INTRA-SEASONAL CHANGES IN DIRECTIONAL PREFERENCES OF ROBINS (*Erithacus rubecula*) CAUGHT ON AUTUMN MIGRATION AT BUKOWO-KOPAŃ RINGING STATION (N POLAND) IN 1996

Marta Ściborska and Przemysław Busse

ABSTRACT

Ściborska M., Busse P. 2004. *Intra-seasonal changes in directional preferences of Robins (Erithacus rubecula) caught on autumn migration at Bukowo-Kopań ringing station (N Poland) in 1996.* Ring 26, 1: 41-58.

Data were collected in 1996 at Bukowo-Kopań ringing station situated on the southern Baltic coast. During the whole autumn migration period 2380 Robins were caught, and 445 of them were tested with Busse's method for directional behaviour.

Birds' headings were grouped in four main axes: ENE-WSW, NNE-SSW, NNW-SSE and WNW-ESE. The seasonal dynamics of birds caught was divided into periods reflecting waves of migration. For each period the percentage shares of these four main axes were extrapolated into the daily numbers of birds caught. The obtained pattern consisted of four migration dynamics characterising differently heading birds.

The total migration dynamics of the Robin at the station is interpreted as follows. In 1996, the intensive migration started around the middle of September with a numerous wave consisting of at least three populations. The peaks of those population waves were shifted in relation to each other in just 1-2 days, and occurred in following order: birds heading to the Apennine winter-quarter, birds heading to the most eastern wintering grounds, and birds heading to the southern parts of Western winter-quarter. The second, numerous wave consisting at least of birds heading to Mediterranean winter-quarter occurred with a peak on 26 September. In two most numerous October waves around 10 and 18 October, birds heading to the northern parts of Western migration route dominated. However, also birds heading to the Balkan (earlier) or even more eastern (later) wintering grounds formed numerous waves around those dates.

The model of Robin migration is proposed, in which the wavy character of migration is generally explained by large-scale factors (like macrosynoptic weather situations, or changes in length of day). Their influence results in the most pronounced waves consisting of populations of different origin. However, the final pattern of dynamics is affected strongly by many other factors: *e.g.* localisation and characteristics of those populations.

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Key words: *Erithacus rubecula*, autumn migration, cage experiments, directional preferences, migration dynamics, waves of migration

INTRODUCTION

During autumn migration birds behave directionally flying from breeding areas toward winter-quarters. In studying direction of these movements several methods have been involved – visual observations, bird ringing and analyses of recoveries, *etc.* Since studies by Kramer (1949) and Sauer (1957), also orientation cages have been used to follow directional preferences of migrants, however, such experiments were performed usually to study mechanisms of orientation and navigation (*e.g.* Weindler *et al.* 1998, Wiltschko *et al.* 1998, Wiltschko *et al.* 2001). A few years ago, a new field technique of directional preferences studies was proposed (Busse 1995), which allows to collect easily quite numerous data. The method was checked on data collected for the Robin in central Poland (Nowakowski and Malecka 1999). Birds tested with it have shown local migratory directions consistent with their migration routes. One of the first stations working within SE European Bird Migration Network (SEEN) and engaged in programme of directional preferences studies was Bukowo-Kopań ringing station, in which one of the most numerous species is Robin. In the paper by Busse *et al.* (2001) the general pattern for this species was presented.

This study is aimed at analysing changes of directional preferences during the season, taking into account catching dynamics, and to compare the results with existing knowledge on the migration of the species in the region of southern Baltic coast (Remisiewicz *et al.* 1997; Remisiewicz 2001, 2003). The article has also a methodical aspect, describing a method of presenting such data. Additionally, a simplified model explaining "wavy" character of Robin migration is proposed.

MATERIAL AND METHODS

Data were collected in autumn 1996 at Bukowo-Kopań ringing station (54°28'N, 16°25'E) situated on the southern Baltic coast. In the study period (31 August – 25 October) 2380 Robins caught with mist-nets were ringed and aged. In total 445 experiments according to a new field method (Busse 1995) used to studying directional preferences of migrating birds were performed on Robins. The seasonal dynamics of birds caught and distribution of tests is shown in Figure 1.

Catching dynamics was divided into waves of migration, based on the assumption that increases and decreases of birds number can reflect groups of birds different in origin, migration routes or winter-quarters (Busse 1996, Remisiewicz and Baumanis 1996, Kopiec-Mokwa 1999). First, strict division (according to all the minima of the dynamics curve) was later revised – the waves with insufficient experiments data were joined with the adjacent ones. The dates of minima were classified to waves according to the run of dynamics or arbitrarily – as a result half of

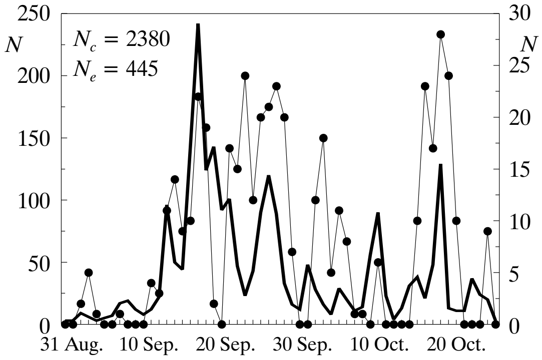

Fig. 1. Catching (thick line) and experiments (thin line with black circles) dynamics of Robins migrating through Bukowo-Kopań ringing station in 1996. N_c – total number of birds caught and ringed, N_e – total number of experiments performed

them were included into the previous periods and the second half – into the following ones. The final division is shown in Table 1 and Figure 2.

Table 1
Division of the season into subsequent periods

No	Dates	Peak(s) of wave(s)	No of birds caught	Days of testing	No of experiments performed	% of exp. in relation to birds caught
1	31 Aug.-10 Sep.	2 Sep., 8 Sep.	94	2-4, 7-9 Sep.	10	11
2	11-15 Sep.	13 Sep.	224	11-15 Sep.	38	17
3	16-17 Sep.	17 Sep.	385	16-17 Sep.	32	8
4	18-19 Sep.	19 Sep.	267	18-19 Sep.	26	10
5	20-23 Sep.	21 Sep.	263	20-23 Sep.	57	22
6	24-30 Sep.	26 Sep.	403	24-29 Sep.	89	22
7	1-6 Oct.	1 Oct., 5 Oct.	149	1-6 Oct.	45	30
8	7-15 Oct.	10 Oct., 15 Oct.	236	7, 10-12, 15 Oct.	20	8
9	16-25 Oct.	18 Oct., 22 Oct.	317	16-20, 22, 24 Oct.	88	28

In the majority of cases (87%), birds passed the test within two hours after catching, sometimes later. A tested bird was located in a flat cage with walls covered with transparent foil, on which the bird made holes and scratches with bill and claws while trying to escape. The cage (with walls divided into 8 sectors) was placed precisely according to compass rose, in the centre of round non-transparent screen, so that the bird in it could not see any surroundings except for the sky. Tested individuals were released after about 15 minutes, all the results were later recalculated into these standardised 15 min. The input data were noted as a set of 8 numbers, representing scratches made on the cage's wall by a tested individual. To the analysis

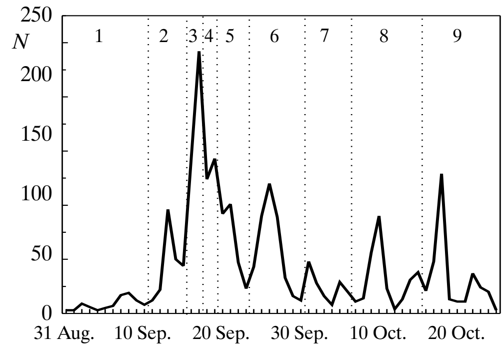

Fig. 2. Division of the season into subsequent periods (numbers above)

more simplified – smoothed by moving average – data were used (Busse 1995, Busse and Trocińska 1999).

The data were elaborated with ORIENTIN software (available from the Bird Migration Research Station, Gdansk University, Poland), that bases on non-standard use of the circular statistics as described and discussed in detail by Busse and Trocińska (1999). The most important assumption in the data elaboration is that the method accepts multimodal distributions of headings. This means that each tested bird can indicate one or more preferred directions, situated on a line (axial) or at different angles. Such assumption is based on a finding that many birds show axial behaviour in the cage (*e.g.* Weindler *et al.* 1998, Busse and Trocińska 1999), and also on the hypothesis that an interpopulational hybrid can have two or more genetically encoded navigational programmes (Busse 1992). Thus, for each individual a simplified distribution of its headings was prepared (*i.e.* local vectors with their directions and lengths). The second important thing in elaboration process is that for the group of birds, local vectors of individuals are not summed up to one resulting vector using circular statistics, but they are shown as summarised distribution and then presented as a radar graph (Fig. 3). Here, due to some limitations of the method (in accuracy of shown directions), distribution of heading indices are grouped in 45°-sectors (*e.g.* WSW, SSW, SSE, ESE, *etc.*), as it was applied in earlier papers (Formella and Busse 2002, Zehtindjiev *et al.* 2003). The third special procedure used is the reversal of return headings – by adding 180° to the vectors heading backwards to standard direction of migration in the season (here: adding 180° to all the northern directions). This is based on the assumption that birds can behave axially, while they really migrate in southern directions in autumn.

The results of experiments were elaborated according to the following procedure: the cases with up to 20 scratches ("inactive" birds) were excluded from the sample, as well as those with random (non-directional) distribution – tested with χ^2-test, as Rayleigh test (used for testing circular data distribution) requires unimodality (Zar 1996). While grouping experiments in the distinguished periods (see Fig. 2), tests performed on retraps were included according to the day of their first catching. If a bird was tested more than once, its second and further results were ex-

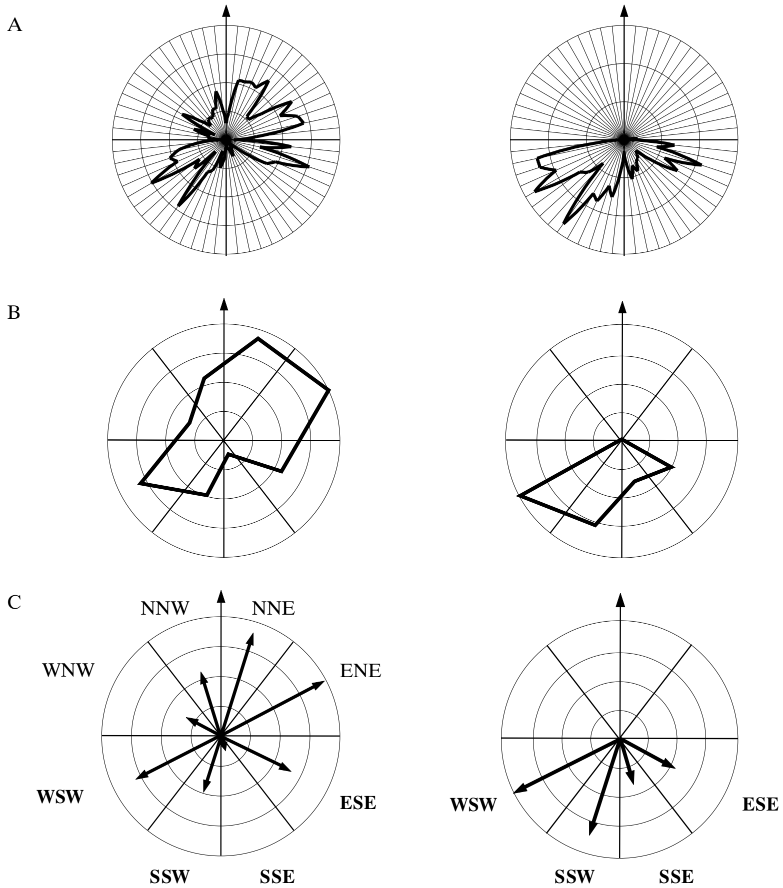

Fig. 3. Total distribution of the headings (N = 439 birds) as shown using different presentation methods: left panels – original data, right panels – reversed data (representing proportion of headings on axes). A – raw data, B – polygon presentation, summed up in 45°-sectors, C – vector presentation, summed up in 45°-sectors.

cluded in order not to disturb the proportion of directions shown in the group. Percentage of heading indices in a given period was extrapolated on daily catch numbers. The next step of the analysis was double smoothing of the obtained dynamics by 5-day moving average, according to the formula:

$$C \quad \frac{a \quad 2b \quad 3c \quad 2d \quad e}{9}$$

Where:
a, b, c, d, e – catch numbers for the subsequent days,
C – smoothed value for the day *c*.

Statistical comparisons between distinguished periods were performed using *G*-test and *t*-test for regression coeficients. Before testing, proportion in headings was recalculated into number of birds in samples, as directionality indices are not independent – they reflect “weight” or determination of a bird to choose given direction and may range in it from 11 to 100. Relations between study periods and percentage share of main directions were described by Spearman rank correlation coeficient (Zar 1996).

To interpretation of the results a map in Mercator projection was used, as this kind of map allows to present easily actual angles, without distortion caused by bend of the Earth surface.

RESULTS

Out of 445 experiments, 439 distributions were significantly different from random (at the level $p < 0.01$). The remaining six (about 1%) were "inactive" birds. After excluding them from the sample the average number of scratches per test was 309. Total picture for the whole season is given in Figure 3 using different presentation methods. Dominating ENE-WSW axis constituted as much as 36.3% of headings, also NNE-SSW was quite pronounced (28.5%, of which 2/3 are northern indices). The least indicated was NNW-SSE axis (only 13.7%), which consisted mostly of northern headings (about 82%). In the following text these axes will be called only by their southern component, *i.e.* WSW, SSW, SSE and ESE.

In subsequent periods of migration (see Fig. 2), frequencies of Robins headings to main directions were differentiated (Fig. 4). In first period of study ESE direction dominated (35%), in next two – SSW (34-42%), later on – WSW (35-45%). The pattern for the whole season was significantly different from expected theoretical distributions (G-test: $G = 39.5$, $df = 24$, $p < 0.05$). Testing subsequent pairs of periods, using G-test and t-test for regression coefficients (Table 2), mostly did not give statistically significant differences or similarities, but periods 2 and 3 seem to be similar (significance at the level 0.05 was nearly reached in G-test and reached in t-test) . The most probable to be different, according to both tests, are periods *3* and *4* as well as *7* and *8* (Fig. 5). The differences do not reach significance level most probably due to small sample sizes or not enough fine analysis of heading distribu-

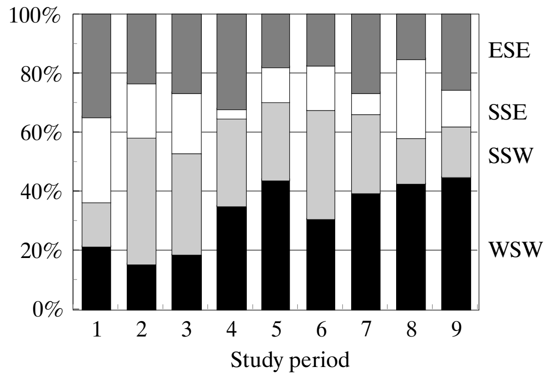

Fig. 4. Percentage share of directionality indices in subsequent periods of migration. For numbers of birds tested see Table 1.

Table 2
Differences in share of headings to main directions (WSW, SSW, SSE, ESE) between subsequent periods (*G*-test values: the smaller the most similar, *t*-test values for regression coefficients: the higher the most similar)

Periods	*G*-value	*t*-value
1-2	2.94	1.09
2-3	0.52	5.64
3-4	5.56	0.33
4-5	3.67	1.35
5-6	3.19	1.35
6-7	4.26	1.15
7-8	5.19	0.57
8-9	2.90	1.39

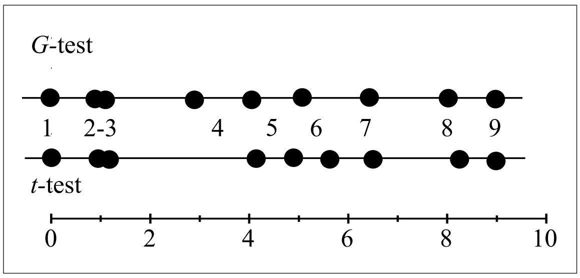

Fig. 5. Relative distances (reflecting similarities or differences) between heading compositions of migrants passing the station in subsequent periods, according to *G*-test values and *t*-values for regression coefficients

tions (*i.e.* grouping by too wide sectors that can cover directions guiding into different winter-quarters).

Changes in share of the main headings in relation to time is shown in Figure 6 (left panel). Only the share of WSW heading is significantly growing in the course of time (Spearman rank correlation: $r_s = 0.8, p < 0.01$). In order to compare migration dynamics of groups that are heading to different sectors the percentages from the samples were extrapolated into the daily numbers of birds caught in a given wave (Fig. 6, right panel). This shows that the total migration dynamics of the Robin at the station is a result of combining four separate migration dynamics characterising differently heading birds. Migration dynamics of birds heading to bordering sectors are significantly different, except for WSW and SSW groups, where the difference does not reach significance level (Fig. 7).

General picture of migration is more simplified when the extrapolated dynamics for each direction was smoothed (Fig. 8). Such presentation of the migration dynamics of differently heading groups allows to compare the course of their migration in relation to others more easily.

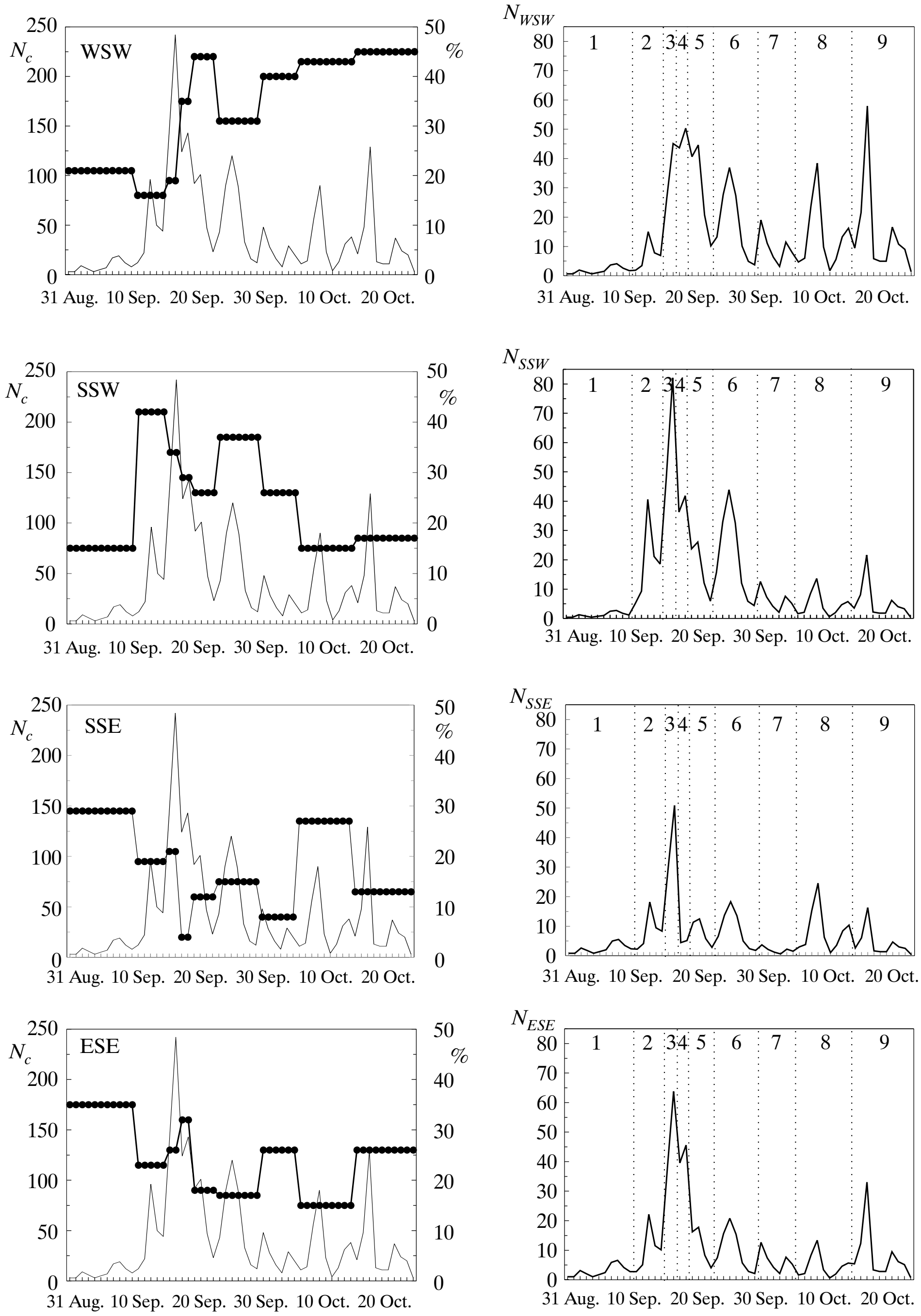

Fig. 6. Changes in the proportions of main directions during the season: in percentage share (left panel) and extrapolated migration dynamics (right panel). Left panels: thin line – catching dynamics, thick line with black circles – percentage share of a given direction by periods; right panels: thick line – dynamics extrapolated for a given direction, dashed vertical lines – division into distinguished periods of migration (numbers above).

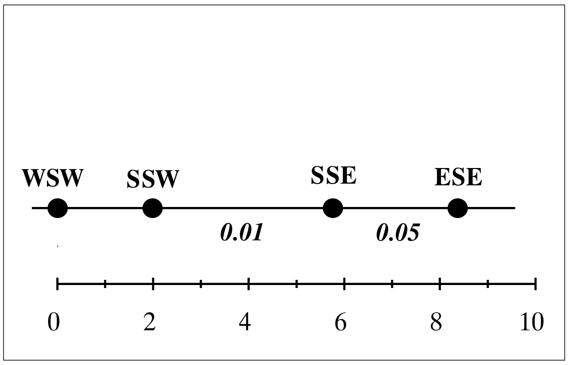

Fig. 7. Relative distances (reflecting similarities or differences) between migration of groups heading to different sectors according to *t*-values for regression coefficients; statistical significance of differences are listed.

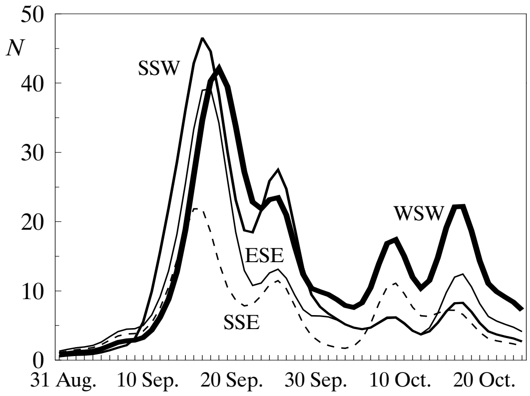

Fig. 8. Smoothed seasonal migration dynamics of birds heading to main directions

DISCUSSION

Although several analyses of cage tests performed using Busse's method has been made (*e.g.* Trocińska *et al.* 2001, Zehtindjiev *et al.* 2003) and quite large amount of data is collected now, so far usually only general pictures of most numerous species migration through chosen stations have been drawn. As for the Robin, such overall pattern was described by Busse *et al.* 2001, where also data from Bukowo-Kopań ringing station were presented. The general picture of migration was made then basing on 46 experiments performed irregularly during first big wave of migration in first half of September 1998. Thus, the comparison with those results is rather useless, as in 1996 this period is "silent" and the migration started more intensively as late as in second half of September. Nevertheless, this can be a good example of the first big problem facing the researcher trying to make a more precise analysis. Although the high number of performed tests seems to be promising, after short insight one can see that tests usually are very irregularly or even accidentally scattered, what may bias the overall pattern. Oversampling in some periods of migration season can lead to overestimation of directions prevailing in these terms, and *vice versa*: undersampling – to underestimation of others in the pattern for the whole season. This problem was discussed by Busse *et al.* 2001. Ideal would be the case, when the sampling is representative in proportion to the catching dynamics – what very often does not take place. In such circumstances any comparisons of overall patterns without regarding the dynamics of catching and testing should be treated very cautiously.

Autumn migration season studied in the present paper was (among years 1995-2002 for Bukowo-Kopań) the most regularly and numerously sampled (although for sure not ideally), and that is why it was chosen for this work. Actually, the first attempt to analyse this material based on daily (not "wavy") sub-divisions – it failed, of course. Nevertheless, during division into the waves of migration, still some difficulties appeared. Some waves were sampled not enough for the reliable analysis (*i.e.* a numerous wave around 10 Oct., the beginning and the end of migration) and also a 2-day-long (19-20 Sep.) "break" in intense testing during the most profound migration took place (see Fig. 1). The final division (Fig. 2) was a compromise between precision and suitability of sample size. Thus, one should borne in mind that some periods should be in fact divided into two waves (possibly differing in pattern of heading indices), and here only averaged picture for both is presented (what can be misleading). This statement is very important for October, with its three very long double-wave periods. Out of these, period *8* is of special interpretative caution, as it is least and unevenly represented (see Fig. 1, Table 1). Uneven sampling inside a single wave (*e.g.* in period *4*) could also bias results, however, this bias is larger when longer periods are analysed. To sum up, the most representative data came from periods: *2*, *3*, *5*, *6*, which cover almost whole migration in September.

Seasonal dynamics of bird migration has been a subject of many ornithological studies (*e.g.* Dorka 1966, Högstedt and Persson 1971, Busse 1996). The increases and decreases in number of birds noted were explained in different ways. Some authors discussed external source of this phenomenon, like weather conditions (Mehlum 1981, Gyurácz *et al.* 2003), others pointed at some innate mechanisms, *e.g.* populational or physiological background (Remisiewicz and Baumanis 1996, Kopiec-Mokwa 1999, Busse 2001). If we assume the first hypothesis, the waves of migration should be similar in internal parameters (*e.g.* in size, morphology, or directional preferences), if the second one holds true – the waves should differ. After testing subsequent periods (generally reflecting waves) in terms of overall pattern of heading indices (Fig. 4 and 5, Table 2), one can say that at least some of them seem to be different. This could indicate biological background of waviness. Only one pair (periods *2-3*) is so similar, that it could suggest that the minimum between them was caused by external factors.

Let us try to look into this problem more carefully. If we analyse not the overall composition of directions in each wave, but we divide it into separate components, *i.e.*: ENE-WSW, NNE-SSW, NNW-SSE and WNW-ESE axes, the left panel of Figure 6 shows clearly that directional preferences of Robins passing through Bukowo-Kopań ringing station vary considerably during the migration season. The most obvious changes refer probably to western directions. A clear increasing trend is visible in WSW component, with its percentage share reaching during October more than 40 percent. In contrast, SSW proportion is high in numerous September waves. Actually, these two directions seem to some extent replace each other during time. Very interesting is the situation around the block of short terms *2-3-4-5*. On the catching dynamics curve it looks like one big wave of birds, however with four peaks. Nevertheless, the percentage share of WSW gradually and consequently increases and SSW – decreases during this time, suggesting that it is not a uniform object. Thus, dividing it into several terms appeared reasonable and allowed to catch this differences. Once again the importance of precise analysis should be emphasised. Changes in eastern directions are more differentiated, they include alternate increases and decreases during whole season, with slight decreasing trend more pronounced for ESE. Both this directions also seem to replace each other (except for the first part of migration), however not so clearly as their western counterparts.

The problem arises how to interpret these findings with regard to the existing knowledge about Robin autumn migration. At first sight changing of dominating direction from eastern to western ones (see *Results*) seems to be very confusing, as many authors working on ringing recoveries reported the opposite situation, *i.e.* intraseasonal shifting of their average angle towards more eastern areas (Högstedt and Persson 1971, Pettersson and Lindholm 1983, Remisiewicz 2001). Hence, the results are so surprising that maybe the explanation for them should be searched in the method?

The orientation experiments are known to bring sometimes unexpected or seemingly illogical data (*e.g.* Rabøl 1981, 1985; Muheim and Jenni 1999). Preferred directions are usually significantly scattered and the influence of several factors has been described (Rabøl 1981, Sandberg *et al.* 1988, Able 1990, Mouritsen 1998, Muheim and Jenni 1999, Huttunen 2004). The influence of such factors is not a subject of this paper. Nevertheless, in other studies on Robins their cage activity became the more clear, the higher was determination of birds to migrate, *e.g.* their fat reserves were larger (Sandberg *et al.* 1988, Bulyuk and Mukhin 1999, Huttunen 2004), they arrived at the ringing place during peaks of migration waves (Bulyuk and Mukhin 1999) or they were caught during crossing ecological barrier – the Baltic Sea – in extensive flight (Sandberg *et al.* 1988). One can imagine that such determination probably increases during migration period – fat-stores become larger (*e.g.* Bairlein 1990, Berthold *et al.* 1991), birds have less time to reach winter-quarters, unfavourable weather conditions occur, *etc*. Thus, if we consider that as the season goes by birds behave in experimental cages more determined and show less accidental directions, we can predict gradual intensification of directions “correct” for the species migration. Maybe such circumstances could explain the significantly increasing trend found for WSW direction – which is known for birds migrating through central Europe from ringing recoveries (*e.g.* Remisiewicz *et al.* 1997).

Even if this explanation seems to be reasonable, still many doubts arise, with maybe one of the most obvious: why such positive trend does not apply to SSW direction, which is also strongly (if not stronger) indicated by ringing recoveries from the southern Baltic coast? Well, let us look into the results once again and more penetratingly. The overall pattern of migration through a given station is not only a matter of proportions in subsequent waves, but also of "size" of these waves, *i.e.* catch numbers in seasonal dynamics. That is why the proportions in study periods were extrapolated into daily catch numbers during the analysis (Fig. 6, right panel). What can be seen after this operation? The first impression is that the dynamics for individual directions differ in relative numbers of birds showing these directions and also in relative changes of these numbers (*cf.* Fig. 7). In WSW direction one can see at least four numerous waves during whole migration season: first – wide but "flat" wave extending through periods *3-4-5*, second – in period *6*, and two others in periods *8* and *9*. All of these waves, although the highest, do not reach 60 birds per day. On the contrary, SSW direction has two or three numerous waves limited to September: first – in period *2*, which in fact could be probably joined with the second – condensed wave *3-4-5* with very high peak (over 80 birds per day) in period *3*, and third – in period *6*. During comparing these two directions a block of terms *2-3-4-5* should be discussed. It was mentioned previously that changes in proportions during this time suggested that it was not a uniform object. Now the situation looks even more clear – the condensed and highest in period *3* wave of SSW birds overlapped with the wide flat wave *3-4-5* of WSW birds. By the way, it is really astonishing that in the latter wave after extrapolating such different percentage share (*cf.* Fig. 6, left panel), so similar numbers of birds caught were obtained, with differences between consequent five days not exceeding 9 birds. SSE direction dynamics comprises in general two groups of not numerous waves: first – in second half of September, and second – after about 10 October, separated by "silent" period *7* (Fig. 6, right panel). As for the ESE direction, it resembles a little bit the SSW dynamics, however, the block *2-3-4-5* is not so numerous, the wave *6* is less pronounced and there is another high peak in period *9*.

To see more generally the trends in directions dynamics, their double smoothing by 5-day moving average was performed. This method used to the reconstructing of real waves of migration was described in detail in a previous paper (Busse 1996). Smoothing, while removing accidental fluctuations of birds number, enlarges standard deviation of the distribution (*i.e.* "flattens" waves), but does not change total number and localisation of distribution maxima, what can be seen in Figure 8 (*cf.* Fig. 6, right panel).

Analysing the obtained pattern some general conclusions can be drawn. If we assume that each direction curve reflects real waves of birds migrating in this direction, one can see that such waves for different directions usually overlap considerably. This fact may be an indicator that the migration of Robins is influenced by some large-scale factors, resulting in similar timing of migration for differently heading population even from distant (from each other) areas. Such factors concerning vast region are, for example, the length of day or some weather phenomena, like cyclonic/anticyclonic situations. Both of mentioned elements affect migration of birds (*e.g.* Alerstam 1978, Elkins 1988, Gwinner 1990, Richardson 1990, Gyurácz *et al.* 2003). This may be the explanation of the most pronounced waves (consisting of populations of different origin), separated, for example, by periods of unfavourable European-scale weather conditions.

Probably the most affected is the onset of migration, thus, as it was already said, differently heading populations from vast areas may start migration even synchronically (for example, populations from the same latitudes). If we consider, however, the place somewhere in the middle of migration route, those populations will pass it not necessarily in the same time (when assuming the same speed of migration), but according to the distance of starting (breeding) area from it (Fig. 9). Thus, some shifting in time may be expected and the results show it – for example in first big wave of migration (Fig. 8).

If we add to the very simple model of a single wave consisting of several populations shown in Figure 9, more groups of populations starting in different time (*e.g.* in differing latitudes or because of the weather), and consider that in each of these groups populations are localised in different distances from the ringing station, migrating with different speed, and comprising different number of birds, we may obtain a pattern similar to the observed one. To sum up: the proposed model of Robin migration generally explains the wavy character of migration by large-scale factors (endogenous or external). However, the resulting pattern of dynamics is influenced strongly by many factors: *e.g.* localisation and characteristics of populations.

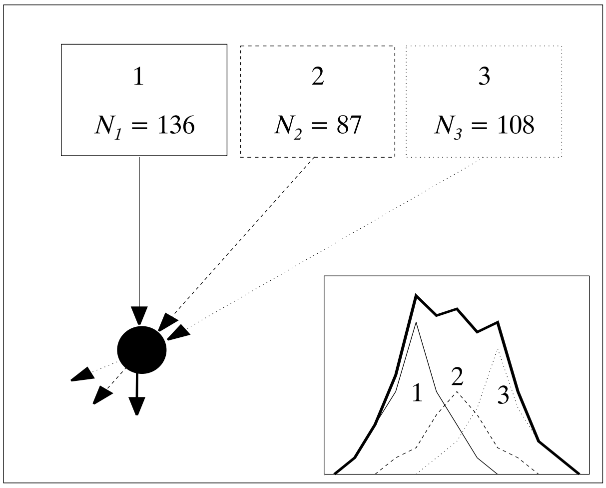

Fig. 9. Hypothetical pattern of the passage through a ringing site localised on the migration route (black circle) of three, not equally numerous (this reflected by numbers of representatives caught), populations synchronically departing from different areas. Arrows indicate directions of migration, lengths of upper arrows represent distances from the breeding grounds to the ringing site. Assuming the same migration speed in these hypothetical groups, the observed pattern of dynamics is shown.

Now, let us look at this pattern considering the existing knowledge about migration of Robins to different winter-quarters. What the directions dynamics really mean? To discover it we should analyse them in relation to the known winter-quarters of Robins (Fig. 10). Quite astonishing and unexpected, but for sure facilitating the interpretation, is the fact that the borders between Busse's cage sectors reflect to a high degree borders between winter-quarters. Nonetheless, both borders between winter-quarters and limits of shown directions should be treated only approximately, as at least in the case of directional preferences of birds significant variation of indices was reported (Sandberg *et al.* 1988, Able 1990, Mouritsen 1998, Muheim and Jenni 1999). Notwithstanding, one can generally say that WSW direction refers to Western winter-quarter, SSW – to both Mediterranean and Apennine, SSE – to Balkan, and ESE – to Balkan as well, but also to some most eastern wintering grounds for the species (east and south-east of the Black Sea).

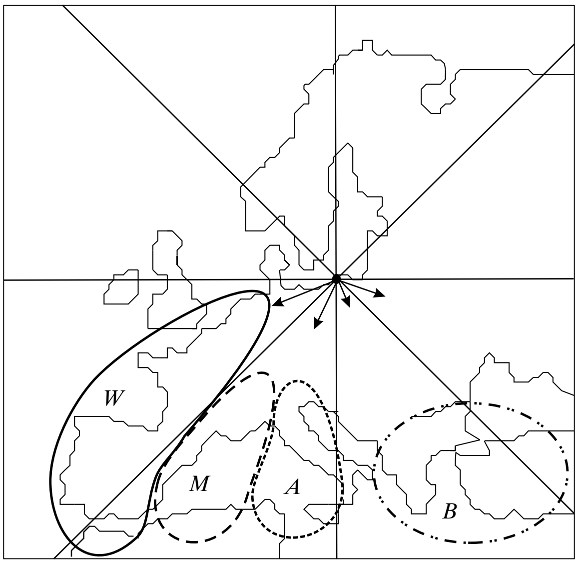

Fig. 10. The pattern of Robin winter-quarters (after Remisiewicz 2001, modified): *W* – Western, *M* – Mediterranean, *A* – Apennine, *B* – Balkan winter-quarter (only approximately delimited). Thin lines radiating from Bukowo-Kopań ringing station (black circle) delimit the ranges of four distinguished directions, arrows represent axes discussed in the paper. A map is drawn according to Mercator projection rules.

As it was mentioned earlier some analyses of ringing recoveries showed intra-seasonal changing of their average angle towards east (Högstedt and Persson 1971, Pettersson and Lindholm 1983, Remisiewicz 2001). Only for birds ringed at Långskär and Signildskär islands (Finland), Saurola (1983) reported a slight shift of gravity centres of recoveries towards west. All of these authors compared only general differences between subsequent months. However, Remisiewicz *et al.* 1997 divided migration season more precisely – into 10-days terms – and found that the average angle of recoveries indeed decreased from 233.5° in August to 219.5° in first decade of October, but afterwards it again increased reaching 226.9° in the last decade of October, what indicates – very similar to this study – the growth of most western directions proportion in October. This increase can be explained by shortening of the distance to the wintering area (reported by Högstedt and Persson 1971, Pettersson and Lindholm 1983, Saurola 1983), which for the region of southern Baltic coast is particularly visible within the Western winter-quarter (Remisiewicz 2001, *cf.* Fig. 10). Possibly, the two October big waves of dominating WSW direction (Fig. 8) can reflect migration of at least one closer-wintering population, as also in a map presenting distribution of ringing recoveries of birds ringed after 10 October (Remisiewicz 2001), a clear concentration of several records in the most northern part of Western winter-quarter is visible. Thus, some sub-divisions within this wintering area are postulated. The more southern areas are probably wintering grounds for the population passing in September big wave of WSW direction (see Fig. 8), and the northern ones – for one or two populations passing through Bukowo-Kopań in October WSW waves.

As for the SSW direction, generally two big waves in September can be distinguished (see Fig. 8). Probably the second one refers to Mediterranean winter-quarter, because: firstly – period *6* containing it comprises also high share of WSW direction (what could be expected if we take into account the scatter of indications and the fact that Mediterranean quarter lies close to WSW range), secondly – this is the second (later) wave of SSW direction, and Remisiewicz (2002) found that ringing recoveries recorded on the Mediterranean route have the mean date of ringing significantly later than those localised in adjacent wintering grounds. Thus, the first SSW wave could be probably regarded as the population heading to Apennine winter-quarter. In both of those waves due to mentioned variation of indications some share of SSE directions may be expected, what is the case (Fig. 8).

What about the south-eastern and less known, because of very low recovery ratio (Kania and Busse 1987), Balkan quarter? Pettersson *et al.* 1990 found that Robins caught in their winter-quarters around the Mediterranean differ in morphology. Probably the most obvious differences related to leg colour – in general, more easterly-wintering populations had darker legs. In a study basing on morphology of Robins passing through Bukowo-Kopań ringing station (Rosińska 2003), the following results were presented. In autumn 2002 (with catching dynamics similar to autumn 1996) the share of darker-legged Robins was the highest at the beginning of migration season (in terms corresponding to first three periods of this study) and at the end (starting from the turn of September). Now, if we join shares of both eastern directions – SSE and ESE heading to the Balkan winter-quarter (in a broad sense), we can see that together the percentage share of eastern directions is also highest (not less than 39%) in first three and last two periods (Fig. 4), however at the end is not so pronounced as in Rosińska (2003). The very high share of darker-legged Robins found by her in October may be connected not only with eastern wintering grounds, but also with northern part of the Western quarter (distinguished in previous considerations as a quarter for populations migrating late in October), as the morphology of Robins wintering there is not known.

Nevertheless, looking at the dynamics of eastern directions (Fig. 6 and 8), the interpretation is not so easy. The SSE dynamics curve in September may be probably, at least partly, a result of already mentioned high variation of SSW indications (a kind of echo). After a "silent" period on the turn of September, however, the numerous wave around 10 October, joining with the second one several days later, is clearly visible. As for the ESE direction, it heads to most eastern winter-quarters, being practically impenetrable by scientists. Thus, the results of these study cannot be referred to other sources of data, like in the case of other directions. It should be only stated that the most pronounced migration of birds heading to ESE direction took place in the middle of September and also at the end of October.

According to all above considerations, the obtained dynamics for Bukowo-Kopań ringing station (Fig. 8) may possibly be, very generally, interpreted as follows. In 1996, the intensive migration started around the middle of September with a numerous wave consisting in fact of at least three populations. The peaks of those population waves were shifted in relation to each other in just 1-2 days, and occurred in following order: birds heading to the Apennine winter-quarter, birds heading to the most eastern wintering grounds, and birds heading to the southern parts of Western winter-quarter. The second, numerous wave consisting at least of birds heading to Mediterranean winter-quarter occurred with a peak on 26 September. In two most numerous October waves around 10 and 18 October, birds heading to the northern parts of Western migration route dominated. Nevertheless, also birds heading to the Balkan (earlier) or even more eastern (later) wintering grounds formed numerous waves around those dates.

Such interpretation in general confirms the alternate passage of populations wintering in Europe from west to east proposed by Remisiewicz (2002). On the other hand, the dates found here are not in full accordance with above model. In September they are significantly shifted towards earlier terms. The reason for those shifting may be various, for example different method of analyses. The author used mean dates to comparing populations passing through the region of southern Baltic coast. Such approach does not regard wavy character of Robin migration. Besides, here only most numerous waves are described, however also the existence of some "background" and less numerous waves is obvious. They can comprise a mixture of birds of different origin and condition (some "delayed" individuals) – present for a long time after the main passage of populations and hence shifting the mean date towards later terms. Also material is not comparable – Remisiewicz (2002) analysed several stations around the Baltic Sea, and many years – starting from 1961. Here, only one season is analysed, and no-one knows if it is representative or if it is rather unusual. In comparison to Bukowo-Kopań catching dynamics from seasons 1995-2002 (own data), it seems to start lately (some waves occurring usually in first half of September are not visible), and also the turn of September is rather "silent" (usually in this period high waves of birds occur).

Despite above difficulties, the analysis of migration dynamics using the results obtained from orientational experiments seems to be a promising method in the studies of bird migration.

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