

AUTUMN MIGRATION DYNAMICS AND BIOMETRICAL
DIFFERENTIATION OF THE DUNNOCK
(*Prunella modularis*) PASSING THE SOUTHERN BALTIC COAST

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ABSTRACT

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The aim of this study is to determine biometrical differentiation among Dunnocks caught at the two ringing sites (Bukowo-Kopań and Mierzeja Wiślana) located on the southern Baltic coast. The distance between those two stations covers 190 km. The material was collected during autumn fieldwork of the Operation Baltic in 1961-2003. The material used for biometrical analysis comprises only immature birds from the period of the most intensive migration, when the numbers of caught individuals allowed to compare the results for both stations. The seasonal dynamics at both sites was pooled for 43 years of catching. Medians of autumn migration for the stations were significantly different. A shift of the median for the eastern site (Mierzeja Wiślana) by 6 days after the median for the western site (Bukowo-Kopań) suggested different origins of birds migrating through the stations. The analysis of standard deviations for the studied biometrical parameters confirms an intra-seasonal change in proportions of birds probably originating from different areas in Europe.

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INTRODUCTION

The knowledge of the Dunnock's migration and its biometrical differentiation is rather fragmentary. Based on the data collected at the Operation Baltic stations some preliminary analyses were made by Busse and Halastra (1981). The first element that was taken into account during biometrical analysis of the species was the comparison of wing shape among four geographical populations (Scott 1962). The difference between the 2nd and 7th primary was examined. Somewhat later, for the stations located on the southern Baltic coast the variation of wing shape was analysed using two more precise indices (*e* and *l*) relating to the wing asymmetry and pointedness (Nitecki 1969).

According to the studies on German populations of Dunnocks it was possible to find a relationship among the wing length, wing formula and migration distance (Mead 1983).

The aim of my study is to determine the differentiation of migration dynamics and biometrical parameters among Dunnocks caught at two distant ringing stations as well as the relationship between those two aspects.

STUDY AREA AND MATERIAL

The data were collected at two stations of the Operation Baltic located on the Polish Baltic coast (Fig 1):

Mierzeja Wiślana (54°21'N, 19°19'E). Catching in mist-nets, in some years additionally in helgoland-type trap. Places of catching were located on the Vistula Spit in young pine stands and middle-aged stands mixed with oak and in reedbeds surrounding the Vistula Lagoon.

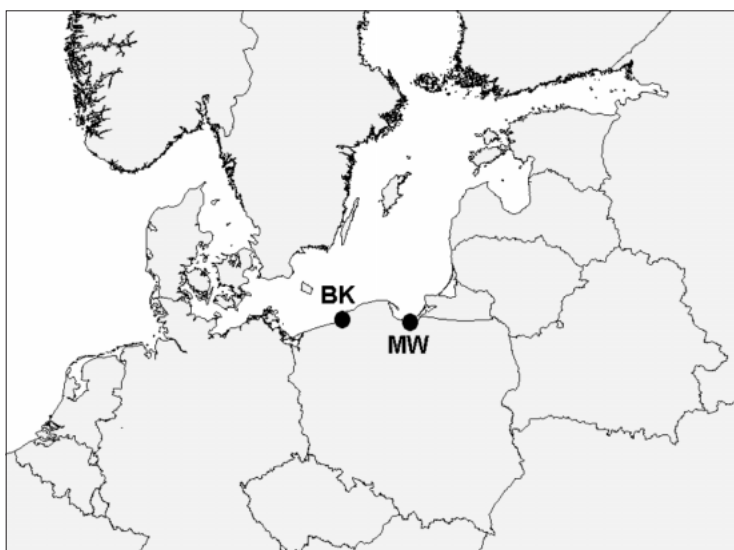


Fig. 1. Localization of ringing stations where the data were collected: BK – Bukowo-Kopań, MW – Mierzeja Wiślana

Bukowo-Kopań (54°21'N, 16°17'E / 54°28'N, 16°25'E). Catching in mist-nets. In 1961-1984, places of catching were located in a narrow stripe of land between the sea and Lake Bukowo, and since 1983 onward – 15 km to the northeast in a narrow stripe of forest lying between the sea and wet meadows neighbouring with Lake Kopań.

Material was collected during autumn migration. The basic standard season was established and standardized to the period 14 August – 31 October in years 1961-2003 (Table 1). Biometrical analyses comprised 653 and 363 individuals (for Bukowo-Kopań and Mierzeja Wiślana stations, respectively).

Table 1
Periods of work of the stations and numbers of caught birds

Years	Bukowo-Kopań		Mierzeja Wiślana	
	Period of work	<i>N</i>	Period of work	<i>N</i>
1961	15 Sep. - 14 Oct.	2	15 Sep. - 14 Oct.	4
1962	11 Sep. - 10 Oct.	34	22 Aug. - 30 Sep.	2
1963	6 Sep. - 15 Oct.	43	17 Aug. - 30 Oct.	15
1964	6 Sep. - 15 Oct.	18	17 Aug. - 25 Oct.	15
1965	7 Sep. - 15 Oct.	18	17 Aug. - 25 Oct.	32
1966	6 Sep. - 15 Oct.	25	17 Aug. - 25 Oct.	26
1967	17 Aug. - 25 Oct.	83	17 Aug. - 25 Oct.	21
1968	17 Aug. - 25 Oct.	44	17 Aug. - 25 Oct.	14
1969	17 Aug. - 25 Oct.	9	17 Aug. - 25 Oct.	19
1970	6 Sep. - 10 Oct.	40	17 Aug. - 14 Nov.	31
1971	17 Aug. - 22 Oct.	36	17 Aug. - 14 Nov.	54
1972	14 Aug. - 27 Oct.	4	14 Aug. - 17 Nov.	13
1973	14 Aug. - 27 Oct.	17	14 Aug. - 16 Nov.	18
1974	14 Aug. - 27 Oct.	15	14 Aug. - 1 Nov.	32
1975	14 Aug. - 27 Oct.	27	14 Aug. - 1 Nov.	44
1976	14 Aug. - 1 Nov.	17	14 Aug. - 1 Nov.	16
1977	16 Aug. - 1 Nov.	27	16 Aug. - 1 Nov.	17
1978	14 Aug. - 1 Nov.	11	14 Aug. - 1 Nov.	9
1979	16 Aug. - 1 Nov.	1	14 Aug. - 1 Nov.	3
1980	14 Aug. - 1 Nov.	4	14 Aug. - 1 Nov.	5
1981	14 Aug. - 1 Nov.	44	14 Aug. - 1 Nov.	32
1982	14 Aug. - 1 Nov.	46	14 Aug. - 1 Nov.	35
1983	14 Aug. - 1 Nov.	30	14 Aug. - 1 Nov.	15
1984	14 Aug. - 1 Nov.	1	14 Aug. - 1 Nov.	15
1985	14 Aug. - 1 Nov.	6	14 Aug. - 1 Nov.	16
1986	14 Aug. - 1 Nov.	0	14 Aug. - 1 Nov.	12
1987	14 Aug. - 1 Nov.	2	14 Aug. - 1 Nov.	25
1988	14 Aug. - 1 Nov.	1	14 Aug. - 1 Nov.	6
1989	14 Aug. - 1 Nov.	4	14 Aug. - 1 Nov.	5
1990	14 Aug. - 1 Nov.	37	14 Aug. - 1 Nov.	17
1991	14 Aug. - 31 Oct.	8	14 Aug. - 1 Nov.	9
1992	14 Aug. - 31 Oct.	3	14 Aug. - 1 Nov.	8
1993	14 Aug. - 31 Oct.	9	14 Aug. - 1 Nov.	30
1994	14 Aug. - 31 Oct.	23	14 Aug. - 1 Nov.	6
1995	14 Aug. - 31 Oct.	27	14 Aug. - 1 Nov.	10
1996	14 Aug. - 31 Oct.	16	14 Aug. - 1 Nov.	29
1997	14 Aug. - 31 Oct.	20	14 Aug. - 1 Nov.	12
1998	14 Aug. - 31 Oct.	42	14 Aug. - 1 Nov.	16
1999	14 Aug. - 31 Oct.	27	14 Aug. - 1 Nov.	8
2000	14 Aug. - 31 Oct.	21	14 Aug. - 1 Nov.	1
2001	14 Aug. - 31 Oct.	41	14 Aug. - 1 Nov.	15
2002	14 Aug. - 31 Oct.	33	14 Aug. - 1 Nov.	15
2003	14 Aug. - 31 Oct.	28	14 Aug. - 1 Nov.	10
Total		944		737

METHODS

Birds were caught mainly in mist-nets controlled every hour from dawn to dusk. Caught birds were ringed and measured using the SEEN standards (Busse 2000). From each Dunnock the following measurements were taken: wing length, tail length and wing formula. Birds were also scored for fat, weighed to the nearest 0.5 g until 1998 and to the nearest 0.1 g since 1998.

Data analyses

Based on the material collected in 1961-2003 two multi-year dynamics were prepared, showing quantitative trends in the catching of Dunnocks for both stations. To compare those two dynamics the catch numbers in a given year were converted to percent values in relation to the average season within the 1961-1970 period according to the formula:

$$n_{\%} = \frac{n_y}{n_p} \times 100\%$$

where:

- $n_{\%}$ – percentage,
- n_y – number of birds caught in a given year,
- n_p – average number of birds caught within a season for the 1961-1970 period.

Next, in order to facilitate the comparison of multi-year dynamics between the stations, the coefficient of fluctuations (CF), which is used for the evaluation of multi-year fluctuations, was calculated according to the formula by Busse (2000):

$$CF = \frac{1}{M} \times \frac{\sum \frac{(X_{oy} - X_y)^2}{X_{oy}}}{N} \times 100\%$$

where:

- X_y – number of birds in year y ,
- X_{oy} – moving average for year y ,
- N – number of study years,
- M – total average.

The moving weighted-average smoothed numbers for five following years (Busse 1973) and was calculated according to the formula by Busse (1996):

$$C_{kn} = 0.06a + 0.24b + 0.4c + 0.24d + 0.06e$$

where :

- C_{kn} – moving weighted-average number of birds in year C ,
- a, b, c, d, e – numbers of birds in the five subsequent years.

Analysis of seasonal migration dynamics

Due to small numbers of Dunnocks caught at both stations within single seasons, the seasonal dynamics was prepared based on all the years jointly, by pooling numbers of birds for each day apart. In order to consider the differences in lengths of catching periods between particular seasons, the sum of birds caught on a given day was first divided by the number of seasons, during which the station actually worked

on that day, and next the result was multiplied by the highest number of working seasons. As a result of this method all the adjacent days obtained the same weight.

Similarly to the multi-year dynamics, the coefficient of fluctuation (*CF*) was used for the comparisons.

The next stage of the analysis was calculating median dates of seasonal dynamics for both stations and comparing them by the Mann-Whitney *U*-test.

In order to determine passage minima, the data pooled for all the 43 years of study were used as well. An advantage of such a method, as compared to the analysis of particular seasons apart, is an insight independent of weather circumstances, which within a single season may essentially influence terms of passage minima. According to the non-smoothed (raw) seasonal dynamics, the standard period was divided into smaller fragments – so called “waves” of migration. The waves of migration were separated by dates on which the numbers of birds caught were clearly lower than on the adjacent days (the passage minima). A detailed description of dividing migration dynamics into waves is given in papers by Busse (1996) and Kopiec-Mokwa (1999). In the next stage, the dynamics curve was three times smoothed by the moving weighted-average, as in the case of multi-year dynamics.

Biometrical analysis

In order to have as homogenous group of birds as possible only young individuals were considered in biometrical analysis. The standard period, in which the numbers of birds caught were high enough, was established for 5 September – 11 October.

Biometrical comparisons were based on wing length, tail length, standardized body mass, as well as on wing pointedness (*L*) and asymmetry (*E'*) indices (Busse 2000).

In order to obtain the standardized body mass, the average weight of birds for each fat score class was calculated. The average weight of birds from the most common fat score class became the basis for comparisons. To obtain body mass of each individual, comparable regardless of its fat load, a correction was subtracted from its actual body mass. These corrections were calculated, according to the formula by Busse (2000):

$$c_i = C_{Ti} - C_{T2}$$

where:

c_i – correction for the fat score T_i ,

C_{Ti} – average body mass of birds with the same fat score,

C_{T2} – average body mass of birds with the most common fat score (T_2).

Wing asymmetry (*E'*) and pointedness (*L*) indices were calculated based on the quantitative wing formula according to the following equations (after Busse 1986):

$$E' = \frac{\sum p - \sum d}{\sum p + \sum d} \times 100\%$$

$$L = \frac{\sum p + \sum d}{w} \times 100\%$$

where:

$\sum p$ – sum of distances from wing tip to the tips of proximal primaries,

$\sum d$ – sum of distances from wing tip to the tips of distal primaries,

w – wing length.

In order to find potential intra-group differentiation, a biometrical method called “correlative topography”, which reveals differences within the group of individuals of the same species (Busse 1968, 2000), was applied. Based on this method and using SURFER software, correlation charts and their three-dimension presentations were prepared, for the stations and pairs of parameters separately.

The next stage of the analysis was calculating multi-year average daily values of wing and tail lengths, standardized body mass, wing pointedness and asymmetry indices as well as wing/tail ratio. These averages were calculated from all birds caught on a given day throughout 43 years of study. Then, seasonal fluctuations of daily averages were illustrated in the form of charts. After their twice smoothing by the moving weighted-average, the trends were compared between the stations within the standard period (5 September – 11 October). Next, for each parameter the Pearson’s correlation coefficient r was calculated for the linear dependence between its changes at both stations.

The next part of the biometrical analysis was calculating differences between the averages of the studied parameters for the adjacent days. The values of the differences were plotted on bar graphs prepared for both stations. Afterwards, the standard period was divided into two equal parts and for both of them standard deviations of the differences were calculated. The standard deviations were compared with the Fisher’s exact test.

RESULTS

The multi-year dynamics of catch numbers for Bukowo-Kopań station within the period from 1961 to 1987 demonstrated a clear declining tendency with slight increases in numbers around the years: 1970, 1976 and 1982 (Fig. 2). Starting from 1982, the numbers remained stable at the average level of 38% with an apparent decrease in 1984-1989. Somewhat different situation developed at Mierzeja Wiślana, where at the beginning a clear decline from the level similar to Bukowo-Kopań appeared, and next, starting from 1970, the numbers were rising again until 1975, when they reached the highest value for this station. The lowest number of caught birds appeared in 1979, afterwards, another increase occurred and subsequent fluctuations remained at the level of 100% of the multi-year average for the 1961-1970 period. The value of the coefficient of fluctuations CF for Bukowo-Kopań was higher than for Mierzeja Wiślana. At Mierzeja Wiślana it reached 35.9, at Bukowo-Kopań – 46.3.

Seasonal dynamics

The extent of seasonal fluctuations defined by the coefficient of fluctuations for the raw data reached 14.5 at Bukowo-Kopań, and at Mierzeja Wiślana it was a bit lower – 13.6. However, the more important factor discriminating these two dynamics was the passage median date, which at Bukowo-Kopań fell on 26 September, whereas at Mierzeja Wiślana – 6 days later, *i.e.* on 2 October (Fig. 3).

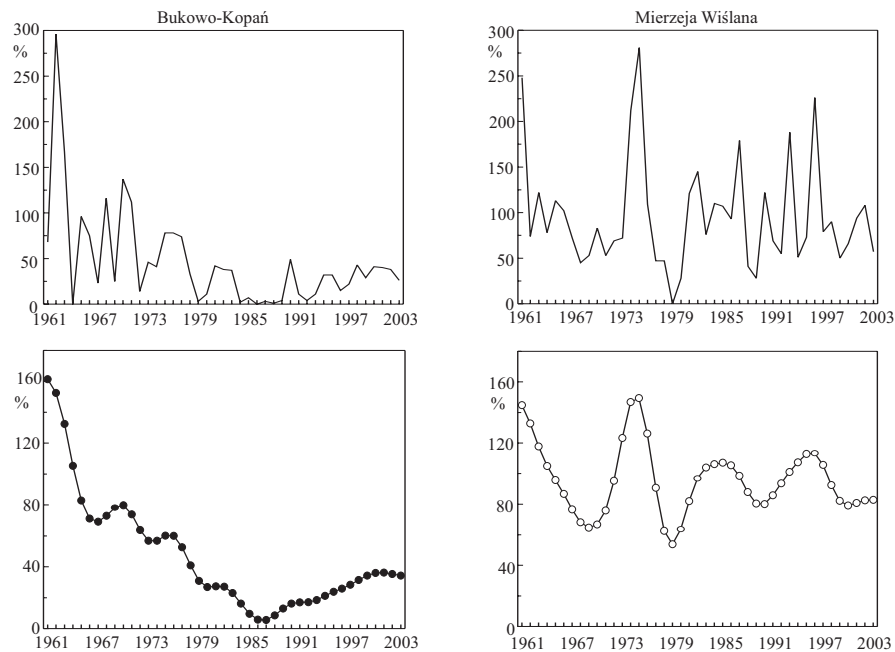


Fig. 2. Long-term dynamics of catch numbers for the Bukowo-Kopań and Mierzeja Wiślana stations (1961-2003). Above: raw data; below: after triple smoothing by 5-year moving weighted-average.

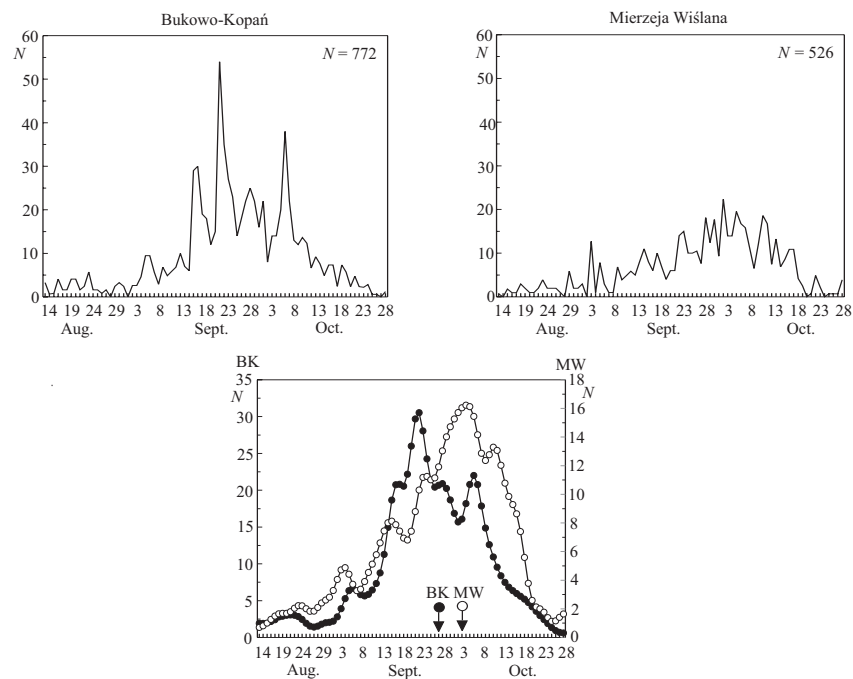


Fig. 3. Seasonal migration dynamics at both stations in the standard period – from 14 August to 31 October. Lower panel: the comparison of dynamics from both the stations – Bukowo-Kopań (BK) and Mierzeja Wiślana (MW) – after triple smoothing by the moving weighted-average. The medians (significantly different – Mann-Whitney U -test: $p < 0.001$) denoted by arrows.

Division into waves of migration

Based on the division of seasonal migration dynamics according to the raw data, in the period from 14 August to 31 October, for the Bukowo-Kopań station 10 waves of passage specified by numbers from 0 to 9, were distinguished (Fig. 4). At Mierzeja Wiślana there were 11 waves (0-10). The waves that least fitted to normal distribution occurred at the beginning and at the end of the standard period of catching (Fig. 4).

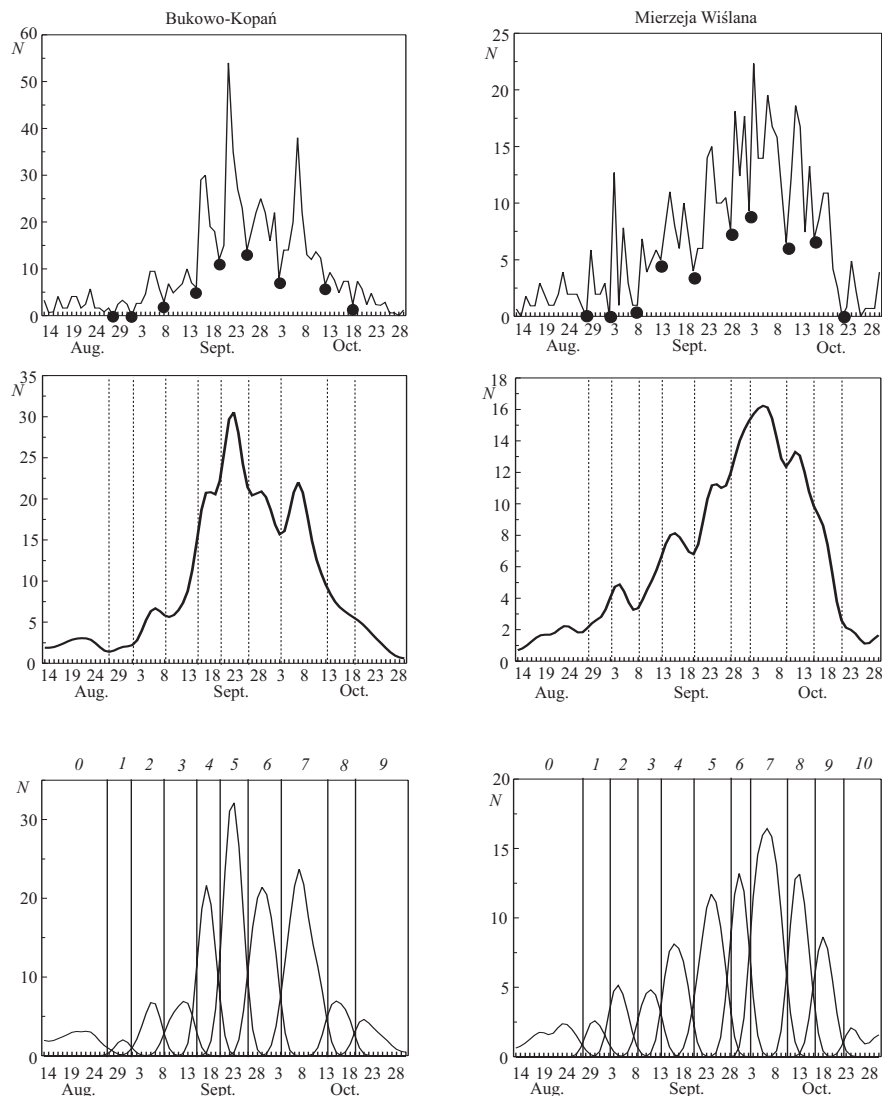


Fig. 4. The procedure of establishing migration waves for both stations: upper panels – passage minima denoted on the seasonal dynamics curves by black dots, middle panels – seasonal dynamics smoothing curves, lower panels – migration waves reconstructed according to the minima of passage (numbers of waves are given).

Within these waves (at Bukowo-Kopań - 0 and 9; at Mierzeja Wiślana 0 and 10), as can be seen on the seasonal dynamics graph, small numbers of birds were caught.

For both analysed stations the terms of the established waves of passage were very close. For waves denoted by 0 their dates were exactly the same, for waves 1-4 the discrepancies did not exceed one day, for waves 5-7 the differences in terms increased to two days, and further, the last two waves established for Bukowo-Kopań at Mierzeja Wiślana became divided into three shorter sections.

As it results from the established borders, the longest at both stations was wave 0. It included the first period of Dunnocks' catching and lasted 15 days. During this time 4.6% and 4.5% of all the birds were caught at the Bukowo-Kopań station and at Mierzeja Wiślana, respectively (Fig. 5). As it represented rather low level of passage (as well as wave 1), these waves revealed probably only postbreeding dispersal of Dunnocks. An increase in percent share of caught birds started gradually from the wave 2 and probably marked the actual beginning of the Dunnock passage through the Polish Baltic coast.

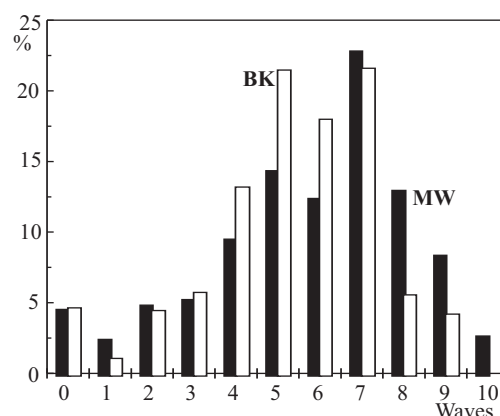


Fig. 5. Percentage share of birds in subsequent waves of migration – a comparison of both the stations: Bukowo-Kopań (BK) and Mierzeja Wiślana (MW).

The subsequent waves differed in percentage of birds caught – within one station as well as between them (Fig. 5). The percent shares of Dunnocks in respective waves were strictly related to the shift of the passage median date.

Biometrical analysis

Standard period, in which the biometrical analysis was possible, consisted of 37 days from 5 September to 11 October (Fig. 6) and comprised the term of the most intensive migration at both stations. During this time 80.5% and 66.7% of Dunnocks were caught at Bukowo-Kopań and Mierzeja Wiślana, respectively. The reason for the lower percentage at Mierzeja Wiślana was the shift in the median date of passage by 6 days in relation to Bukowo-Kopań, and thus failure in establishing dates of standard period that would include similar percentage of migrating Dunnocks.

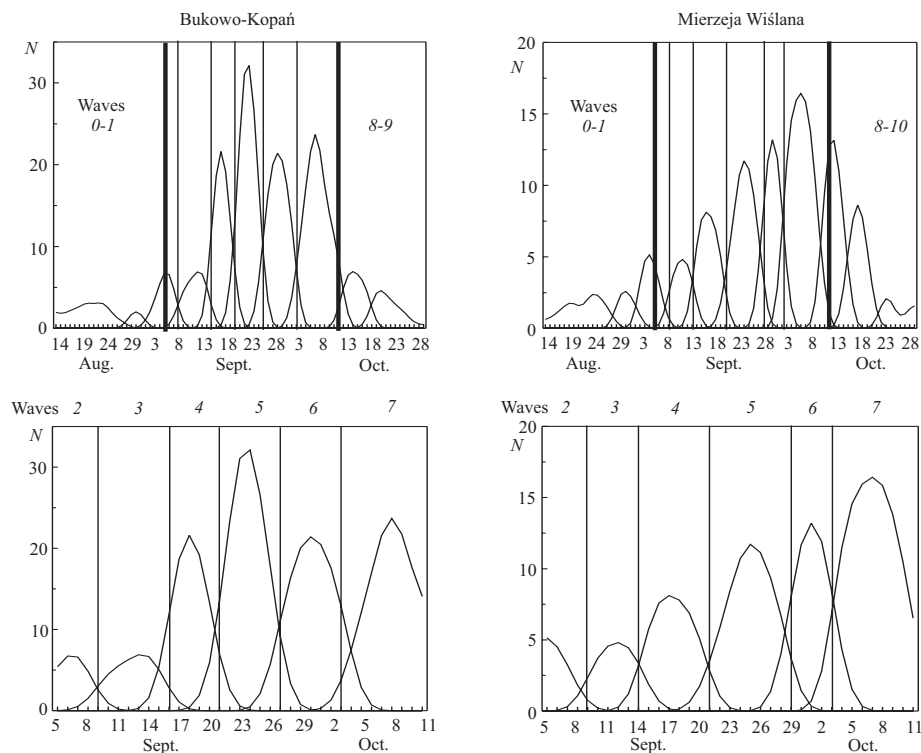


Fig. 6. Standard period established for biometrical comparisons. Upper panels: the standard period (from 5 September to 11 October) limited by thick vertical lines, lower panels: subsequent waves of the standard period. Numbers of waves are given.

At both stations the standard period for biometrical analysis comprised 6 subsequent waves of migration, specified by numbers from 2 to 7.

Verifying biometrical homogeneity of the material

At both charts presenting relations of wing length to tail length and also numbers of caught birds with definite combinations of these two parameters three peaks are clearly visible (Fig. 7). The peaks are marked by black dots.

The first combination of wing and tail lengths (denoted by I) is identical for both stations (Table 2). The only differences concern the numbers of birds in this group – at Bukowo-Kopań the birds were relatively more numerous. The second peak is characterized by the same wing length for both stations, however differences in tail length occurred. At Mierzeja Wiślana the tail was 1 mm longer. In the next group of birds, denoted by III, there were not any differences in the wing length either, and, similarly to the second group, at Mierzeja Wiślana the tail was 1 mm longer.

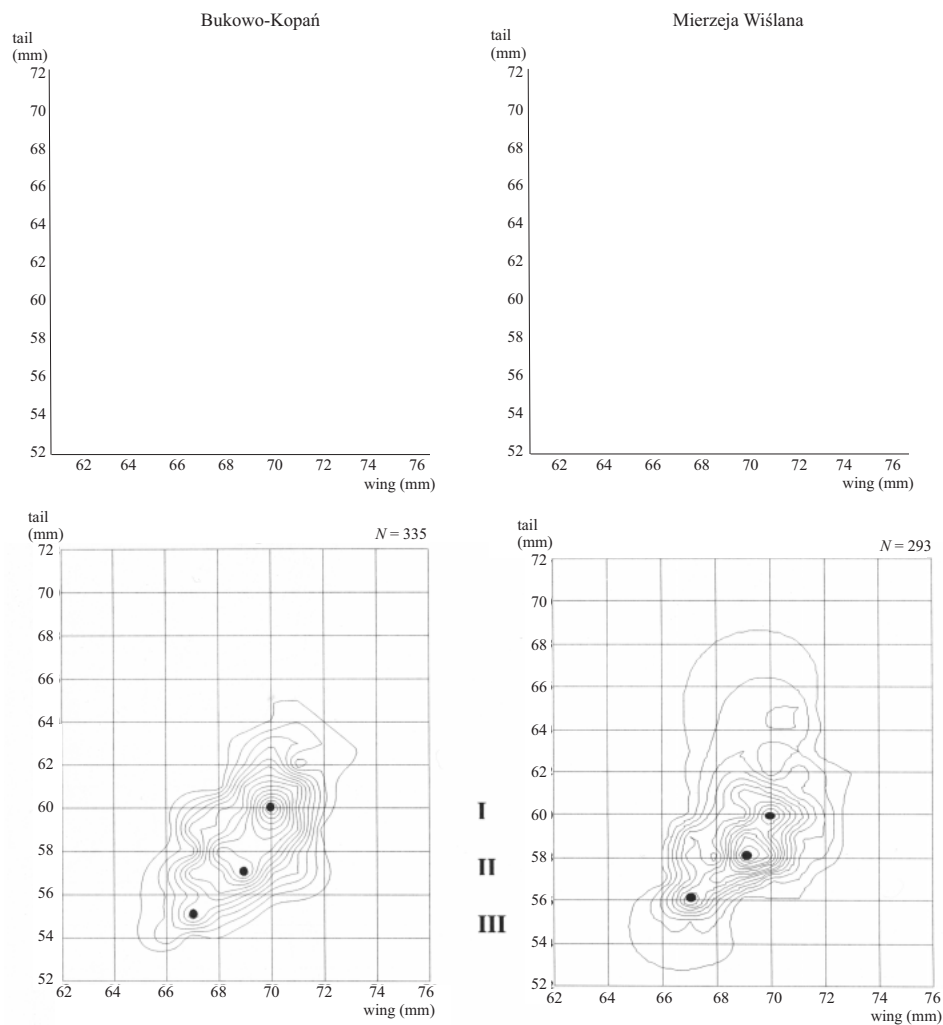


Fig. 7. Presentation of percentage shares of Dunnocks representing particular combinations of wing and tail lengths: correlation charts (below) and their three-dimension images (above). Prepared according to krigging procedures.

Table 2
Three most numerous combinations of wing and tail lengths (mm)
at Bukowo-Kopań and Mierzeja Wiślana stations

Bukowo-Kopań				Mierzeja Wiślana			
Peaks	Wing	Tail	<i>N</i>	Peaks	Wing	Tail	<i>N</i>
I	70	60	15	I	70	60	12
II	69	57	12	II	69	58	15
III	67	55	8	III	67	56	10

Fluctuations of daily averages for the studied parameters

The comparison of daily averages' dynamics (Fig. 8) revealed considerable differences between Bukowo-Kopań and Mierzeja Wiślana stations. This is also confirmed by the weakness of correlations between the same parameters at both stations.

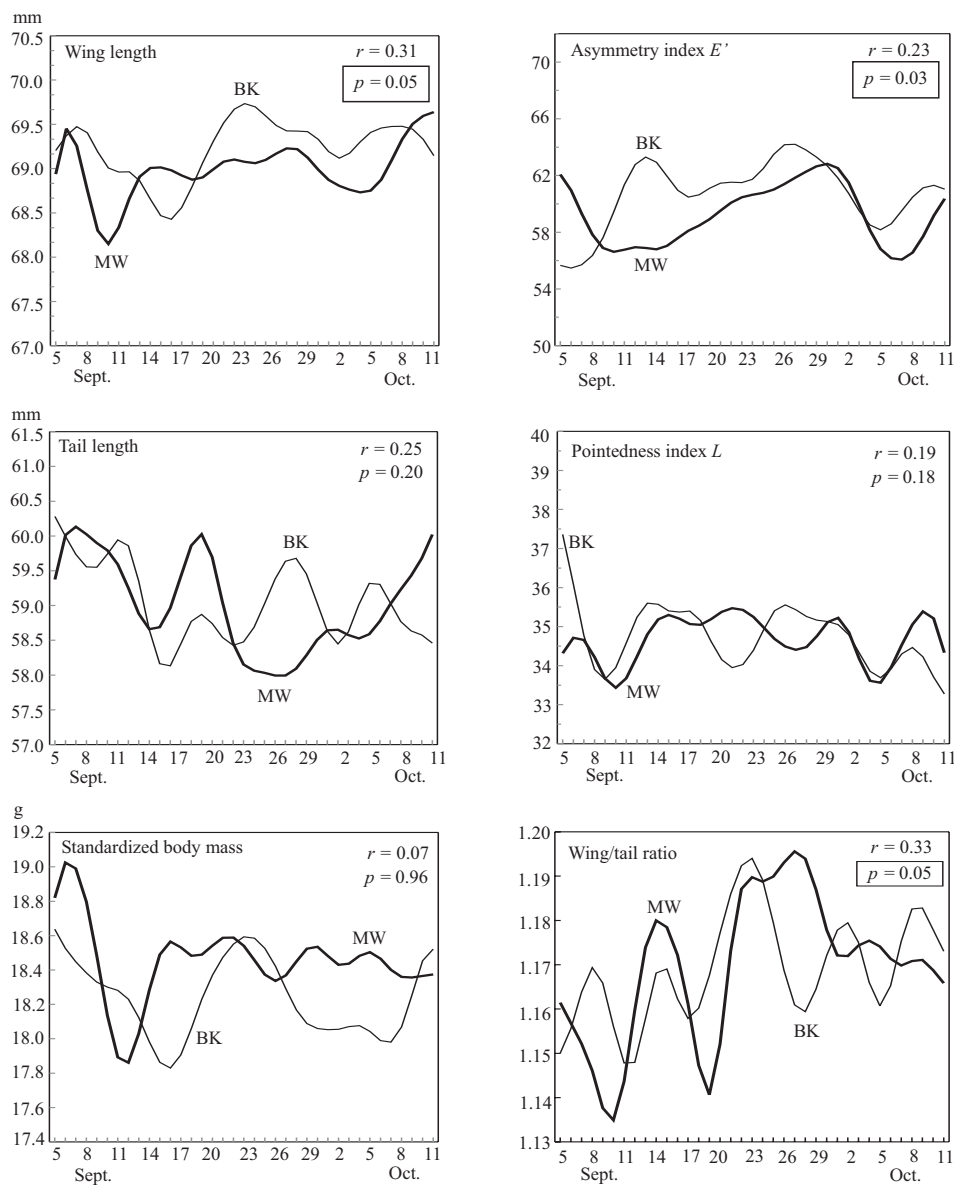


Fig. 8. Changes of daily average values for all the analysed parameters at Bukowo-Kopań (BK) and Mierzeja Wiślana (MW). The dynamics smoothed twice by five-day moving average.

The analysis of the fluctuations of the differences between adjacent days (expressed by *SD*) in the averages of the parameters describing size of birds (*i.e.* standardized body mass, wing and tail lengths) revealed considerable directional differentiation appearing up to the middle of the study period (23 September) at Mierzeja Wiślana (Fig. 9). Large differences occurring at this time may reflect high intra-group

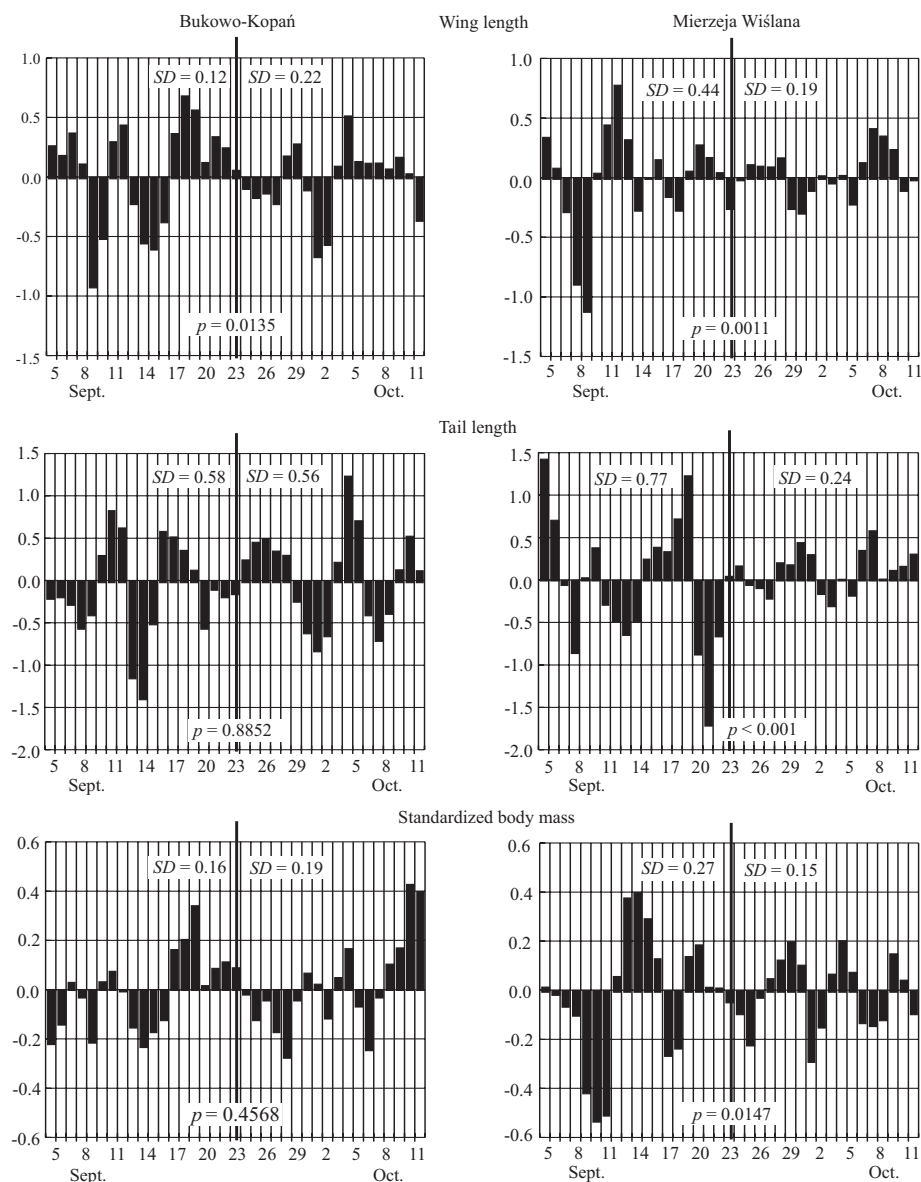


Fig. 9. Differences in average values of size parameters between the adjacent days. The border between the first and second half of the standard period for biometrical analysis marked by a thick vertical line. The value of *p* for difference of *SD* are given according to Fisher's exact test.

diversity of Dunnocks passing through this station. Moreover, it is noticeable that the changes were not accidental, what is confirmed by directionally changing differences forming quite regular several-days-long blocks on the chart. Afterwards, the “wavy” character of differences’ dynamics still continued, however the differences between

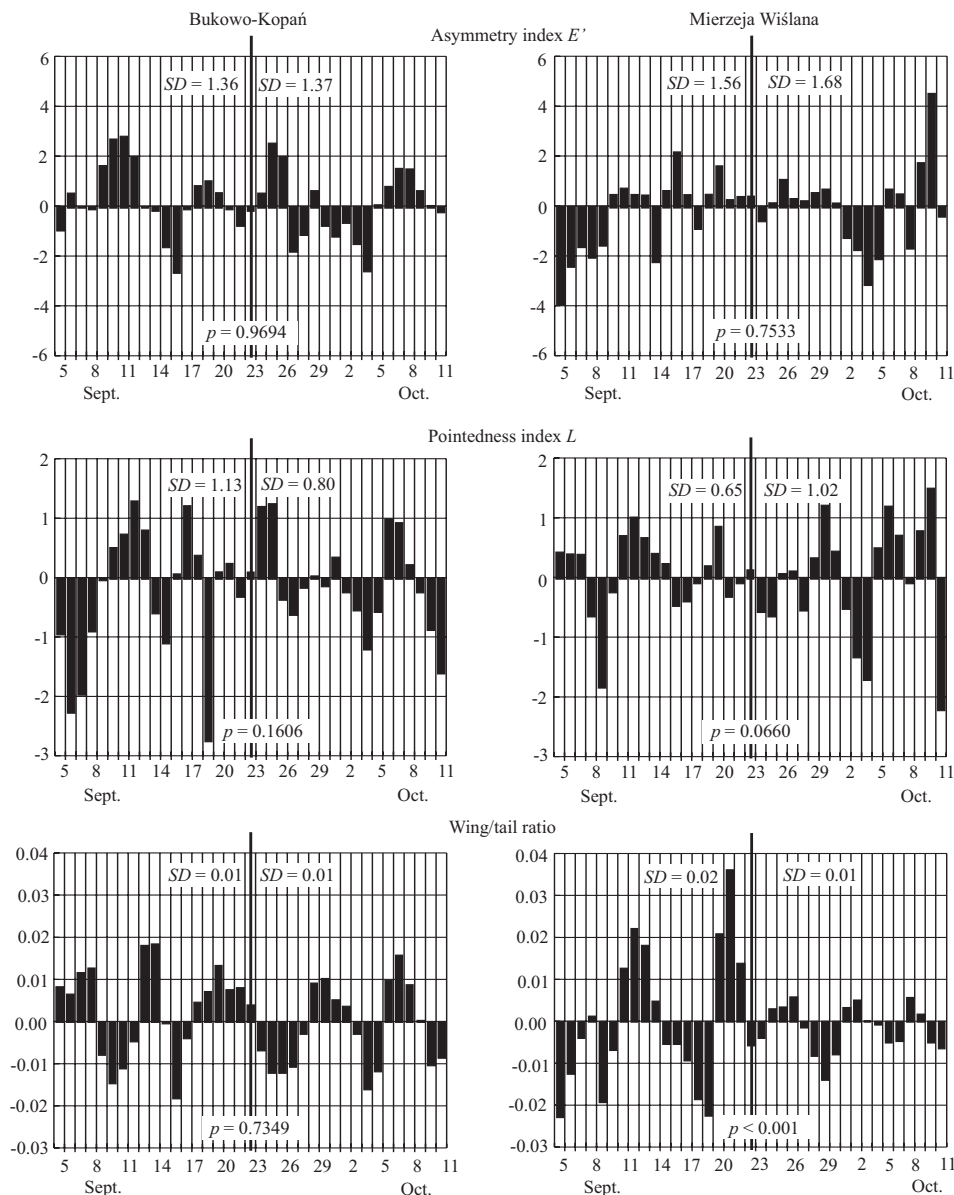


Fig. 10. Differences in average values of shape parameters between the adjacent days. The border between the first and second half of the standard period for biometrical analysis marked by a thick vertical line. The value of p for difference of SD are given according to Fisher's exact test.

averages clearly decreased, what is confirmed by large differences in standard deviations calculated for both halves of the analysed period. This may indicate more homogenous groups of birds migrating in the second half of the study period. The differences between standard deviations were statistically significant for all three size parameters. The situation at Bukowo-Kopań was different – only for the wing length the differences between standard deviations were statistically significant. For the rest of the analysed parameters the values were similar in both halves of the study period.

The analysis of shape parameters, (*i.e.* wing/tail ratio, asymmetry and pointedness indices) revealed statistically significant differences between both halves of the study period only in the standard deviations for the wing/tail ratio at the Mierzeja Wiślana station (Fig. 10). At Bukowo-Kopań the standard deviations for all these parameters did not differ significantly between the parts of the analysed period.

Biometrical differentiation among the waves

The average wing lengths for particular waves were different, however the directions of their changes were similar at both the stations (Fig. 11, Table 3). Only between wave 3 and 4 there were slight differences in the course of these values. At Mierzeja Wiślana the average wing length in wave 4 was larger than in wave 3, while at Bukowo-Kopań in both waves the values were similar. At Bukowo-Kopań within the standard period established for biometrical analysis statistically significant differences occurred between waves 2 and 3, 4 and 5, as well as 5 and 6, whereas at Mierzeja Wiślana there were not any significant differences.

Concerning the wave averages of the tail length the directions of their changes were similar at the two stations only at the beginning and at the end of passage (Fig. 11, Table 3). For waves 4-6 the directions of changes differed between the stations. There were no statistically significant differences between the analysed waves at both stations.

The directions of changes in the average standardized body mass for waves 4-6 were analogous to the tail length at both stations (Fig. 11, Table 3). Statistically significant differences occurred at Bukowo-Kopań between waves 4 and 5 as well as 5 and 6. At Mierzeja Wiślana there was only one difference between wave 2 and 3.

In the case of shape parameters a larger differentiation was revealed for the wing asymmetry index E' (Fig. 12, Table 3). Its wave averages were diverse at both ringing stations. A statistically significant difference occurred at Bukowo-Kopań between wave 2 and 3. At Mierzeja Wiślana there was a difference between wave 6 and 7.

The wing pointedness index L was the last analysed parameter. The directions of changes in its wave average values were the most similar between the stations and no significant differences between the waves of the analysed period were revealed (Fig. 12, Table 3).

Having compared between the stations the corresponding wave averages for all the analysed features one can say that they are very similar and no essential differences were shown within the period of study.

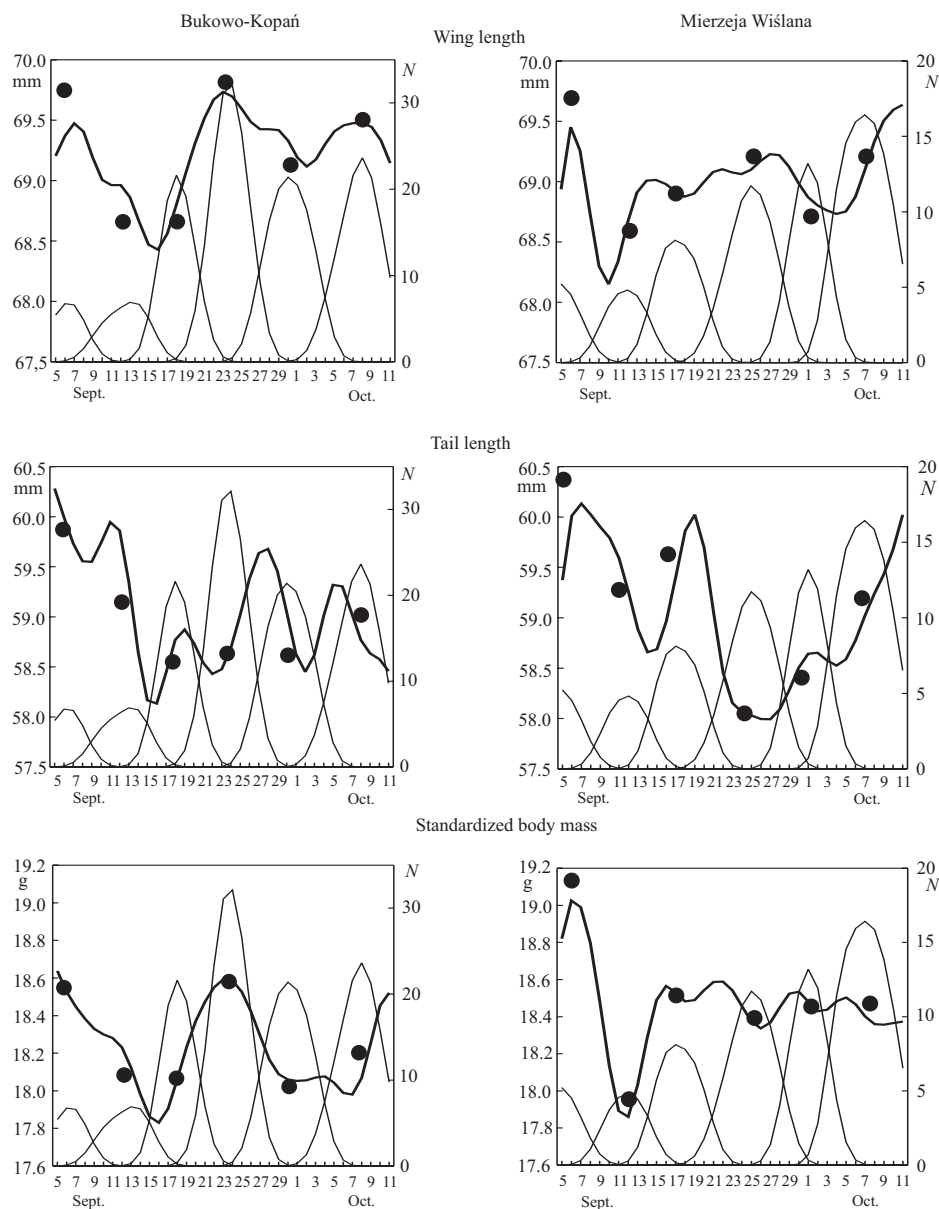


Fig. 11. Changes of wave average values for size parameters. The averages for particular waves of passage (presented in the background by thin lines) marked by black dots. The dynamics of changes (thick lines) smoothed twice by moving weighted-average.

Table 3
Biometrical differentiation among the waves of passage with regard
to the analysed parameters: sample sizes, wave averages and standard deviations.

Standardized body mass						
Waves	Bukowo-Kopań			Mierzeja Wiślana		
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>
0 and 1	34	19.44	1.64	19	19.01	2.10
2	19	18.55	1.27	10	19.12	1.15
3	25	18.08	1.15	13	17.96	1.46
4	34	18.07	1.25	26	18.54	1.39
5	69	18.60	1.28	48	18.41	1.37
6	51	18.03	1.22	44	18.44	1.58
7	44	18.20	1.45	48	18.46	1.48
8 to 10	18	18.58	1.45	71	18.61	1.52
Wing length						
Waves	Bukowo-Kopań			Mierzeja Wiślana		
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>
0 and 1	42	68.85	1.84	19	68.52	2.06
2	20	69.75	2.29	10	69.70	1.41
3	28	68.64	1.47	14	68.57	1.94
4	47	68.63	2.20	27	68.93	1.63
5	71	69.76	1.76	47	69.21	1.89
6	70	69.14	2.01	47	68.74	1.97
7	73	69.49	2.10	54	69.22	2.07
8 to 10	46	69.32	1.97	80	69.14	2.09
Tail length						
Waves	Bukowo-Kopań			Mierzeja Wiślana		
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>
0 and 1	41	58.87	2.58	18	58.33	2.65
2	20	59.90	3.98	10	60.40	2.22
3	28	59.14	2.97	14	59.29	2.26
4	46	58.54	3.39	27	59.63	4.86
5	70	58.65	2.80	46	58.07	1.80
6	69	58.64	2.75	47	58.43	2.11
7	73	59.01	2.65	54	59.17	2.77
8 to 10	44	59.25	3.08	78	59.52	3.08
Assymetry index <i>E'</i>						
Waves	Bukowo-Kopań			Mierzeja Wiślana		
	<i>N</i>	Mean	<i>SD</i>	<i>N</i>	Mean	<i>SD</i>
0 and 1	36	61.50	9.78	13	61.69	9.16
2	17	55.50	10.37	10	59.70	9.87
3	21	61.61	5.97	12	56.67	11.55
4	33	59.81	9.75	25	58.32	7.69
5	62	62.48	8.25	34	61.09	6.42
6	51	61.54	9.33	38	62.82	7.48
7	64	59.39	9.12	31	56.19	12.88
8 to 10	42	66.74	15.29	60	60.65	8.84

Table 3 – continued

Waves	Pointedness index L					
	Bukowo-Kopań			Mierzeja Wiślana		
	N	Mean	SD	N	Mean	SD
0 and 1	36	35.25	5.09	13	36.08	6.65
2	15	35.26	4.28	10	35.00	2.78
3	21	34.85	4.13	12	33.92	2.06
4	33	35.27	5.04	25	35.40	5.18
5	63	34.47	4.65	34	34.59	3.25
6	52	35.06	4.85	38	35.39	3.93
7	64	34.34	4.23	31	34.16	6.12
8 to 10	45	33.33	5.04	60	33.31	3.98

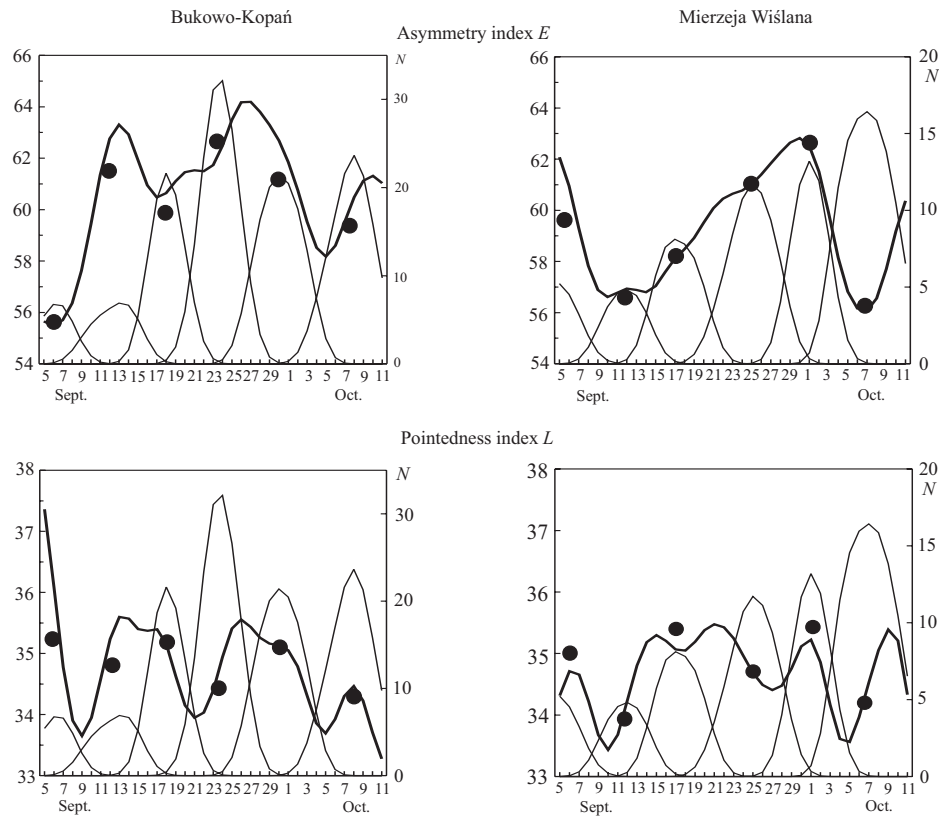


Fig. 12. Changes of wave average values for shape parameters. The averages for particular waves of passage (presented in the background by thin lines) marked by black dots. The dynamics of changes (thick lines) smoothed twice by moving weighted-average.

DISCUSSION

There is a lot of factors that may be responsible for the long-term changes in the number of caught birds. The changes concerning vast areas undoubtedly are influenced by weather conditions, which directly or indirectly may affect the number of individuals undertaking autumn migration to winter quarters – indirectly through the influence on alimentary conditions on breeding grounds, and consequently on birds' breeding success; directly through the probable influence on decision between starting migration or wintering, particularly in the case of not obligatory, partial migrants, for example tits.

The local factor causing differences in many-year dynamics between the neighbouring stations, such as Bukowo-Kopań and Mierzeja Wiślana, can surely be a different habitat, which for many species is closely connected with the intensity of catching at a station, *e.g.* for birds from genera *Acrocephalus* or *Sylvia* (Chernetsov 2006).

The succession of vegetation at a place of catching can also influence the number of birds caught (the passage takes place higher, out of net reach), which does not mean that the intensity of species migration over a given area changes. The more detailed considerations about the influence of successional changes one can find in a paper by Cofta (1985).

The type of migration characterizing a given species can also affect the number of birds migrating over a given area in the course of time. For example, in the invasive species, *e.g.* the Coal Tit (*Parus ater*) and many species from the finches family, the very high numbers of migrating birds in some years result mainly from the high breeding success in a given season (Kerlinger *et al.* 1985, Berthold 1993, Newton 2008). In Europe the Dunnock is considered as a partial migrant, what means that not all its sub-species undertake the migration. Only the nominate sub-species regularly migrates to the winter quarters, hence it is considered as an obligatory migrant (Cramp 1993). Birds migrating through the Polish Baltic coast belong to this group.

The long-term dynamics of Dunnocks caught in autumn at Bukowo-Kopań and Mierzeja Wiślana stations are clearly different, what is confirmed by a much higher number of caught birds at Bukowo-Kopań and a difference in values of the coefficient of fluctuation. With regard to the standardization at the stations of the Operation Baltic, the variable number of mist-nets used for catching can not influence this. The only factors that could cause such differences may be different habitat conditions for the stations or different routes of migration for bird groups passing through them. It is supposed that in the case of Dunnock also the weather circumstances in winter quarters can influence the number of individuals on breeding grounds (Svensson 1986).

In the studies comprising the 1961-1970 period it was noticed that for a bulk of species, among others also for the Dunnock, the long-term dynamics of catch numbers were similar at two ringing stations: Bukowo-Kopań and Hel, which were located west to Mierzeja Wiślana (Busse 1973). One of the explanations was the presence of an inter-populational migratory division between Hel and Mierzeja Wiślana stations. This division was defined also for the Dunnock. The hypothesis about the

existence of such border is supported by relatively high numbers of Dunnocks caught at the Wilga station, located at the Vistula riverbank, south to Warsaw (Maluchnik 1988). This may be also connected with preferring areas adjacent to water by this species, particularly during autumn migration (Bezzel 2000). Such preferences could canalize the passage of continental Dunnocks along the Vistula.

Due to the lack of literature relating to the passage of Dunnocks through the southern coast of the Baltic, their seasonal dynamics were compared to better studied species, such as the Robin (*Erithacus rubecula*) and the Song Thrush (*Turdus philomelos*), which could migrate in a similar way. Probably the most, close pattern of migration occurs for the Robin. Both species are night migrants with comparable distribution range and both winter in western and south-western Europe and in the Balkans (Cramp 1993). Moreover, a high correlation between the long-term changes in the numbers on breeding grounds as well as the large convergence of many-year autumn dynamics was shown for these species at a Swedish station – Ottenby located on the Oland island (Svensson 1986).

In this study the pooled seasonal dynamics for Bukowo-Kopań and Mierzeja Wiślana stations and Mierzeja Wiślana stations differed not only in the number of caught birds, but also in the median date of passage. At Mierzeja Wiślana the median occurred on 2 October, whereas at Bukowo-Kopań, located *ca* 190 km west, six days earlier, *i.e.* on 26 September. A highly significant statistical difference between these medians was also shown. The later occurrence of the autumn passage median date at the station located east excludes the same proportion of particular groups of birds passing through both the stations of study. Similar conclusions were drawn by Nitecki (1969), who based the likelihood of different origin of Dunnocks caught at eastern (Mierzeja Wiślana, Hel) and western (Bukowo, Wapnica) stations on the comparison of pentads (five-day periods), in which the intensity of catching was the highest. In 1962-1966, at the eastern sites the most intensive passage occurred in the first decade of October, which corresponds with the median of passage for the Mierzeja Wiślana station in my study. At the western sites the maximum of catching took place in the third decade of September, which is also confirmed by the median of passage in present work.

Recoveries from the areas of Germany indicated Danish, Swedish and Norwegian origin of birds caught (Hudde and Vohwinkel 1997). Also the analysis of recoveries from a Swedish station Falsterbo confirmed the migration of Scandinavian Dunnocks along the western route through Germany and France (Roos 1984). It is possible that also a considerable part of birds caught at Bukowo-Kopań have similar origin, but the lack of the species recoveries from this station does not allow to state this unambiguously. Taking into account the material used for the biometrical analysis by Nitecki (1969), some regularity becomes noticeable: namely, the farther west located station, the higher number of Dunnocks caught. Hence, in 1963-1966, starting from the most eastern sites the material comprised 17, 43, 60 and 842 indiv. (at Mierzeja Wiślana, Hel, Bukowo-Kopań and Wapnica, respectively). Similar tendency appears for this study, where at Bukowo-Kopań considerably more Dunnocks were caught than at Mierzeja Wiślana. Unfortunately, these data can not be compared with the results from the German stations as the tape luring greatly enlarged the effectiveness of catching.

Nevertheless, taking into consideration the number of 47 thousand Dunnocks caught during seven years (Hudde and Vohwinkel 1997), one can only suppose that the passage there was rather intensive. The regularities shown above may suggest a numerous migration of Scandinavian Dunnocks within the broad stream of passage, and its greatest concentration runs west of Polish stations located at the coast. Based on the differences in the median dates of passage it is supposed that the birds migrating along the "Western" route have also more western winter quarters. The earlier occurrence of Dunnocks at Bukowo-Kopań may correspond with migration pattern of the Song Thrush. For this species the analysis of recoveries revealed that the proportion of birds migrating to the "Western" winter quarter decreased in subsequent waves of passage, while there was an increase in the proportion of birds wintering at the Balkans (Busse and Maksalon 1978). The analysis of recoveries from Robins caught at the Baltic stations also showed that birds passing through the "Western" route (along the Atlantic coast) appear on the Polish coast the earliest, and their passage in this direction lasts until the end of autumn migration. In turn, the migration of Robins directing to the "Balkan" winter quarter begins on the Polish coast the latest, however it also lasts until the end of autumn passage (Remisiewicz 2002).

With regard to the comprehensive literature describing seasonal dynamics of the passerine migration, the analysis of such phenomenon should not be approached generally, without taking into consideration some periodical changes in numbers, so called "waves of passage". The wavy pattern of migration was showed among others for the species such as Redstart – *Phoenicurus phoenicurus* (Busse 1972), Meadow Pipit – *Anthus pratensis* (Petryna 1976), Coal Tit (Busse 1978), Song Thrush (Busse and Maksalon 1978), Robin (Larm 1996) or Blackcap – *Sylvia atricapilla* (Kopiec 1997). The most often described reasons for the waves of passage were: populational differentiation, weather conditions during migration and birds' internal rhythms related to changes of their fatness (Blyumenthal 1971, Busse 1978).

For the Dunnocks the division into the waves of passage was based on the seasonal migration dynamics pooled for 43 years of study. Due to the small amount of material, it was impossible to present such division for single years. Moreover, the data collected only in one season could be affected by weather conditions, what masks general pattern of migration. Based on the division according to the minima of passage, 10 waves for Bukowo-Kopań and 11 waves for Mierzeja Wiślana station were recognized. Two first waves, in which the numbers of birds were low, and in which considerable fluctuations occurred, represent probably postbreeding dispersal. For both stations this period is parallel, and the beginning of regular increase in numbers of caught Dunnocks occurs for Bukowo-Kopań on 3 September, and for Mierzeja Wiślana on 4 September.

Regarding the hypothesis by Nitecki (1969) about the origin of passing Dunnocks, the most numerous peak at Bukowo-Kopań (taking into account the combination of wing and tail lengths) could be represented by birds originating from Scandinavia. The corresponding peak at Mierzeja Wiślana comprises however lower number of individuals than at Bukowo-Kopań. In the case of Mierzeja Wiślana the most numerous peak could be represented by birds of more continental origin, migrating from Russia and Baltic countries. Such situation at both stations may be additionally complicated

by different fractions of birds from different geographical latitudes. Taking into account as short as 200 km distance between these stations, one cannot generalise completely different origin of birds passing them. Most probably at both stations the same groups are present, but in different proportions. As a general rule, the Scandinavian populations may predominate at Bukowo-Kopań, whereas the continental ones – at Mierzeja Wiślana. The lack of recoveries between Bukowo-Kopań and Mierzeja Wiślana may result from the more southern than the shoreline direction of passage (the birds leave the shoreline before they reach the Bukowo-Kopań station), as in the case of the Song Thrush (Busse and Maksalon 1978).

Another possible explanation of such differentiation could be the differences in wing and tail lengths between males and females. The male Dunnocks have on average longer wings and tails than the females, however broad ranges of the parameters allow to sex only a small proportion of individuals (Cramp 1993). The sexual and populational differentiation can overlap, which obviously makes drawing any conclusions more difficult, particularly based on the analysis of not very numerous data. It should also be borne in mind that the described populational differentiation concerns migrational populations, which are rather hard to determine. Nevertheless, in the areas with less complicated routes of migration a clear gradient of changing features related to migration becomes visible. As for the wing length, an apparent increasing trend during the migration time (even within one season) has been observed in Dunnocks passing through the area of Germany (Zaniewicz in prep.).

Based on the comparisons of daily averages for the analyzed size and shape parameters, it may be stated that there are differences between Dunnocks passing through the studied stations. It is confirmed by the weak correlation between the values of studied parameters at both stations. The correlations are statistically significant only for three of six parameters. Analysis of the same parameters with regard to their standard deviations in first (5-23 September) and second (24 September – 11 October) halves of the standard period reveals some relations. At Mierzeja Wiślana after the mid-period, *i.e.* after 23 September, a rather sudden change of values of these deviations occurred. The significant differences concerned five of six analysed parameters. Comparing date of this change with seasonal dynamics it is noticeable that the passage through Bukowo-Kopań is much more intensive than through the Mierzeja Wiślana station at this time. It may be assumed, that large deviations in the first part of the standard period at Mierzeja Wiślana result from an increased share of individuals from Scandinavian populations or from certain geographical latitudes (for which the passage is more concentrated in the western part of Polish coast). A decrease in deviations in the second part of the standard period may be caused by declining of passage of the above mentioned individuals and intensified passage of continental populations or birds that fly with more eastern routes. The increase in proportion of such individuals reduces the heterogeneity of the passage. At Bukowo-Kopań the level of variation for the analysed daily averages does not change so much in the course of season. The only statistically significant differences occur in the case of wing length. The obtained pattern corresponds with the results of the correlative topography method (Busse 1968, 1999), which were described in the previous paragraph.

The most unlike wave at Bukowo-Kopań is wave 5, which significantly differs from the adjacent waves with regard to the average wing lengths and standardized body mass. Possibly it may be represented by the most homogenous group of passing individuals, what could cause its biometrical distinction. The other statistically significant differences at this station occurred between waves 2 and 3 in the wing length and asymmetry. At Mierzeja Wiślana the variation of average values for particular waves is smaller, and significant differences occurred only in two cases, which does not allow for drawing any conclusions. In general, one can say that the differences among average values for waves are smaller between the stations (for the corresponding waves) than between the adjacent waves at the same station.

Most probably, in the case of the Dunnock, the established borders of migration waves are too short (the waves actually overlap in time) to analyse precisely their biometrical differentiation based on the accessible material.

CONCLUSIONS

1. The long-term dynamics of passage differ between Bukowo-Kopań and Mierzeja Wiślana stations, what may indicate partly different migration routes of Dunnocks from different areas of Europe.
2. The differences in seasonal dynamics between the stations are clear, what is confirmed among other things by statistically significant shift between the median dates of passage. Such differences may result from the location of the stations in relation to the most concentrated stream of passage migrants and from different proportion of migrational populations at both stations.
3. At both the stations three birds' groups were distinguished by the method of correlative topography, what indicates a biometrical differentiation of migrational populations.
4. The Dunnocks caught at the Mierzeja Wiślana station showed temporal differences in the variation of analysed biometrical parameters. At Bukowo-Kopań, however, during the whole season of study the standard deviations for these parameters remained at similar level. This could result from different proportion of populations during the passage of this species through the southern Baltic coast.

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REFERENCES

- Berthold P. 1993. *Bird Migration. A General Survey*. Oxford Univ. Press, Oxford – New York – Tokyo.
- Bezzel E. 2000. [*Birds-lexicon*.] Multico, Warszawa. (In Polish).
- Blyumenthal T.I. 1971. [*The development of the autumnal migratory state in some wild passerine birds: bioenergetic aspect*.] In: Bykhovsky B.E. (Ed.) [*Ecological and physiological aspects of bird migration*.] Nauka Press, Leningrad: 111-182.

- Busse P. 1968. *Correlative topography – the metod of analysis of the population differentiation*. Not. Orn. 9, 3: 1-8.
- Busse P. 1972. *Autumn migration of the Redstart Phoenicurus phoenicurus (L.) along the Polish coast of the Baltic*. Acta orn. 13, 6: 193-241.
- Busse P. 1973. *Populational differentiation analysis based on many years dynamics of number in migrants*. Not. Orn. 14: 49-61.
- Busse P. 1978. *Wave and population structure during Coal Tit autumn migration in 1974*. Not. Orn. 19, 1-4: 15-26.
- Busse P., Maksalon L. 1978. *Some aspects of Song Thrush migration at Polish Baltic coast*. Not. Orn. 19, 1-4: 1-14.
- Busse P., Halastra G. 1981. *The autumn migration of birds on the Polish Baltic sea coast*. Acta orn. 18, 3: 167-290.
- Busse P. 1986. *Wing-shape indices and the problems with their interpretation*. Not. Orn. 27, 3-4: 139-155.
- Busse P. 1984. *Key to sexing and ageing of European passerines*. Beitr. Naturk. Niedersachsen 37, Suppl.
- Busse P. 1996. *Modelling the seasonal dynamics of bird migration*. Ring 18, 1-2: 97-119.
- Busse P. 1999. *Correlative topography by Krigging – a useful method to study intra-group biometrical differentiation*. Ring 21, 2: 145-159.
- Busse P. 2000. *Bird station manual*. SE European Bird Migration Network. Univ. of Gdańsk: 5-264.
- Chernetsov. N. 2006. *Habitat selection by nocturnal passerine migrants en route: mechanisms and results*. J. Ornithol. 147: 185-191.
- Cofta T. 1985. *The comparison of studying the migration dynamics of Great Tit and Blue Tit by catching and visual observations*. Not. Orn. 26, 1-2: 61-71.
- Cramp S. (Ed.) 1993. *The Birds of the Western Palearctic. Handbook of the Birds of Europe, the Middle East and the North Africa*. vol. 7. Oxford. Univ. Press, Oxford – New York.
- Hudde H., Vohwinkel R. 1997. *Zur Phänologie des Herbstzuges der Heckenbraunelle (Prunella modularis)*. Vogelwarte 39: 48-60.
- Larm G. 1996. *[Autumn migration dynamics of the Robin (Erithacus rubecula) through the Polish Baltic coast]*. M.Sc. thesis, Univ. of Gdańsk. (In Polish).
- Kerlinger P., Lein M.R., Sevic B.J. 1985. *Distribution and population fluctuations of wintering Snowy owls (Nyctea scandiaca) in North America*. Can. J. Zool. 63: 1829-1834.
- Kopiec K. 1997. *Seasonal pattern of Blackcap (Sylvia atricapilla) autumn migration at the Polish Baltic coast*. Ring 19, 1-2: 41-58.
- Kopiec-Mokwa K. 1999. *Dates of migration waves – a coincidence or an effect of biologically based mechanism? Improvement of the method of analysing the seasonal migration dynamics*. Ring 21, 2: 131-144.
- Newton I. 2008. *The Migration Ecology of Birds*. Acad. Press: 976 pp.
- Nitecki C. 1969. *Variability of the wing-formula in Dunnock, Prunella modularis*. Not. Orn. 10, 1: 1-8.
- Maluchnik R. 1988. *[The autumn migration of the Dunnock (Prunella modularis) in central Poland.]* M.Sc. thesis, SGGW. (In Polish).
- Mead C. 1983. *Bird Migration*. Country Life Books: 244 pp.
- Petryna A. 1976. *The autumn migration of Meadow Pipit on the Polish coast of the Baltic*. Not. Orn. 17, 3-4: 51-73.
- Remisiewicz M. 2002. *The spatio-temporal pattern to Robin Erithacus rubecula migration: evidence from ringing recoveries*. In: Both C., Piersma T. (Eds). *The avian calendar: exploring biological hurdles in the annual cycle*. Proc. 3rd Conf. European Orn. Union, Groningen, August 2001. Ardea 90, 3 (special issue): 489-502.
- Roos G. 1984. *Migration, wintering and longevity of birds ringed at Falsterbo (1947-1980)*. Anser, Suppl. 13: 1-208.
- Scott R.E. 1962. *Wing-formula variation in Dunnock populations*. Bird Migr. 2: 118-120.
- Svensson S., Hjort C., Pettersson J., Roos G. 1986. *Bird population monitoring: a comparison between annual breeding and migration counts in Sweden*.