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Authors: Nowakowski, Jarosław K., Remisiewicz, Magdalena, Keller, Marek, Busse, Przemysław, and Rowiński, Patryk

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Synchronisation of the autumn mass migration of passerines: a case of Robins *Erithacus rubecula*

Jarosław K. Nowakowski[1*], Magdalena Remisiewicz[2], Marek Keller[3], Przemysław Busse[1] & Patryk Rowiński[3]

[1]Bird Migration Research Station, University of Gdańsk, Przebendowo 3, 84–210 Choczewo, POLAND
[2]Department of Vertebrate Ecology and Zoology, University of Gdańsk, Legionów 9, 80–441 Gdańsk, POLAND
[3]Department of Forest Protection and Ecology, Warsaw University of Agriculture, Nowoursynowska 159, 02–776 Warszawa, POLAND
[*]Corresponding author: e-mail: jaroslaw.nowakowski@gazeta.pl

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Abstract. The pattern of autumn migration of the Robin was studied through an analysis of daily dynamics for the birds caught in the years 1984-1997 at four ringing stations (two on the Baltic coast and two in inland Poland). In a given year, migration dynamics was found to be distinctly similar at all stations. It showed conspicuous consistence (± 2 days) in the dates with peak numbers. This could be explained by assuming that Robins take off at the same time across a large breeding ground, and arrive almost simultaneously at stopover sites located over extensive areas. Moreover, migration dynamics from year to year at a given station was also remarkably similar, though this phenomenon was more distinct at the inland stations than at the coastal ones. Day-to-day fluctuations in numbers were on an average the highest at the coastal station most exposed to variable weather, the lowest at the inland stations, and intermediate at the more "sheltered" of the coastal station. The paper discusses the extent to which such results can reflect the influence of weather conditions on passage, or else a precise internal (physiological and genetic) mechanism responsible for the timing of migration.

Key words: Robin, *Erithacus rubecula*, autumn migration, migration timing, synchronised passage, migration mechanisms

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INTRODUCTION

Many authors have discussed the extent to which subsequent elements of the life cycle (including the migratory behaviour) of an individual bird are determined by internal mechanisms (e.g. genetic or/and physiological), and the extent to which they represents a response to external conditions (e.g., Dolnik 1977, Piersma et al. 1990, Alerstam 1993, Berthold 1993, Weber et al. 1998a, Weber & Hedenström 2000, Zehnder et al. 2001, Dawson 2002). In the case of small passerines, it has been shown experimentally that basic parameters of migratory behaviour (onset, the period of migratory restlessness and direction) are determined genetically and controlled by internal timing system called circadian clock (e.g. Biebach 1983, Helbig 1991, Berthold & Helbig 1992, Berthold 1993). However, it is believed that the timing of migration is not fixed strictly as to the day, but rather that departures from the breeding grounds and stop-over sites take place within some wider period of genetically-set migratory restlessness, depending upon a bird's physiological predisposition and external stimuli (e.g. Dolnik & Blyumental 1967, Blyumental 1971, Dolnik 1977, Berthold 1993). The external factor considered to influence movement most strongly is the weather (e.g. Alerstam 1979, 1993, Elkins 1983, Richardson 1990, Žalakevičius 1990), particularly — winds (Weber & Hedenström 2000, Åkesson et al. 2001, Zehnder et al. 2001). A favourable pattern of weather conditions can trigger migration (e.g. Busse 1972, Richardson 1990, Alerstam 1993, Berthold 1993, Žalakevičius 1994, Remisiewicz et al. 1997, Åkesson et al. 2001). During movement, weather influences the "timetable", affecting, for example, flight speed or stopover duration (Dolnik 1977, Elkins 1983, Berthold 1993, Liechti & Bruderer 1998, Weber et al. 1998a). Other factors, such as behavioural and physiological determinants of migration set-off and continuation, are imposed upon the ones described.

Recently, several theoretical models for optimal bird migration strategies have been developed to consider the above relations (Alerstam & Lindström 1990, Weber et al. 1998a, Åkesson & Hedenström 2000). Passerines using on migration abundant habitats and food resources seem to realise the time-minimisation strategy (Lindström & Alerstam 1992, Åkesson & Hedenström 2000). The Robin, as a feeding opportunist associated with coppices (Cramp 1988) that is widespread in Europe, could be a good example of such a species.

Recent amendments to the optimal migration theory (Weber et al. 1998a, Weber & Hedenström 2000) ushered in the concept of the endogenously (most probably genetically) determined several-day "departure time window", which means the range of days over which a bird has to decide to depart from a given stopover site. According to this model, the extent of the influence of wind conditions on this decision depends on the probability of occurrence and gain from tailwind assistance. If the expected wind support is low and not likely, birds wait for it for only some certain period of time (the "departure window") before departing anyway, even with headwinds (after the "giving-up time"). The occurrence of this mechanism was confirmed by the studies of Åkesson & Hedenström (2000) and Åkesson et al. (2001), in which — despite a general tendency for migrants to depart with tailwinds and visible orientation cues — some cases of departure with unfavourable weather conditions were noted. This happened especially after birds encountered with a series of days affording. This also shows that, while internal factors are decisive for departure time, external ones can modify it within some limits only.

In passerines, endogenous mechanisms of migratory behaviour have usually been studied on captive individuals and only to a limited extent has work been done in the field (e.g. Dolnik & Blyumental 1967, Blyumental 1971, Biebach 1983, Berthold 1984, Helbig 1991, Berthold & Helbig 1992). However, recent field studies (Møller 2001, Both & Visser 2001), point to a strictly endogenous regulation of migration timing in long-distance passerine migrants, while the study by Møller (2001) attests to the genetic basis underpinning this behaviour. Papers concerning the phenomenon of a synchronised mass passage of birds over large areas (e.g. Žalakevičius & Petraitis 1992, Švažas 1993, Žalakevičius 1994, Liechti & Bruderer 1998, Åkesson et al. 2001) discussed the impact of weather conditions. The evidence of a strict endogenous (internal clock) control of large-scale migration from field research thus seems to be lacking.

The aim of the work was to establish the level of synchronisation of migration in a single species over an extensive area, and on this basis to analyse the balance of internal and external factors that determine migration timing. These problems are discussed using an example of the autumn migration of the Robin across Polish territory. Autumn was selected as the first migration season for immature birds, which rely mostly on internal cues during movement (e.g. Berthold 1993). The Robin was chosen as a model species because its migration pattern through Europe is quite complicated (Remisiewicz 2002), which may act as the factor that enforces precise control of passage of different populations. Poland is mostly lowland country without any geographical barriers, which could disturb expression of internal mechanisms that drive birds' migratory movements.

MATERIALS AND METHODS

On the basis of good recognition of the migration routes taken by the Robin over Europe (Remisiewicz et al. 1997, Remisiewicz 2002), 4 ringing stations were selected. At each of them birds were exposed to different weather conditions. It is generally known that weather over the sea and on the coast is much more harsh and variable than inland (for Poland, see climate data given by Kwiecień 1987). Migration observed at the Bukowo-Kopań station (abbreviation BK, 54°28′N, 16°25′E), is affected most by marine weather, as all Robins that arrive there have to fly at least the last stage of passage over the sea or along the seacoast (see Fig. 1). Mierzeja Wiślana (MW, 54°21′N, 19°19′E) is also located on the seacoast, though at least some birds arrive there from inland (Fig. 1). Both coastal stations were located in young pine stands on narrow land strips between coastal lakes, or between the open sea and a lagoon. Robins caught at the two inland stations (IN: Wilga, 51°52′N, 21°23′E, Brzumin, 51°57′N, 21°16′E) came there across the extensive

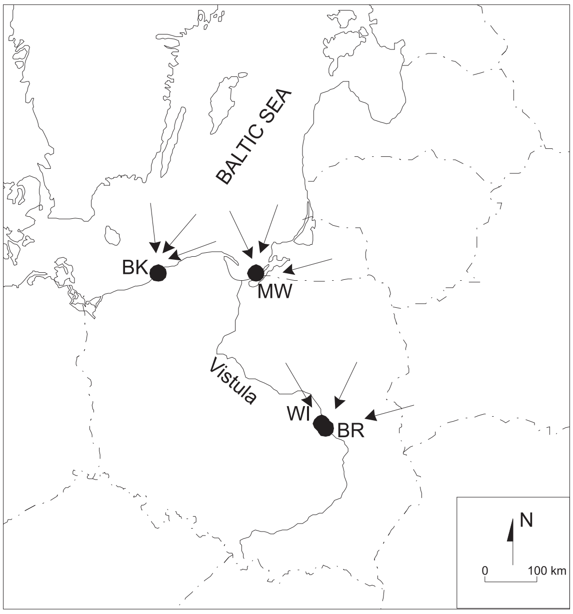

Fig. 1. Location of bird ringing stations. Operation Baltic stations: BK — Bukowo-Kopań (54°28'N, 16°25'E), MW — Mierzeja Wiślana (54°21′N, 19°19′E); inland (IN) stations: BR — Brzumin (51°57'N, 21°16'E), WI — Wilga (51°52'N, 21°23'E). Arrows indicate three main directions from which Robins come to the region of the stations; according to Remisiewicz et al. (1997).

Central European Lowland, thereby encountering the mildest and most stable weather conditions on the way (Fig. 1). At these stations birds were caught in a humid willow-poplar woodland covering the flood terrace of the Vistula River.

At all stations, mist-nets remained open for 24-hours and were checked every hour from dawn to an hour after dusk. A more detailed description of the ringing stations and methods of work can be found in other papers (Busse & Kania 1970, Keller et al. 1997, Busse 2000).

The study employed a season lasting 1 September–15 October in the supply of catch data. This covers most of the Robin's migration period and is useful in that all stations were working during it, in all of the studied years.

The material was collected during the 14 autumn migration seasons of 1984–1997 inclusive. Bird ringing was conducted over the entire period at Bukowo-Kopań and Mierzeja Wiślana, while that at two of the stations, located inland and just 40 km apart was done in different years of this period — at Wilga in 1984–1988, and at Brzumin in the years 1991–1992, 1994–1995 and 1997. Only first captures of individuals were used. The numbers of Robins caught were as presented in Table 1.

The material was analysed through: I) comparison of daily migration dynamics (between stations within a season and between years at a station), II) analysis of day-to-day changes in the numbers of caught birds at each station.

For comparisons of migration dynamics between stations and seasons, the numbers of birds ringed on successive days at each site were expressed as percentages of the total number of Robins ringed at the station in the analysed period of a given year (N%). Daily migration dynamics was compared in pairs by using a similarity index *S*, which was calculated by summing up the lower percent values N% (out of the two compared for each day) from the whole season, in line with the equation:

$$S = \Sigma \min (N\%_{di}, N\%_{dj})$$

where: S — similarity index, $N\%_{di}$, $N\%_{dj}$ — the percentage of birds caught in day "d" in years (or at stations) "i" and "j" in relation to the total number of birds caught during the season at a given station.

Index *S* is in fact identical to the Renkonen coefficient, which is used in comparing the structures of different species communities (Balogh after Trojan 1978). In our study, this index allowed for comparisons to be made between sites, regardless of absolute numbers of migrating birds. The index can range from 0% (a complete separation of the migration periods) to 100% (an identical course for daily migration dynamics) and illustrates the percentage shares of the area under the

Table 1. Working seasons of the stations, numbers (N) and daily means ($\bar{x}$) of Robins caught, in the standard period 1 September-15 October. Station symbols: BK — Bukowo, MW — Mierzeja Wiślana, WI — Wilga, BR — Brzumin.

Season	BK		MW		WI		BR	
	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$
1984	1678	37	608	14	127	3	-	-
1985	396	9	770	17	163	4	-	-
1986	318	7	1155	26	194	4	-	-
1987	520	12	558	12	207	5	-	-
1988	1426	32	439	10	271	6	-	-
1989	1379	31	1297	29	-	-	-	-
1990	1348	30	1134	25	-	-	-	-
1991	483	11	447	10	-	-	166	4
1992	350	8	1183	26	-	-	329	7
1993	1531	34	1652	37	-	-	-	-
1994	1084	24	1679	37	-	-	307	7
1995	1839	41	1892	42	-	-	461	10
1996	1996	44	1475	33	-	-	-	-
1997	767	17	800	18	-	-	369	8
Total	15115		15089		962		1632	
Mean	1080	24	1078	24	192	4	326	7

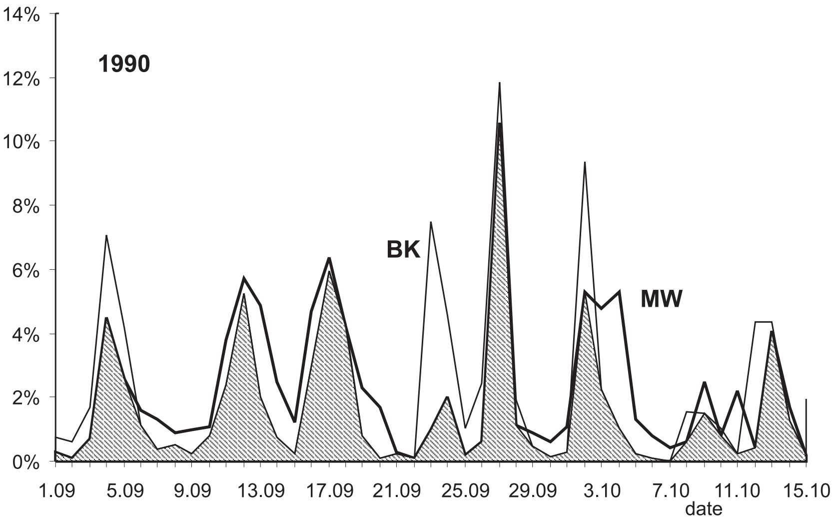

Fig. 2. Comparison of the similarity index *S* of daily migration dynamics of Robins at the BK and MW stations in 1990. The lined area common to both curves represents $S = 70$ % ($p < 0.001$).

curves of compared dynamics that are in common (Fig. 2). The presented method considers both the difference in the dates of peaks and minima for the curves and relative differences in the numbers of birds caught within each migration peak.

The similarity indices *S* were calculated for all pairs of stations within each year and between all pairs of years at a given ringing station (Appendix). To asses whether the obtained *S* value reflects a real or only a random correspondence of the course of migration dynamics, the probability that the resulted *S* value could be obtained randomly was calculated according to the following procedure. The compared migration dynamics was randomly changed — maintaining the number of birds caught on a given day but changing the sequence of these days in migration dynamics. By this method, the general characteristics of the dynamics was retained (the proportion of days of a different intensity of migration in a given year and at a given station remained the same), but its course was changed (i.e. the days in which minima and maxima occurred). Two casual migration dynamics obtained in this way were compared by calculating the *S* index. The random selection of the sequence of days was repeated for each pair of dynamics 50 times. In this way a sample of indices S_r was obtained, having of certain distribution, which for each of the comparisons (in total n = 261 pairs of dynamics) fitted the normal distribution (K-*S* test, in each case $p > 0.05$). The random selection of days was done 50 times, as from ca the 35rd time mean S_r and standard deviations for the sample did not change at the first two significant places. The distribution of the indices S_r was compared with the value of the *S* index calculated for the real course of the compared pair of dynamics, and the probability of obtaining such an index randomly was found. Subsequently, combining these individual probabilities (χ^2 test of joint probabilities e.g. Guilford 1956), the joint probability (p_j) of an event that migration dynamics observed in subsequent years at one station resembled each other more than it would result from the random course of migration dynamics was calculated. In the same way the joint probability that migration dynamics observed at subsequent stations in one season were more similar to each other than it would result from the random course of migration dynamics was found.

In order to compare daily fluctuations in Robin numbers between stations, the coefficient of fluctuations, F, was calculated. This illustrates deviations of daily migration dynamics from the five-day weighted moving average calculated in accordance with the formula:

$$A_{\%d}=(N_{\%d-2}+2N_{\%d-1} + 3N_{\%d}+2N_{\%d+1}+N_{\%d+2})/9$$

where: $A_{\%d}$ — five-day weighted moving aver age calculated for day "d", $N_{\%}$ — the percentage of the total number of birds caught during the season at a given station, caught on: $_{d}$ — day "d", $_{d-1, d+1}$ — days neighbouring day "d", $_{d-2, d+2}$ — days with two-days span from day "d".

For the two border days beginning and closing the standard period only three or four items respectively were taken to the calculations.

The coefficient of daily fluctuations, F, was calculated using the formula:

$$F = \Sigma(N_{\%d} - A_{\%d})^2$$

where: F — the coefficient of daily fluctuations, $N_{\%d}$ — the percentage of birds caught on day "d" in relation to the total number of birds caught during the season at a given station, $A_{\%d}$ — five-day moving average calculated for day "d" using the formula given above.

Coefficient F is in essence the same as the coefficient of fluctuations used in comparisons of multi-year fluctuations in bird numbers (Busse 1994).

The majority of comparisons were made in two ways. Firstly, 14-year results from MW and BK (treated as two separate stations) were compared with 10-year data from the inland stations (IN). This approach allowed for the describing of relations among the coastal and inland stations. To check if pooling the data from two inland stations was justified, we divided material from coastal stations (which remained in the same localities during all studied years) into two groups of years corresponding with the years of activity at the Wilga and the Brzumin stations. We calculated similarity indices between seasons within each of these groups of years, and between seasons from different groups (Table 2). At both MW and BK stations, catch dynamics from the 1980s resembled one another to a lesser extent than those from the 1990s. The same tendency can be seen at the inland stations, thus we assumed that possible differences between catch dynamics at Wilga and Brzumin would be the effect of the different years in which they were operational, rather than that of their different locations.

In order to present daily migration dynamics clearly, the period of the peak intensity of Robin migration (15 September –10 October) was chosen for some illustrations (Table 2).

Table 2. Between-year comparisons for similarity indices *S* (in %), as calculated for years in which there worked inland stations: Wilga (1984–1988) and Brzumin (1991–1992, 1994–1995, 1997).

	Mean $_{\text{Years WI}}$	Mean $_{\text{Years BR}}$
IN	55	61
MW	45	49
BK	35	42

RESULTS

Similarity of daily catch dynamics among stations and seasons

The catch dynamics for Robins was similar (*S* values in the range 42–74%, all averages over 50 %) among all the stations in subsequent years (Table 3). The relatively high *S* values reflect not only the general resemblance of migration dynamics at all the stations in a given season, but also a high consistency to the dates of peaks at the different stations (see Figs 2 and 3). Random occurrence of such a correspondence is extremely unlikely for some years (e.g. for comparison of MW and IN in 1997, $p = 9*10^{-12}$; for comparison of MW and BK in 1992, $p = 10^{-16}$), thus in these cases we can regard it as a true synchronisation. On the other hand, for 4 (out of 34) pairs of stations compared in subsequent years, it is possible that synchronisation was casual (this is most probable for the comparison of MW and BK in 1993, p = 0.36). Despite these differences, joint probability that the revealed synchronisation between compared pairs of stations occurred randomly is very low (in every case $p_j < 10^{-13}$, Table 3).

The comparison of *S* indices for daily catch dynamics between sites and years showed that the similarity among stations in the same season (mean = 57, min = 42, max = 74, n = 34) was higher (Mann-Whitney U-test, $p < 10^{-6}$) than the similarity between seasons at the same station (mean = 47, min = 26, max = 69, n = 34). However, even at the same station migration dynamics

Table 3. Similarity indices *S* (%) between all pairs of described ringing stations in consecutive years. BK — Bukowo, MW — Mierzeja Wiślana, IN — inland stations treated jointly, p_j — joint probability (see Methods): $^+$ — p < 0.1, * — p < 0.05, ** — p < 0.01, *** — p < 0.001.

Year	BK/MW	MW/IN	IN/BK
1984	42**	53**	46*
1985	49*	51*	52*
1986	48***	51**	56***
1987	65***	61***	52**
1988	57***	61*	47*
1989	65***	-	-
1990	70***	-	-
1991	60***	55	50**
1992	73***	53+	47*
1993	58	-	-
1994	60*	54	58*
1995	63**	66*	56*
1996	66***	-	-
1997	57***	74***	55**
Mean	60	58	52
SD	8.7	7.9	4.3
p_j	2.3^{-46}	4.2^{-19}	2.3^{-13}

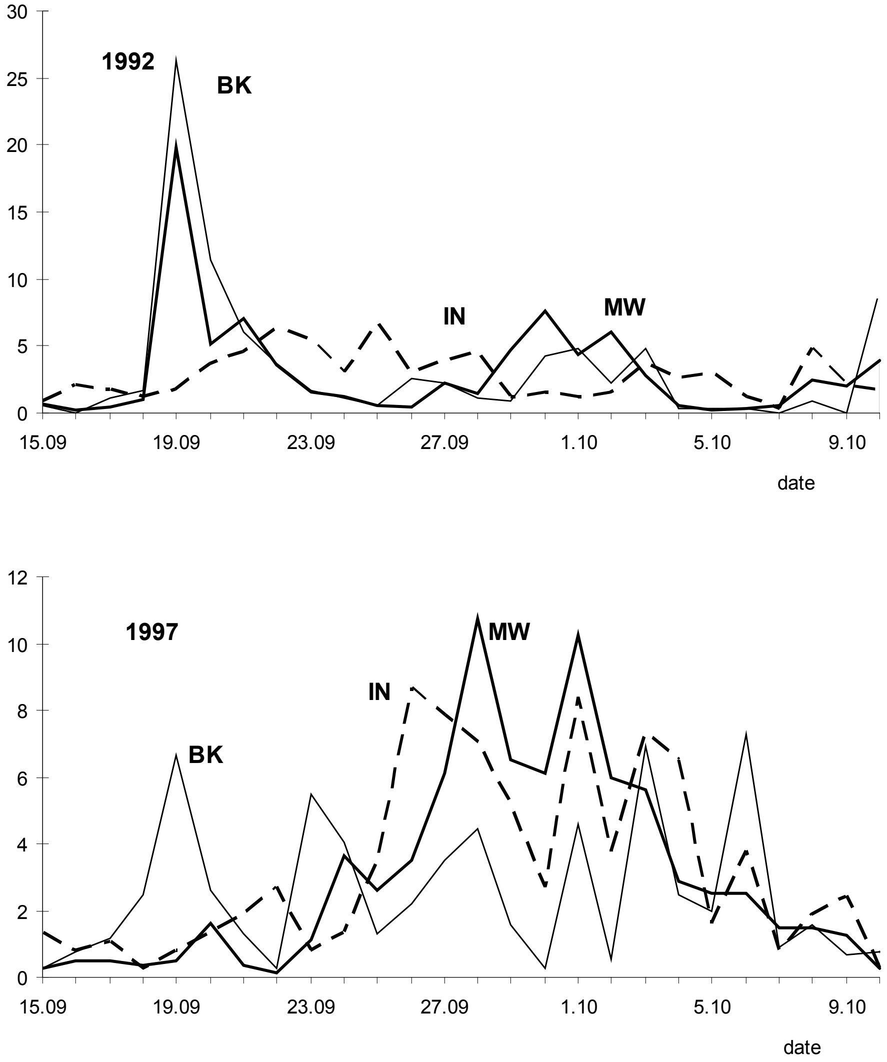

Fig. 3. Comparison of daily migration dynamics (N%) at the described ringing stations in years: 1992, and 1997. Station symbols as in Fig. 1.

was not randomly synchronised in subsequent years (for each of the three stations $p_j < 10^{-12}$; Appendix).

The resemblance of catch dynamics among stations is visualised in Fig. 4, where each side of the triangle represents mean *S* index for comparisons of migration dynamics between linked stations. So that the dynamics at coastal stations (BK and MW) was significantly more similar to each other than that at BK and the inland stations (IN), as is shown by comparing respective means for *S* indices (mean *S* values and statistics at Fig. 4, for source data — see Table 3). But surprisingly in the face of the coastal character of the MW station, the course to catch dynamics there was intermediate between those of the BK and inland sites (IN). This is demonstrated by closer correspondence (i.e. significantly lower mean *S* value) of migration dynamics at two latter sites than for relation between MW and each of these sites (Fig. 4). In fact, the Robin catch dynamics at MW was in some years similar to that observed at BK (1990, 1992 — $S_{MW/BK} > 70\%$, Figs 2 and 3, Table 3), and in others more similar to that at the IN (maximum $S_{IN/MW} = 74\%$ in 1997 — Fig. 3). This variation is also documented in the SD associated with *S* index values (Table 3), which were higher for relations between MW and each of the remaining localities in consecutive years, than for the com-

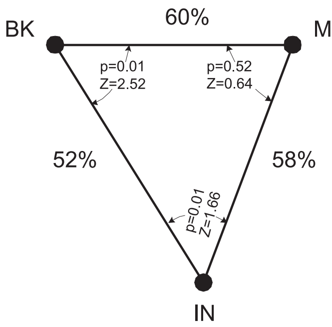

Fig. 4. The resemblance of migration dynamics among stations. Percentage values are the means of the *S* index between pairs of linked stations; the distance between each pair of stations (length of respective triangle side) represents the difference in their migration dynamics (100% — mean *S*); p is the statistical significance (Mann-Whitney U-test, Z values given) of differences between neighbouring values of *S* indicated by arrows. Station symbols are as in Fig. 1.

parison between BK and IN — despite their lowest level of similarity.

As has been shown, the highest dissimilarities in catch dynamics characterised BK as compared with the IN. Notwithstanding these differences, the resemblance between BK and the inland stations in the same years was greater (mean $S_{IN/BK}$ = 52, n = 10) than the similarity noted for dynamics at BK itself in different years (mean S_{BK} = 41%, n = 91, Mann-Whitney U-test Z = 3.74, p = 0.0002).

Table 4. Comparison among the stations of similarity indices *S* (in %) of Robin migration dynamics between years (source data and station symbols as in Table 3). N — number of similarity indices calculated for each station. Differences between each pair of stations — significant at $p < 10^{-6}$ (Mann-Whitney U-test).

	Mean S (min-max)	N
IN	57 (43-69)	45
MW	48 (31-63)	91
BK	41 (26-60)	91

Variations in daily catch dynamics from season to season differed significantly in line with which station was being considered (Table 4), apparently being dependent on location. *S* indices were highest when the different seasons at inland stations were compared and the lowest when the site situated in the central part of the coast (BK) was considered. Values were intermediate on the eastern coast (MW). At inland sites, the *S* indices between some years were so high that they could not be explained only by a general similarity of the courses of catch dynamics, but must rather have resulted from conspicuous consistency in the dates of migration peaks (Fig. 5).

Intra-seasonal fluctuations in migration intensity

At the BK station each year witnessed some days of rapid increase in the number of caught birds, even to the point where totals could be 128 times higher on a given day than on the day before. Day-to-day changes in Robin numbers

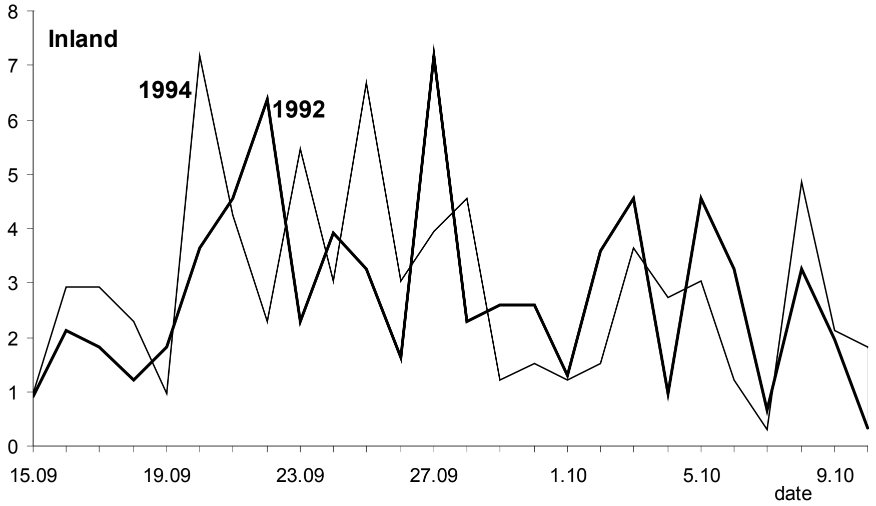

Fig. 5. Comparison of daily migration dynamics (N%) at the inland station of Brzumin in the years 1992 and 1994; *S* = 69 %, p < 0.001.

were also relatively great at MW, though the difference was never of more than 31-fold. At the IN, bird numbers were at most 16 times higher on a given day than on the previous day. These maximal values make clear the extent to which the fluctuations in daily numbers at BK exceed those occurring at the remaining stations. In all the studied seasons the values for coefficients of fluctuation F for BK were higher than those for the IN — on average more than four times as great (Table 5). In the case of MW, it was usual for values of the coefficient to be intermediate, though there are some years for which the observed fluctuations were even greater than at BK. Equally, there were other years for which the fluctuations were much less marked even than those noted inland (Table 5).

DISCUSSION

As both Zehnder & Karlsson (2001) and Nowakowski (2002) have shown, catch dynamics does offer a good reflection of the real intensity of migration (daily migration dynamics). The presented synchronicity to migration dynamics suggests that Robins start off together from their extensive breeding grounds and arrive simultaneously (accurately to within 2–3 days) at stopover sites also located across an extensive area (at least half as big as Poland). The literature provides some evidence for the simultaneous departures of birds from a breeding and stopover sites (Dolnik & Blyumental 1967, Dolnik 1977, Alerstam 1993, Berthold 1993, Remisiewicz & Baumanis 1996, Fransson 1998). The mass-scale migration of birds (including Robins) over an area of several hundred square kilometres has been well documented (Žalakevičius 1990, 1994, Žalakevičius & Petraitis 1992, Švažas 1993). Also Nowakowski (2001) showed that Great Tits *Parus major* do indeed seem to synchronise the speed of migration on the large scale if passage is intensive.

Table 5. Maximal seasonal values of fluctuation coefficient *F* (as % of total number of birds caught during the season at a given station — see text). Difference among stations statistically significant ($H_{2,38} = 16.78$, $p = 0.002$, Kruskall-Wallis test), p — significance of differences between pairs of stations connected by arrows (Dunn post-hoc test); N — number of seasons at a given station; station symbols as in Table 3.

	Mean *F* (± SD)	Min-max	N	p	
IN	0.56 ± 0.253	0.23-1.05	10		
				0.1 < p	
MW	1.17 ± 1.057	0.34-4.60	14		p < 0.001
				0.1 > p > 0.05	
BK	2.34 ± 1.921	0.49-5.98	14		

This phenomenon supports the idea that its basis is a genetically-determined period for migration within each individual. A question then arises as to how such a mechanism could bring about the coordination of passage with such a high degree of accuracy, within the population over an area of several hundred square kilometres. Two alternative hypotheses could be advanced to explain the observed synchronisation: 1) external synchronising control or 2) strict endogenous control, described as follows:

1) the onset of migration is only determined genetically to within a wide range of possible dates, such that the main fine-tuning factor allowing the described synchronic passage to arise would be similar weather conditions, particularly winds;

2) the onset of migration and the departures from stopover sites are determined endogenously (genetically) at least in some species, to a degree of accuracy far higher than was previously thought to be the case, with whole populations moreover being genetically homogenous in this respect, ensuring the high level of repeatability noted for the timing of migration from year to year, as well as the spatial synchronisation of passage within a season.

The first hypothesis seems to be a more probable explanation of the wide-scale synchronisation of passage. Conditions in the breeding grounds determine the breeding period and, to some extent thereby, the moment when birds are physiologically enough mature for migration (Berthold 1993). As similar weather factors apply in a given season over large areas of breeding range, birds from a given area may indeed become ready to migrate at the same time. Also the configuration of weather factors may determine the moment of birds' departure from the breeding grounds and, once they are en route, the possibility for the passage to continue (e.g. Busse 1972, Richardson 1990, Alerstam 1993, Berthold 1993, Švažas 1993, Žalakevičius 1994, Remisiewicz et al. 1997, Weber et al. 2000, Åkesson et al. 2001). Evidence for a strong correlation between mass-scale migration of different species over extensive areas and the occurrence of favourable weather conditions there has been given by Žalakevičius (1990, 1994), Švažas (1993) and Žalakevičius & Petraitis (1992), so it would seem that the hypothesis of weather impact could provide a satisfactory explanation of the described synchronisation of migration throughout the studied area within a season. However, the similarity to migration dynamics between seasons cannot be explained by influence of weather conditions. While showing a general trend towards a repeatability in subsequent years, configurations of weather factors are ultimately objects of irregular character, even being regarded as typical examples of chaotic phenomena (Lorenz 1979 after Gleick 1996). It is thus impossible that weather conditions are solely responsible for the observed high degree of repeatability to the times of peaks in occurrence noted in subsequent years at this study's inland stations (Fig. 5). The observed similarity of the migration pattern between years is greater at the IN than in the coastal stations because weather conditions favourable and unfavourable to birds' take-off do not occur in subsequent years with a higher degree of repeatability inland than on the coast. Therefore, it is clear that the first hypothesis cannot account for the whole of the determined repeatability in migration dynamics.

Our results can be explained well by the second hypothesis. If the onset of migration is indeed determined genetically to an accuracy of within 2–3 days, and the population over the territory of the described size is genetically homogeneous in this respect, then the influence of weather conditions on migration timing should disturb the repeatability of the patterns for passage in subsequent years and also, albeit to a smaller extent for the reason given above, at the different stations in the same season. This disturbance should be greater the greater the exposure of birds observed at the station to changing weather conditions.

In fact, the ringing stations compared were selected in such a way that Robins arriving at each of them (Fig. 1) would indeed face different levels of exposure to weather conditions (including winds — see Material and Methods). In line with the second hypothesis, we would expect that the BK station (at which birds are most exposed to strong sea winds) would be associated with the weakest (i.e. most disturbed) expression of any strict internal (genetic) mechanism. The migration dynamics should thus be less similar between years here than at the other stations. In contrast, at the inland stations, where birds are very seldom faced with weather conditions making passage impossible, the expression of the intrinsic migration drive should be strongest (least hindered). Additionally, the risk of flying over the mainland is lower than that faced over the sea, as passage can be easily interrupted if weather conditions become unfavourable (Richardson 1990, Alerstam 1993, Bruderer & Liechti 1998). Thus, in consistency with the second hypothesis, the inland stations can be expected to show a marked repeatability of migration dynamics from year to year. Furthermore, BK, with its most variable weather conditions, should witness the highest day-to-day fluctuations in bird numbers. Conversely, we would expect day-to-day fluctuations in numbers to be less marked inland. For MW the second hypothesis would indeed predict intermediate variation in the course of migration, as only some of the birds arriving there have been exposed to the variable weather conditions to be anticipated at sea (Fig. 1). It is clear that all of these implications inherent in the second hypothesis were supported by the results presented (Tables 4 and 5).

To our knowledge, nobody has yet proposed a model which predicts that the timing of migration would be under such precise control of the "internal clock" variety. However, many studies have shown that such a mechanism can be manifested strongly. Berthold et al. (1971) demonstrated that captive individuals showed migration restlessness in the same period in consecutive years. Moreover, this was the same in birds from the same population (Dolnik & Blyumental 1967, Berthold et al. 1971, Berthold 1990). Møller (2001) showed that arrival dates observed in the field were also repeated and inherited. Furthermore, caged birds presented changes in the intensity of migratory restlessness at times when they would have been negotiating geographical barriers had they been allowed to fly (Berthold 1988). These results show the fundamental importance of a precise internal clock in the realisation of the migration timetable. These endogenous mechanisms are thought to express themselves with particular intensity in juvenile birds on their first migration, as has been shown for the Robin by Mouritsen (2001). In our study, 90 % of all Robins caught were first-year birds in which the observed manifestation of these innate factors should be strong.

The occurrence of such a precise mechanism may or may not be common, but the model of Weber and co-authors (1998a, 1998b, Weber &

Hedenström 2000) indicates that its evolutionary appearance is particularly probable over the extensive lowlands of Eastern and Central Europe, in which the convenient stopover sites for such birds as the Robin are both abundant and spatially and temporally stable with respect to food availability and predation pressure. In this entire area there is only a low probability of the occurrence in autumn of the tailwinds that would be favourable to birds migrating to western and south-western wintering grounds (i.e. N, NE and E winds). At the same time, the occurrence of very unfavourable weather conditions is distinctly rare both on the coast and inland (Woś 1999). Thus, while on the one hand birds can hardly count on wind assistance, on the other hand they are not likely to be forced to wait for an opportunity to fly. Even where tailwinds do occur, they are generally weak (Remisiewicz 1996, Woś 1999), so the advantage likely to be obtained is anyway very low. In such conditions the model proposed by Weber et al. (1998a) anticipates an optimal strategy of departure on the first day of the "departure window" (immediately after physiological readiness has been reached), with no waiting for possible tailwinds. The manifestation of internal factors is in these circumstances very strong.

If the hypothesis of a strict genetic background to migration timing is true with respect to the Robin, then further questions arise. What benefits of the evolution of such a precise mechanism are sufficient to encourage retention through natural selection? What are the genetic benefits for individuals that undertake migration at exactly the same time as other birds from the same population?

We may point to at least two such benefits. Firstly, frequent communication between flying groups of birds of the same species (especially night migrants flying under an overcast sky) probably helps in the constant fixing of positions in relation to neighbours and the more precise setting of the direction of migration (Thake 1981, Alerstam 1993, Simons 2004). As a night migrant flying in dispersed flocks, the Robin could use this mechanism, especially in order to maintain a vocal contact while migrating (Cramp 1988). Secondly, precise timing may help groups of birds coming from different directions, which is the case in Poland (Fig 1., for details see Remisiewicz 2002), to avoid each other in a junction points. The mixing of different groups at stopover sites can be disadvantageous, because of higher competition for food resources (Rappole & Warner 1976, Moore & Yong 1991) or because of the risk that some individuals will depart with a group migrating in different directions.

Apart from weather and endogenous factors, other factors connected with the initiation and the continuation of migration, e.g. behavioural mechanisms, can affect the observed spatial synchronisation of passage. Individuals call each other while starting off or passing over, something which can stimulate other birds to take off (Dolnik & Blyumental 1967, Dolnik 1977, Piersma et al. 1990, Berthold 1993) and can entail a migration "avalanche" spreading out across space. On the other hand, birds which are not physiologically ready for departure can hold back the ready ones (Dolnik & Blyumental 1967).

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STRESZCZENIE

[Synchronizacja masowej jesiennej migracji ptaków wróblowych na przykładzie rudzika]

Na podstawie dziennych dynamik chwytania rudzika z lat 1984–1997 analizowano synchronizację jesiennego przelotu tego gatunku na czterech

stacjach obrączkowania — dwu usytuowanych na wybrzeżu Bałtyku (Mierzeja Wiślana, Bukowo-Kopań) i dwu w centralnej Polsce (Wilga, Brzumin) (Fig. 1). Stwierdzono, że w danym roku dynamika przelotu jest silnie i w sposób nieprzypadkowy zsynchronizowana między wszystkimi sta-cjami (Tab. 3). Dni najintensywniejszego przelotu rudzików (lokalne maksima dynamik) pokrywały się we wszystkich stacjach na ogół z dokładnością do 2 dni, a często przypadały na tą samą datę (Fig. 2 i 3). Wyniki te wskazują, że rudziki startują z obszarów lęgowych i przybywają na miejsca odpoczynku jednocześnie na dużych obszarach. Co więcej, dynamiki migracji w danej stacji były również nieprzypadkowo podobne w kolejnych latach (Fig. 5), a podobieństwo to było większe w stacjach śródlądowych, niż w tych położonych na wybrzeżu Bałtyku (Tab. 4). W stacjach śródlądowych zanotowano również najmniejsze wahania liczebności ptaków z dnia na dzień, podczas gdy w najbardziej eksponowanej na oddziaływanie morskiej pogody stacji Bukowo-Kopań, zmiany te były gwałtowne (Tab. 5). W pracy przedyskutowano czy zaobserwowana synchronizacja może być odzwierciedleniem wpływu pogody, która podobnie oddziałuje na migrację ptaków na dużych obszarach (hipoteza zewnętrznej regulacji synchronizującej), czy raczej jest odbiciem precyzyjnego zegara wewnętrznego, który uruchamia wędrówkę ptaków na dużych obszarach w tym samym czasie (hipoteza precyzyjnej regulacji wewnętrznej). Wydaje się, że zaobserwowane fakty lepiej tłumaczy druga hipoteza.

Appendix. Similarity indices *S* (in %) between all pairs of years at the described ringing stations. Station symbols as in Table 3. p_j — joint probability (see Methods): $^+$ — $p < 0.1$, * — $p < 0.05$, ** — $p < 0.01$, *** — $p < 0.001$.

IN

Years	1984	1985	1986	1987	1988	1991	1992	1994	1995
1985	51$^+$								
1986	56$^+$	46							
1987	57*	47	57*						
1988	64$^+$	57*	59	57					
1991	43	53*	48	49	65*				
1992	55	54$^+$	58	60	59	62*			
1994	58*	53	60*	57	61	60	69***		
1995	60**	62***	59	59$^+$	61	60	67*	67*	
1997	54**	55*	58**	58**	64***	54$^+$	54$^+$	62***	56$^+$

Mean *S* = 57%
p_j = 5.1^{-23}
SD = 5.5%

MW

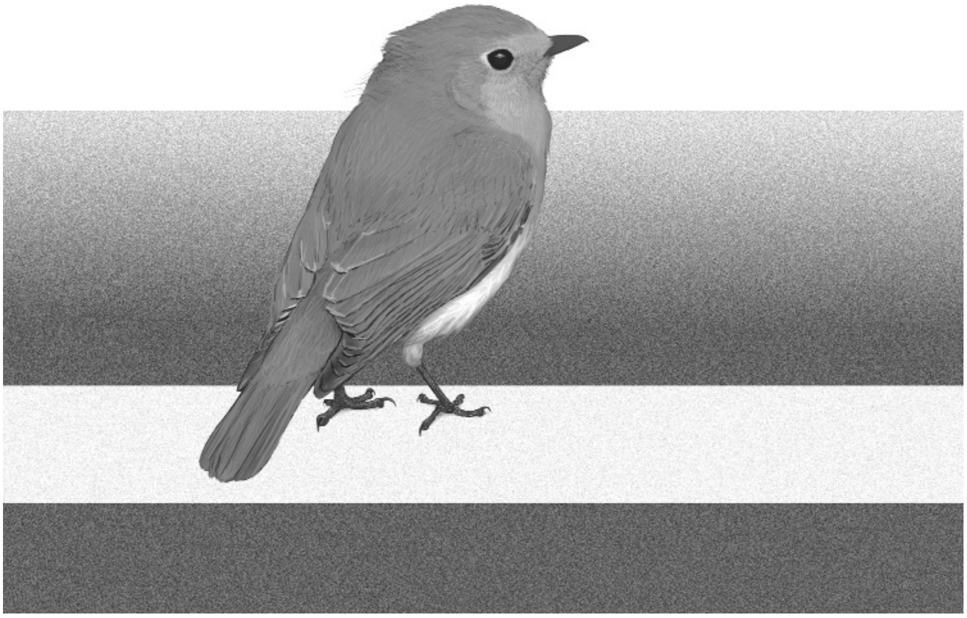
Years	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
1985	54***												
1986	39	40											
1987	50**	48*	35										
1988	48*	49+	34	53*									
1989	50+	48	38	48	53								
1990	41	50	34	48+	48	56							
1991	43	54*	45+	59***	46	54	49						
1992	46*	39	31	54**	41	50	46	45					
1993	47	44	40	43	44	67***	43	51	55*				
1994	40	47	48**	49	48	49	44	61**	42	50			
1995	39	46	40	57**	57+	60	52	54	45	52	50		
1996	40	46	35	46	51	57	52	48	53*	63**	56+	56	
1997	60***	62***	40	63***	51*	54*	46	54**	49*	47	39	49	38

Mean *S* = 48%
p_j = 6.6^{-22}
SD = 7.3%

BK

Years	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
1985	31												
1986	32	45^{+}											
1987	36^{+}	35	35										
1988	42*	36	32	31									
1989	31	40	44	34	35								
1990	33	38	47**	36	31	46							
1991	31	37	50**	40^{+}	33	39	33						
1992	26	30	26	41*	26	49*	30	35					
1993	35	55**	43	36	40	57*	48	38	38				
1994	39	38	35	47*	32	53	40	33	46*	51			
1995	42*	37	37	60***	38	46	39	29	43*	53	49		
1996	41	43	41	46*	36	61**	46	46*	58***	56^{+}	60**	47	
1997	32	47^{+}	49*	41	31	50	51^{+}	43^{+}	45^{+}	50	49	44	57**

Mean S = 41%
$p_j = 5.6^{-12}$
SD = 8.5%



T. Cofta

ADAPTATIONS AND CONSTRAINTS OF HOLE USING

HOLE-BREEDING PASSERINES CONFERENCE 2007

(Białowieża, Poland, 7–12 September 2007)

Most of long-term studies of Passerine have been based on birds that breed in tree holes or nest boxes. They offer an almost unparalleled resource in answering important questions about ecology and behavior of the hole-nesters. The forthcoming conference will be held in Białowieża, a famous village located in the heart of the beautiful, primeval forest, NE Poland. A dozen or so hole-breeding Passerines nest there. Some of them have been intensively studied since late 1980s. Now there is an excellent opportunity to meet in this Forest and to discuss major advances of the hole-nesters population and evolutionary ecology.

We shall try to keep costs as low as possible, to make participation easy for ornithologists from all parts of Europe as well as for guests from farther away.

We very much look forward to the meeting and welcoming you in Białowieża!

Secretary address:
Dorota Czeszczewik
Department of Zoology, University of Podlasie
Prusa 12, 08–110 Siedlce, Poland
Phone +48 25 6431207; Fax +48 25 6435959
e-mail: hole-breeding-meeting@ap.siedlce.pl

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