METHODS

MODELLING OF THE SEASONAL DYNAMICS OF BIRD MIGRATION

Przemysław Busse

ABSTRACT

Busse P. 1996. *Modelling of the seasonal dynamics of the bird migration*. Ring, 18, 1-2: 97-119.

The basic model as to structure of the seasonal migration pattern of the bird species are: (1) the pattern is the normal distribution altered by environmental factors, and (2) it is composed of a number of waves of migrants cases of which are explained variously. According to the first model the pattern can be described by means of average date and standard deviation or by median day and percentiles. The second model needs other methods of presentation of the seasonal dynamics pattern. The aim of this paper is to discuss the problem how to describe the seasonal dynamics of the bird migration. Analyses of many year migration data suggest that the second model is right. The modelling of the patterns as a row of waves of migrants is discussed theoretically. This is illustrated by an example of the seasonal migration pattern (1961-1990) of Willow Warbler at two bird ringing stations located at the southern Baltic coast. It is concluded that: (1) the pattern of the passage is repeated year by year with quite high accuracy being, however, altered by random fluctuations of environmental variables, (2) the average seasonal migration dynamics can be described by pooling yearly dynamics data into the total composed distribution, (3) subsequent waves can be reconstructed from the total pattern as a row of quasi-normal distributions by means of iterative modelling procedure, (4) obtained reconstruction of the contents of the seasonal dynamics pattern can be used for the estimation of relative frequencies of birds belonging to subsequent waves. These results could be useful for deeper monitoring studies and for comparisons between passage patterns at different bird stations, (5) the wave-like structure of the seasonal migration pattern cause that attempts of the statistical description of the pattern by means of average day and the standard deviation as well as by median day and percentiles are biologically meaningless.

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INTRODUCTION

Seasonal dynamics of bird migration is rarely studied as a separate problem. Usually it is shown as a descriptive data being a background for discussing other problems, e.g. influence of weather factors on migration or shift in migration time over a large territory. To discuss weather influence on migration the authors stress occurrence of pronounced daily peaks of the species number as well as days when the species is not observed there. These peaks and minima of migration are assumed there as deviations from an "ideal" course of migration pattern which is silently assumed to be a normal distribution of numbers of migrating birds. The same assumptions are made when shift in the time of migration is studied. In that case, however, mentioned irregularities of migration pattern are frequently taken into consideration and statistical problems whether mean date of migration should be presented as an arithmetic average or as a median are discussed. To describe the migration dynamics better some percentile values are added to the median.

Contrary to the assumed normal distribution of seasonal migration pattern of the species some authors consider migration to be rather wave-like than one-mode distributed. They look for different causes of such pattern, suggesting migration of various populations or suspect physiological processes being a background of creating some waves starting from the same area in differentiated time. Despite various mechanisms which could be involved in formation of waves along migration route, the wave-like dynamics cannot be described by means of both arithmetic average nor median and percentiles. In such case all mentioned statistical measures of migration timing are incorrect as they depend not only on the time of migration of the species, but on frequencies of birds migrating in subsequent waves. They can contain completely different populations migrating from several breeding areas to some separated winter-quarters.

The aim of this paper is to discuss the problem how to describe the seasonal dynamics of the bird migration.

MATERIAL

The material presented in the paper as an illustration of the methods of analyzing seasonal migration pattern was collected in years 1961-1990 at the Operation Baltic bird stations Bukowo/Kopań (54.21 N, 16.17 E/ 54.28 N, 16.25 E) and Mierzeja Wiślana (54.21 N, 19.19 E) located at the southern Baltic coast. The seasonal dynamics is described here as a number of individuals caught daily throughout autumn migration season by means of stable number of mist-nets. Details of the field methods were given in the paper by Busse and Kania (1970). As the example species Willow Warbler (*Phylloscopus trochilus*) was chosen as the relatively numerous species having a long enough period of migration. Altogether 13 946 individuals were caught at Bukowo and 10 201 at Mierzeja Wiślana, as shown in the Table 1.

The problem

Typical patterns of yearly seasonal dynamics of migration of small passerines are presented at Figure 1. There are shown raw data (daily catches) and the data smoothed. Both are expressed in a percent of an average number of individuals caught per day in a particular year. The smoothing was four time repeated 5-day running average using the formula:

$$D_x = 0.06d_{x-2} + 0.24d_{x-1} + 0.40d_x + 0.24d_{x+1} + 0.06d_{x+2},$$

where: D_x – smoothed value for a day X; d_{x-2}, d_{x-1} ... – raw values for 2 and 1 days respectively before day X and after it; 0.06, 0.24, 0.40 – y values of normal distribution with SD = 1. The weights chosen force forming quasi-normal distributions. Similar idea of smoothing weights other than traditional was applied by Ader (1993) to follow large scale bird migration waves.

Table 1
Catching periods and numbers of Willow Warbers caught
(after Piotrkowska 1995)

Year	Bukowo		Mierzeja Wiślana	
	Catching period	N	Catching period	N
1961	14.09-15.10	14	13.09-14.10	0
1962	10.09-10.10	12	20.08-03.10	57
1963	05.09-15.10	31	16.08-30.10	133
1964	03.09-15.10	231	16.08-25.10	560
1965	06.09-15.10	76	15.08-25.10	1159
1966	04.09-25.10	120	16.08-26.10	419
1967	16.08-25.10	255	16.08-27.10	371
1968	16.08-25.10	274	16.08-25.10	904
1969	16.09-25.10	305	16.08-25.10	478
1970	05.09-11.10	39	16.08-01.11	723
1971	16.08-22.10	240	16.08-01.11	681
1972	14.08-29.10	127	14.08-01.11	170
1973	14.08-29.10	221	14.08-01.11	286
1974	14.08-28.10	263	14.08-01.11	482
1975	14.08-28.10	104	14.08-01.11	325
1976	14.08-01.11	218	14.08-01.11	363
1977	15.08-01.11	178	15.08-01.11	380
1978	14.08-01.11	202	14.08-01.11	330
1979	15.08-01.11	160	14.08-01.11	88
1980	14.08-01.11	140	14.08-01.11	80
1981	14.08-01.11	851	14.08-01.11	374
1982	14.08-01.11	1122	14.08-01.11	395
1983	14.08-01.11	507	14.08-01.11	98
1984	14.08-01.11	190	14.08-01.11	82
1985	14.08-01.11	188	14.08-01.11	94
1986	14.08-01.11	91	14.08-01.11	156
1987	14.08-01.11	39	14.08-01.11	284
1988	14.08-01.11	36	14.08-01.11	272
1989	14.08-01.11	54	14.08-01.11	194
1990	14.08-01.11	234	14.08-01.11	263

Willow Warbler migration at Bukowo station (Fig. 1) is composed usually of 5 distinct waves which can include one or more peak days. They are more or less distinctly separated by days with no migration (e.g. in 1975 from 9th to 15th September) or days when migration was clearly less intensive than in the peak days (e.g. in 1967 on 14-15 Sept.). Periods when such waves pass the station in different years are relatively stable. This phenomenon was found for many species (Busse 1976, Busse and Maksalon 1978, Maksalon 1983, several diploma works at the University of Gdańsk). However, the analysis of 30 year data show that sometimes two neighbouring waves touch each other in particular year or some of them seem to disappear in this season.

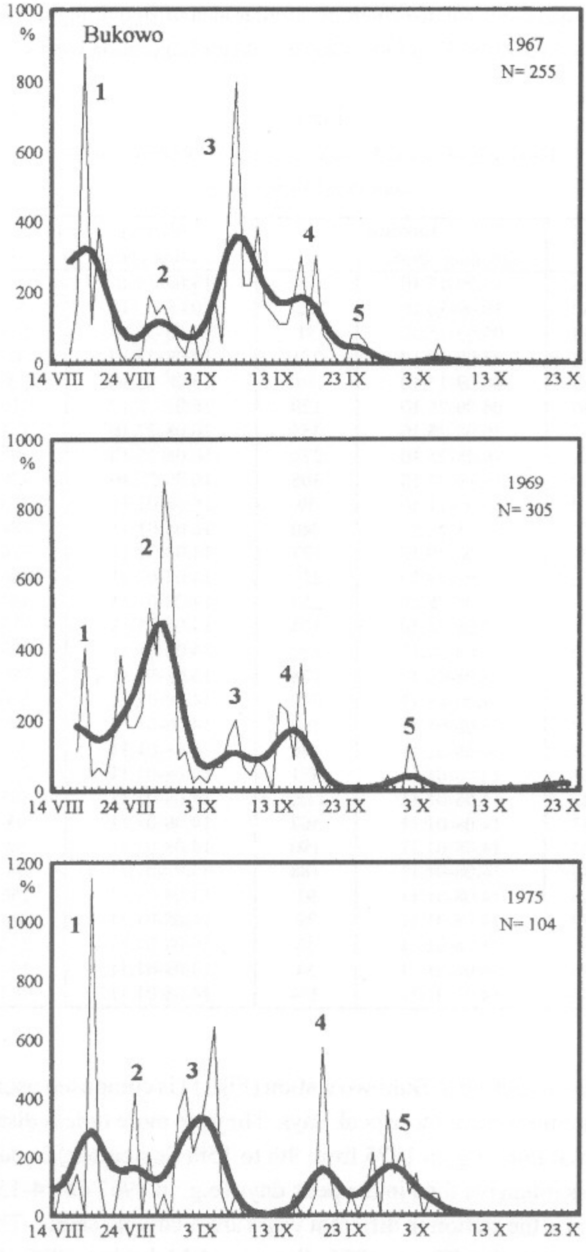

Fig. 1. Examples of yearly seasonal dynamics patterns of Willow Warbler at Bukowo. Raw (thin lines) and smoothed (thick lines) data are presented. Subsequent main waves are numbered.

Leaving apart the nature of waviness of migration, which is not a matter of this paper, the phenomenon can be described by means of listing the periods when tips of waves occur or by giving border dates between the subsequent waves. This last method was used in some cases when the main problem was in looking for population differentiation in migrants. To compare biometrics of populations passing the station one must have the migration period cut into pieces of time when passage of different groups is suspected. Individuals caught within such period of time are assumed, in the first approximation, as being members of one population. When species is so numerous that every year subsequent groups are represented by a high enough number of individuals caught the problem is simpler and every year birds can be analysed separately. Unfortunately, many species are less abundant and so detail analyses are not possible. However, as it was stated earlier, the wave pattern of seasonal migration seems to be repeatable throughout years. Basing on this finding the birds measurements taken from individuals caught in the same wave (e.g. wave number 3), but in different years can be pooled together to reach sample size big enough for statistical treatment. This idea was applied earlier when Song Thrush migration was analysed (Busse and Maksalon 1986).

Figure 2 shows border days between waves as estimated for Willow Warbler at Mierzeja Wiślana. The procedure leading to this picture is somewhat subjective as every

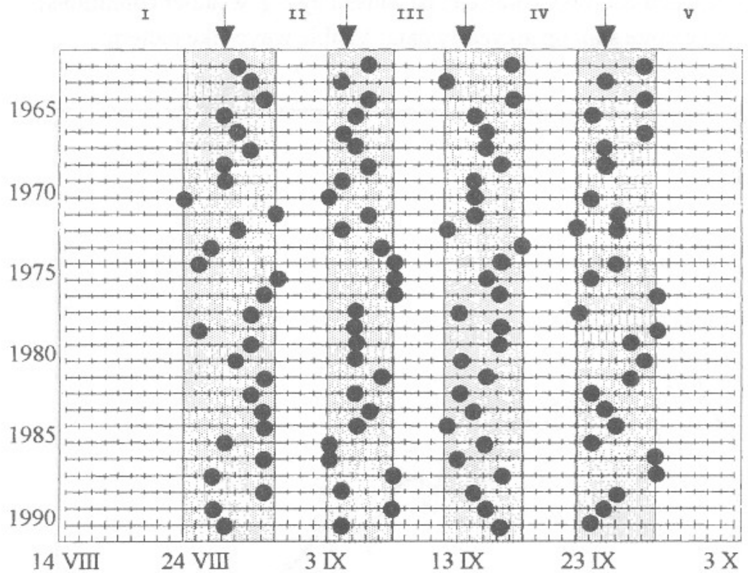

Fig. 2. Distribution of wave border days in different years (Willow Warbler, Mierzeja Wiślana), (after Piotrkowska 1995).

year migration dynamics (such as these at Figure 1) was cut onto pieces estimating border days from more or less clear patterns of peaks and minima of migration. However, the wave pattern seems to be acceptable as estimated variation between years is not too high (Table 2). So, basing on this procedure 5 waves of Willow Warblers passing Mierzeja Wiślana were set up.

Table 2

Estimated wave border days at Mierzeja Wiślana

Year	Estimated wave borders (dates)			
	I/II	II/III	III/IV	IV/V
Mode	28 Aug.	4 Sept.	15 Sept.	23 Sept.
Avg. date	**26 Aug.**	**4/5 Sept.**	**13/14 Sept.**	**24 Sept.**
Avg. day	26.1	4.4	13.7	23.9
SD	1.87	1.57	1.56	1.87

The most controversial point in this method is the subjectivity of divisions. Let us check whether the estimation procedure is good enough.

Assumptions:

1. Waves are a real phenomenon,
2. Timing of passing of the waves through the station is stable from year to year, disturbed by random fluctuations only (they can be caused by e.g. weather conditions)

Expected when one sum up all yearly data: Visible wave-like pattern.

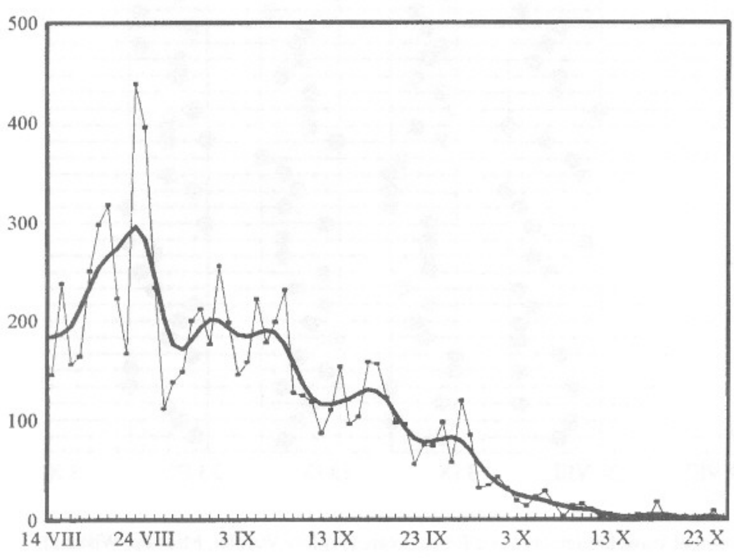

Fig. 3. Total (1961-1990) seasonal migration dynamics pattern at Bukowo. Raw (thin line) and smoothed (thick line) data are shown.

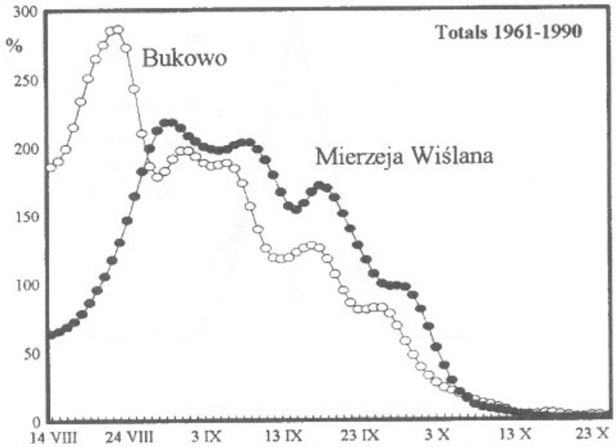

Fig. 4. Comparison of the total smoothed seasonal migration dynamics patterns for Bukowo and Mierzeja Wiślana (after Piotrkowska 1995, modified).

To avoid too strong influence of years with very numerous catches every year data were recalculated to percents of yearly average daily catches and then pooled as unweighted average.

The pattern obtained for Bukowo (1961-1990) is shown at Figure 3. As expected smoothed curve shows a row of waves. The number of waves is as shown at Figure 1. However, it is worth mentioning that day to day differentiation of pooled values is surprisingly high. All main smoothed waves include at least two peaks, which suggests that there is possible intra-wave differentiation not fixed yet by applied estimation procedure. So, the wave structure could be more complicated than expected.

Figure 4 shows that the total wave patterns at different stations can be clearly different. Deeper analysis of this phenomenon opens new possibilities to study general migration pattern of the species.

The problem is whether we can describe in more detail time location and number relations between subsequent waves of migration.

BASICS OF THE MODELLING OF THE SEASONAL DYNAMICS PATTERN

The smoothing procedure as described above has some consequences which must be taken into consideration when analysing seasonal migration patterns:

1. Every single peak of birds number (e.g. 100 birds in day "0" at Figure 5) is transformed by one pass of the smoothing procedure into normal distribution with the average equal

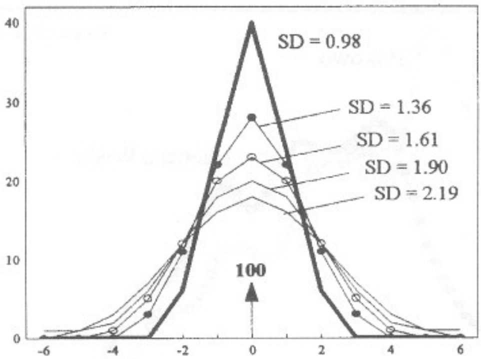

Fig. 5. Illustration of the results of repeated smoothing procedure. The starting value is 100 individuals in a day „0"; SD of subsequent smoothed distributions are given.

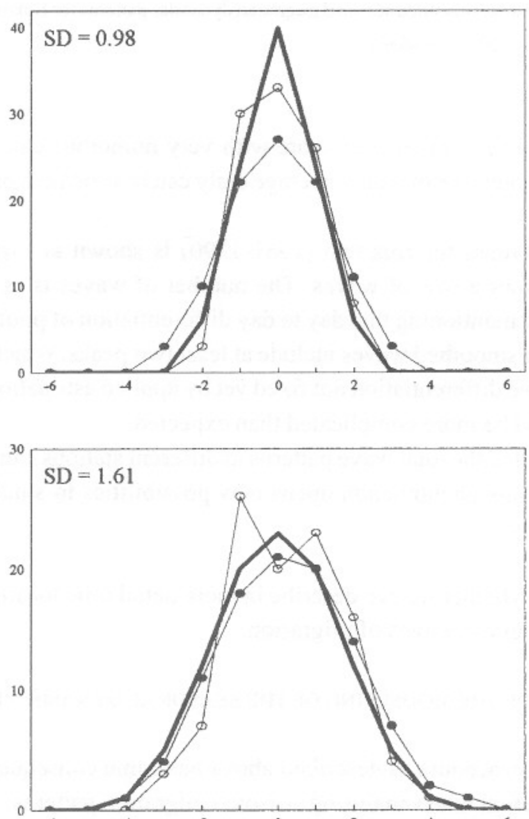

Fig. 6. Comparison of the results of smoothing (black circles) of normal distributions altered by random (generated by a computer) numbers (open circles) with source normal distributions (thick line).

to the original value (zero), SD equal 1 (exactly 0.98) and total number of birds within distribution (sum of abcisses) equal starting value (100).

2. Subsequent passes of smoothing do not change average and total values, but subsequently enlarge standard deviation of the distribution which covers more and more days.
3. Application of smoothing to the normal distribution altered by random deviations (Fig. 6) force returning the shape of the curve into symmetric quasi-normal distribution with variation (SD) a little bit bigger than original. Smoothing can cause loss of precision in estimating wave boundaries, but do not change total number and localization of distribution maximum.

The general assumption to the modeling is that the seasonal dynamics pattern is a composition of a row of waves. Every wave is assumed to be a normal distribution of numbers of passing birds belonging to the particular wave. These distributions can be altered by random environmental factors.

The shape of the total pattern being a sum of two source distributions depends on three parameters of included distributions: their numbers (N1, N2), variation within (SDs1, SDs2) and distance between source distributions averages which can be expressed in relation to the variation of the source distributions (Dr). Figures 7 and 8 give some idea how resulting distribution shapes look like when two groups of different parameters are added. When both numbers and variations of source distributions are equal (Fig. 7) resulting distributions are symmetric and they are unimodal below the distance between peaks around 2 SDs. The only difference from the simple normal source distribution is that resulting SD (SDr) is higher than that of the source ones. As in the original data we do not know natural variation therefore such distributions cannot be separated from a single wave case. Border date between source distributions can be found when bimodality is visible. As the border day we use a day when both source distributions have the same number share. Distributions composed of two ones, but not equal as to number of birds included (Fig. 8) are unimodal when distance between peaks is less than around 3 SDs (but this level depends on number difference between both source distributions). These unimodal distributions are usually clearly asymmetric which can be checked by a calculation of the skewness index value. Estimation of the border day is possible in some cases of a clear bend along the tail of the distribution. When bimodality is visible the border day can be more easily estimated. Depending on distribution parameters estimation could be more or less exact. Generally, it can be stated that the estimated border day tend to be shifted from the correct one towards the peak of more numerous source distribution.

Figure 9 shows simulated seasonal dynamics pattern composed of 6 source distributions of different numbers and located at different distances between peaks. For simplicity, all source "waves" within one graph have the same raw standard deviations. Depending on this parameter "wave" contents of the resulting distribution is more or less visible – when leptocurtic distributions (lower SDs) are combined wave composition is better visible and border days can be better estimated, when more platycurtic ones (higher SDs) the wave composition is less visible and border days can be sometimes hard to estimate. In an ex-

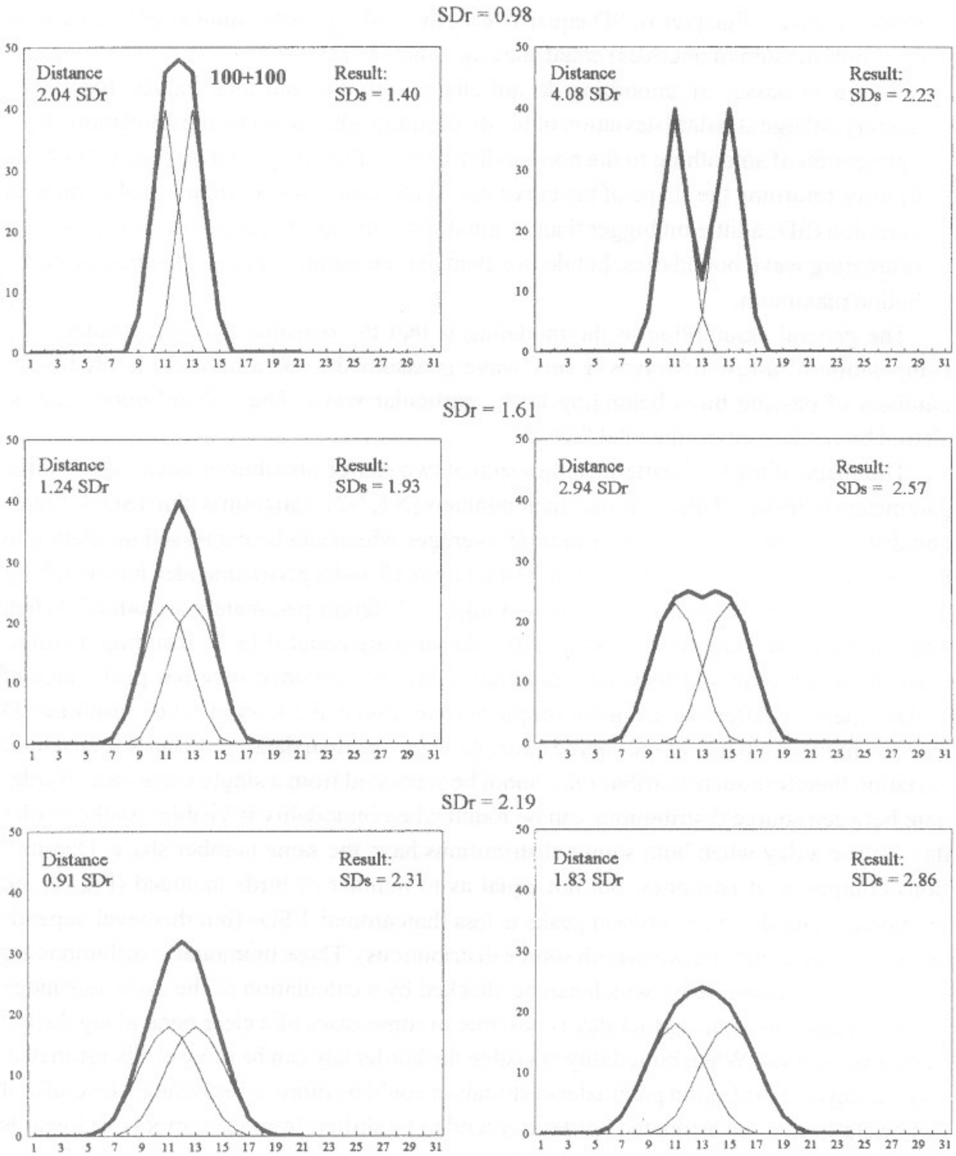

Fig. 7. Results of pooling of two normal distributions of equal numbers and the same variation. Three levels of source variation (SDr) are shown. Distances between averages of distributions are expressed in relation to source distribution variation (SDr). SDs – standard deviation of the total distribution.

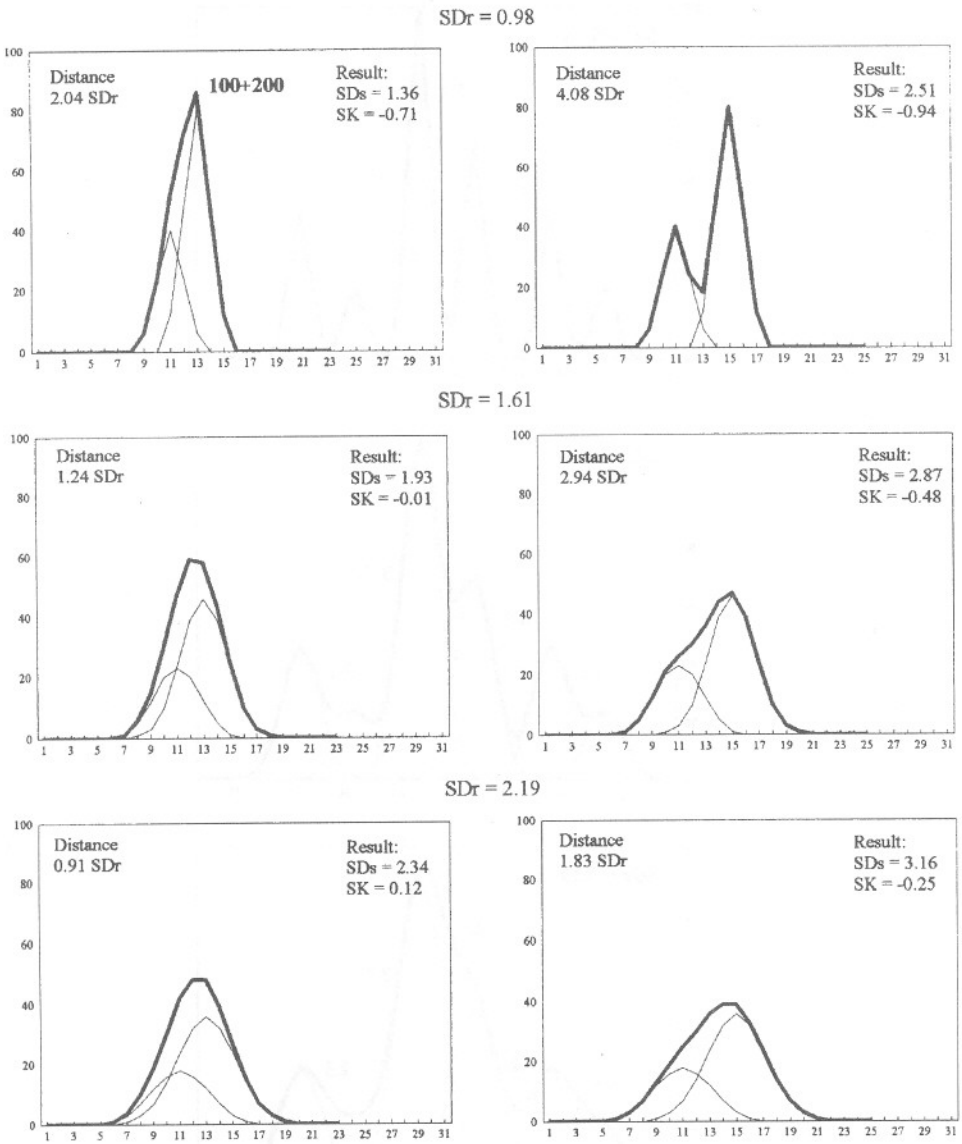

Fig. 8. Results of pooling of two normal distributions of not equal numbers, but the same variation. SK - skewness index. Other explanations as at Fig. 7.

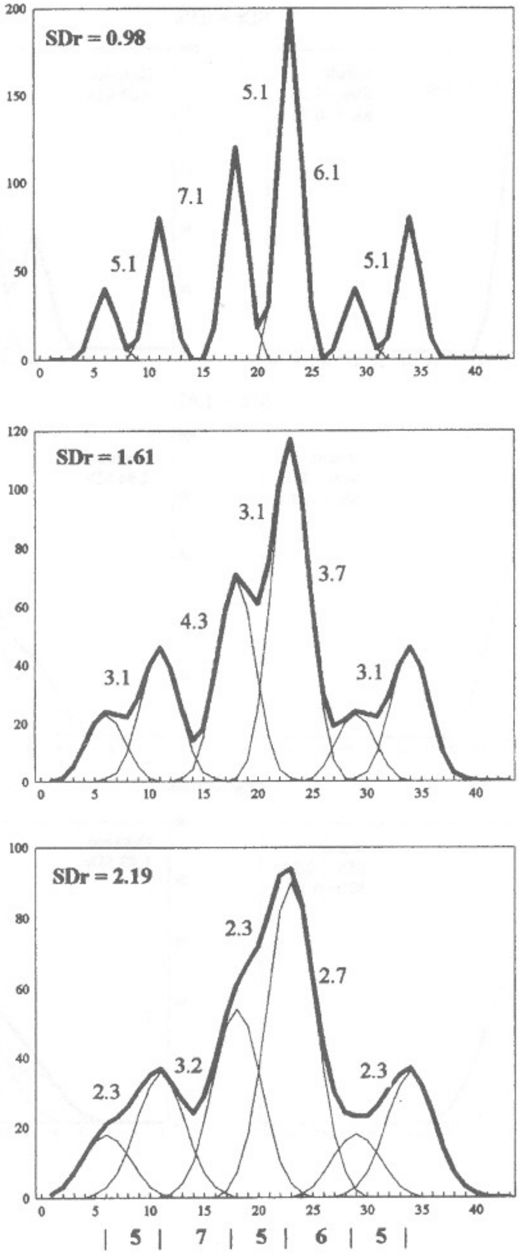

Fig. 9. Simulated seasonal migration pattern composed of 6 subsequent waves of different size (100, 200, 300, 500, 100, 200), but the same variation. Three levels of variation are illustrated. Distances between tips of distributions are given in days (below the graphs) and in relation to variation within the source distributions (SDr; values on graphs).

treme case of not numerous wave located between two more numerous ones this small wave could be not found at all.

The basic idea of the modeling is that when we know the border days between source distributions or, at least, we can estimate them exactly enough, we are able to reconstruct source distributions from the observed composed pattern. The basic procedure of modelling is as follows:

1. Choose estimated border days (basing on a shape of the total distribution),
2. cut the total distribution data onto pieces limited by border days; border days values should be divided by two (the shares of bordering waves are equal here) and these halves should be used as this day values in both waves; in a case when we decide to put the border between two days (e.g. in a case of two equal low number days) we use the earlier day value to the earlier wave and accordingly the later one to the later wave),
3. smooth the values in every part of data separately using the mentioned earlier smoothing formula; the smoothing procedure add lower and upper tails to the modeled distribution (wave),
4. plot obtained distributions against the time scale.

Let us check the idea on simulated distributions shown at Figure 9. The case of the most leptocurtic source distributions (Dr = 0.98) will be omitted. Figure 10 presents the results of the described modelling procedure. Agreement of reconstructed distributions with the original ones seems to be good enough. The only bigger deviation can be observed in the case of the situation mentioned earlier when small wave is located between two bigger ones. The deviation is bigger when the source distributions variation is higher. To check total exactness of the reconstruction the original composed distribution and distribution being a sum of the reconstructed waves are compared at the Figure 11. Differences are negligible (Table 3), so proposed modelling procedure could be accepted as enough robust.

Table 3

Reconstruction of simulated 6-wave seasonal migration pattern (see Fig. 10). Deviations of estimated peaks from the correct date are given in days.

Groups (N)	Border (no. of day)	Peaks (no. of day)	Distance (days)	Reconstruction of peaks (deviations) SDr = 1.61	Reconstruction of peaks (deviations) SDr = 2.19
100		6		0	0
	8		5		
200		11		0	-0.5
	14		7		
300		18		-0.5	-0.5
	20		5		
500		23		0	0
	27		6		
100		29		-1	-1
	31		5		
200		34		0	0

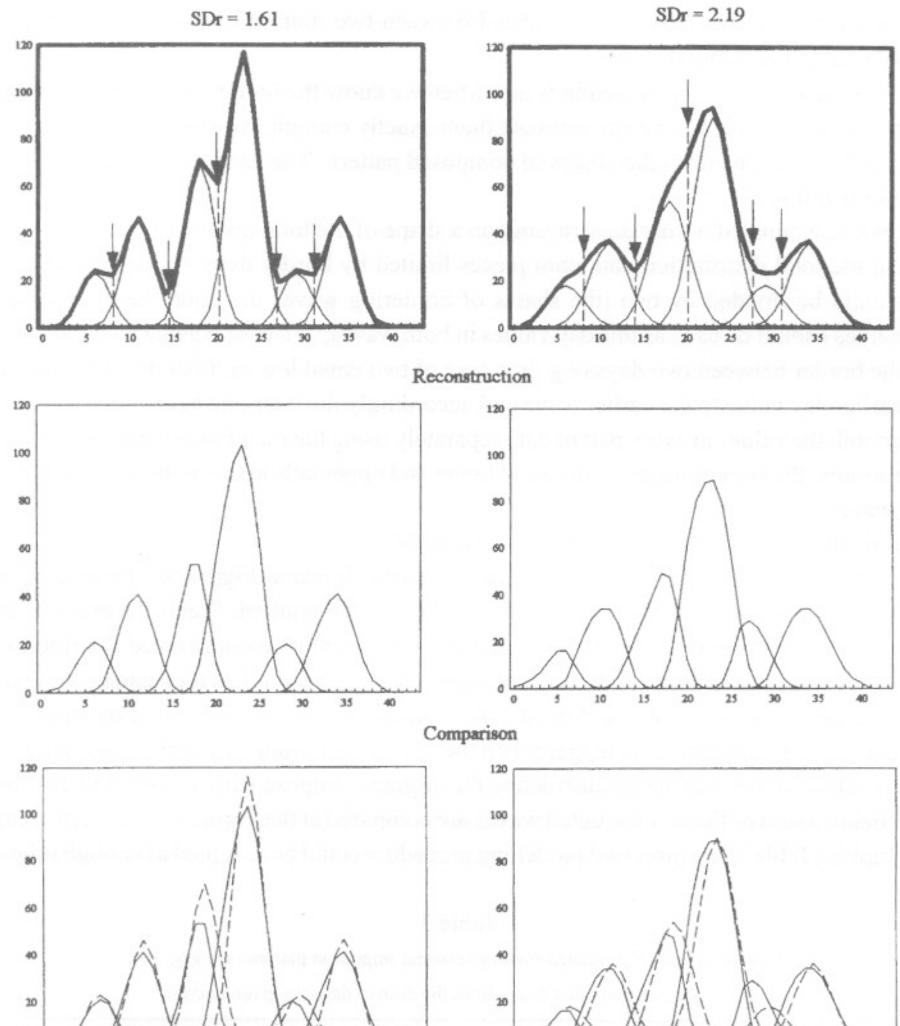

Fig. 10. Reconstruction of source distributions from the simulated seasonal dynamics pattern (see Fig. 9). Two levels of source distributions variation (SDr) are shown. Top graphs: thin line – source distributions, thick line – total distribution, arrows – border days used in reconstruction (selected as they really were); middle graphs – reconstructed waves; lowest graphs – comparison of source (continued lines) and reconstructed (dashed lines) distributions.

The next problem in such modelling is vulnerability of the method to inaccuracy of the estimated border days. The example test is presented at Figure 12. The same as at Figure 10

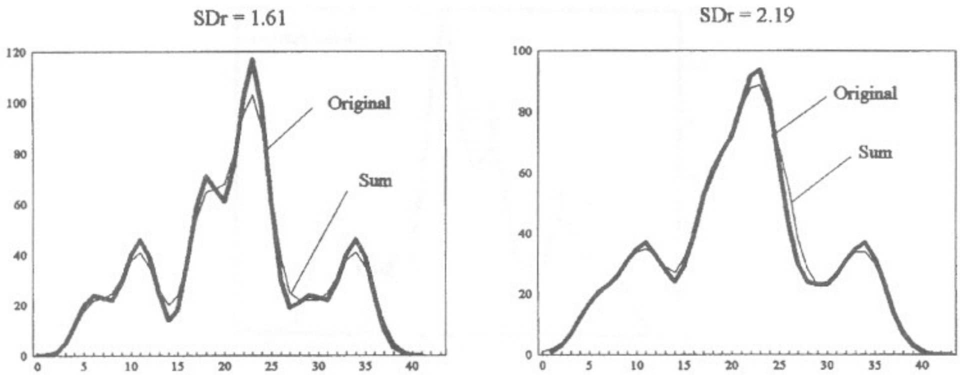

Fig. 11. Comparison of backward summed up reconstructed distributions and original simulated seasonal dynamics patterns (see Fig. 10).

Table 4

Deviations in peaks estimation when simulated pattern is reconstructed with false borders of waves (see Fig. 12)

Groups	Real borders (no. of day)	Real peaks (no. of day)	Deviations from the real values: False borders	Resulted peaks	Corrected borders (1)	Resulted peaks	Corrected borders (2)	Resulted peaks
100		6		0		0		0
	8		0		0		0	
200		11		-1		0		0
	14		-3		0		0	
300		18		-1*		-1		-0.5
	20		-2		-2		0	
500		23		0		0		0
	27		+1		+1		+1	
100		29		+0.5		+0.5		+0.5
	31		0		0		0	
200		34		0		0		0
Sum of deviations			-4	-1.5	-1	-0.5	+1	0

* - additional peak found

composed distribution is cut on waves by incorrect border days. After first reconstruction one of the resulting waves is clearly bimodal, which is not acceptable according to general assumptions of the method (the pattern is composed of normal distributions). It is necessary to correct the wrong border date to the most probable one. Second reconstruction gave acceptable shape of the second wave, but the third one is still asymmetric which suggests second correction. After the second correction reconstructed waves are quite acceptable (Fig. 13, Table 4). Table 4 points at an additional rule which is important when one wants

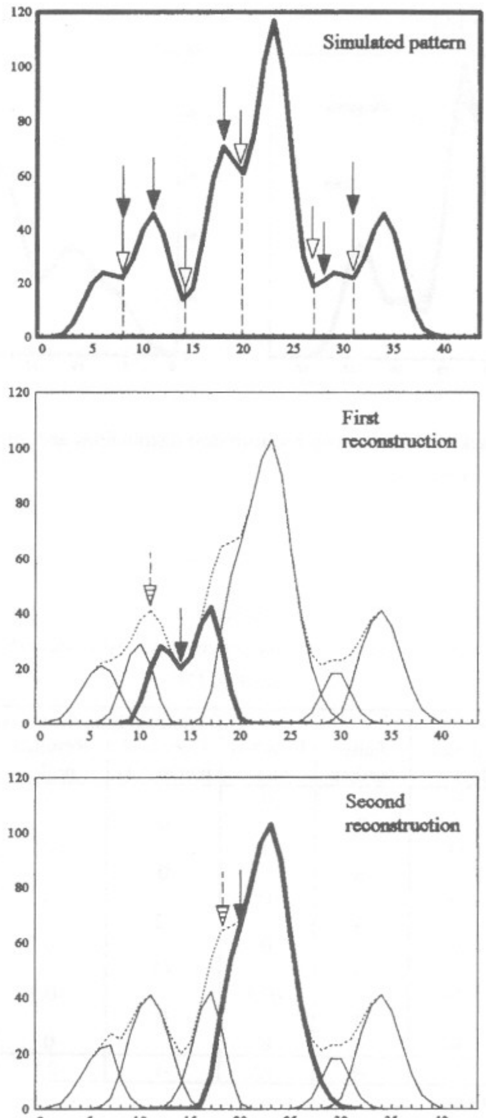

Fig. 12. Iterative modelling of source distributions from the simulated seasonal dynamics pattern (see Fig. 9) when first attempt was made with intentionally mislocated border days. White-headed arrows – exact border days which should be used for efficient modelling (as at Fig. 10), black-headed arrows – these used for reconstruction, hatched-headed arrows – erroneously selected border days corrected in subsequent iterations.

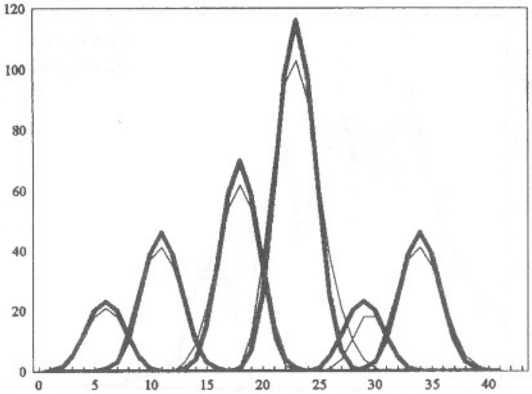

Fig. 13. Comparison of source (thick lines) distributions and these reconstructed (thin lines) in second iteration as shown at Fig. 12.

to estimate size of possible errors in location of the waves tips – these errors are at level of half of the size of the errors made in estimation of wave border days.

Modelling the Willow Warbler seasonal dynamics pattern as an example of the modelling pooled (1962-1990) Willow Warbler seasonal dynamics data from Mierzeja Wiślana are used. Figure 14 contains summarized daily data and smoothed patterns for this station. As at Bukowo station (Fig. 3) the summarized data show quite pronounced day to day differentiation in number of birds. The first pass of smoothing does not smooth out all these differentiations and peak pattern shows at least 8 peaks. The third pass of smoothing suggests that there are four main waves of migrating Willow Warblers. Figure 15 presents the results of modelling procedure. In the first step the pattern was cut onto four pieces according to the most pronounced border days. These days were selected on the basis of raw data close to minima of the smoothed curve. The first step of reconstruction gave four curves, most of them irregular. Irregularities are visible both on reconstructed and once more smoothed distributions. So, corrections were necessary and additional 5 border days were selected according to minima at curves obtained in the first reconstruction and adjusted using raw data curve. Second reconstruction gave 9 waves, three of them a little bit irregular. As these irregularities are small the modelling stopped at this stage.

It is a matter for discussion how to check obtained wave pattern. Some additional data on peaks distribution and border days between them can be obtained when year by year analysis of seasonal dynamics of migration is performed. For every year pattern some most pronounced peak days are selected as well as top days of smoothed yearly dynamics pattern (Fig. 16). Then for every day of the whole period of migration number of found peaks is counted. This is made separately for daily peaks and top days of the smoothed patterns. Obtained distributions point at days when peaks of migration occur most frequently in the

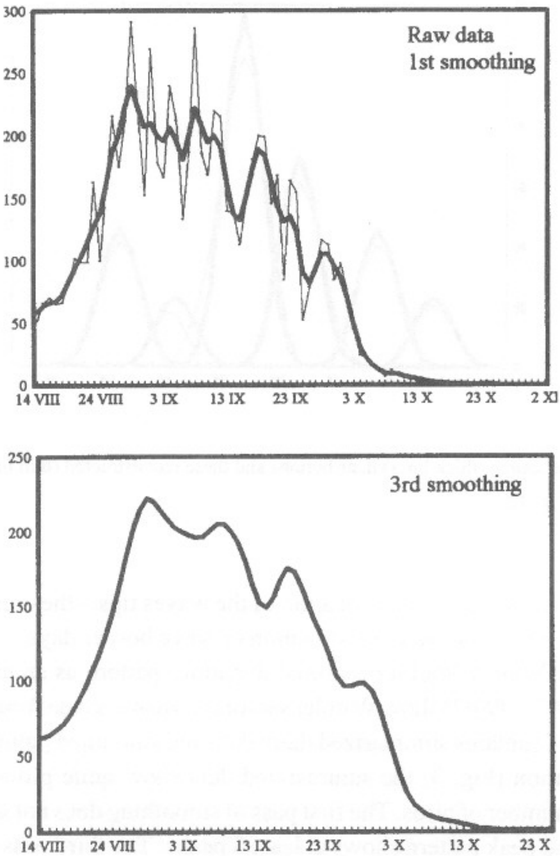

Fig. 14. Total (1962-1990) seasonal dynamics pattern of Willow Warbler migration at Mierzeja Wiślana. Thin line – raw data, thick lines – 1st and 3rd smoothing.

many year dimension. After smoothing these distributions can be compared with each other (Fig. 17). Agreement of the patterns obtained by these three methods is very good and one can conclude that at Mierzeja Wiślana four main waves occur and additional one at the beginning of migration is suggested by distribution of peaks at smoothed yearly patterns. It is natural that daily peaks in this time are rather low in relation to these from the main migration period, so they were not counted as conspicuous ones and they are not shown at the daily peaks pattern.

The general model of Willow Warbler migration over Mierzeja Wiślana can be summarized as shown at Figure 18 and in the Table 5. The most detailed division of the migration onto 9 waves was obtained by means of iterative reconstruction of the wave composi-

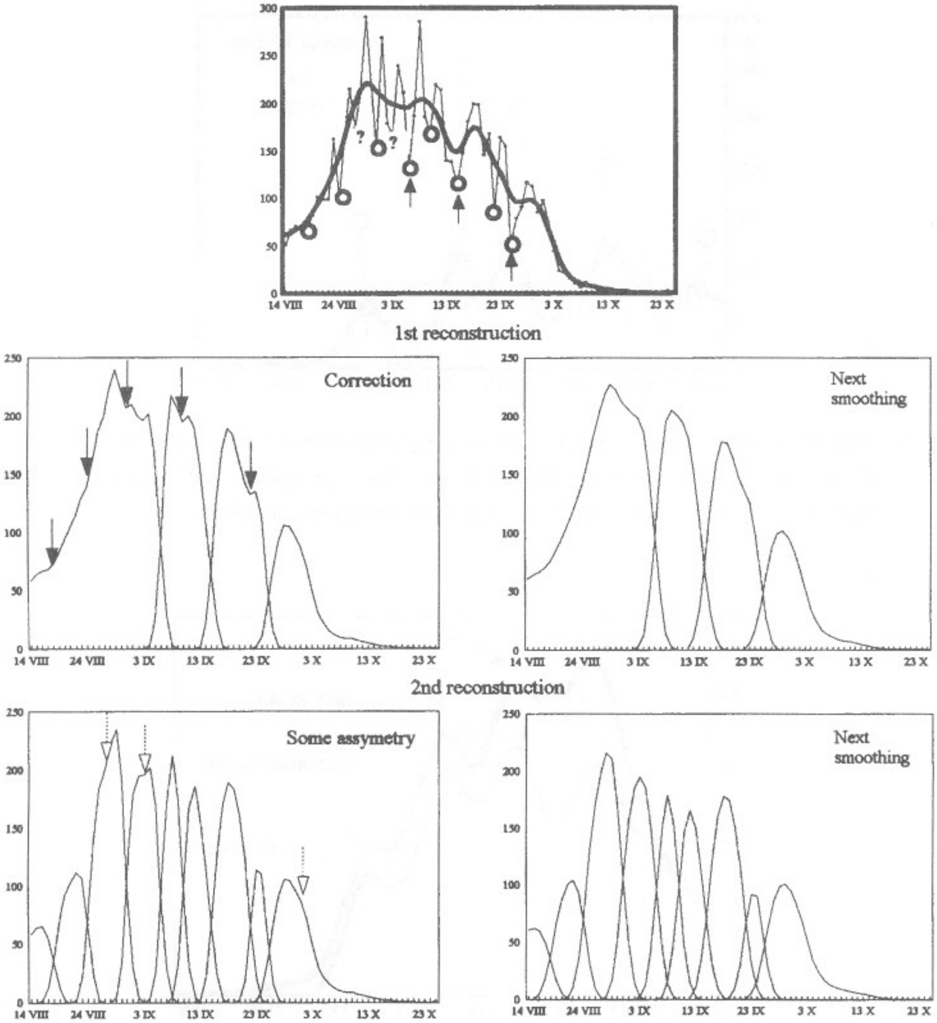

Fig. 15. Iterative modelling of the wave structure of the total seasonal migration pattern shown at Fig. 14 (Willow Warbler, Mierzeja Wiślana). Top graph: total pattern with locations of more pronounced minima (circles), black-headed arrows – minima used as border days in the first step of modelling; middle graphs: result of the first step of the modelling, arrows show additional border days used for the second step of the procedure; bottom graphs: results of the second step of the modelling, arrows point at some residual asymmetries within waves.

tion. This method bases on the assumption that the general seasonal dynamics pattern is the result of summing up series of normal distributions, being representations of subsequent waves of migrants. Other methods applied in the analysis are directed to find the most

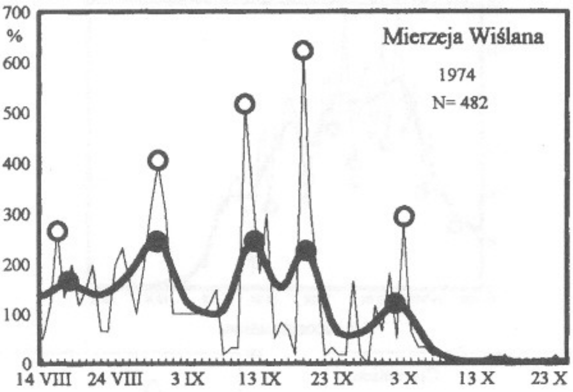

Fig. 16. Example of peaks selected from yearly seasonal migration pattern of Willow Warbler at Mierzeja Wiślana for use in supplementary methods of the modelling. Open circles – daily peaks of migration, black circles – tip days of smoothed curve (after Piotrkowska 1995, modified).

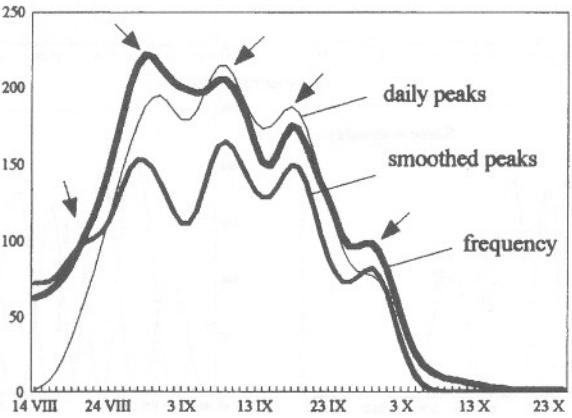

Fig. 17. Main wave structure of Willow Warbler seasonal migration pattern at Mierzeja Wiślana according to different methods: total frequency, yearly daily peaks and yearly smoothed peaks (after Piotrkowska 1995).

pronounced differentiations and they all point in agreement at 5 main waves (I-V) which are equivalents to waves 2, 3, 5 and 9 found according to the wave modelling method. Agreement in the estimation of peak days by means of all methods is very high (Table 5).

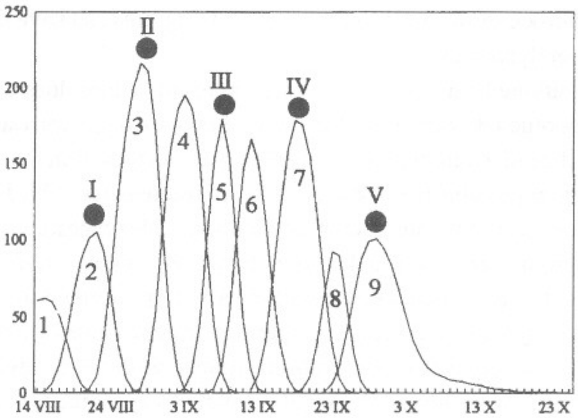

Fig. 18. Wave structure of seasonal migration of Willow Warbler at Mierzeja Wiślana according to the modelling procedure (waves 1 to 9). Main waves as shown by other methods are pointed by black dots and roman numbers (I-V).

Table 5

Seasonal peaks of migration of Willow Warbler at Mierzeja Wiślana according to different methods

Wave (estimated)	Yearly peaks daily	Yearly peaks smoothed	Total (smoothed)	Reconstructed	Wave (see Fig. 18)
	–	–	–	16 Aug.	1
I	–	21 Aug.	–	21/22 Aug.	2
II	30 Aug.	28 Aug.	29/30 Aug.	28 Aug.	3
	–	–	–	3 Sept.	4
III	8 Sept.	9 Sept.	9 Sept.	8 Sept.	5
	–	–	–	12 Sept.	6
IV	18 Sept.	18 Sept.	18 Sept.	19 Sept.	7
	–	–	–	23/24 Sept.	8
V	29 Sept.	29 Sept.	29 Sept.	29 Sept.	9

Estimation of relative frequency of birds in different waves

Comparing seasonal migration dynamics patterns at different bird stations show that relative abundance of migrants passing the stations can be differentiated very much as it is seen e.g. at Figure 4. At Bukowo the most numerous is the first main wave while at Mierzeja Wiślana the most intensive migration takes place 10 days later. In this context estimation of the birds frequencies in waves of migration could be important for monitoring analyses. Some data, both published (Petryna 1976) and preliminary ones (diploma theses written at

University of Gdańsk), show that different waves of migrants can have their own long-term population number dynamics.

As it was mentioned earlier (p. 103) smoothing procedure does not change the total number of the smoothed distribution. Because of that one can accept a sum of values within the wave as an indice of a number size of the particular wave within the whole migration by the station. The other possibility to estimate relative frequencies of birds in different waves is to compare tip values of reconstructed distributions. This measure would be exact only when variance within every wave is the same. However, as it is visible at Figure 18 and in the Table 6, it is not a case when we deal with distributions derived from a real data. Table 6 shows that some estimations done by comparing the peak values are much deviated from the values obtained taking into consideration variance within the waves. Despite that the average size of deviations is lower when higher level of smoothing is used it seems that this last method of estimation is not acceptable for monitoring purposes.

Table 6

Estimated variance and size of Willow Warbler waves at Mierzeja Wiślana

Wave (see Fig. 18)	SD	Number indice		Distribution maximum					
				1st smoothing			2nd smoothing		
		Value	%	Value	%	Deviation	Value	%	Deviation
1	1.62	290	**3.8**	65	4.6	0.8	62	4.8	1
2	2.21	629	**8.3**	112	7.8	-0.5	105	8.1	-0.2
3	2.36	1404	**18.5**	235	16.5	-2	216	16.7	-1.8
4	2.22	1210	**15.9**	202	14.2	-1.7	195	15.1	-0.8
5	1.76	810	**10.7**	213	15.1	4.4	179	13.8	3.1
6	1.98	854	**11.2**	186	13.1	1.9	166	12.8	1.6
7	2.39	1140	**15.1**	189	13.3	-1.8	178	13.7	-1.4
8	1.59	387	**5.1**	114	8.1	3	92	7.1	2
9	4.77	865	**11.4**	106	7.4	-4	101	7.8	-3.6
Average size of deviation						2.23			1.72

CONCLUSIONS

1. Seasonal dynamics pattern of the species is composed of a row of waves of birds migrating through the particular locality one after another.
2. The pattern of the passage is repeated year by year with quite high accuracy being, however, altered by random fluctuations of environmental variables.
3. The average seasonal migration dynamics can be described by pooling yearly dynamics data into the total composed distribution.
4. Subsequent waves can be reconstructed from the total pattern as a row of quasi-normal distributions by means of iterative modelling procedure:

   I. choose estimated border days (basing on a shape of the total distribution),

II. cut the total distribution data onto pieces limited by border days; border days values should be divided by two (the shares of bordering waves are equal here) and these halves should be used as these day values in both waves; in a case when we decide to put the border between two days (e.g. in a case of two equal low number days) we use the earlier day value to the earlier wave and accordingly the later to the later wave),

III. smooth the values in every part of data separately using the mentioned earlier smoothing formula; the smoothing procedure add lower and upper tails to the modeled distribution (wave),

IV. plot obtained distributions against the time scale,

V. check unimodality and skewness of resulted distributions; when any of them is still asymmetric or polymodal, add next estimated border days and repeat procedures I to IV as the next step of iteration.

5. Obtained reconstruction of the contents of seasonal dynamics pattern can be used for the estimation of relative frequencies of birds belonging to subsequent waves. These results could be useful for deeper monitoring studies and for comparisons between passage patterns at different bird stations.
6. The wave-like structure of the seasonal migration pattern cause that attempts of the statistical description of the pattern by means of average day (and the standard deviation) as well by median day and percentiles are biologically meaningless.

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