# DATES OF MIGRATION WAVES – A COINCIDENCE OR AN EFFECT OF BIOLOGICALLY BASED MECHANISM? IMPROVEMENT OF THE METHOD OF ANALYSING THE SEASONAL MIGRATION DYNAMICS

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## ABSTRACT

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The main problem considered in this work was to check whether the distribution of migration peaks was similar in subsequent seasons, or was accidental, depending mainly on variable weather conditions. By definition, a peak of a passage (or a maximum) was a day that the number of migrants was higher than the day before and the day after. The analysis of the migration dynamics was done on ringing data from autumn migration of the Blackcap (Sylvia atricapilla) from two Operation Baltic stations. Data from 1961-1997 were used. The repeatability of distribution of the peaks (maxima) was tested basing on the analysis of probability that the particular number of peaks occurs accidentally on the same day during 37 years of study. Several dates were found where number of peaks was high enough to be statistically significant or very close to this level. In some periods these dates were very concentrated, and the days in-between were characterised by a very low number of peaks, that in some cases was also statistically significant. These results were considered as a proof of the migration pattern repeatability in subsequent seasons and the high density of the peaks' dates - as a proof of high precision in timing of migrating birds. An assumption was made that the structure of migration dynamics was biologically based, thus an attempt to divide the passage into different waves was undertaken. The method by Busse (1996), who used previously on the same data, was modified. The aim of this modification was to improve this method and to make it more precise. Higher number of waves was found according to the new division. Despite the modification of the method the dividing dates found previously were only slightly different. The structure of passage at two stations obtained with the modified method was compared. The maximum difference in the border dates, found independently at both stations, was two days and it was found only in two cases out of twelve established. The analogous difference was three days in the previous analysis and was found in three cases out of eight. The results obtained with the use of the modified method were found much more precise, than those of the basic method. Most differences in the dates defined with both methods were not larger than one day; thus the basic method was recognised as precise enough to get a general structure of the passage. The modified method can be used when much more detailed division of the passage into waves is essential for analysis.

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## INTRODUCTION

Different scientists working on bird migration have found large fluctuations in numbers of birds migrating in following days. This phenomenon defined as a wave pattern of migration (Busse 1991) was interpreted in many ways. The most common one was that the migration waves were caused by meteorological factors that could either pause or favour migration (Žalakevičius 1990). According to such interpretation, the dates of the subsequent waves were completely accidental. This phenomenon was interpreted differently by authors that tried to find out its reasons in biology of migrating species of birds. Berthold et al. (1972) described behaviour of hand-raised warblers based on regular, annual rhythm. Studies done by Gwinner's group (after Alerstam 1990) on night migrants, proved that this rhythm was hormonally controlled and known as "biological clock" synchronised by the altering day length in autumn and spring. It was also proved, by the same scientists, that there was a relationship between the period of migration restlessness and the distance of migration. According to these results it can be said that populations of birds from different areas can differ in their annual rhythm of migration behaviour. This could also support the hypothesis of Busse (1973) of the populational origin of different waves of the passage. According to this author, weather conditions only modify regular year-to-year pattern of migration dynamics based on biological rhythms.

I accepted the occurrence of a migration peak (a clearly pronounced increase in number of migrating birds) in this work, as a determinant of a potential wave, therefore I concentrated on two main problems. The first task was to find out whether the wave distribution is similar in subsequent seasons. These results were a clue to the next step of analysis which was a division of the migration dynamics into waves with maximal precision. If the result of the first stage of the study was that the migration pattern was unpredictable in subsequent seasons, it would have to be stated that the variation in number of birds during the passage had no connection with their biological rhythms or this connection was not possible to be proved. In such a case, migration dynamics in subsequent seasons based mainly on different weather conditions, should be recognised as completely accidental, thus improvement of the method of defining the waves would have no sense. On the other hand, if the first stage of the analysis proved that the pattern of migration dynamics is repeated in subsequent seasons, it would be important to develop a precise method of dividing the passage into waves and to compare the results of this work with the previous studies. As the basis of the current work, the previous analysis of migration dynamics of the Blackcap (Kopiec 1997) based on the method of wave defined by Busse (1996), was used.

### MATERIAL

The analysis of migration dynamics was made on the ringing data of the Blackcap (*Sylvia atricapilla*) on autumn migration. Data from 1961-1997, from two stations of the Operation Baltic located on the Polish Baltic Coast: Bukowo-Kopań (54°21'N, 16°17'E / 54°28'N, 16°25'E) and Mierzeja Wiślana (54°21'N, 19°19'E) were used. The standard period of fieldwork was 14 Aug.-1 Nov. Series of data were shortened for analysis to the most intensive period of migration: 17 Aug.-6 Oct. The period of work of the stations was shorter in some years that the one accepted for this analysis. This fact was taken into consideration in calculations.

Birds were caught with mist-nets – their numbers and placement were stable throughout the season. The nets were controlled every hour from dawn to dusk. Busse and Kania (1970) give detailed description of the work standards of the Operation Baltic. The analysis was based entirely on the raw data, calculated into percent values in relation to the average daily number of birds caught in a season. This calculation eliminated the influence of the years with high number of caught birds on the general migration dynamics model. Seasons with the low number of caught birds (less than 100 individuals) were excluded when pooled curve of migration dynamics was made. In such years the distribution of peaks could have been much more a result of an incident, and high variation in calculated percent data could have deformed considerably general pattern of migration dynamics. Regarding the different length of catching period in some years, average percent values for each day of the season were calculated, thus giving a comparable sequence of data.

### METHODS AND RESULTS

The similarity of distribution of the peaks (maxima) in subsequent seasons was estimated on the basis of the analysis of probability that a particular number of peaks occurs on the same day during the 37-year study. For the days that the maxima sum was calculated for less than 37 years, the values were extrapolated to the standard (37 years) period and rounded to whole number. The average number of maxima in one day was 9.37, and was the same at both stations - Mierzeja Wiślana and Bukowo-Kopań. Because of that, distributions of the number of maxima at both stations were combined. With the Chi-square test, I learnt that pooled distribution was significantly (p < 0.05) different from the normal one. This result suggested that the distribution of maxima throughout the time was not an accidental one. To check, at what dates the distribution of the peaks differed most from the average one, there was done the analysis of probability of accidental occurrence of the found numbers of the peaks on the same day within 37-year period. I assumed that the peaks were accidentally distributed on different days of the studied period and that probability of occurrence of a particular peak in each season was equal. The probability was calculated on the average number of maxima in a season during the 37-years study, according to the following formula:

$$p = \frac{a}{n} \tag{1}$$

where:

a - the average number of peaks during the studied period (17 Aug.-6 Oct.), n - the number of days in the studied period.

The probability of accidental occurrence of found number of peaks, was calculated according to the following formula (Łomnicki 1995):

$$P(k) = \frac{N!}{k!(N-k)!} p^{k} (1-p)^{(N-k)}$$
(2)

where:

k – the number of peaks,

N – the number of years (here: 37);

p – the probability of occurrence of a peak in a season.

The probability of the occurrence of a particular peak in a season at Bukowo-Kopań station (formula 1) was p = 0.24, at Mierzeja Wiślana p = 0.25. The lowest values of probability of the accidental occurrence of the defined number of peaks on the same day, calculated with the formula (2), are given in the Table 1. Some of these values were statistically significant, some were very close to this level. Figure 1 shows the dates listed in the Table 1 in comparison with the migration dynamics curve and the maxima number curve. Sometimes these dates were highly concentrated (with 2-4 day intervals), and the dates in-between were characterised by very low number of peaks, in some cases also statistically significant. This was observed at Mierzeja Wiślana both at the beginning and in the second half of the studied period (Fig. 1) and at Bukowo-Kopań clearly in the first half of this period (Fig. 1). It is worth to note this, as because of such short time-intervals, rather intermediate frequencies of the peaks' occurrence were expected on those days: high, though not statistically significant.

These, very low values of probability of accidental occurrence of the peaks and their frequency calculated throughout 37-year period, suggested the high repeatability of the migration pattern in subsequent seasons. The high density of the dates of significant, high frequency of maxima occurrence, separated by the days with the very low frequency of maxima, can suggest the high precision in timing of the peaks occurrence, therefore also of migration waves.

Recognising migration pattern as constant in subsequent years, I assumed that it was based on biological mechanisms.

The next stage of this analysis was an attempt to divide precisely the passage into waves. The method by Busse (1996) used for the same purpose in the previous work (Kopiec 1997) offered a possibility to compare migration dynamics pattern only generally. The phenomenon of occurrence of short waves, highly precise as to their timing in subsequent seasons, made the improvement of the method of division of passage into waves necessary. With the use of the earlier method, peak dates of the

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Fig. 1. Comparison of numbers of peaks found on each day during the period 1961-1997 (line with dots, right axis) and pooled percent number dynamics of the Blackcap in that time (thick line, left axis). Arrows – days with the lowest probability values of accidental occurrence of exceptionally high and low number of peaks: black arrow – P(k) < 0.05, empty arrow – P(k) < 0.1.

passage and border dates separating different waves, were found in several, different ways. Ultimate peak and border dates were averages of the dates obtained from all calculations that were made. The first way was to find all maxima on the pooled twice-smoothed curve separately for the raw and the percent data. Next, for each day of the studied period, I summed up maxima from all seasons, in the same way as it was done in the analysis described above. Because of different period of the study in several years, maxima counted for the subsequent days were divided by the number of years in which the fieldwork was done on that day. The results were smoothed twice and on this basis the days with the most numerous peaks of the passage were found. The same procedure was applied to minima – which were the days

<sup>\*</sup> Smoothing: (a + 2b + 3c + 2d + e)/9; a ... e – subsequent days.

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of the lowest intensity of the passage. The border dates that were found were then used to divide the study period into fragments corresponding theoretically to the terms of the passage of subsequent waves. By smoothing the data from these fragments two times, hypothetical curves of migration for each wave were reconstructed, giving then the sequence of several distributions similar to the normal distribution. The result of the division made with the method described above, for the Bukowo-Kopań station is given in the Figure 2.

Mierzeja Wiślana			Bukowo-Kopań		
Date	k	P(k)	Date	k	P(k)
18 Aug.	6	0.076	18 Aug.	5	0.053
19 Aug.	16	0.007	19 Aug.	14	0.023
21 Aug.	12	0.083	21 Aug.	1	0.0005
25 Aug.	15	0.016	24 Aug.	12	0.071
26 Aug.	5	0.043	27 Aug.	12	0.071
29 Aug.	14	0.030	29 Aug.	15	0.011
3 Sept.	6	0.076	30 Aug.	4	0.026
12 Sept.	14	0.030	1 Sept.	14	0.023
13 Sept.	12	0.083	2 Sept.	4	0.026
17 Sept.	12	0.083	3 Sept.	12	0.071
19 Sept.	12	0.083	4 Sept.	4	0.026
24 Sept.	15	0.016	6 Sept.	15	0.011
26 Sept.	6	0.076	8 Sept.	14	0.023
27 Sept.	16	0.007	20 Sept.	12	0.071
28 Sept.	6	0.076	3 Oct.	6	0.090
29 Sept.	6	0.076	5 Oct.	12	0.071
30 Sept.	14	0.030	6 Oct.	12 .	0.071
l Oct.	6	0.076			
5 Oct.	5	0.043			

Values of the probability of accidental occurrence of defined number of peaks falling on the same date within the 37-year study. k – the number of peaks, P(k) – the probability of accidental occurrence of found number of peaks. Bold – P(k) < 0.05.

Table 1

In the modified method of dividing the migration dynamics into waves, the data were not smoothed, because of the high precision of the dates of the waves that was proved in the first stage of the analysis. Dates with minima common for both pooled and maxima number curves were found in the first division (Fig. 3). All cases when the defined dates marked periods shorter than 3 days were recognised as uncertain ones, and were left to further verification. As the result the preliminary sequence of the terms was obtained.

The second, final division was made separately for each period defined earlier. The average number of peaks was calculated for each of them, and this was a deter-







Fig. 3. The first stage of the passage (pooled number dynamics) division, according to the modified method. Thick vertical lines are the border dates found where on pooled percent data curve and maxima number curve, minima can be found (see Fig. 1). Dotted lines – the dates left for the further verification (see text for details). Arrows – see Fig. 1.

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minant of the number of waves in each period. Two different procedures were applied: border date was included in or excluded from the given period. In years when the period of study was shorter and the data did not come off the whole standard period, the calculated number of maxima was extrapolated to the appropriate number of days. If the average calculated according to the second procedure was higher, it was considered as a possible but less certain number of waves in a given period. Usually, border dates were found with distinct minima of the pooled curve. But if on the adjacent day there was a clearly marked minimum of the maxima number curve, I assumed that the border was between these two dates. Figure 4 shows the result of division made for both stations. Not all border dates between different waves were found with the same reliability, nevertheless the scope of these differences did not exceed one day. The defined periods did not always cover one-



Fig. 4. The final division of the passage according to the modified method. Thick, vertical lines – as at Fig. 3, dashed lines – the border dates found with the second stage of division, dotted line means less certain division date (see text for details).

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peak fragments of the pooled curve. At Mierzeja Wiślana only the wave no 12 had two peaks, but at Bukowo-Kopań waves no 2, 8, 10, 11 and 12 two had peaks. This fact remarkably complicated the procedure of setting the dates of subsequent waves. If, within the given period, there were the dates of the statistical significance (or close to this level) of the frequency of maxima occurrence, I considered them as the peak dates of the wave. In other cases, the peaks were found both on the pooled and maxima number curve, and the ultimate peak-date was calculated as an average of these two.

Next, I compared the results of division of migration dynamics into waves made according to the method given above, with the results of the basic method (Kopiec 1997). Border and peak dates defined with both methods: the basic and modified one, are given in Tables 2 and 3. The second method is a detailed one, thus some dates found with the first method fell in-between the dates given with the second one. Also some difference in border and peak days can be found. Most differences were maximum one-day. As the analysed species is a night migrant (it starts and ends the following stage of migration in one night) these differences could be con-

#### Table 2

Comparison of the border dates, separating subsequent waves of the passage, found with the use of two methods. Method I – basic method; Method II – modified method. The complete correspondence of the dates, and allowed difference of +/- one day,

was marked with "=" symbol or thin arrows. Thick arrows – more than one-day difference.

the second se	Da	ates of borders			
Mierz	eja Wiślana	Bukov	Bukowo-Kopań		
Method I	Method	II Method I	Method II		
20 Aug.	= 20 Aug 24 Aug	18 Aug. 23 Aug. <	21 Aug.		
26 Aug.	= 26 Aug. 30 Sept	29 Aug. <	28 Aug.		
4 Sept.	= 3/4 Sept 6/7 Sept	4 Sept.	= 4 Sept.		
11 Sept.	= 10 Sept.	10 Sept.	= 10 Sept.		
15 Sept.	= 14/15 Sep 18/19 Sep	ot. 14 Sept.	= 14/15 Sept.		
		18 Sept.	= 19 Sept.		
	1	22 Sep.	= 21 Sept.		
22 Sept.	= 23 Sept.				
27 Sept.	= 26 Sept.		<b>2</b> 6 Sept.		
5 Oat	1 Oct.	28 Sept 2 Oct	= 1 Oct.		

Table 3						
Comparison of the dates of the peaks of the subsequent migration waves						
found with two methods. Explanations as in Tab. 2.						

	Dates o	f peaks		
Mierzej	a Wiślana	Bukowo-Kopań		
Method I	Method II	Method I	Method II	
	19 Aug.	20 Aug.	= 19 Aug.	
22 Aug. =	= 21 Aug.			
	25 Aug.		24 Aug.	
		26 Aug.	= 27 Aug.	
20.4	> 29 Aug.		29 Aug.	
30 Aug.	→ 31 Aug.	2.0	1 Sept.	
	5 Sept.	2 Sep. <	→ 3 Sept.	
9 Sept. =	9 Sept. = 8 Sept. 13 Sept. = 12/13 Sept.		6 Sept.	
13 Sept. =			► 8 Sept.	
18 0	▶ 17 Sept.	12 Sept.	= 12 Sept.	
18 Sept.	▶ 19 Sept.	17 Sept.	= 17 Sept.	
24 Sept. =	24 Sept.	20 Sept.	= 20 Sept.	
	27 Sept.	24 Sept.	= 24 Sept.	
10.	> 30 Sept.	30 Sept.	= 28/29 Sept.	
1 Oct. <	> 2/3 Oct.	4 Oct.	= 5/6 Oct.	

sidered as marginal. When comparing the results of both methods in one table, their convergence with one-day precision seems to be good enough. When we put the border dates defined in the first study, on the pooled curve (Fig. 5), one can find that there are some cases, when the border data falls on the date, where according to the new method and the analysis of probability, there should be highly significant peak of the passage (e.g. border date between waves no 7 and 8 at Mierzeja Wiślana or waves no 3 and 4 at Bukowo-Kopań). Generally lower number of waves found with the first method was the reason of the lack of border dates in the days when one could expect them (Mierzeja Wiślana: waves no 2, 4 and 8; Bukowo-Kopań: waves no 2, 3 and 9). It is worth to note that some of the dates found previously, did not change though the method was altered.

In the previous work (Kopiec 1997), I compared the terms of passage at three different stations. Figure 6 illustrates a similar analysis made for Mierzeja Wiślana and Bukowo-Kopań stations with the modified method. Border dates found with the new method of division are the same to a large extent. This can suggest that the waves are present at both stations at the same time, thus enabling to make some hypothesis on the origin of migrants. The maximum difference was two days and was found only in two cases out of twelve border dates (also probable border date within the wave no 6 at Bukowo-Kopań station was considered). In the previous analysis, these differences in the border dates were even 3 days in three cases out of eight, thus the present result can be considered as much more precise.



Fig. 5. Border dates found with the basic method



Fig. 6. Comparison of the border dates found with the modified method at two stations. Dotted lines – less certain division date.

#### DISCUSSION

Many authors characterising migration give the terms of beginning, end and the highest intensity of passage, sometimes also the median date (Bauer and Keiser 1991, Granadio 1997, Hudde and Vohwinkel 1997). More detailed description of migration dynamics is usually lacking because of difficulties in interpretation caused by, according to conviction of authors, remarkable influence of external factors disturbing migration. Žalakevičius (1990) studied the influence of weather conditions on migration dynamics and found out that the high intensity of some factors could block the passage. According to this author, birds, to some extent could oppose unfavourable weather conditions, but later their migration behaviour was restrained. Izhaki and Mativ (1998) noticed a clear influence of bad weather condi-

tions on delay of spring migration as well as on the reduction of the interval between the beginning of migration of males and females, during studies on migration of the Blackcap in Israel. In both papers (Žalakevičius 1990, Izhaki and Mativ 1998) as a basis for conclusions on the modifying influence of external factors on the timing of bird migration was an assumption that there were several internal mechanisms stabilising the timing of passage. When we analyse one or even several seasons' migration dynamics, the data are to a large extent modified by external factors. This analysis of repeatability of migration dynamics pattern in subsequent years was made on 37-year series of data. Defined numbers of the peaks of the passage falling on the same date were so high in some cases, that their accidental occurrence would be of a very low probability. Now, what about the interpretation of these results? With such high repeatability of the dates of the migration peaks in subsequent years, the wave pattern of migration can be considered as based on biological mechanism. What kind of mechanism is this - remains yet unknown. One of interpretations could be that this complicated structure of migration is caused by the passage of the subsequent groups of birds that differ in their origin and the migration flyway they take. Remisiewicz and Baumanis (1996) compared the migration dynamics of the Goldcrest (Regulus regulus) at several stations located on the Baltic coast. Supplementing the study with analysis of ringing recoveries they found a relation in "membership" of the certain wave and chosen direction of the passage in the studied species. If such interpretation is also valid for the Blackcap, passing groups of birds, that form the peaks of the passage with high repeatability of the dates in subsequent years, should differ in their strategy of migration. Very short intervals between the dates in which the peaks fall with high statistical significance in the course of many years, and very rare peaks in days in-between, can prove birds' ability to settle their passage very precisely in time. This phenomenon needs further studies as it can be regulated by an unknown mechanism that isolates birds from different populations during migration. In the study of migration dynamics of the Blackcap on the Polish Baltic Coast (Kopiec 1997) I used a method of division of the passage into waves elaborated by Busse (1996). On different stages of the analysis I smoothed the data. Considering present results that allow for presumption that subsequent waves of the passage can be of a very short-term and considerably concentrated in time, one could be cautious that smoothing the data can blur important information. Thus, I omitted this procedure in the modified method. Instead, using several approximations, I tried to get as detailed structure of migration dynamics as possible. With the second stage of division, I calculated the average number of peaks in each period that was defined in the first stage. In that way I tried to avoid the effect of multiplying number of waves when summing up the peaks in each day during 37-year period, that could happen because of their displacement in time in some seasons. The mechanism of such error is illustrated on a scheme (Fig. 7). Securing ourselves from this kind of error in interpretation, we could be endangered by a different one. When we assume that there is an accidental lack of one or more



Fig. 7. The model presenting the mechanism of possible overestimating of the number of waves when counting the peaks falling on the same day in all studied seasons: on every "year" line only three dots occur, while distribution of them by days show four peaks.

peaks in each season, then when interpreting the calculated average, we reduce the actual number of waves. Nevertheless it seems that this inaccuracy is not so vital. Being aware of constraints of this method, when we get a wave with more than one peak, we can always suspect that in fact it is not a single wave. In the division made by me, some of the waves had two peaks. Similar problem faced Remisiewicz and Baumanis (1996) in their analysis. These authors assumed that the distance between two waves could be, as a rule, so small that it was impossible to find the border between them. Thus such waves should be treated as a single wave, bearing in mind that it could consist of different groups of birds. The final stage of my analysis was the comparison of the previous method of defining the waves with the modified one. The basic difference in the division made with both methods was the number of the waves that were found. With the use of the basic method less border dates were found as this method was more general. Most of the differences between the dates found with both methods were one day. Conclusions from the comparison of the passage structure at the two stations made with the modified method were similar to the previous study when the basic method was used. Small difference, in independently set border dates, that support simultaneous occurrence of the waves at both stations, were interpreted as the same origin of migrants - presumably Scandinavian. In the modified method the differences in the border dates at two stations were even smaller - this supports the above hypothesis and emphasises the described effect of the simultaneous occurrence of the waves. The basic method can be considered as precise enough to get a general pattern of the passage. When more detailed division is necessary for the analysis, the modified method can be used. When trying to divide the passage into waves, we have to accept that we will get several approximations that give us only more or less detailed impression of actual structure of the passage.

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