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Influence of temperatures on breeding grounds and migration routes on timing of autumn migration of Garden Warbler *Sylvia borin* and Lesser Whitethroat *S. curruca* at the Baltic coast.

Praca magisterska wykonana
na Stacji Badania Wędrówek Ptaków
pod kierunkiem
dr. hab. Magdaleny Remisiewicz, prof. UG

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Podziękowania

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Contents

1. Introduction

1.1. Annual bird migration

Seasonal migration is observed in all classes of vertebrates, especially in birds. Most bird species that breed in the northern hemisphere undertake migrations to and from wintering grounds twice a year (Newton 2008). The ultimate reason behind bird migration in the northern hemisphere is the seasonality of the environment, including seasonal changes in weather conditions and thus in food supplies (Berthold 1993, Newton 2008, Conklin et al. 2013). To adjust to these seasonal changes birds developed genetically controlled migratory behaviour (Berthold & Querner 1981, Gwinner 1996, Tøttrup et al. 2006, Dawson 2008). In this study we will focus on regular migrations on two species of long-distance migrants, the Garden Warbler *Sylvia borin* and the Lesser Whitethroat *Sylvia curruca*.

In such regular obligatory migrants, the timing of migration is controlled by endogenous factors, which respond to seasonal changes in photoperiod (Gwinner 1996, Jonzén et al. 2007, Knudsen et al. 2011). Although birds rely on the endogenous rhythm, the timing of migration is somewhat flexible and can be adjusted to environmental conditions (Coppack & Pulido 2004, Dawson 2008, Newton 2008). External factors, such as temperatures or feeding conditions, might influence the timing of subsequent stages in birds' life cycle, including migration, and modify it at any site along the migration routes and at the breeding or wintering grounds (Sparks 1999, Cotton 2003, Strode 2003, Newton 2008, Ockendon et al. 2013, Briedis et al. 2019, Lehikoinen et al. 2019).

1.2. Changes in timing of spring and autumn migrations

Many recent studies have shown that the timing of migration and breeding in some migrant passerine species in the northern hemisphere altered during the last decades (Sokolov et al. 1999ab, Cotton 2003, Jenni & Kéry 2003, Ahola 2004, Lehikoinen et al. 2004, Tøttrup et al. 2006a, Tøttrup et al. 2006b, Miles 2016, Kluen 2017). The majority of these studies show earlier spring arrival of migrants at the breeding grounds in recent years as compared to a few decades ago, for example Spotted Flycatcher *Muscicapa striata* and Common Whitethroat *Sylvia communis* in the United Kingdom (Cotton 2003) or Willow Warbler and Blackcap in Russia (Askeyev et al. 2009). Usually, the higher the spring temperatures are, the earlier the birds arrive in spring, and in many species trends for advance of spring migration have been explained by increased spring temperatures and climate warming, as e.g. in Pied Flycatchers *Ficedula hypoleuca* in Finland (Ahola 2004) and Song Thrushes *Turdus philomelos* on migration through the Baltic coast in Poland (Redlisiak et al. 2018). In the timing of autumn migration advances, delays or no long-term changes, have been observed in different species of passerines. For example, advancement in autumn migration timing was observed in Blackcaps *Sylvia atricapilla* ringed in Denmark (Tøttrup et al. 2006b) and Willow Warblers in United Kingdom (Cotton 2003), delays were observed in Wood Warblers and no changes in Common Whitethroats in Denmark (Tøttrup et al. 2006b). These shifts might depend on breeding biology, including the tendency for single or multiple broods, and on migration distance of a bird species.

During warm springs adult birds might arrive early and start breeding early, as for example Pied Flycatchers and Willow Warblers ringed on the Courish Spit (Sokolov 1998, Sokolov 2006). In single-brooded species, if they begin and end breeding early, adults and immatures might also depart early in autumn from the breeding grounds, as observed in Bluethroats *Luscinia svecica*breeding in Sweden (Ellegren 1990). In contrast, multiple-brooded species might lay additional clutches if their breeding period is extended by early and warm spring and possibly by warm autumn, as for example in Barn Swallows in Denmark (Moller 2002). Immatures from these additional clutches would be ready to depart from the breeding grounds later, and thus have delayed autumn migration, than those from the first clutches, as in Song Thrushes in Poland (Redlisiak et al. 2018) or in Great Tits in Russia (Bojarinova et al. 2002).

Short-distance and long-distance migrants are under different pressures during autumn migration, which affects their migration strategy and other life stages (Jenni & Kéry 2003). For short-distance migrants, environmental conditions on their wintering grounds, for example in the Mediterranean region, improve with the progress of autumn that brings rainfall, which pacifies summer droughts. Therefore, short-distance migrants which arrive at these wintering grounds too early might experience unfavorable conditions, which would reduce their chances for survival (Newton 2008, Hałupka 2017). Thus, staying longer at the breeding grounds might increase the chances of survival for short-distance migrants (Jonzén et al. 2007b, Newton 2008). Species that migrate for long distances begin autumn migration as soon as possible after breeding, to take advantage of peak abundance of food supplies at the beginning of autumn at their stopover sites and at the wintering grounds (Morel 1973 after Gordo 2007, Remisiewicz et al. 2018). In this study we examine influence of the temperatures on autumn migration timing of Garden Warbler and Lesser Whitethroat, both long-distance migrants, but with different wintering grounds and migration distances.

1.3. Study species

1.3.1. Garden Warbler

Garden Warbler *Sylvia borin* (Fig. 1) is a passerine bird that belongs to typical warblers family Sylvidae. In breeding and non-breeding seasons this species inhabits riparian woodlands, mixed woodlands with shrubbery, dense bushes, woodland edges, parks and large gardens (Cramp et al. 1992, Svensson et. al 2019). Garden Warbler is a long-distance migrant, with breeding grounds that extend across almost whole Europe and part of west Asia, and wintering grounds that span sub-Saharan west, central, east and south Africa (Fig. 3a). Garden Warbler is a single-brooded species (Cramp et al. 1992). The life-cycle of the central and north European populations of this species includes: breeding mostly in June–July, autumn migration to the south from August to mid-November, wintering from about mid-November to mid-March, and spring migration to the north from mid-March to the end of May (Cramp et al. 1992, Fig. 4a). This species occurs in Poland from May to September (Svensson 2019). Autumn migration of Garden Warblers across Poland lasts from beginning of August to mid-September, then they continue migration to the south (Cramp et al. 1992).

Fig. 1. Garden Warbler *Sylvia borin* (photo by Andrzej Olczyk, http://aolczyk.pl/galeria/fotografia/ptaki/gajówka/).

1.3.2. Lesser Whitethroat

Lesser Whitethroat *Sylvia curucca* (Fig. 2) is a passerine bird of the same family Sylvidae as the Garden Warbler. This species inhabits semi-open areas with woodlands, mainly young conifers, hedges, dense bushes and thorny bushes in breeding and non-breeding seasons (Cramp et al. 1992, Svensson et al. 2019). Lesser Whitethroat is also a long-distance migrant, but with shorter migration distance and more eastern wintering grounds than the Garden Warbler (Fig. 3b). Breeding grounds of the Lesser Whitethroat include most of Europe except the southwest, and western and central Asia, and wintering grounds include sub-Saharan central, east Africa, Middle East and India (Fig. 3b). Usually the Lesser Whitethroat has one brood a year, however sometimes second broods are possible (Cramp 1992). The life cycle of this species (Fig. 4b) includes breeding from mid-May to July, autumn migration from August to October, wintering from November to February, and spring migration from March to mid-May (Cramp et al. 1992). This species occurs in Poland from April to September (Svensson et al. 2019).

Fig. 2. Lesser Whitethroat *Sylvia curruca* (photo by Jaysukh Parekh, http://orientalbirdimages.org/search.php?Bird_ID=1410&Bird_Image_ID=85394).

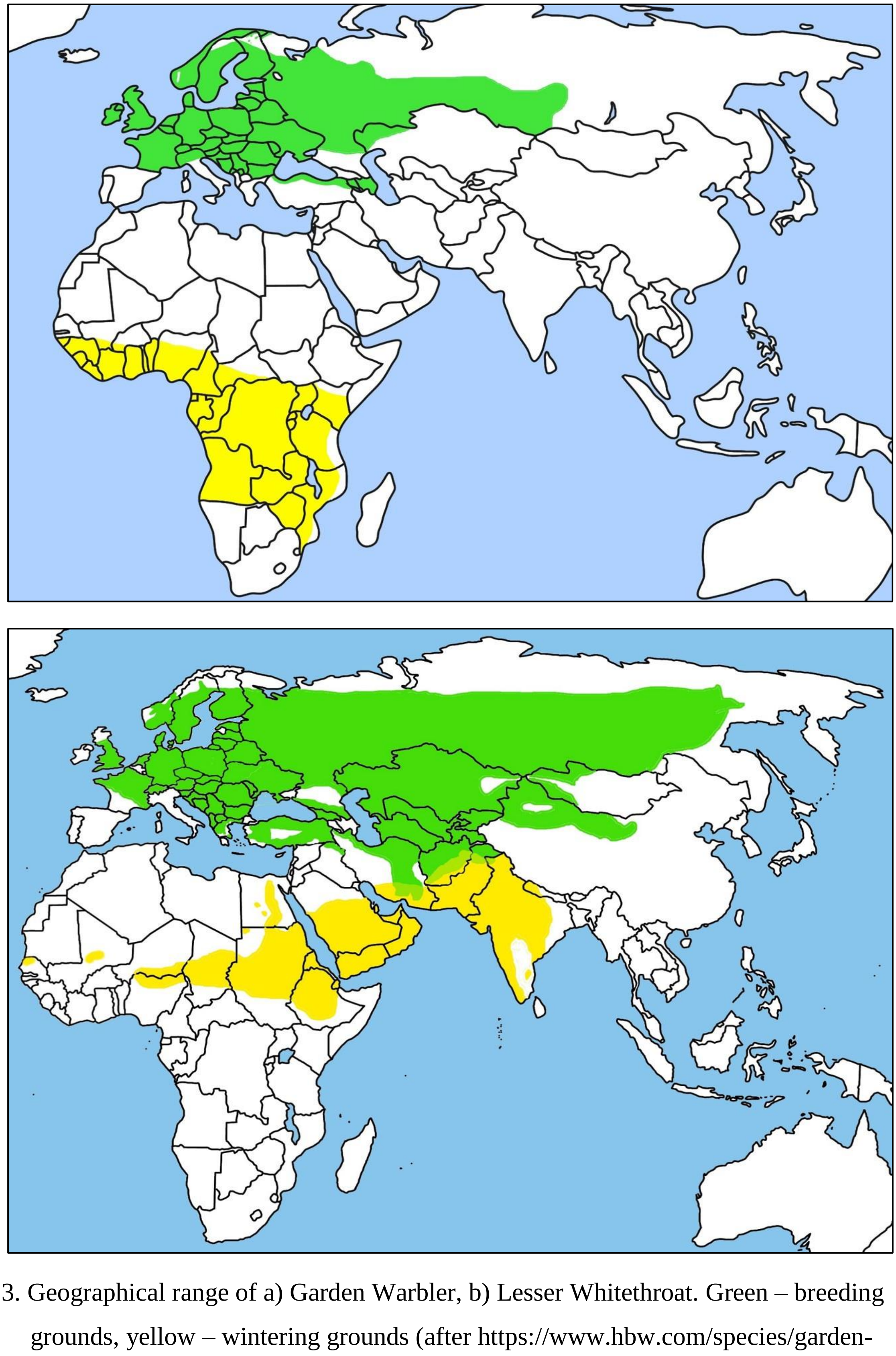

Fig. 3. Geographical range of a) Garden Warbler, b) Lesser Whitethroat. Green – breeding grounds, yellow – wintering grounds (after https://www.hbw.com/species/garden-warbler-sylvia-borin; https://www.hbw.com/species/lesser-whitethroat-sylvia-curruca, modified).

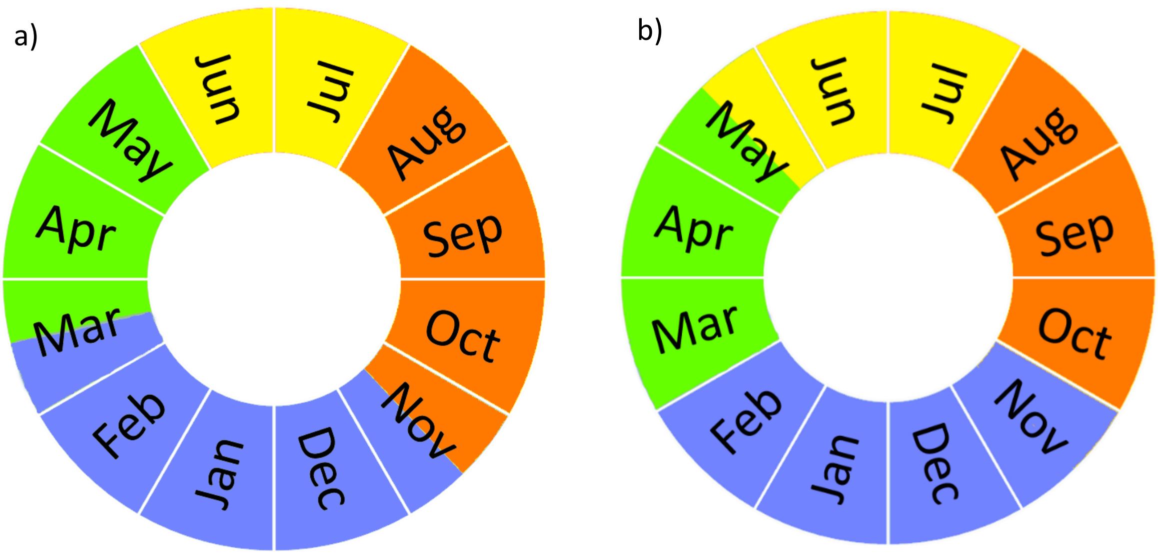

Fig. 4. Life cycles of a) Garden Warbler, b) Lesser Whitethroat. Yellow – breeding, orange - autumn migration, blue – wintering, green - spring migration (timing of life stages after Cramp et al. 1992).

1.4. Aims of the study.

In this study I aimed to:

a) Identify any changes in the timing of autumn migration of Garden Warbler and Lesser Whitethroat at the Polish Baltic coast.

b) Determine if any changes in the timing of autumn migration in these species were related to temperatures on their spring migration routes and at the breeding grounds before autumn migration.

2. Study sites

Study sites consisted of two bird ringing stations: Bukowo-Kopań and Mierzeja Wiślana (Table 1, Fig. 5). Both stations moved locations within a few kilometres over the years as habitat changed. But these were small movements within the same coastal zone, which channels birds’ passage, so we combined data from all locations for each station as one dataset.

Table 1. Operation Baltic ringing stations.

Station	Location	Coordinates
Bukowo-Kopań	Bukowo Lake spit, West Pomeranian voivodeship	54°19,38″-54°27'54″N; 16°13,33″-16°25,15″E
Mierzeja Wiślana	Vistula Spit, Pomeranian voivodeship	54°21,10″-54°21,57″N; 19°17'30″-19°23'30″E

Fig. 5. Location of Operation Baltic ringing stations. Red circles – current locations of the stations, orange circles – previous locations of the stations, BK – Bukowo-Kopań, MW – Mierzeja Wiślana (http://akbalt.ug.edu.pl/stacje/stacje-historia, modified).

3. Material

Data was collected during autumn migration, from 14th August to 15th October, at Bukowo-Kopań in 1967–2018 and at Mierzeja Wiślana in 1965–2018. During all the years of study all the Operation Baltic stations used the same standard protocol (Busse & Meissner 2015). Migrating birds were captured daily in the mist nets from dusk till dawn. The number of mist nets ranged from 25 to 89 throughout the years but remained constant during each season. Birds caught in the nets were brought to the ringing stand, ringed, aged and measured. Garden Warblers and the Lesser Whitethroats were aged as immatures and adults using their plumage features (Svensson 2006, Demongin 2016). All the collected data was recorded in ringing notebooks and then typed into Operation Baltic database.

The daily numbers of Garden Warblers and Lesser Whitethroats caught in each year of study were extracted from this database, for adults and immatures separately. I used only the first captures of a bird in the season, the recaptures in the same season were excluded. In the study I used only data on immature birds, as they were the majority of caught birds. Adults were too few to analyse, and they might show different responses to climate change than immatures, thus I did not include them in this study. In the database with the daily catches in each year and at each station the few gaps in data were filled in for days when bird catching ringing was suspended from various reasons, such as storms, rain etc. Those gaps in data were imputed with the numbers of birds estimated as the mean number of birds captured on those dates in 6 previous years and 6 following years (Redlisiak et al. 2018). Such gaps in data occurred in 12 years of the study period and were no longer than 3 days in one season at a station. In total, I analysed data on 6905 Garden Warblers and 2545 Lesser Whitethroats (Table 2, Table 3). I analysed only these years when more than 10 immatures of a species were captured at the station (Table 2, Table 3).

Table 2. The numbers of immature Garden Warblers caught each year from 14 August to 15 October at each station (BK – Bukowo-Kopań, MW – Mierzeja Wiślana) in years of the period 1965–2018 used in the study; “-“ – years in which less than 10 individuals were caught.

Year	Total BK	Total MW	Year	Total BK	Total MW	Year	Total BK	Total MW
1965	-	87	1983	42	15	2001	236	10
1966	-	41	1984	50	-	2002	214	27
1967	100	112	1985	37	24	2003	133	11
1968	106	116	1986	20	39	2004	68	-
1969	82	107	1987	16	11	2005	147	25
1970	-	107	1988	56	19	2006	159	17
1971	60	44	1989	25	46	2007	110	29
1972	102	103	1990	55	55	2008	104	27
1973	52	68	1991	20	11	2009	66	11
1974	122	132	1992	22	18	2010	126	42
1975	64	131	1993	60	71	2011	-	23
1976	52	72	1994	84	24	2012	69	11
1977	75	76	1995	111	55	2013	67	24
1978	86	78	1996	199	63	2014	91	-
1979	53	21	1997	247	47	2015	105	-
1980	25	93	1998	148	11	2016	43	-
1981	151	110	1999	178	45	2017	89	18
1982	103	30	2000	67	15	2018	38	-
						Total each station	4533	2372
						Total	6905	

Table 3. The numbers of immature Lesser Whitethroats caught each year from 14 August to 15 October at each station (BK – Bukowo-Kopań, MW – Mierzeja Wiślana) in years of the period 1965–2018 used in the study; “-“ – years in which less than 10 individuals were caught.

Year	Total BK	Total MW	Year	Total BK	Total MW	Year	Total BK	Total MW
1965	-	32	1983	40	19	2001	102	14
1966	-	23	1984	11	-	2002	82	14
1967	25	26	1985	-	-	2003	96	12
1968	11	22	1986	10	10	2004	55	-
1969	20	25	1987	-	14	2005	49	-
1970	-	42	1988	-	12	2006	93	-
1971	43	26	1989	-	10	2007	54	-
1972	12	10	1990	16	-	2008	69	-
1973	30	16	1991	-	-	2009	72	-
1974	27	45	1992	10	10	2010	68	-
1975	23	34	1993	39	14	2011	-	-
1976	34	16	1994	40	12	2012	23	-
1977	36	27	1995	57	14	2013	33	-
1978	38	18	1996	81	18	2014	26	-
1979	25	-	1997	95	14	2015	38	-
1980	-	-	1998	88	-	2016	21	-
1981	36	-	1999	87	-	2017	-	-
1982	69	18	2000	67	-	2018	29	-
						Total each station	1978	566
						Total	2545	

4. Methods of data analysis

4.1. Calculating daily cumulative catches in each year.

For each station in each year we determined how many immatures of the species in total were caught each day of the season. Then, for each day we presented this number as a percent of the total number of immature Garden Warblers or Lesser Whitethroats caught in each autumn at a station. For each species, these values on each consecutive day were added to the values from the previous days, accumulating to 100% of the birds caught at the station in the season. These cumulative percent values in the scale 0%-100% were then presented in the scale 0 to 1, to facilitate further calculations. Based on these values, the daily cumulative curves were drawn for each species at each station, which reflected the pattern of autumn migration in each year of the study (Fig. 6).

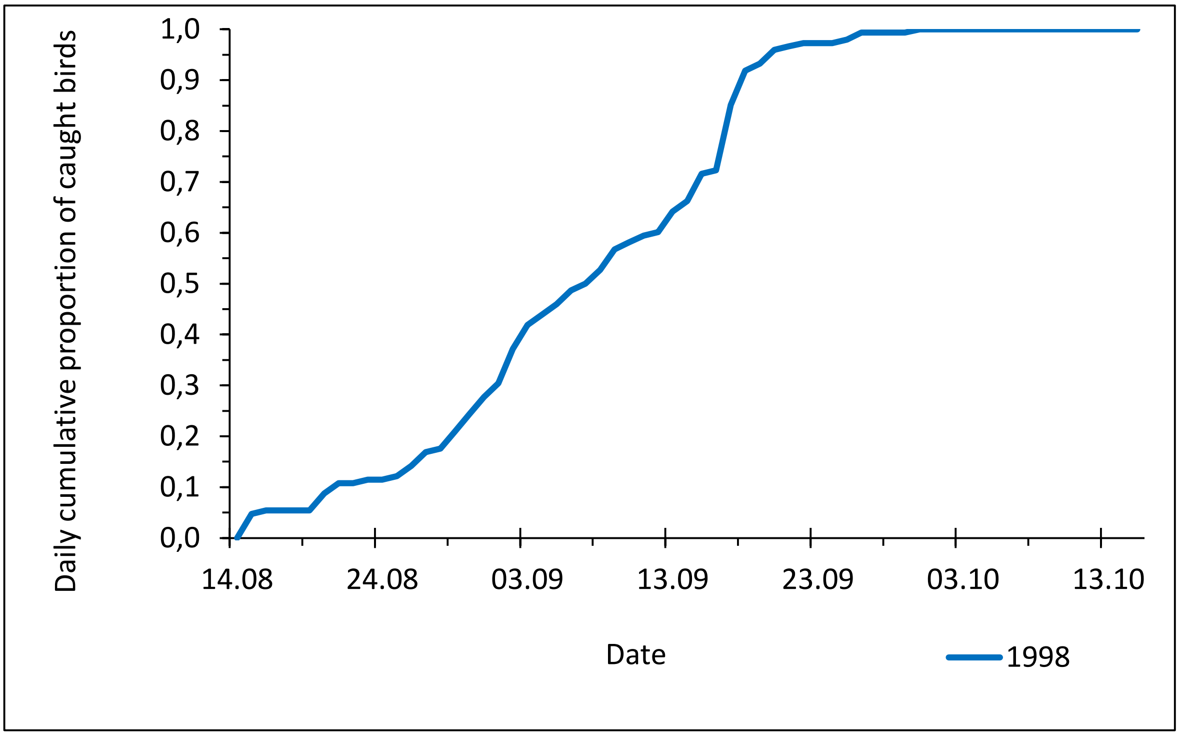

Fig. 6. Daily cumulative proportion curve of Garden Warblers in year 1998 at Bukowo-Kopań station.

4.2. Calculating the annual anomaly (AA).

For each species at each station, the Annual Anomaly (AA) of migration pattern in an autumn was determined as the area between the daily cumulative curve in that year and the many-year average daily cumulative curve. The area above the average daily cumulative curve (lined in red at Fig. 7) had the negative value and the area below this curve had positive value (area lined in green at Fig. 7). Those positive and negative values for each day of a season were then summed up over the whole season to give the Annual Anomaly (AA). The overall negative Annual Anomaly (AA) occurred when passage in that year was earlier than the many-year average pattern, and positive annual anomaly occurred when passage in that year was later than the average (Fig. 7).

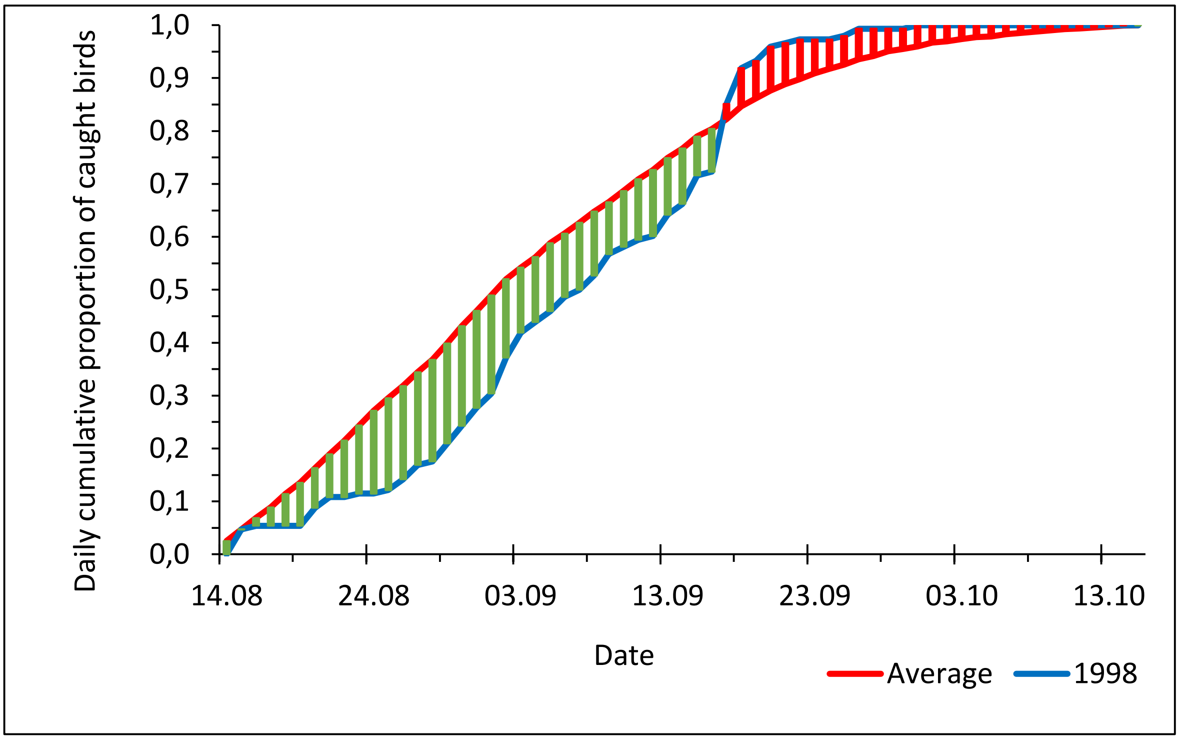

Fig. 7. Daily cumulative curve in 1998 (blue line) and the many-year average cumulative curve (red line) of the Garden Warbler at Bukowo-Kopań in 1967-2018. Area lined red – the part of 1998 passage that was earlier than the many-year average and thus had negative daily values for departure from the many-year average, area lined green – the part of 1998 passage that was later than average, and thus had positive values.

4.3. Deriving the dates for the percentiles of passage.

To show the changes in autumn migration timing of Garden Warbler and Lesser Whitethroat in more detail, from the daily cumulative curves I derived the dates, when 5%, 10%, 25%, 50%, 75%, 90% and 95% of the total number of Garden Warblers, and Lesser Whitethroats, respectively, was captured at each station in consecutive autumns each year. These dates were used in further analyses as Julian days, i.e. the day numbers from 1st January.

4.4. Many-year trends in timing of autumn migration and duration of passage.

For each species at each station I plotted the migration dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% of immatures against the years. Then I checked for any many-year trends in the dates for each percentile over the years, fitting the Generalized Additive Models (GAM). In this way I aimed to determine if the dates of percentiles showed any many-year trends, and to check if any occurring tendencies were linear or curved trends. Because most trends were linear, I plotted the dates for each percentile of passage against the years and fitted regressions line to reflect the many-year trends in these dates. For each station and each species I also calculated the duration of passage for 90% of birds migrating each year, as the difference (in days) between the dates when 5% and 95% of birds passed.

4.5. Estimating variation of annual anomalies around the many-year linear trends.

I determined the many-year trend in Annual Anomaly (AA) by using linear regression of the AA against the year. To estimate year-to-year variation of Annual Anomalies around the many-year trend, for each species and each station, I estimated the average values of the trend each year using the relevant regression equation. Then I calculated the difference between the AA value for the year and the value estimated from the trend for that year, to obtain the residual for that year. Those residuals were then squared, and those squares of residuals were summed up for each station. To obtain the mean deviation this sum of squares was divided by the number of years in which they were derived. This mean deviation I then treated as the coefficient of variation (CV) for the annual values around the many-year trend, which could be compared between the stations and species.

4.6. Comparing migration timing between the two stations.

To determine any similarities in migration timing at both stations over the years I correlated the Annual Anomalies at Bukowo-Kopań and at Mierzeja Wiślana, for each species. Similarly, for each species I correlated the dates (as Julian days) for each percentile of passage between Bukowo-Kopań and Mierzeja Wiślana, to test for any similarities between these stations.

4.7. Testing relationships between the timing of autumn migration and temperatures on spring route and at breeding grounds.

To determine the relationship between temperatures and the timing of autumn migration I used mean temperatures from weather stations on spring migration routes and breeding grounds of the study species (Fig. 8, Fig. 9). Those locations were selected based on the locations of ringing recoveries of Garden Warblers and Lesser Whitethroats, respectively (Maciąg et al. 2017). Using mean daily temperatures from these weather stations, from April to September 1965–2018 (http://www.ecad.eu, 2018) I calculated bi-monthly mean temperatures of April and May, June and July, August and September. These bi-monthly means corresponded with consecutive stages in life cycles of Garden Warblers (Table 4) and Lesser Whitethroats (Table 5).

For each species, these bi-monthly means of daily temperatures in consecutive years were correlated with the dates of passage for each percentile (as Julian day), and with AA at each station, using Pearson’s correlation coefficient.

Table 4. Weather stations on routes of autumn and spring migration and at breeding grounds of Garden Warblers, from which the mean bi-monthly temperatures of the listed months were used in the study (see Fig. 8).

Region (months)	Weather station (country)
Spring migration routes (April–May)	Brindisi (Italy)
	Lugano (Switzerland)
	Eindhoven (Netherlands)
	Łeba (Poland)
Breeding grounds (June–July) and autumn migration routes (August –September)	Gardermoen (Norway)
	Bergen (Norway)
	Skovde (Sweden)
	Kalmar (Sweden)
	Juupajoki (Finland)

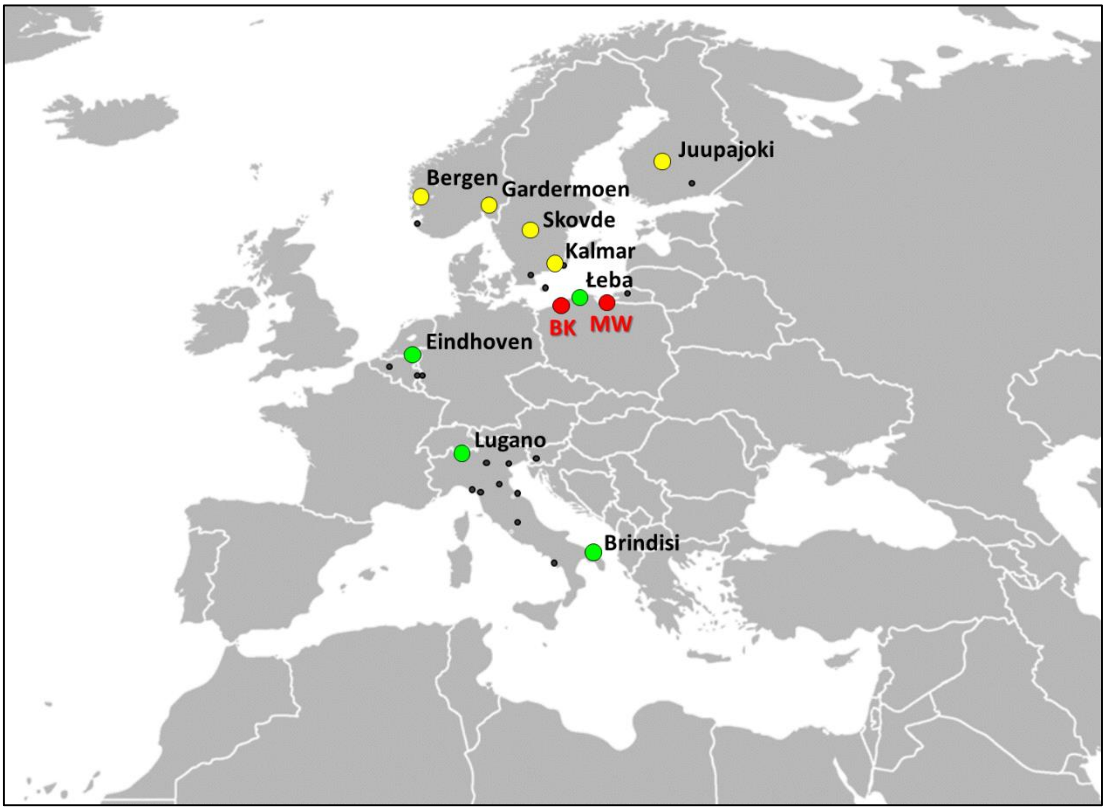

Fig. 8. Distribution of ringing recoveries of Garden Warblers ringed at Operation Baltic and recovered elsewhere (black circles), Operation Baltic stations (red circles): MW – Mierzeja Wiślana, BK – Bukowo-Kopań, and weather stations from which data were used in this study (yellow circles – stations at breeding grounds and autumn migration routes, green circles – stations on spring migration route). Locations of ringing recoveries after Maciąg et al. (2017).

Table 5. Weather stations on routes of autumn and spring migration and at breeding grounds of Lesser Whitethroats, from which the mean bi-monthly temperatures of the listed months were used in the study (see Fig. 9).

Region (months)	Weather station (country)
Spring migration routes (April–May)	Lod (Israel)
	Edirne (Turkey)
	Szeged (Hungary)
	Łeba (Poland)
Breeding grounds (June–July) and autumn migration routes (August –September)	Gardermoen (Norway)
	Bergen (Norway)
	Skovde (Sweden)
	Kalmar (Sweden)
	Juupajoki (Finland)

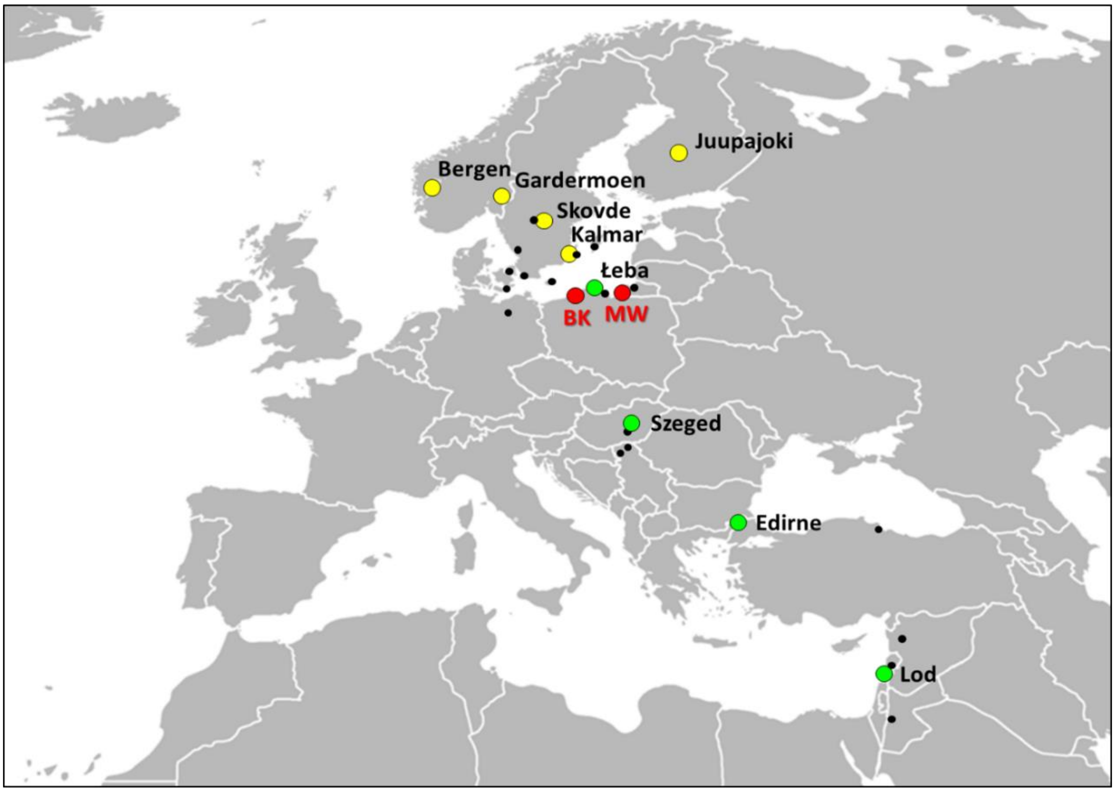

Fig. 9. Distribution of ringing recoveries of Lesser Whitethroats ringed at Operation Baltic and recovered elsewhere (black circles), Operation Baltic stations (red circles): MW – Mierzeja Wiślana, BK – Bukowo-Kopań, and weather stations from which data were used in this study (yellow circles – stations at breeding grounds and autumn migration routes, green circles – stations on spring migration route). Locations of ringing recoveries after Maciąg et al. (2017).

4.8. Software used for statistical analysis.

I used R 3.4.0 (R Core Development Team 2018) and Rstudio 1.0.143 (RStudio, Inc. 2017) to fit and draw General Additive Models (GAM) and linear regressions, to calculate the regression coefficients, and to derive Pearson's correlation coefficients. The remaining calculations and figures were prepared using Excel 2013.

5. Results

5.1. Timing of Garden Warbler migration at Bukowo-Kopań.

The overall timing of autumn migration for Garden Warblers at Bukowo-Kopań station, expressed as AA, advanced on average by 6 days over 1967–2018 (Fig. 10, Table 6). The timing of autumn migration for 75%, 90% and 95% of all Garden Warblers captured at Bukowo-Kopań advanced over these 52 years, and all the significant trends by GAM were linear (Fig. 11). According to these linear trends, the passage of 75% of captured Garden Warblers advanced by 10 days, the passage of 90% of birds by 11 days, and the passage of 95% of birds by 13 days, over the 52 years (Fig. 12, Table 6). The duration of autumn migration of Garden Warblers at Bukowo-Kopań shortened on average by 11 days in 1967–2018 (Fig. 13, Table 6). This shortening of the passage occurred because the end (95%) of autumn migration advanced while no changes occurred in the beginning (5%) of migration (Fig. 12).

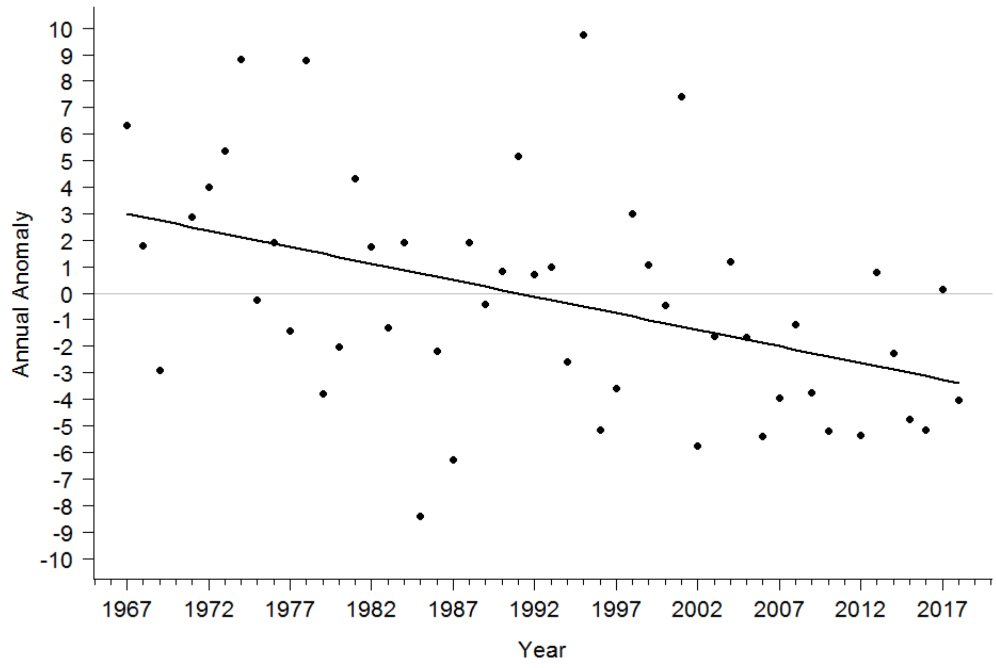

Fig. 10. Annual Anomalies of autumn migration for Garden Warbler at Bukowo-Kopań in 1967–2018, and the linear trend, parameters of the regression line are presented in Table 6.

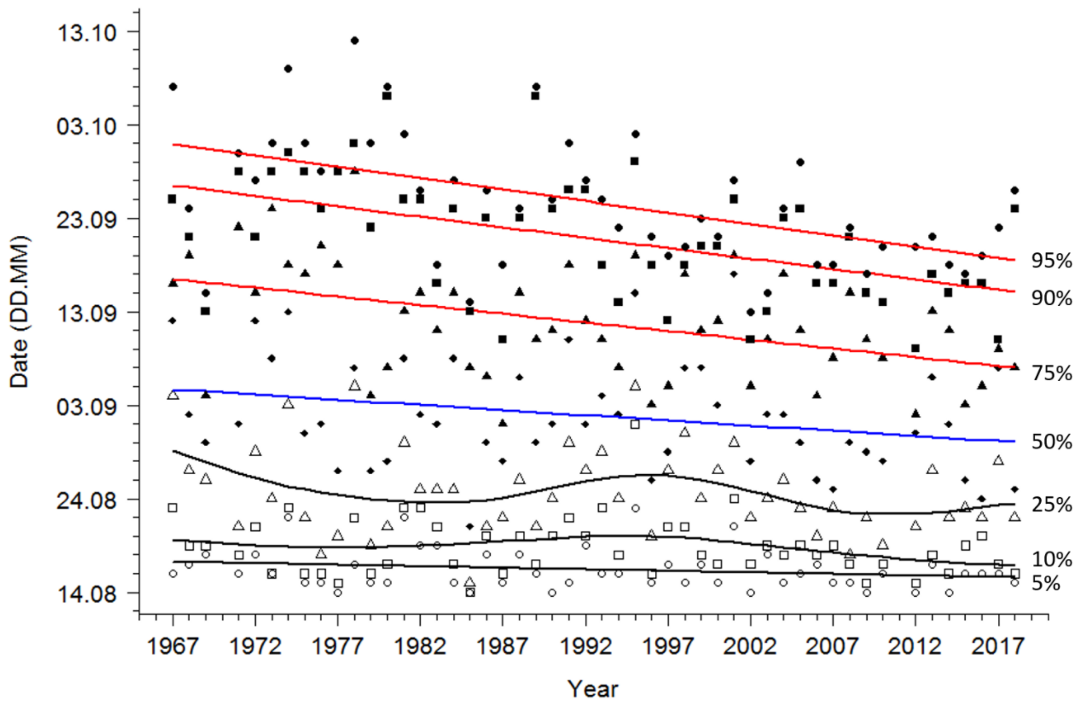

Fig. 11. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% of autumn migration for immature Garden Warblers at Bukowo-Kopań in 1967–2018 and trends for these dates by GAM; black line – trend non-significant, red – trend significant at $p < 0.05$, blue - $p < 0.1$.

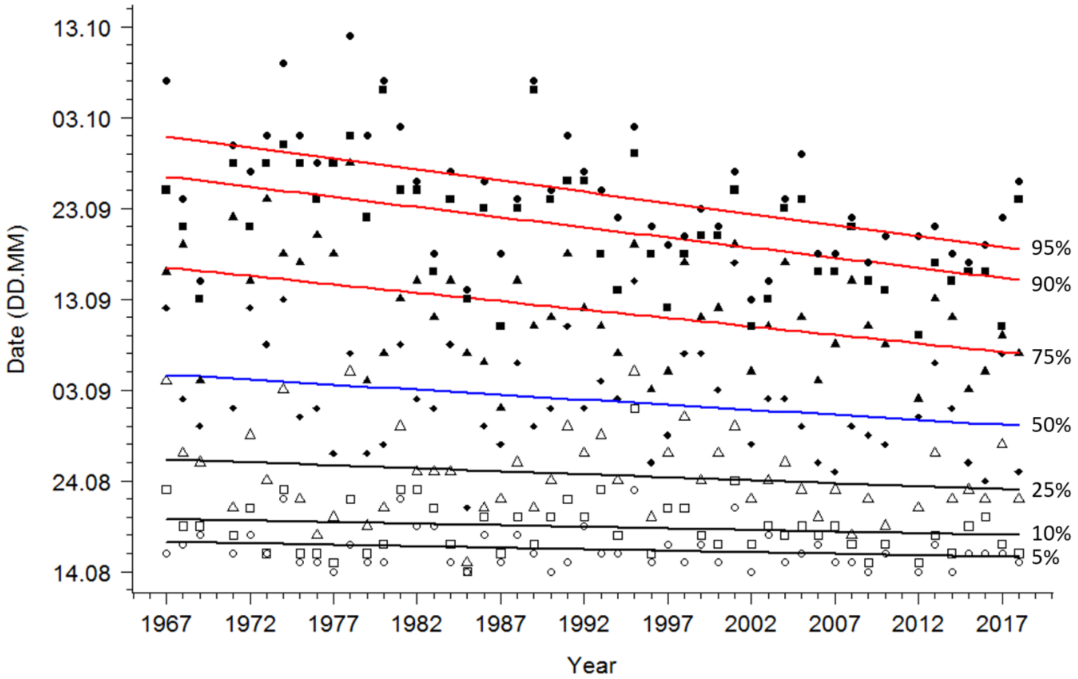

Fig. 12. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% autumn migration for immature Garden Warblers at Bukowo-Kopań in 1967–2018 and trends for these dates by linear regression; black line – trend non-significant, red – trend significant at $p < 0.05$, blue – $p < 0.1$, parameters of regression equations are presented in Table 6.

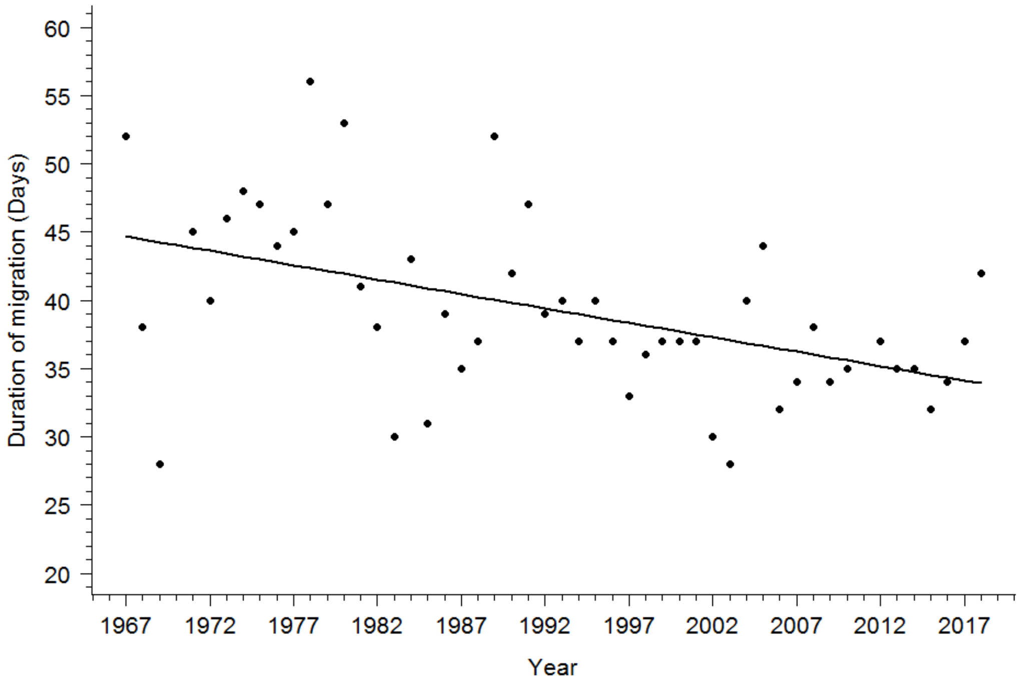

Fig. 13. Duration of autumn migration of immature Garden Warblers at Bukowo-Kopań in 1967–2018 and the trend by linear regression; parameters of the regression equation are presented in Table 6.

Table 6. Coefficients of regression equations for subsequent percentiles of immature Garden Warbler passage at Bukowo-Kopań in 1967– 2018 (Fig. 10, Fig. 12, Fig. 13); a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, 52*β – change in autumn migration dates and duration of migration (in days) during 52 years, negative values indicate earlier arrival at Bukowo-Kopań and shortened migration duration, respectively.

Parameter	Mean arrival date	a	β	SE	p	R^2	52*β
Annual Anomaly	-	3.12	-0.12	0.04	< 0.05	0.19	-6
5%	16 Aug	229.29	-0.03	0.02	0.12	0.05	-2
10%	19 Aug	231.80	-0.03	0.03	0.26	0.03	-2
25%	25 Aug	238.41	-0.07	0.04	0.15	0.04	-3
50%	2 Sep	247.80	-0.11	0.06	0.06	0.07	-6
75%	12 Sep	259.68	-0.19	0.05	< 0.05	0.20	-10
90%	21 Sep	269.72	-0.22	0.06	< 0.05	0.25	-12
95%	25 Sep	274.15	-0.24	0.06	< 0.05	0.28	-13
Duration of migration (5%--95%)	-	44.89	-0.21	0.06	< 0.05	0.23	-11

5.2. Timing of Garden Warbler migration at Mierzeja Wiślana.

The changes of the overall timing of autumn migration for Garden Warblers at Mierzeja Wiślana reflected by AA were not significant at over 1965–2018, although there was some tendency for advance (Fig. 14, Table 7). For the timing of autumn passage of 75%, 90% and 95% of Garden Warblers at Mierzeja Wiślana, the trends by GAM showed fluctuations, and indicated the delay of passage in 1965–1975, advance in 1976–1997, and again a delay in 1997–2017 (Fig. 15). The passage of 90% and 95% of Garden Warblers at Mierzeja Wiślana generally advanced in 1965–2017, by 7 and 11 days on average, respectively, as reflected by significant linear trends (Fig. 16, Table 7). The duration of autumn migration for Garden Warbler at Mierzeja Wiślana shortened on average by 13 days during these 53 years (Fig. 18, Table 7). This shortening of migration duration was the effect of the advance in the end (95%) of autumn migration while the dates of the beginning (5%) of migration showed no significant change (Fig. 16).

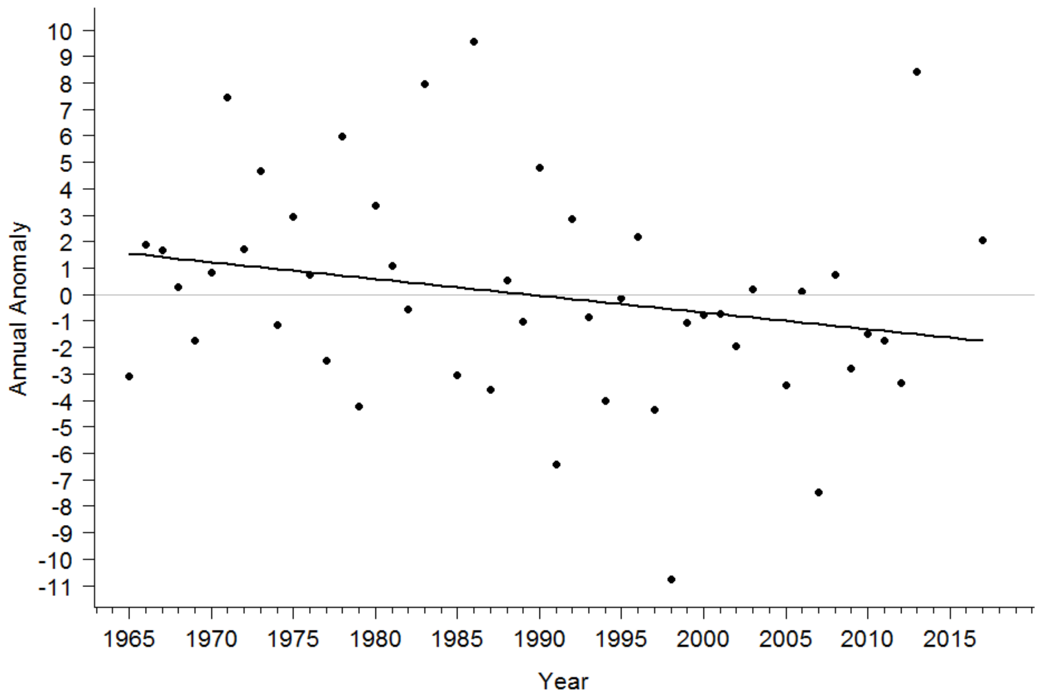

Fig. 14. Annual Anomalies of autumn migration for Garden Warbler at Mierzeja Wiślana in 1967–2017, and the linear trend, parameters of the regression line are presented in Table 7.

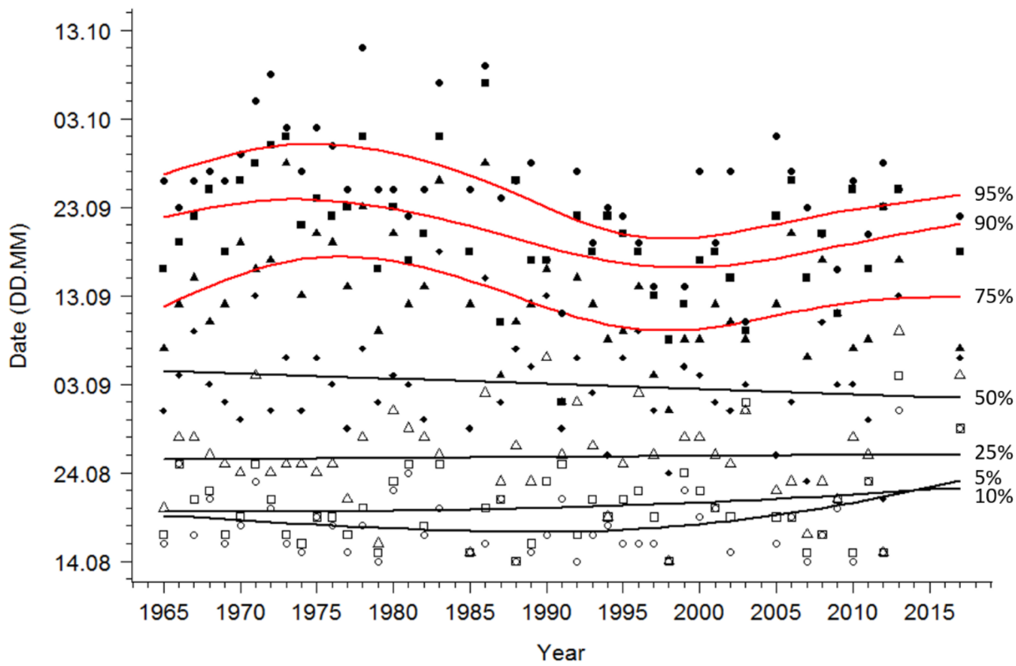

Fig. 15. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% of autumn migration for immature Garden Warblers at Mierzeja Wiślana in 1967–2017 and trends for these dates by GAM; black line – trend non-significant, red – trend significant at $p < 0.05$.

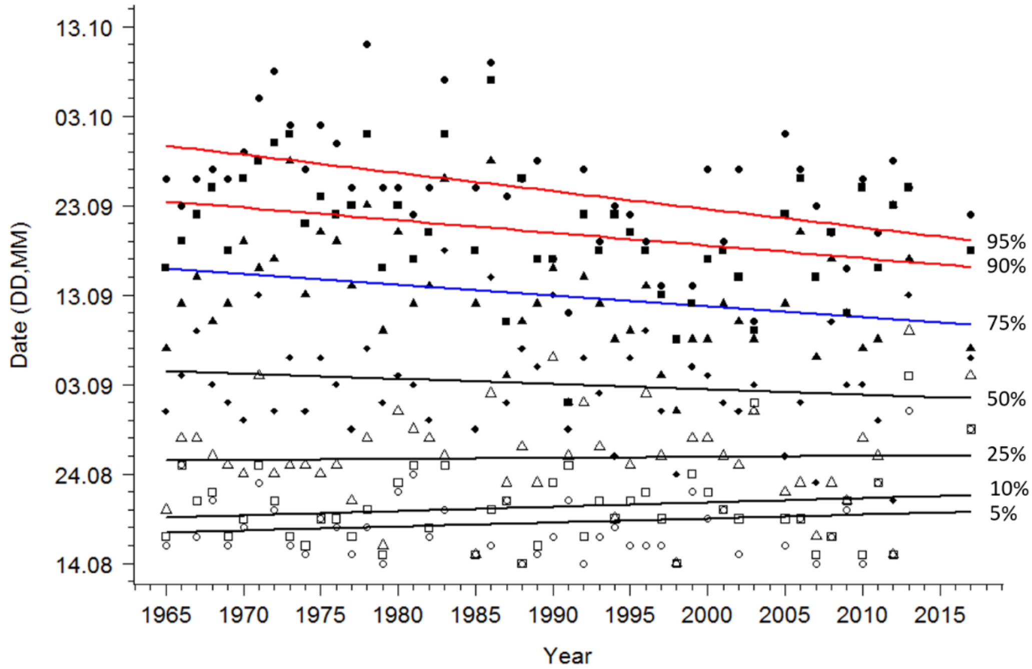

Fig. 16. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% autumn migration for immature Garden Warblers at Mierzeja Wiślana in 1967–2017 and trends for these dates by linear regression; black line – trend non-significant, red – trend significant at $p < 0.05$, blue – $p < 0.1$, parameters of regression equations are presented in Table 7.

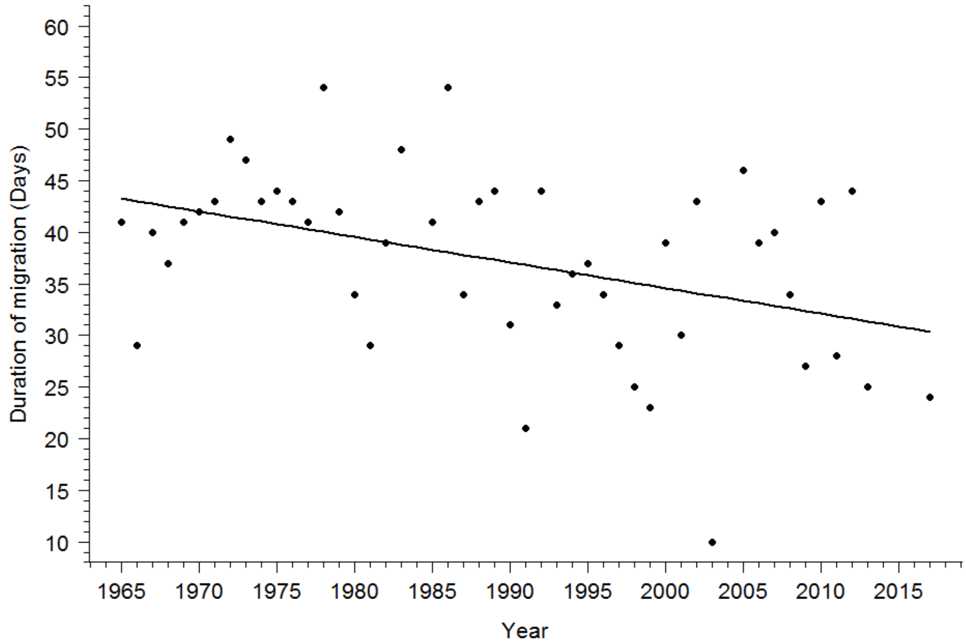

Fig. 17. Duration of autumn migration of immature Garden Warblers at Mierzeja Wiślana in 1967–2017 and the trend by linear regression; parameters of the regression equation are presented in Table 7.

Table 7. Coefficients of regression equations for subsequent percentiles of immature Garden Warbler passage at Mierzeja Wiślana in 1967– 2017 (Fig. 14, Fig. 16, Fig. 17); a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, 53*β – change in autumn migration dates and duration of migration (in days) during 53 years, negative values indicate earlier arrival at Mierzeja Wiślana and shortened migration duration, respectively.

Parameter	Mean arrival date	a	β	SE	p	R^2	53*β
Annual Anomaly	-	1.61	-0.06	0.04	0.11	0.05	-3
5%	19 Aug	229.39	0.04	0.04	0.29	0.02	2
10%	20 Aug	231.05	0.05	0.04	0.27	0.03	3
25%	25 Aug	237.46	0.01	0.06	0.84	0.001	1
50%	3 Sep	247.55	-0.06	0.06	0.31	0.02	-3
75%	13 Sep	259.04	-0.12	0.06	0.06	0.08	-6
90%	20 Sep	266.63	-0.14	0.06	< 0.05	0.10	-7
95%	25 Sep	272.91	-0.20	0.06	< 0.05	0.18	-11
Duration of migration (5%--95%)	-	43.51	-0.25	0.08	< 0.05	0.17	-13

5.3. Migration timing of Lesser Whitethroats at Bukowo-Kopań.

The Annual Anomalies of immature Lesser Whitethroats at Bukowo-Kopań in 1967–2018 showed no significant trend (Fig. 18, Table 8). We also found no changes in timing for any percentiles of autumn migration of Lesser Whitethroats at Bukowo-Kopań over the 52 years of study (Fig. 19, Fig. 20, Fig. 21, Table 8).

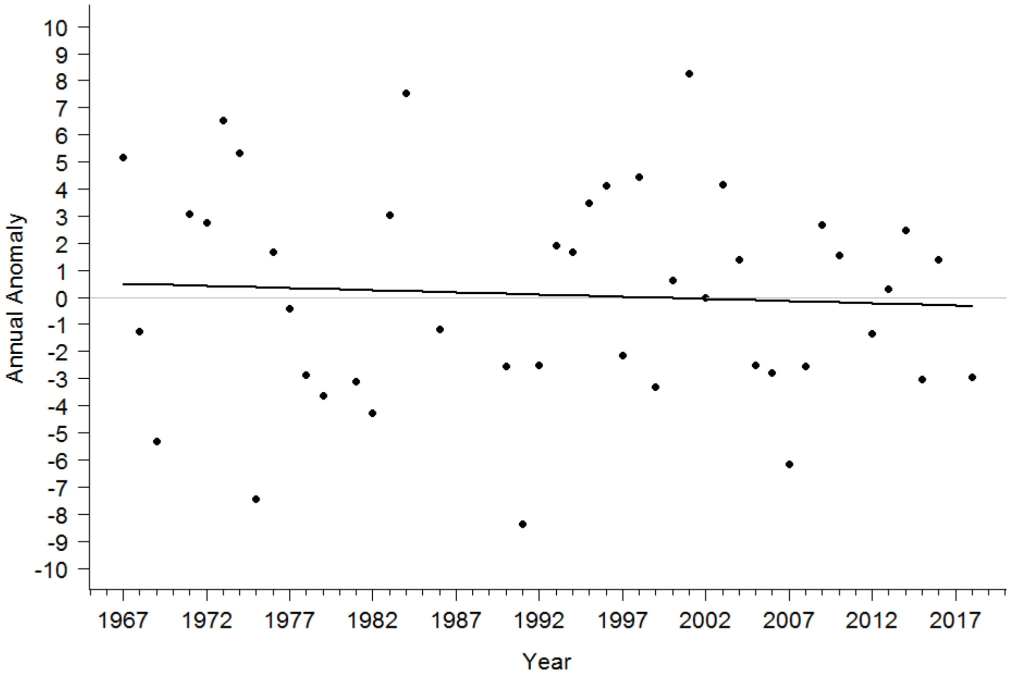

Fig. 18. Annual Anomalies of autumn migration for immature Lesser Whitethroats at Bukowo-Kopań in 1967–2018, and the linear trend, parameters of the regression line are presented in Table 8.

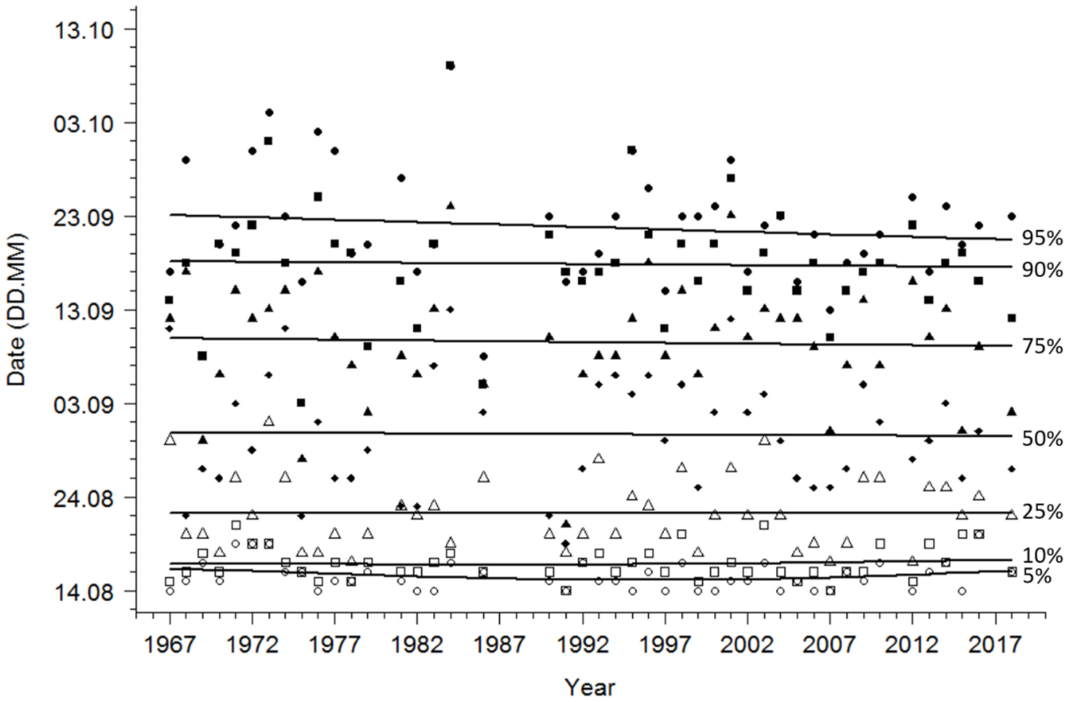

Fig. 19. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% of autumn migration for immature Lesser Whitethroats at Bukowo-Kopań in 1967–2018 and trends for these dates by GAM; black line – trend non-significant.

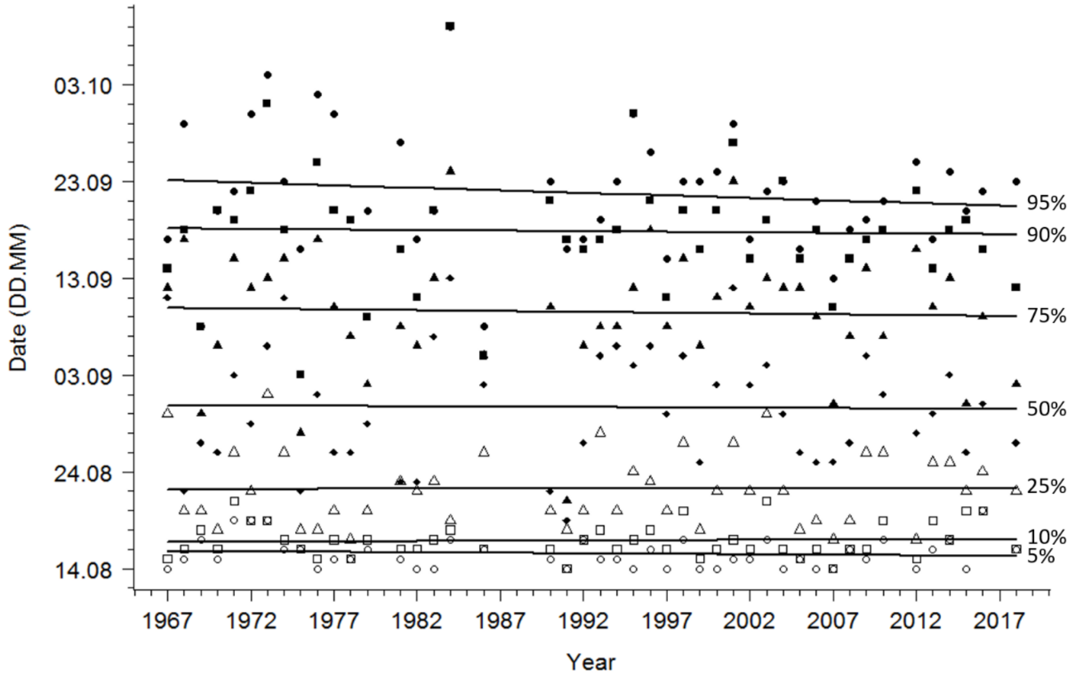

Fig. 20. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% autumn migration for immature Lesser Whitethroats at Bukowo-Kopań in 1967–2018 and trends for these dates by linear regression; black line – trend non-significant, parameters of regression equations are presented in Table 8.

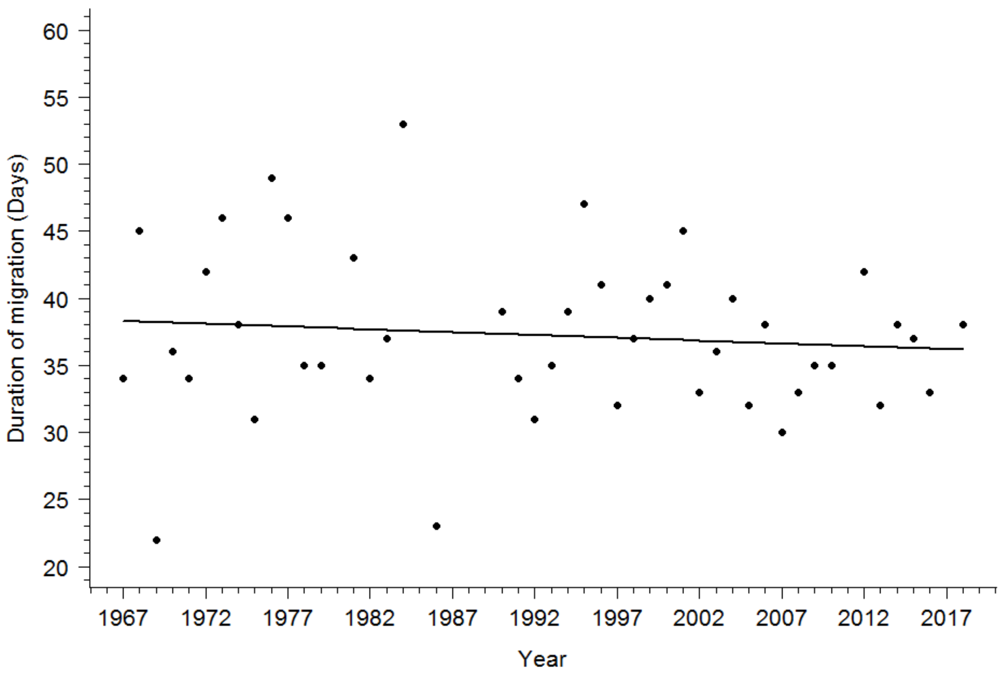

Fig. 21. Duration of autumn migration of Lesser Whitethroats at Bukowo-Kopań in 1967–2018 and the trend by linear regression; parameters of the regression equation are presented in Table 8.

Table 8. Coefficients of regression equations of subsequent percentiles of passage for immature Lesser Whitethroats at Bukowo-Kopań in 1967– 2018 (Fig. 10, Fig. 12, Fig. 13); a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, 52*β – change in autumn migration dates and duration of migration (in days) during 52 years, negative values indicate earlier arrival at Bukowo-Kopań and shortened migration duration, respectively.

Parameter	Mean arrival date	a	β	SE	p	R^2	52*β
Anomaly Index	-	0.51	-0.02	0.04	0.69	0.004	-1
5%	16 Aug	227.83	-0.01	0.02	0.51	0.01	-1
10%	17 Aug	228.70	0.01	0.02	0.73	0.003	0
25%	22 Aug	234.20	0.00	0.04	0.97	0.00004	0
50%	31 Aug	242.87	-0.01	0.06	0.90	0.0004	0
75%	10 Sep	252.93	-0.02	0.06	0.79	0.002	-1
90%	18 Sep	261.14	-0.01	0.06	0.85	0.001	-1
95%	22 Sep	266.15	-0.05	0.06	0.40	0.02	-3
Duration of migration (5%--95%)	-	38.35	-0.04	0.06	0.49	0.01	-2

5.4. Migration timing of Lesser Whitethroats at Mierzeja Wiślana.

Although Annual Anomalies showed a tendency for advance in the overall migration timing of Lesser Whitethroats at Mierzeja Wiślana over 1965– 2003, the linear trend was not significant (Fig. 22, Table 9). The dates for 75% of immature Lesser Whitethroats passing through Mierzeja Wiślana showed a trend for advance over 39 years of study, which was nearly significant ($p = 0.064$) (Fig. 23, Fig. 24, Table 9).

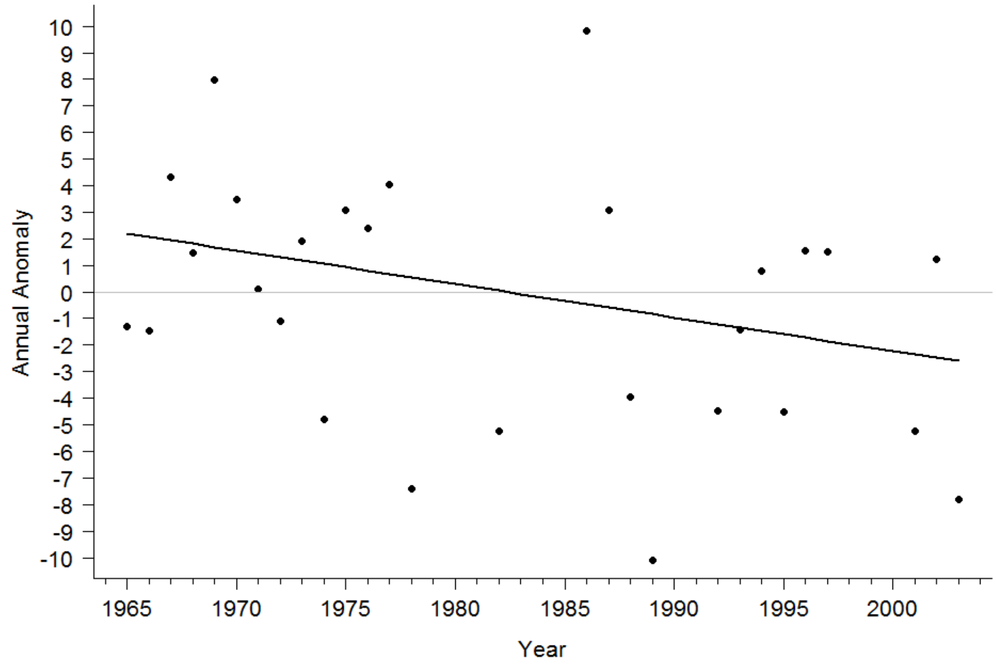

Fig. 22. Annual Anomalies of autumn migration for immature Lesser Whitethroat at Mierzeja Wiślana in 1967–2003, and the linear trend, parameters of the regression line are presented in Table 9.

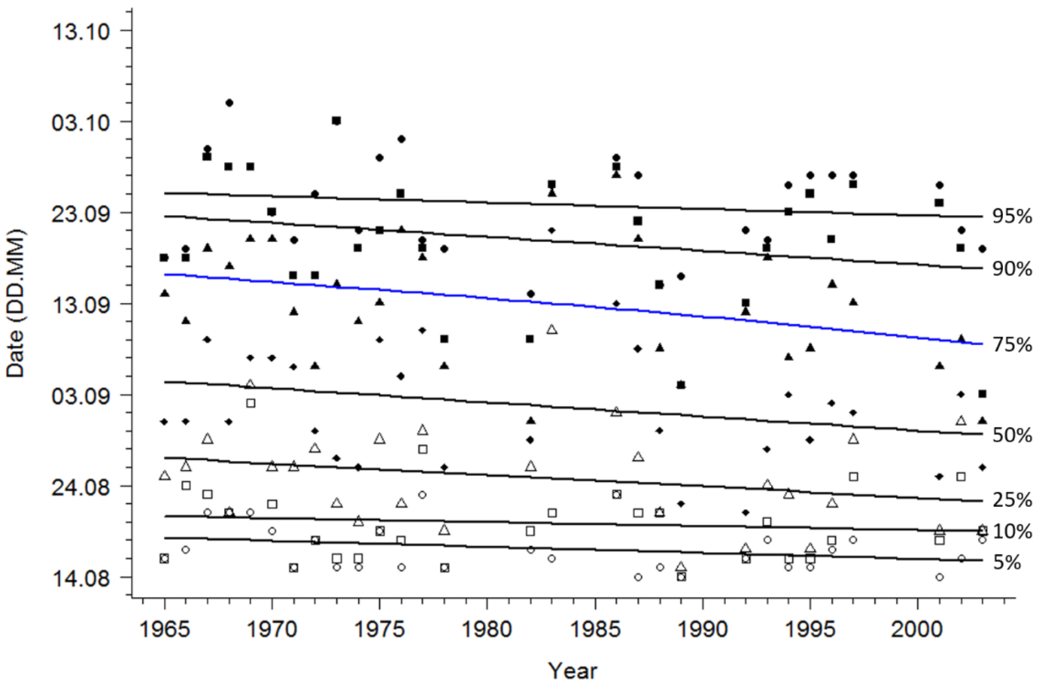

Fig. 23. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% of autumn migration for immature Lesser Whitethroats at Mierzeja Wiślana in 1967–2003 and trends for these dates by GAM; black line – trend non-significant, blue - $p < 0.1$.

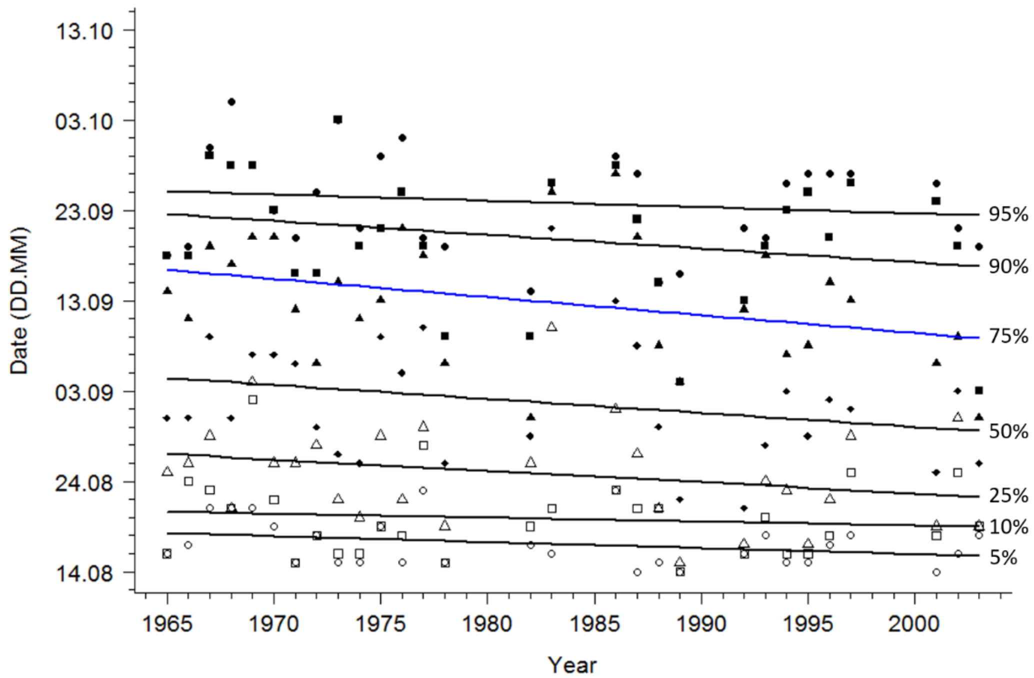

Fig. 24. Dates of 5%, 10%, 25%, 50%, 75%, 90% and 95% autumn migration for immature Lesser Whitethroats at Mierzeja Wiślana in 1967–2003 and trends for these dates by linear regression; black line – trend non-significant, red – trend significant at $p < 0.05$, blue – $p < 0.1$, parameters of regression equations are presented in Table 9.

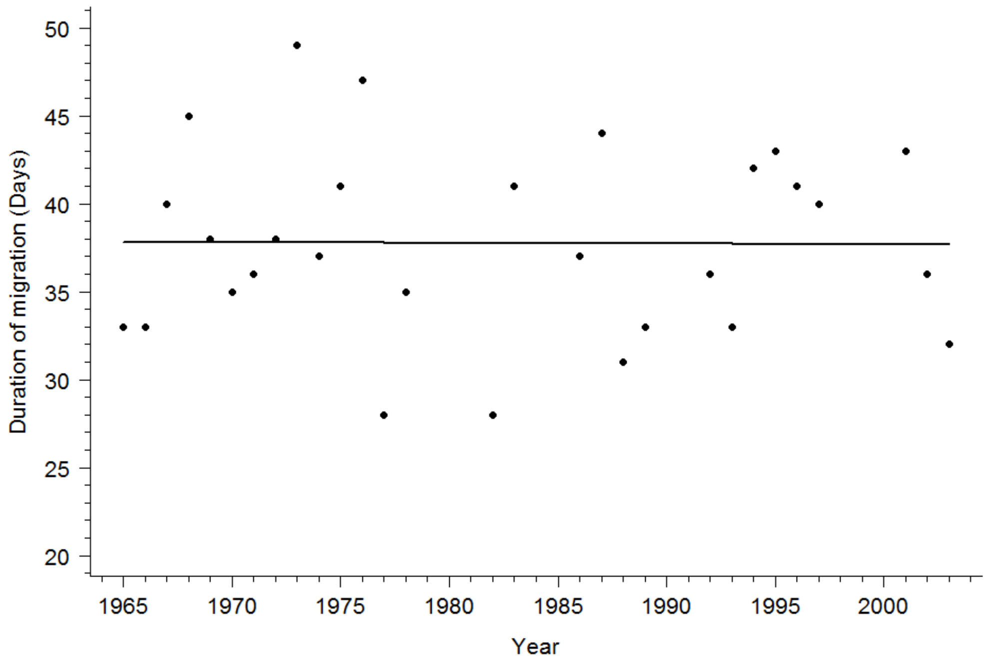

Fig. 25. Duration of autumn migration of immature Lesser Whitethroats at Mierzeja Wiślana in 1967–2003 and the trend by linear regression; parameters of the regression equation are presented in Table 9.

Table 9. Coefficients of regression equations of subsequent percentiles of Lesser Whitethroat passage at Mierzeja Wiślana in 1967– 2017 (Fig. 14, Fig. 16, Fig. 17); a – intercept, β – slope of regression line, SE – standard error, p – statistical significance, 39*β – change in autumn migration dates and duration of migration (in days) during 39 years, negative values indicate earlier arrival at Mierzeja Wiślana and shortened migration duration, respectively.

Parameter	Mean arrival date	a	β	SE	p	R^2	39*β
Anomaly Index	-	2.32	-0.13	0.08	0.12	0.09	-5
5%	17 Aug	230.32	-0.07	0.04	0.11	0.09	-3
10%	20 Aug	232.65	-0.04	0.07	0.54	0.01	-2
25%	25 Aug	239.16	-0.13	0.09	0.18	0.07	-5
50%	2 Sep	247.61	-0.15	0.11	0.16	0.07	-6
75%	13 Sep	259.61	-0.20	0.10	0.064	0.12	-8
90%	20 Sep	265.74	-0.15	0.11	0.19	0.06	-6
95%	24 Sep	268.15	-0.07	0.09	0.42	0.02	-3
Duration of migration (5%--95%)	-	37.83	-0.004	0.09	0.97	0.0001	0

5.5. Inter-annual variation of Annual Anomalies.

Annual Anomaly values of each species at each station varied around the average values defined by the respective regression lines (Figs 10, 14, 18, 22). For Garden Warblers year-to-year variations were similar at both stations (Table 10). Variation of Lesser Whitethorat migration at Bukowo-Kopań was at a similar level as for the Garden Warbler at the same site. The Annual Anomaly showed the greatest year-to-year variation for Lesser Whitethroats at Mierzeja Wiślana (Table 10).

Table 10. Coefficients of Variation (CV) of Annual Anomalies around the the many-year linear regression trends for Garden Warbler and Lesser Whitethroat at Bukowo-Kopań (BK) in 1967–2018, and for Garden Warbler at Mierzeja Wiślana (MW) in 1965–2017 and Lesser Whitethroat in 1965–2003.

Species	Garden Warbler		Lesser Whitethroat	
Station	BK	MW	BK	MW
CV	3.80	3.88	3.86	4.86

5.6. Correlations of Annual Anomalies and migration dates of subsequent percentiles between the two Operation Baltic stations.

Annual Anomalies were not significantly correlated between Bukowo-Kopań and Mierzeja Wiślana station for any of the studied species in the studied years that were common for both stations (Table 11). Migration dates of 95% of Garden Warblers were significantly correlated between Bukowo-Kopań and Mierzeja Wiślana, and for the dates for 90% correlation was nearly significant (Table 11). For Lesser Whitethroats migration dates for none of the percentiles of passage were correlated between Bukowo-Kopań station and Mierzeja Wiślana (Table 11).

Table 11. Correlation coefficients between Bukowo-Kopań and Mierzeja Wiślana for Annual Anomalies and migration dates for subsequent percentiles of for Garden Warblers in 1967– 2017, and for Lesser Whitethroats in 1965–2003; red box – $p < 0.05$; blue box – $p < 0.1$.

Species/Parameter	Annual Anomaly	5%	10%	25%	50%	75%	90%	95%
Garden Warbler	0.23	0.13	0.11	0.20	0.11	0.19	0.27	0.33
Lesser Whitethroat	-0.20	-0.05	-0.15	-0.11	-0.01	-0.09	0.07	0.22

5.7. Correlations of migration dates with temperatures on migration routes and at breeding grounds.

The higher spring temperatures on migration routes of Garden Warblers were the earlier those birds arrived in autumn at Bukowo-Kopań in 1967–2018, as indicated by negative correlation coefficients (Table 12). The dates of 25% and 50% of autumn migration were correlated with spring temperatures in Italy, the date of 75% was correlated with spring temperatures in Italy and Switzerland, and the dates of 90% and 95% were negatively correlated with spring temperatures from all weather stations on spring migration routes of this species in Italy, Switzerland, Netherlands and at the Polish coast (Table 12).

The higher the summer temperatures on the breeding grounds in Norway and at the Polish costs the earlier Garden Warblers arrived at Bukowo-Kopań in autumn, as indicated by negative correlations. The dates of 25% and 50% Garden Warblers passage were negatively correlated with summer temperatures in Norway, for 90% with summer temperatures at the Polish coast, and the dates for 95% were correlated with summer temperatures both in Norway and at the Polish coast (Table 12).

The higher autumn temperatures in Norway and Sweden were the earlier last percentiles of Garden Warblers migrated through Bukowo-Kopań (Table 12). The dates for 75% of autumn passage were negatively correlated with autumn temperatures in Sweden, and the dates for 90% and 95% were also correlated with autumn temperatures at two weather stations in Norway (Table 12).

Table 12. Correlation coefficients of dates for subsequent percentiles of Garden Warblers autumn migration at Bukowo-Kopań with bi-monthly means of daily temperatures of April–May (IV-V), June–July (VI-VII), and August–September (VIII-IX) from weather stations on spring and autumn migration routes and at breeding grounds of the species (Fig. 8).

Bi-monthly mean of daily temperatures	**Weather station**	**Percent of the total population passing**						
		5%	10%	25%	50%	75%	90%	95%
IV-V	Łeba (Poland)	-0.19	-0.10	-0.06	-0.12	-0.22	-0.34	-0.41
	Lugano (Switzerland)	-0.07	-0.08	-0.17	-0.24	-0.30	-0.42	-0.49
	Eindhoven (Netherlands)	-0.12	-0.22	-0.28	-0.30	-0.40	-0.51	-0.56
	Brindisi (Italy)	-0.13	-0.07	-0.11	-0.23	-0.25	-0.29	-0.37
VI-VII	Łeba (Poland)	0.05	0.00	-0.13	-0.12	-0.21	-0.30	-0.36
	Gardermoen (Norway)	0.03	-0.16	-0.28	-0.27	-0.21	-0.14	-0.27
	Bergen (Norway)	-0.08	-0.08	-0.15	-0.20	-0.11	-0.16	-0.27
	Kalmar (Sweden)	0.13	-0.02	-0.15	-0.14	-0.22	-0.15	-0.27
	Skovde (Sweden)	0.04	-0.17	-0.27	-0.22	-0.13	-0.09	-0.20
	Juupajoki (Finland)	0.20	0.02	-0.02	0.08	-0.04	0.07	0.00
VIII-IX	Łeba (Poland)	-0.02	-0.03	-0.03	-0.12	-0.23	-0.23	-0.24
	Gardermoen (Norway)	0.04	0.04	-0.03	-0.15	-0.25	-0.31	-0.41
	Bergen (Norway)	-0.04	-0.02	0.02	-0.07	-0.17	-0.28	-0.34
	Kalmar (Sweden)	0.07	0.06	0.03	-0.08	-0.17	-0.18	-0.23
	Skovde (Sweden)	0.03	-0.01	-0.06	-0.17	-0.22	-0.25	-0.34
	Juupajoki (Finland)	-0.04	-0.07	-0.08	-0.15	-0.20	-0.14	-0.17

The higher spring temperatures in Switzerland and Netherlands were the earlier last percentiles of autumn passage Garden Warblers occurred at Mierzeja Wiślana. Migration dates of 75%, 90% and 95% of Garden Warblers at Mierzeja Wiślana were negatively correlated with spring temperatures at several weather stations in Switzerland and Netherlands (Table 13).

The lower summer temperatures in Sweden were the earlier were the dates for 90% of Garden Warblers' autumn passage at Mierzeja Wiślana, as indicated by the negative correlations (Table 13).

The dates of 90% and 95% of autumn passage for Garden Warblers at Mierzeja Wiślana were negatively correlated with autumn temperatures in Norway, and the dates of 95% were also negatively correlated with autumn temperatures in Sweden (Table 13).

Table 13. Correlation coefficients of autumn migration dates for subsequent percentiles of Garden Warblers at Mierzeja Wiślana with bi-monthly means of daily temperatures of April–May (IV-V), June–July (VI-VII), and August–September (VIII-IX) from weather stations on spring and autumn migration routes and breeding grounds of the species (Fig. 8).

Bi-monthly mean of daily temperatures	Weather station	Percent of the total population passing						
		5%	10%	25%	50%	75%	90%	95%
IV-V	Łeba (Poland)	-0.19	-0.10	-0.06	-0.12	-0.22	-0.34	-0.41
	Lugano (Switzerland)	-0.07	-0.08	-0.17	-0.24	-0.30	-0.42	-0.49
	Eindhoven (Netherlands)	-0.12	-0.22	-0.28	-0.30	-0.40	-0.51	-0.56
	Brindisi (Italy)	-0.13	-0.07	-0.11	-0.23	-0.25	-0.29	-0.37
VI-VII	Łeba (Poland)	0.05	0.00	-0.13	-0.12	-0.21	-0.30	-0.36
	Gardermoen (Norway)	0.03	-0.16	-0.28	-0.27	-0.21	-0.14	-0.27
	Bergen (Norway)	-0.08	-0.08	-0.15	-0.20	-0.11	-0.16	-0.27
	Kalmar (Sweden)	0.13	-0.02	-0.15	-0.14	-0.22	-0.15	-0.27
	Skovde (Sweden)	0.04	-0.17	-0.27	-0.22	-0.13	-0.09	-0.20
	Juupajoki (Finland)	0.20	0.02	-0.02	0.08	-0.04	0.07	0.00
VIII-IX	Łeba (Poland)	-0.02	-0.03	-0.03	-0.12	-0.23	-0.23	-0.24
	Gardermoen (Norway)	0.04	0.04	-0.03	-0.15	-0.25	-0.31	-0.41
	Bergen (Norway)	-0.04	-0.02	0.02	-0.07	-0.17	-0.28	-0.34
	Kalmar (Sweden)	0.07	0.06	0.03	-0.08	-0.17	-0.18	-0.23
	Skovde (Sweden)	0.03	-0.01	-0.06	-0.17	-0.22	-0.25	-0.34
	Juupajoki (Finland)	-0.04	-0.07	-0.08	-0.15	-0.20	-0.14	-0.17

Migration dates of subsequent percentiles of the Lesser Whitethroat at Bukowo-Kopań showed no correlations with spring temperatures in weather stations along their assumed spring migration routes, summer temperatures at the breeding grounds, and with temperatures on autumn migration routes (Table 14).

Table 14. Correlation coefficients of autumn migration dates for subsequent percentiles of immature Lesser Whitethroats at Bukowo-Kopań with bi-monthly means of daily temperatures of April–May (IV-V), June–July (VI-VII), and August–September (VIII-IX) in weather stations on spring and autumn migration routes and breeding grounds of the species (Fig. 9).

Bi-monthly mean of daily temperatures	Weather station	Percent of the total population passing						
		5%	10%	25%	50%	75%	90%	95%
IV-V	Łeba (Poland)	0.05	0.12	0.17	0.10	0.06	-0.02	-0.03
	Szeged (Hungary)	0.14	0.14	0.17	0.09	0.07	-0.20	-0.14
	Edirne (Turkey)	0.13	0.19	0.19	0.15	0.18	-0.15	0.03
	Lod (Israel)	0.25	0.25	0.06	-0.03	0.03	-0.08	0.08
VI-VII	Łeba (Poland)	0.12	0.00	0.01	-0.22	-0.18	-0.16	-0.14
	Gardermoen (Norway)	0.18	-0.04	-0.04	-0.09	-0.14	-0.25	-0.19
	Bergen (Norway)	0.04	-0.10	-0.12	-0.19	-0.05	-0.08	-0.14
	Kalmar (Sweden)	0.14	0.01	0.00	-0.12	-0.18	-0.16	-0.15
	Skovde (Sweden)	0.25	0.03	-0.05	-0.15	-0.16	-0.20	-0.12
	Juupajoki (Finland)	0.31	0.11	0.14	0.00	-0.06	-0.09	-0.03
VIII-IX	Łeba (Poland)	-0.14	-0.12	-0.10	-0.17	-0.24	-0.23	-0.21
	Gardermoen (Norway)	-0.25	-0.09	-0.17	-0.17	-0.06	-0.13	-0.15
	Bergen (Norway)	-0.15	0.05	-0.10	-0.11	0.00	-0.01	-0.06
	Kalmar (Sweden)	-0.23	-0.17	-0.18	-0.15	-0.18	-0.18	-0.18
	Skovde (Sweden)	-0.20	-0.11	-0.20	-0.21	-0.17	-0.22	-0.21
	Juupajoki (Finland)	-0.17	-0.06	-0.05	-0.04	-0.01	-0.10	-0.04

In contrast, migration dates of Lesser Whitethroats at Mierzeja Wiślana were correlated with temperatures in some locations on migration routes and breeding grounds (Table 15). The lower spring temperatures in Turkey were the earlier were the beginning (5%) and the end (95%) of Lesser Whitethroats autumn migration at Mierzeja Wiślana (Table 15). The dates of 25%, 50%, 75% and 90% of migration at Mierzeja Wiślana were negatively correlated with spring temperatures in Israel, and the higher spring temperatures in Israel were the earlier in autumn these dates were at Mierzeja Wiślana.

The higher summer temperatures in Norway and at the Polish coast were the earlier immature Lesser Whitethroats migrated through Mierzeja Wiślana in autumn. The dates of 50% and 75% of Lesser Whitethroats passage at Mierzeja Wiślana were negatively correlated with summer temperatures in Norway. The migration dates of 75% were also negatively correlated with summer and autumn temperatures at the Polish coast (Table 15).

Table 15. Correlation coefficients of autumn migration dates for subsequent percentiles of immature Lesser Whitethroats at Mierzeja Wiślana with bi-monthly means of daily temperatures of April–May (IV-V), June–July (VI-VII), and August–September (VIII-IX) from weather stations on spring and autumn migration routes and breeding grounds of the species (Fig. 9).

Bi-monthly mean of daily temperatures	**Weather station**	**Percent of the total population passing**						
		5%	10%	25%	50%	75%	90%	95%
	Łeba (Poland)	-0.12	-0.11	-0.03	-0.12	-0.14	-0.16	-0.11
	Szeged (Hungary)	-0.30	-0.08	-0.24	-0.29	-0.42	-0.27	-0.18
	Edirne (Turkey)	0.38	0.11	0.23	0.33	0.20	0.30	0.50
	Lod (Israel)	-0.11	-0.24	-0.46	-0.40	-0.66	-0.54	-0.26
VI-VII	Łeba (Poland)	-0.04	0.07	-0.07	-0.22	-0.36	-0.05	0.06
	Gardermoen (Norway)	0.04	0.23	0.04	-0.05	-0.17	0.05	0.12
	Bergen (Norway)	-0.12	0.07	-0.18	-0.38	-0.47	-0.27	-0.14
	Kalmar (Sweden)	-0.04	0.11	0.00	-0.17	-0.24	0.02	0.11
	Skovde (Sweden)	0.01	0.13	-0.02	-0.15	-0.26	-0.01	0.12
	Juupajoki (Finland)	-0.03	0.11	0.01	-0.15	-0.23	0.10	0.05
VIII-IX	Łeba (Poland)	-0.11	0.01	0.05	-0.08	-0.38	-0.05	0.02
	Gardermoen (Norway)	0.00	0.30	0.17	0.06	-0.24	0.04	0.07
	Bergen (Norway)	-0.03	0.22	0.00	-0.10	-0.27	0.01	0.04
	Kalmar (Sweden)	-0.11	0.06	0.07	-0.04	-0.33	0.05	0.14
	Skovde (Sweden)	0.00	0.21	0.14	0.03	-0.29	0.04	0.13
	Juupajoki (Finland)	-0.16	-0.24	-0.10	-0.11	-0.42	-0.18	-0.10

6. Discussion

6.1. Changes in the timing of autumn migration of Garden Warbler on the Polish Baltic coast compared to other locations in Europe.

Our study showed that the overall autumn migration timing (AA) and migration timing of the last stages of passage (75% – 95%) of the Garden Warbler at the Polish coast of Baltic advanced over 1976 – 1997, similarly as on the Danish island Christiansø on the southern Baltic, located only ca 130 km north-west of Bukowo and 290 km from Mierzeja Wiślana, in this period (Tøttrup et al. 2006, Table 16). This correspondence may indicate similar effect of some common environmental factors, possibly of temperatures, which we analysed, on autumn migration of Garden Warblers through the Baltic region.

Table 16. Slopes of regression lines (β) of the dates of passage of 5%, 50% and 95% of Garden Warblers captured in 1976 – 1997; BK – Bukowo-Kopań, MW – Mierzeja Wiślana (this study), CH – Christiansø (after Tøttrup et al 2006). Red – $p < 0.05$

Station	5%	50%	95%
BK	0.06	0.13	-0.38
MW	-0.09	0.01	-0.61
CH	-	-0.09	-0.88

Steeper slopes for the dates of 95% in 1976 – 1997 (Table 16) than in 1965 – 2018 (Tables 6 and 7) at both Operation Baltic stations indicate that in 1976 – 1997 stronger advance occurred in the last stage of passage of Garden Warblers. possibly in response to more rapid climate warming in Europe in that period than during all 53 years of our study. Similarly as in our study last autumn departure dates of the Garden Warbler advanced in 1971–2000 in Oxfordshire, England (Cotton et al. 2003). Although these advances of the end of autumn migration of Garden Warblers, studies from other locations in Europe showed different patterns. The dates of 5%, 10%, 25% and 50% of autumn migration of Garden Warblers captured on Fair Island, Scotland, advanced significantly over 1955 – 2014, but the dates of 75%-95% did not advance (Miles et al. 2017). Those results suggest that the populations of Garden warblers that breed in west Europe tend to advance their autumn migration timing.

On the other hand, the median passage date (50^{th} percentile) of immature Garden warblers captured at Ottenby Bird Observatory in Sweden did not show any significant trend over 1950 – 2008 (Iwajomo et al. 2012), similarly as in my results for Mierzeja Wiślana (Table 7, Fig 19); for Bukowo the trend was nearly significant (Table 6, Fig 16). At Rybachy station on the Courish spit (Russia), about 130 km east of Mierzeja Wiślana, the mean dates of autumn migration of Garden Warbler were delayed over 1959 – 1976 and 1985 – 1998, but no trend was found in 1976 – 1990 (Sokolov et al. 1999). At Mierzeja Wiślana, a similar delay occurred in 1965 – 1975 (Fig. 14), but later the trends were different than at Rybachy. These results, showing alternate periods of delays and advances, suggest that the populations of this species breeding more to the east, which migrate through these Baltic stations, show different patterns to those breeding in the UK and Scotland.

No changes in the early and the middle stage of Garden Warbler autumn migration of (5% – 75%) but advances in the last stages of migration (90% and 95%) at both Operation Baltic stations might indicate that Garden Warblers migrating early in autumn are under influence of different factors than those migrating late in autumn. These differences might result from different breeding origins of Garden Warblers migrating early and late in autumn trough the Polish coast.

The duration of autumn passage of Garden Warblers at both Operation Baltic stations shortened over the studied period because the last stage of their autumn migration advanced, which is in contrast with most literature. More frequently an extension of the duration of autumn bird migration has been observed in short- and long-distance migrants in temperate and boreal zones of the northern hemisphere, because of earlier beginning and later end of migration than several decades ago (Lehikoinen et al. 2019). The meta-analysis of the duration of breeding revealed that single-brooded species in the northern hemisphere shortened their breeding season during last decades, in response to increasing temperatures, similarly as I found for autumn migration, in contrast to multi-brooded species that extended breeding period (Hałupka & Hałupka 2017). These authors suggest that the shortening of the breeding season in single-brooded species might results from their fine-tuning laying dates to match the time of maximum energetic demands of their offspring and the peak of food resources, which might shift early in birds that begin their breeding season late in relation to food resources should shorten breeding (Hałupka & Hałupka 2017). Therefore, Garden Warblers, which are long-distance migrants arriving on the breeding grounds later than other species, should shorten their breeding season.

6.2. Patterns in timing of autumn migration of Lesser Whitethroat on the Polish Baltic coast compared to other locations in Europe.

No changes in overall migration timing and autumn migration dates for any of the percentiles for Lesser Whitethroat occurred at both Operation Baltic stations, similarly as on Christiansø. At that location the trends for 5%, 50% and 95% of passage were not significant in 1976 – 1997, I also found no trends in the same period (Table 19) as well in the longer periods covered by my study (1967 – 2018 for BK, 1965 – 2003 for MW; Tables 8, 9).

Table 19. Slopes of regression lines (β) of the dates of passage of 5%, 50% and 95% of Lesser Whitethroats captured in 1976 – 1997; BK – Bukowo-Kopań, MW – Mierzeja Wiślana (results of this study), CH – Christiansø (after Tøttrup et al 2006).

Station	5%	50%	95%
BK	0.003	0.20	-0.25
MW	-0.07	-0.38	0.12
CH	0.07	-0.02	-0.29

At Rybachy, the mean dates of autumn migration dates for Lesser Whitethroats did not change in 1959 – 1976, but advanced strongly in 1976 – 1990 and then delayed strongly in 1985 – 1998 (Sokolov et al. 1999). Abrupt changes of autumn migration timing of this species at Rybachy station suggests that Lesser Whitethroats strongly react to changes of climate.

But in Oxfordshire, England, the last autumn departure dates of Lesser Whitethroats advanced in 1971 – 2000 (Cotton et al. 2003), but the dates for 75 and 95% of Lesser Whitethroat autumn migration delayed in 1955 – 2014 on Fair Island, Scotland (Miles et al. 2017). In Eilat, Israel, the median (50%) passage date of Lesser Whitethroats in autumn significantly delayed by 21.5 days in 1985 – 2004 (Horev et al. 2010). Comparisons of my results with those from these studies suggest that Lesser Whitethroats that migrate in autumn through different areas, even as closely located Bukowo-Kopań and Christansø, or as Fair Island and Oxfordshire, show very different patterns.

I have two hypotheses to explain why would the Lesser Whitethroats migrating through the Polish Baltic coast show no long-term trend in the timing of their autumn passage, in contrast to the pattern in some other sites in Europe. Firstly, we suggest that Lesser Whitethroats respond to temperatures in some locations on route (Table 15), which might explain large year-to-year fluctuations of their migration dates I found (Figs 18, 22, Table 10). But no significant linear trend would reflect such inter-annual variation, as indicated by low determination coefficients R^2 for all the regression lines (Tables 8, 9). Large coefficients of variations for Annual Anomalies around the linear trend for Lesser Whitethroats at Bukowo-Kopań, and even greater variation at Mierzeja Wiślana (Table 10) indicate these year-to-year fluctuations. Secondly, small numbers of Lesser Whitethroats captured at Operation Baltic stations and the resulted gaps in series of years I analysed (Table 3) might bias the results for this species.

6.3. Correlations in migration patterns of both species between two Operation Baltic stations.

For none of the two species were the Annual Anomalies correlated between the two stations (Table 11), which shows that their overall migration patterns differed between the stations. However, for Garden Warblers autumn migration dates of 95% were correlated between Bukowo-Kopań and Mierzeja Wiślana. This correlation suggests that similar factors in a similar way affected the last stages of autumn migration of this species at both stations.

6.4. Timing of Garden Warbler autumn migration in relation to temperatures on migration routes and breeding grounds.

This study showed that the temperatures on spring and autumn migration routes, and on the breeding grounds, are related with the timing of autumn migration of immature Garden Warblers at the Polish Baltic coast. The timing of their autumn migration was related the strongest with the temperatures on spring migration route of this species. The higher spring temperatures on route were the earlier the immatures arrived at both Operation Baltic stations in autumn. This influence could only be indirect, as the immatures I analysed had not existed yet in spring, thus the spring conditions most likely influenced their parents. Warm springs might encourage early arrival of adults at the breeding grounds and early nesting, thus earlier hatching and maturity of immatures, followed by earlier departure of both age groups from the breeding grounds than in years with cold springs (Ellegren 1990, Sokolov et al. 1999, Gordo 2007). Negative correlations found between May temperatures on migration route and spring migration dates of Garden Warblers passing through Hanko in Finland, seem to confirm the assumption that warm springs encourage early arrival of adult birds at the breeding grounds (Halkka 2011). The correlation of spring temperatures with autumn migration dates in birds seem to be a novel approach in this field of study, as I found no other studies that would relate autumn migration to spring temperatures.

Immature Garden Warblers migrated through the both Operation Baltic stations in autumn the earlier the higher were June–July summer temperatures on the breeding grounds. Warm summers may enable immatures to grow earlier and faster, and thus depart earlier from the breeding grounds, than after cold and rainy summers (Redlisiak et al. 2018). In my study the last percentiles (90%-95%) of autumn migration were related to summer temperatures on the breeding grounds in Norway (Table 12, 13) in a similar way as in Oxfordshire, where the last 95% of Garden Warblers passed earlier with the higher summer temperatures in Oxford (Cotton 2003).

The end (95%) of immature Garden Warblers passage occurred at the Polish coast in autumn the earlier with the higher temperatures in August–September on the initial stage of their migration route, in Norway and Sweden. This pattern might reflect earlier and faster growth of immatures, and their readiness for migration, when beginning of autumn is warm at their breeding grounds, than in cold autumns, similarly as in the Song Thrush (Redlisiak et al. 2018). Earlier departure of Garden Warblers from the breeding grounds in Scandinavia in warm autumns might explain the correlation I found between early migration dates of 90% and 95% of Garden Warblers at Bukowo-Kopań and local August–September temperatures. At Rybachy station in Russia the higher local temperatures in August–September were the later the median (50%) of Garden Warblers migrated through this station (Sokolov 2006). This is in contrast to my results which showed no correlations between the median passage dates of Garden Warblers at both Operations Baltic stations and any autumn temperatures locally or in Scandinavia (Table 12, 13). This suggests that Garden Warblers migrating through Rybachy might come from different breeding grounds than Garden Warblers migrating through the two Polish stations.

6.5. Timing of Lesser Whitethroat autumn migration in relation to temperatures on migration routes and breeding grounds.

Autumn migration timing of immature Lesser Whitethroats passing through the Operation Baltic stations was related the strongest to temperatures on spring migration routes, as I also found in Garden Warbler. The higher spring temperatures in Hungary and Israel on the spring migration route of adult Lesser Whitethroats the earlier the immatures arrived at Mierzeja Wiślana (Table 15).

The explanation could be that, similarly as in Garden Warbler, warm springs might entail early arrival of adults at the breeding grounds and early nesting, and thus earlier departure of immatures and adults from the breeding grounds (Ellegren 1990, Sokolov et al. 1999, Gordo 2007).

No similar correlations with temperatures were observed at Bukowo-Kopań station, which suggests that Lesser Whitethroats migrating through Bukowo-Kopań and Mierzeja Wiślana stations in autumn come from different breeding grounds and use partly different migration routes. Most likely, in this study we did not identify the weather stations on route of spring migration and breeding grounds of the Lesser Whitethroats that migrate through Bukowo-Kopań.

Our results also revealed that the higher spring temperatures were in Edirne, Turkey, on spring migration route of Lesser Whitethroats, the later the 5%, 50% and 95% of immatures occurred the following autumn at Mierzeja Wiślana. This result is opposite to any relations we found between spring temperatures in other locations in Europe (Table 19), and in Garden Warbler (Tables 12, 13). If warm springs enable early arrival of adults at the breeding grounds in spring, and in this way spring temperatures are related to the timing of autumn migration of their offspring, then warm springs on route should cause advances, not delays, in migration of immatures. As this result seems to be odd and is unexpected, we compared it with a study showing correlations of spring arrival of Lesser Whitethroats in Finland (Halkka et al. 2011). Spring arrival dates of the first 5% of Lesser Whitethroats in SW Finland were negatively correlated with April temperatures in various stations in Europe, including the region of Edirne (Halkka et al. 2011, Fig. 27). No correlations were found between the date of the 50% spring migration of Lesser Whitethroats with April temperatures in central and east Europe, as well as with those near Edirne, Turkey (Halkka et al. 2011, Fig. 27). The positive correlations we found with the temperature in Edirne might be similar to the seemingly positive relationships to temperatures areas in western Europe, in areas that the Lesser Whitethroats do not migrate (areas marked in blue, Fig. 27).

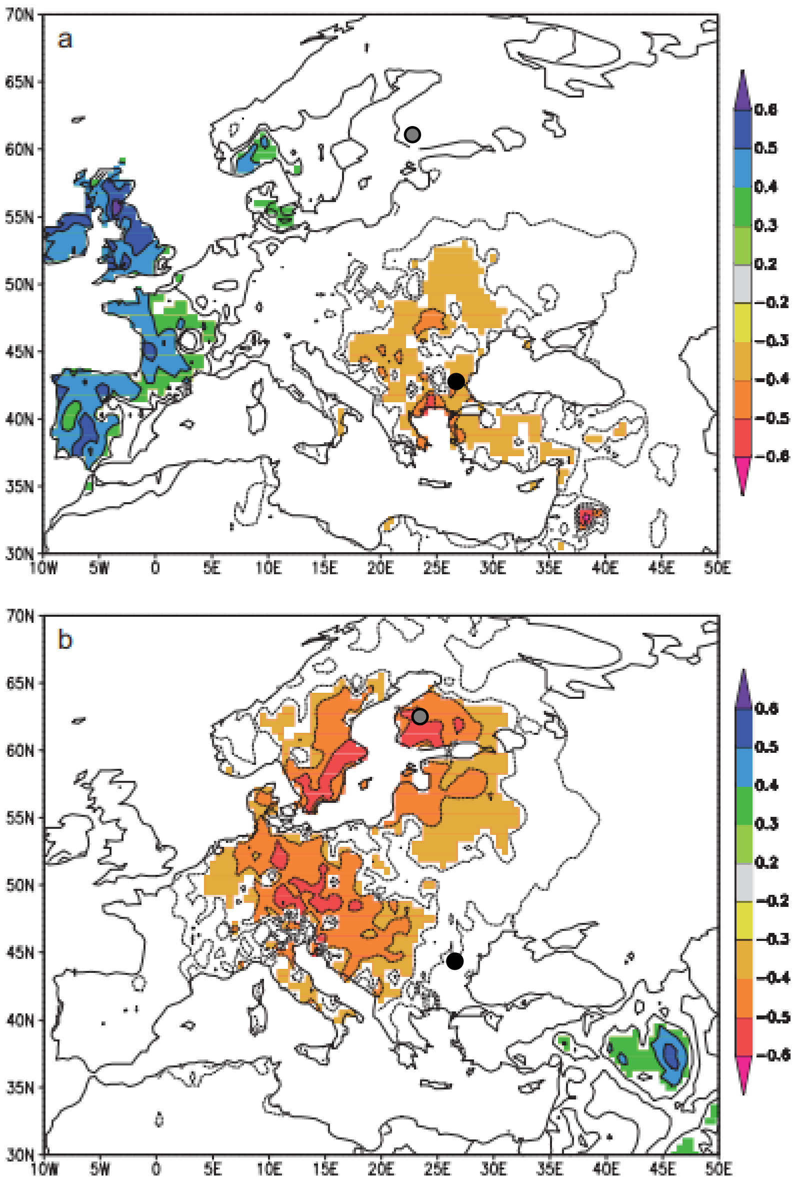

Fig. 27 (a-b). Correlation between the spring arrival dates of Lesser Whitethroats in Hanko, SW, Finland and the monthly GHCN/CAMS-gridded temperate. (a) Early (5% of seasonal sum of migrants) arrival dates vs. temperature in April, (b) median (50%) arrival dates vs. temperature in May. The legends of the figures refer to correlation coefficients (negative of positive). Coloured parts of the maps show only significant correlations (two-sided t-test: p < 0.1) with the degrees of freedom equal to the number of dates. Weather station in Edirne, Turkey, is marked with a black circle and Hanko Bird Observatory is marked with gray circle (after Halkka et al. 2011, modified).

Following the assumption that warm springs affect autumn migration timing through early arrival of adults on the breeding grounds in spring I correlated spring migration dates of Lesser Whitethorats at Bukowo-Kopań in 1982 – 2017 with mean April–May temperatures on spring migration routes. In most cases, the higher April temperatures on spring migration routes in Poland, Hungary, Turkey and Israel, the earlier Lesser Whitethroats arrived in spring at Bukowo-Kopań (Table 20). The correlations of spring passage dates at Bukowo-Kopań station with spring temperatures in Edirne were all negative and were the strongest of all the correlations (Table 20). We suggest that the differences in the pattern of correlations with spring temperatures, especially in Edirne, between the timing of spring and autumn migration of Lesser Whitethroats at the Operation Baltic stations might be biased by too many years within the period 1965–2003 that were excluded from analyses at both stations, and by generally small number of birds in years that were included (Table 3).

The contrast between significant correlations of spring temperatures in Israel and autumn migration dates at Mierzeja Wiślana and no correlations for Bukowo-Kopań suggest that different populations of Lesser Whitethroats migrate through these two Operation Baltic stations. An alternative explanation for negative correlations with spring migration timing of Lesser Whitethroats passing through Mierzeja Wiślana and the contrasting positive correlations of the timing in first and the last stages of autumn migration and spring temperatures in Edirne might be that warm springs there encourage early passage of Lesser Whitethroats through Bukowo-Kopań station and early arrival on the breeding grounds, for example in Finland (Halkka et al. 2011), and those birds that arrived early in spring might have additional clutches. Immature birds from the first and second clutches might stay at the breeding grounds longer to take advantage of the available food to fuel and moult so they leave breeding grounds in autumn later than in years with cold springs in Edirne.

Table 20. Correlation coefficients of spring migration dates of subsequent percentiles of the Lesser Whitethroats at Bukowo-Kopań during 23 March–15 May in 1982–2017 against bi-monthly means of daily temperatures of April–May (IV-V) from weather stations on spring migration routes.

Bi-monthly mean of daily temperatures	Weather station	Percent of the total population passing						
		5%	10%	25%	50%	75%	90%	95%
IV-V	Łeba (Poland)	-0.53	-0.52	-0.40	-0.31	-0.19	-0.08	0.01
	Szeged (Hungary)	-0.54	-0.47	-0.51	-0.40	-0.13	-0.15	-0.03
	Edirne (Turkey)	-0.64	-0.52	-0.53	-0.52	-0.30	-0.32	-0.12
	Lod (Israel)	-0.28	-0.28	-0.21	-0.22	-0.18	-0.25	0.03

7. Conclusions

1. The timing of the end (95%) of Garden Warbler autumn migration through the Polish Baltic coast advanced by 7 – 13 days during 53 years of research.
2. The end of autumn migration of Garden Warbler was the earlier the higher mean spring and autumn temperatures were on route, and the higher mean summer temperatures were on the breeding grounds.
3. The timing of Lesser Whitethroat autumn migration through the Polish Baltic coast did not change during 53 years of research. A lack of trend might be explained by small numbers of Lesser Whitethroats captured at Operation Baltic stations and the resulted gaps in series of analysed years. Another explanation might be large year-to-year fluctuations I found in autumn migration timing of , Lesser Whitethroats, which were related to inter-annual variation in temperatures.
4. The median dates (50%) of autumn migration of Lesser Whitethroat at Mierzeja Wiślana station advanced the more the higher the mean spring and autumn temperatures were on route, and the higher the mean summer temperatures were on their breeding grounds.

5. Warm springs might encourage early arrival and nesting of adult Garden Warblers. The resulted early hatching and fast growth and early maturity of juveniles during warm summers. These combined effects would enable the immature Garden Warblers to begin and end autumn migration earlier after warm spring and summers.
6. We suspect that early arrival in spring, might enable Lesser Whitethroats to lay additional clutches, and immatures from the first and additional clutches leave the breeding grounds late in warm autumns. In the effect autumn migration of this species does not advance.
7. The differences between the two Sylvia species in their response to temperatures might be attributed to their different wintering grounds and migration distances. We suggest that because Garden Warblers migrate very long distances in autumn, they might not have enough time to have second broods. On the other hand Lesser Whitethroats that migrate shorter distances than Garden Warblers might be able to have additional broods.

8. Bibliography

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