus*, Bensch *et al.* (1999) point to the importance of Ice-Age allopatry in shaping presently-observed differences in the morphology and migratory behaviour of adjacent breeding populations. The migratory divide was in this case interpreted as the zone of secondary contact of two populations due to range expansion from the refugia in the SW and SE. It is conspicuous that this divide is only 350-km wide, similarly as divides found in some other passerines species (Busse 1987). A corresponding course to northward range extension has been noted in the last few decades for the Song Thrush (Spencer 1975) and the Yellowhammer *Emberiza citrinella* (Sutherland 1998). In other songbirds – like e.g. the Starling *Sturnus vulgaris* or the Blackcap – recent changes in wintering areas and, in consequence – in migration routes, have also been described (Sutherland 1998).

In the Robin it is remarkable that the spatial segregation of birds with different migration timing occurs within a subspecies. Its breeding range is only partly divided by the Baltic Sea, and separation in the non-breeding period is also incomplete, as the results show. Variation in a few morphological traits – wing length, amount of grey plumage on flanks and leg coloration – was descri-

bed from wintering grounds and on migration routes by Lövei *et al.* (1986) and Pettersson *et al.* (1990); the latter authors assuming that analogous differences occurred across the breeding range. Studies of Wennerberg *et al.* (1999) and Wennerberg (2001) on the Dunlin *Calidris alpina* also revealed genetic variation among populations from adjacent winter quarters corresponding to differences in their morphology, migration routes and timing, and in the areas of breeding origin. In the studies on the Willow Warbler (Bensch *et al.* 1999; Chamberlain *et al.* 2000), morphological differences in two adjacent breeding populations were also associated with different migratory behaviour.

Assuming a genetic basis to timing and direction of migration in the Robin, two scenarios of the history of spatio-temporal segregation across the non-breeding range of the species can be hypothesised: 1) that the variation is the result of expansion from the historical range - towards central and northern Europe - of populations separated during the last glaciation (with the segregation between them probably being maintained at present by some isolation mechanisms at the breeding grounds, e.g. assortative mating or selection against hybrids). 2) that the described segregation has evolved recently in response to diverse selection pressures in different parts of the breeding range.

The facts that the courses of migration routes in the Robin correspond with the distribution of Ice-Age refugia, and that birds breeding in the Baltic area use all the described migration routes, would seem to offer support for the first hypothesis. The issue could be further addressed by way of studies concerning morphological variation at the breeding and wintering grounds, supported by novel methods involving genetic markers and stable isotopes.

ACKNOWLEDGEMENTS

I am very grateful to the staff of the ringing stations and ringing centres that collected and kindly provided the

material for this study, in particular to (in alphabetical order): Janis Baumanis, Casimir Bolshakov & Nadejda Zelenova, Przemysław Busse, Anders Hedenström & Jonas Waldenström, Lennart Karlsson, and Pertti Saurola. I am indebted to Przemysław Busse for constant support with expertise and for valuable comments to this paper. I owe thanks to Jarosław Nowakowski for creative discussions at successive stages of the work and also to Włodek Meissner for his advice, not only on the statistical procedures. Finally, I am grateful to Christiaan Both and Theunis Piersma for inviting me to publish this paper, and to two anonymous referees for comments that helped to improve the manuscript. The research gained the financial support of the Polish Committee for Scientific Research (KBN project no 1062/P04/2000/19).

REFERENCES

- Adriaensen F. 1987. The timing of Robin migration in Belgium as shown by ringing recoveries. *Ring. & Migr.* 8: 43-55.
- Adriaensen F. 1988. An analysis of recoveries of Robins (*Erithacus rubecula*) ringed or recovered in Belgium: age and mortality, speed, distance and direction of migration. *Le Gerfaut* 78: 25-43.
- Alerstam T. 1990. Bird migration. Cambridge Univ. Press, Cambridge.
- Bensch S., T. Andersson & S. Åkesson 1999. Morphological and molecular variation across a migratory divide in Willow Warblers, *Phylloscopus trochilus*. *Evolution* 53: 1925-1935.
- Berthold P. 1993. Bird migration: a general survey. Oxford Univ. Press, Oxford.
- Berthold P. & A. Helbig 1992. The genetics of bird migration: stimulus, timing and direction. *Ibis* 134, Suppl. 1: 35-40.
- Berthold P., A.J. Helbig, G. Mohr & U. Querner 1992. Rapid microevolution of migratory behaviour on a wild bird species. *Nature* 360: 668-669.
- Berthold P., G. Mohr & U. Querner 1990. Steuerung und potentielle Evolutionsgeschwindigkeit des obligaten Teilziehverhaltens: Ergebnisse eines Zweiweg-Selektionsexperiments mit der Mönchsgrasmücke (*Sylvia atricapilla*). *J. Orn.* 131: 33-45.
- Berthold P. & F. Pulido 1994. Heritability of migratory activity in a natural bird population. *Proc. R. Soc. Lond. B* 257: 311-315.
- Berthold P. & U. Querner 1981. Genetic basis of migratory behaviour in European warblers. *Science* 212: 77-79.
- Biebach H. 1983. Genetic determination of partial

- migration in the European Robin (*Erithacus rubecula*). Auk 100: 601-606.
- Blondel J. 1997. Evolution and History of the European Bird Fauna. In: E.J.M. Hagemeijer & M.J. Blair (eds) The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T. & A.D. Poyser, London.
- Burton J. F. 1995. Birds and climate change. Christopher Helm, London.
- Busse P. 1969. Results of ringing of European *Corvidae*. Acta Orn. 11: 236-328.
- Busse P. 1987. Migration patterns of European passerines. Sitta 1: 18-36.
- Busse P. 2001. European Passerine migration system – what is known and what is lacking. Proc. 2nd EOU Conference, Gdańsk 1999. Ring 23: 3-36.
- Busse P. & W. Kania 1970. Akcja Bałtycka 1961-67. Metody pracy. Acta Orn. 12: 232-267.
- Busse P. & G. Halastra 1981. Jesienny przelot ptaków na polskim wybrzeżu Bałtyku. Acta Orn. 18: 167-290.
- Busse P. & L. Maksalon 1986. Wędrowniki europejskich populacji drozda śpiewaka (*Turdus philomelos*). Not. Orn. 37, 1-2: 3-30.
- Chamberlain C. P., S. Bensch, X. Feng, S. Akesson & T. Andersson 2000. Stable isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. Proc. R. Soc. Lond. B 267: 43-48.
- Erard C. 1966. Sur le mouvements migratoires du Rougegorge *Erithacus rubecula* (L.) à l'aide des données du fichier de baguage français. L'Oiseau et R. F. O. 36: 4-51.
- Harrison C. 1982. An Atlas of the Birds of the Western Palearctic: 24-41. Collins, London.
- Helbig A.J. 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating Blackcaps (*Sylvia atricapilla*). Behav. Ecol. Sociobiol. 28: 9-12.
- Hildén O. 1974. Finnish bird stations, their activities and aims. Ornis Fenn. 51: 10-35.
- Högestedt G. & C. Persson 1971. Phänologie und Überwinterung der über Falsterbo ziehenden Rotkehlchen (*Erithacus rubecula*). Vogelwarte 26: 86-98.
- Imboden C. & D. Imboden 1972. Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. Vogelwarte 26: 336-344.
- Jenni L. 1987. Analysis of recoveries of same species subgroups with similar potential recovery rates. Acta Orn. 23: 129-132.
- Kania W. 1981. The autumn migration of the Chaffinch *Fringilla coelebs* over the Baltic coast in Poland. Acta Orn. 18: 371-414.
- Lövei G. L., S. Scebbba, F. Minchiello & M. Milone 1986. Seasonal activity, wing shape, weights and fat reserve variation of Robins (*Erithacus rubecula*) in southern Italy. Rich. Biol. Selvag. 10: 22-241.
- Mayr E. & W. Meise 1930. Theoretisches zur Geschichte des Vogelzuges. Vogelzug 1: 149-172.
- Mead Ch. 1989. Robins. Whittet Books.
- Moreau R.E. 1955. The Bird-Geography of Europe in the Last Glaciation. Acta IX Congr. Int. Orn. Basel 1954: 401-405.
- Mouritsen H. 2001. Ringing recoveries contain hidden information about orientation mechanisms. Ardea 89 (special issue): 31-42.
- Nowakowski J.K. 2000. System jesiennej wędrówki bogatki (*Parus major*) w środkowej i północnej Europie. Doctoral thesis, Univ. of Podlasie, Siedlce, Poland.
- Payevsky V. A. 1998. Age structure of passerine migrants at the eastern Baltic coast: the analysis of the 'coastal effect'. Ornis Svecica 8: 171-178.
- Pettersson J. & C-G. Lindholm 1983. The sequential passage of different Robin *Erithacus rubecula* populations at Ottenby. Ornis Fennica, Suppl. 3: 34-36.
- Pettersson J., Ch., Hjort, A. Lindström & A. Hedenström 1990. Wintering Robins, *Erithacus rubecula*, in the Mediterranean region and migrating Robins at Ottenby – a morphological comparison and an analysis of the migration pattern. Vår Fågelvärld 49: 267-278.
- Pulido F., P. Berthold, G. Mohr & U. Querner 2001. Heritability of the timing of autumn migratory activity in a natural bird population. Proc. R. Soc. Lond. B 268: 953-959.
- Remisiewicz M. 2001. The pattern of winter-quarters of Robins (*Erithacus rubecula*) migrating in autumn through the Baltic coast. Ring 23: 37-53.
- Remisiewicz M., J.K. Nowakowski & P. Busse 1997. Migration pattern of Robin (*Erithacus rubecula*) on the basis of Polish recoveries. Ring 19: 3-40.
- Rendahl H. 1966. Die Zugverhältnisse schwedischer Rotkehlchen (*Erithacus rubecula* L.). Mit Berücksichtigung der norwegischen und finnischen Beringungsergebnisse. Ark. Zool. 18: 462-488.
- Roos G. 1984. Migration, wintering and longevity of birds ringed at Falsterbo (1947-1980). Anser, Suppl. 13, Lund.
- Salomonsen F. 1955. The evolutionary significance of bird migration. Dan. Biol. Medd. 22, no 6.
- Saurola P. 1983. Autumn migration and wintering of Robins (*Erithacus rubecula*) ringed in Finland. Lintumies 18: 108-115.
- Scebbba S. & M. Olivieri del Castillo. 1983. Migrazione e svernamento del Pettiroso *Erithacus rubecula* in Italia: analisi delle riprese. Atti III Conv. Ital. Orn.: 105-106.

- Spencer R. 1975. Changes in Distribution of Recoveries of Ringed Blackbirds. *Bird Study* 22: 177-190.
- Sutherland W. J. 1998. Evidence for flexibility and constraint in migration systems. *J. Avian Biol.* 29: 441-446.
- Wennerberg L., N. M. A. Holmgren, P.-E. Jönsson & T. von Schantz 1999. Genetic and morphological variation in Dunlin *Calidris alpina* breeding in the Palearctic tundra. *Ibis* 141: 391-398.
- Wennerberg L. 2001. Breeding origin and migration pattern of Dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. *Mol. Ecol.* 10: 1111-1120.
- Zar J.H. 1996. *Biostatistical analysis*. Prentice-Hall International, Inc.

SAMENVATTING

Veel trekvogelsoorten broeden over een enorm geografisch gebied, waarbinnen verschillen tussen populaties kunnen bestaan in trekroutes en daardoor in gebieden waar deze vogels de winter doorbrengen. Een mogelijke oorzaak van deze variatie is de wijze waarop zo'n soort na de ijstijden Europa vanuit de zuidelijk gelegen

refugia weer heeft gekoloniseerd. Op basis van 1082 terugmeldingen van in het Baltische gebied geringde Roodborsten *Erithacus rubecula* is onderzocht of groepen vogels die in de loop van de tijd hier doortrekken in verschillende gebieden in Europa overwinteren. De Roodborsten werden teruggemeld uit een groot gebied dat zich uitstrekte van Marokko in het westen tot Turkije in het oosten. De tijd waarop de Roodborsten in het Baltische gebied waren geringd, verschilde duidelijk voor de vogels uit de verschillende delen van het overwinteringsgebied. Roodborsten die op de Balkan overwinterden, passeerden veel later het Baltische gebied dan vogels die in het westen van Europa overwinterden. Binnen westelijk Europa passeerden de meer zuidelijk overwinterraars eerder dan noordelijke overwinterraars. Verder werden Roodborsten aan de 'flanken' van de hoofdtrekbaan eerder teruggemeld dan de vogels in het centrum van de trekbaan. Hieruit ontstaat het beeld dat er door het Baltische gebied verschillende trekbanen van Roodborsten lopen en dat deze variatie door historische oorzaken, zoals het herkoloniseren van het noorden van Europa na de ijstijden veroorzaakt zou kunnen zijn.

(CB)