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Body condition of long-distance migrant birds from the Eastern Baltic before and after a population decline

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ABSTRACT

According to standardized bird trapping for banding purposes the population trends of Wrynecks (*Jynx torquilla* Linnaeus, 1758), Lesser Whitethroats (*Sylvia curruca* Linnaeus, 1758), Tree Pipits (*Anthus trivialis* Linnaeus, 1758), and Red-backed Shrikes (*Lanius collurio* Linnaeus, 1758) over 45 years in the Courish Spit, Eastern Baltic, indicate two periods, an initial population growth and a subsequent significant decline. All results, including the already published data on the Barred Warblers, indicate that 5 species of long-distance trans-Saharan migrants experienced a significant decline in numbers since the mid-1970s. Ringing protocol included determination of age and taking biometric measurements, the wing length as a proxy of structural size, and body mass. During the period of population decline, neither wing length, nor body mass of birds changed. None of the indicators of population productivity (clutch size, average brood size, breeding success) did not change, either. Presumably this may mean that the reasons for the population decline of the species are related to factors affecting birds on migration route or in wintering areas, and not on their breeding grounds. It is known that in catastrophic droughts on the African continent, the quality of habitats deteriorates, and competition for food leads to an increase in the mortality rate of wintering birds.

Keywords: body condition, droughts in Africa, Lesser Whitethroat, population decline, Red-backed Shrike, Tree Pipit, Wryneck

Состояние тела птиц – дальних мигрантов из Восточной Прибалтики до и после сокращения численности популяций

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РЕЗЮМЕ

По данным стандартного отлова птиц в целях кольцевания на Куршской косе в Восточной Прибалтике тенденции изменения численности популяций вертишейки (*Jynx torquilla* Linnaeus, 1758), славки-завирушки (*Sylvia curruca* Linnaeus, 1758), лесного конька (*Anthus trivialis* Linnaeus, 1758) и сорокопужулана (*Lanius collurio* Linnaeus, 1758) за 45 лет свидетельствуют о двух периодах: первоначальном популяционном росте и последующем достоверном спаде. Все результаты, включая уже опубликованные данные о ястребиной славке, указывают на то, что с середины 1970-х годов численность популяций 5 видов дальних транс-сахарских мигрантов значительно сократилась. Все птицы при кольцевании подвергались измерению крыла и взвешиванию. В период снижения численности ни длина крыла, ни масса тела птиц исследованных популяций не изменились. Ни один из показателей продуктивности популяции (размер кладки, средний размер выводка, успешность размножения) также не изменился.

Предположительно это может означать, что причины популяционного спада могут относиться к факторам, влияющим на птиц в местах зимовки или на миграционном пути, а не на местах гнездования. Наиболее вероятной причиной представляется влияние изменения климатических факторов, приводящих к засухам на африканском континенте, в тех областях, где зимуют обсуждаемые виды птиц. Известно, что при катастрофических засухах на африканском континенте ухудшается качество местобитаний, а конкуренция за пищу приводит к увеличению смертности зимующих птиц.

Ключевые слова: состояние тела, засуха в Африке, популяционный спад, славка-завирушка, лесной конек, сорокопуд-жулан, вертишейка

INTRODUCTION

Since the last century's fundamental contributions to population studies, especially by Lack (1954, 1966) and others, many publications have discussed research into population dynamics, both in animals in general but more specifically in birds. The analysis of population, in its turn, is based on the data on numbers and how they fluctuate. Identification of environmental factors that determine population size in natural habitats is one of the tasks of animal population ecology. Population size fluctuates due to changes in environmental conditions or to changes in the density of the population itself (Berryman 2004). A poorly studied aspect of population research is the possibility to forecast the population condition on the basis of parameters including morphological changes during the periods of different population trends. Body condition, e.g. size and mass can inform demographic and ecological inferences. Although still small in number, there are articles on this topic for both mammals and birds (Pavlova and Vysotsky 1989; Calkins et al. 1998; Laidre et al. 2006). The methods for diagnosing causes of declines in bird numbers use of comparisons between time periods with different trends. It is necessary to compare body condition during different periods in the life of population, i.e. when numbers are stable or increasing, and when the numbers are decreasing (Green 1999).

Many population studies have been conducted on birds. Apart from annual fluctuations in population size, there long-term declines or increases in numbers, as well as periodic fluctuations with different amplitudes occur (Newton 2003, 2008). One of the many ways to account for avian population numbers is the standardized annual trapping. The effectiveness of long-term trapping is increased when biometric data is collected following standardized protocols. It provides valuable information on body condition, fuel stores and structural size. These indicators may

be compared between different periods of the life of populations, i.e. during population growth and decline. Such research was conducted in the Eastern Baltic of Barred Warbler (*Sylvia nisoria*) population, whose numbers after a period of some growth began to decline catastrophically (Payevsky et al. 2003). Afterwards, in addition to Barred Warblers, similar population changes were also found in the Eastern Baltic populations of 4 other species of long-distance trans-Saharan migrants. Increases in trapping figures were replaced by gradual but significant declines. This new data is analyzed here. My main goal was to find out whether body mass and wing length of captured birds changed during the period of population decline. If this happened, it would mean that during the breeding season, the populations are affected by factors that lead to insufficient development of young individuals (as happened in the cases cited above). If not, as previously shown in Barred Warbler, this can most likely mean that the causes of the population decline relate to the factors acting on migratory route or in wintering areas, i.e. not in the breeding area.

MATERIALS AND METHODS

Wrynecks (*Jynx torquilla* Linnaeus, 1758), Lesser Whitethroats (*Sylvia curruca* Linnaeus, 1758), Tree Pipits (*Anthus trivialis* Linnaeus, 1758), and Red-backed Shrikes (*Lanius collurio* Linnaeus, 1758) analyzed here were trapped on the Courish (= Curonian) Spit in the Eastern Baltic. The multi-year data presented here were collected by the staff of the Biological Station Rybachy of the Zoological Institute, Russian Academy of Sciences. This long-term bird trapping project is carried out in order to study migration and population ecology.

Research area. The Courish Spit is a narrow strip of land separating the Courish Lagoon from the Baltic Sea. The spit is stretched in the direction from north-east to south-west, which coincides with the

Table 1. Wing length (mm) of the measured birds in different periods.

Periods of years	n	lim	cv, %	Average \pm SE	Difference between the averages		
					<i>t</i>	<i>df</i>	<i>P</i>
Wryneck ad							
1957–1971	44	80.0 – 93.0	1.7	88.6 \pm 0.12	0.8	111	>0.01
1972–2001	69	78.0 – 95.0	1.8	87.6 \pm 0.28			
Wryneck juv							
1957–1971	74	74.0 – 91.0	2.7	82.5 \pm 0.18	1.1	250	>0.01
1972–2001	178	74.0 – 93.0	3.0	85.8 \pm 0.24			
Tree Pipit ad							
1957–1974	231	82.0 – 95.0	2.5	88.5 \pm 0.14	0.1	572	>0.01
1975–2001	343	80.0 – 95.0	2.5	88.7 \pm 0.14			
Tree Pipit juv							
1957–1974	1424	78.0 – 98.0	2.5	88.2 \pm 0.11	0.4	2971	>0.01
1975–2001	1549	81.0 – 97.0	2.4	88.6 \pm 0.13			
Lesser Whitethroat ad							
1957–1980	662	60.0 – 74.0	2.8	65.7 \pm 0.08	0.3	2099	>0.01
1981–2001	1439	57.0 – 72.0	2.6	65.9 \pm 0.07			
Lesser Whitethroat juv							
1957–1980	2373	57.0 – 71.0	2.1	66.4 \pm 0.05	1.9	6475	>0.01
1981–2001	4104	61.0 – 71.0	2.5	66.1 \pm 0.08			
Red-backed Shrike males ad							
1957–1973	98	88.0 – 98.0	2.3	94.6 \pm 0.21	1.9	132	>0.01
1974–2001	36	87.0 – 100.0	2.2	94.2 \pm 0.35			
Red-backed Shrike females ad							
1957–1973	84	85.0 – 98.0	2.3	93.8 \pm 0.22	1.2	128	>0.01
1974–2001	46	84.0 – 98.0	2.3	93.4 \pm 0.33			
Red-backed Shrike juv							
1957–1973	178	84.0 – 98.0	2.2	94.1 \pm 0.23	1.3	557	>0.01
1974–2001	381	88.0 – 99.0	2.4	93.2 \pm 0.32			

main direction of bird migration in the Eastern Baltic (Fig. 1) Annual trapping of birds has been carried out in three Rybachy-type funnel traps since 1957 at “Fringilla” field station (55°05' N, 20°44' E) by a method which strictly standardized trapping effort.

The Rybachy-type trap is described in detail elsewhere (Dolnik and Payevsky 1976; Payevsky 2000). The traps operate around the clock for 7 months of the year, from the end of March to the beginning of November. Every year the same trapping season and the same daily trapping effort were maintained. The traps control the same populations, and the number of birds caught is a proxy of their numbers. We consider all our captured birds as a complex of populations from the all Eastern Baltic territories, and all

our measurement data are averaged for this entire complex.

Ringling protocol included determination of sex and age, if possible (following Svensson 1970, 1992; Vinogradova et al. 1976), and taking biometric measurements, including wing length as a proxy of structural size, and body mass. Wing length, i.e. distance between the carpal joint and the tip of the longest primary, was measured to the nearest 1 mm on a wing flattened and pressed to the ruler (method 3 in Svensson 1992). Birds were weighed to the nearest 0.1 g.

Much data obtained on the number of both migrants and birds nesting on the Courish Spit have been published (Payevsky 1973, 1985, 1999, 2009;

Table 2. Body mass (g) of the measured birds in different periods.

Periods of years	n	lim	cv, %	Average \pm SE	Difference between the averages		
					t	df	P
Wryneck ad							
1957–1971	26	29.8 – 37.4	3.8	33.8 \pm 0.43	0.2	86	>0.01
1972–2001	62	29.2 – 38.1	5.8	35.1 \pm 0.28			
Wryneck juv							
1957–1971	38	25.0 – 37.1	7.2	32.2 \pm 0.47	2.0	205	>0.01
1972–2001	169	25.8 – 41.1	3.0	37.0 \pm 0.29			
Tree Pipit ad							
1957–1974	169	16.2 – 25.5	6.4	21.4 \pm 0.11	0.5	503	>0.01
1975–2001	336	16.6 – 26.4	6.6	21.5 \pm 0.13			
Tree Pipit juv							
1957–1974	680	18.2 – 26.3	6.6	21.5 \pm 0.10	0.3	1753	>0.01
1975–2001	1075	17.4 – 25.1	3.9	28.3 \pm 0.11			
Lesser Whitethroat ad							
1957–1980	563	9.6 – 16.2	7.4	11.3 \pm 0.05	1.1	1960	>0.01
1981–2001	1399	9.0 – 15.6	7.0	11.4 \pm 0.08			
Lesser Whitethroat juv							
1957–1980	2052	9.1 – 13.8	4.8	11.9 \pm 0.25	0.4	6189	>0.01
1981–2001	4139	9.4 – 14.2	5.4	11.7 \pm 0.12			
Red-backed Shrike males ad							
1957–1973	98	25.0 – 32.0	5.5	29.0 \pm 0.13	0.6	132	>0.01
1974–2001	36	26.0 – 31.2	5.7	28.7 \pm 0.16			
Red-backed Shrike females ad							
1957–1973	84	26.0 – 32.3	2.3	29.3 \pm 0.23	0.4	128	>0.01
1974–2001	46	25.0 – 31.8	2.3	29.4 \pm 0.32			
Red-backed Shrike juv							
1957–1973	141	25.4 – 34.3	5.3	29.4 \pm 0.18	0.7	492	>0.01
1974–2001	353	24.6 – 36.8	5.8	28.5 \pm 0.22			

Bolshakov et al. 2001). The published data on the number of captured birds for 1957–1981 (Payevsky 1985), as well as unpublished data from the database of the Biological Station Rybachy for 1982–2001, were used for the analysis of population changes. The size and body mass of the four studied species for the 45-year study period (1957–2001) are also taken from archival data. This period was chosen due to the fact that during this time, the studied populations first grew, and then declined. The total number of all birds measured, excluding nestlings, was as follows: 365 Wrynecks, 8578 Lesser Whitethroats, 3547 Tree Pipits and 1159 Red-backed Shrikes. From these samples, subsamples for analysis of body size and mass were taken for two periods (Table 1 and Table 2).

The inspection and measurement of captured birds began in 1960, but in the first years not all birds were measured and weighed. Due to the greater number of years in the period of population decline, the number of birds measured during this period was greater than during the period of population growth. The calculations were carried out in MS Excel.

In addition, during the entire period, we studied reproduction biology of birds in the Courish Spit, including the 4 species discussed here. We found the following number of nests with eggs or chicks: 63 in the Wryneck, 565 in the Lesser Whitethroat, 38 in the Tree Pipit, and 138 in the Red-backed Shrike. The results of these studies are published (Payevsky 1985, 1991, 1999, 2009; Shapoval 1988).

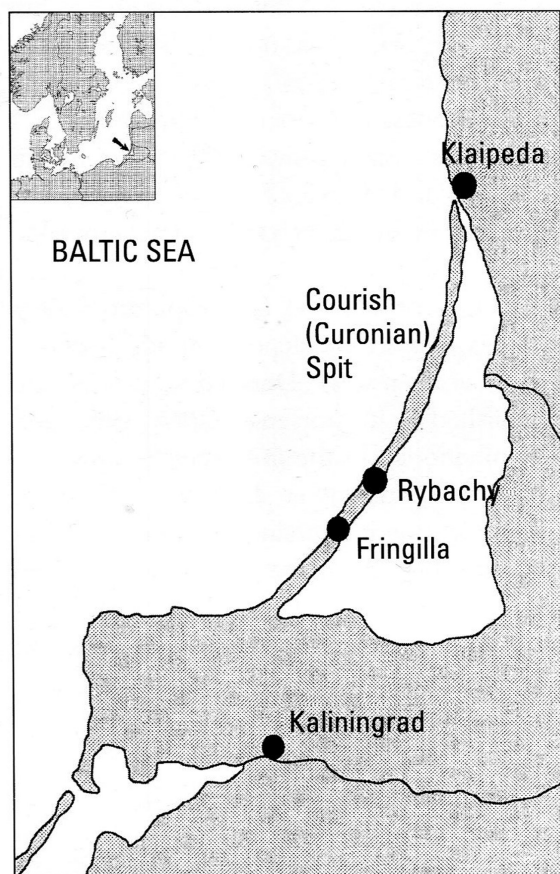


Fig. 1. Map chart of the Courish Spit.

Population trends were analyzed by the Spearman's rank correlation coefficient, where one set of variables is represented by consecutive years, and the other by the number of birds caught. The periods of population growth and decline are analyzed separately. The highest number value was the peak between these two periods.

RESULTS

Trends in the total number of the studied birds of 4 species over 45 years (1957–2001), presented in the form of unaligned curves (Fig. 2), indicate 2 periods, the initial population growth and subsequent population decline. The beginning of the population decline falls on 1972 in the Wryneck, 1974 in the Red-backed Shrike, 1975 in the Tree Pipit and 1981 in the Lesser Whitethroat. Spearman's rank correlation coefficients between trapping totals and periods of the

growth and decline separately are shown in Figure 2 for each species. With one exception (the period of population decline in Tree Pipits), all other coefficients showed a significant relationship of growth or decline with different time periods within 45 years. All results, including the already published data on the Barred Warblers (Payevsky et al. 2003), indicate that 5 species of long-distance trans-Saharan migrants from the Eastern Baltic experienced a significant decline in numbers since the mid-1970s.

Analyses of size (Table 1) and body mass (Table 2) during the periods of population growth and decline were conducted for different age groups, and in the Red-backed Shrike for adult males and adult females. According to t-test, the mean values for the 2 samples were not significantly different in any case. It means that neither the size of the birds nor their body mass changed during the period of population decline.

DISCUSSION

Our results indicate no change in wing length and body mass of the studied birds during the periods of population decline. In addition, according to previously published data on the reproduction of the 4 studied species during the study period gave reason to believe that none of the indicators of population productivity (clutch size, average brood size, breeding success, the ratio of the number of young and adult individuals) changed during the period of population decline (Payevsky 1985, 1991, 1999, 2009; Shapoval 1988). During ringing, no changes were observed in their visible subcutaneous fat deposits during this time. Presumably this may mean that the reasons for the population decline of the 4 species are related to factors affecting birds on migration route or in wintering areas, and not on their breeding grounds. Of course, I can agree with the statement that our present knowledge about migration patterns of different bird populations remains dramatically poor even as individual populations of migratory birds face different pressures from climatic variation at winter quarters and while on passage (Busse 2018).

Do my assumptions apply equally to all 4 species? On the one hand, numerous publications on the population decline of Wryneck and Red-backed Shrike in different countries of Western Europe and in different biotopes confirm this assumption. On the other hand for the Tree Pipit and Lesser Whitethroat an alternative hypothesis is possible. On the Courish

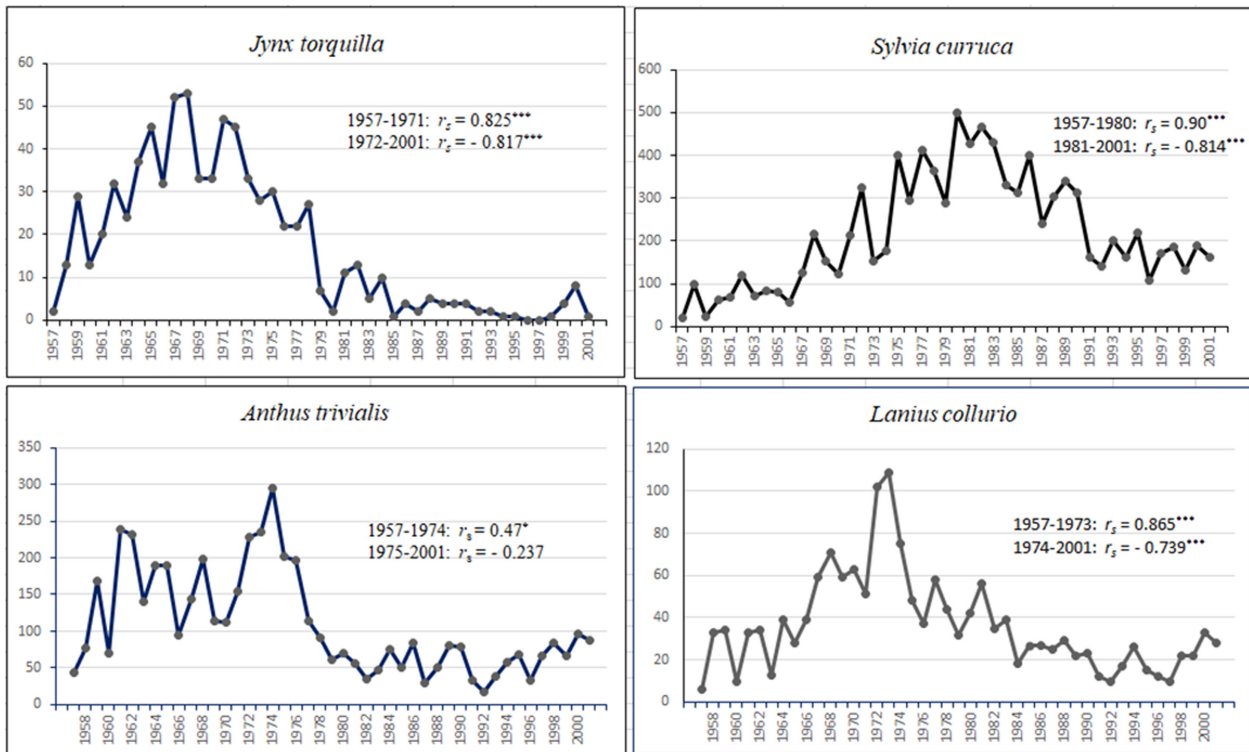


Fig. 2. Trends in the numbers of the studied populations of 4 species over 45 years (1957–2001), presented in the form of unaligned curves of annual totals. On the ordinate axis, the number of birds trapped. Spearman's rank correlation coefficients between trapping totals and periods of the growth and decline separately are shown. Significance levels: * = $p < 0.05$, *** = $p < 0.001$.

Spit, where the traps are located, over the years there has been a gradual change of the biotope. The open sandy territory is gradually overgrown with a dense pine forest (with the exception of high bare sand dunes). It cannot be excluded that the reduction in the number of trapped Tree Pipit and Lesser White-throat could be caused by these changes and the corresponding redistribution of the birds, not only breeding on the Courish Spit, but also migrating birds of these species.

The first reports on population declines in Palearctic species wintering in Africa appeared in the 1970s and 1980s (Berthold 1973; Dolnik and Payevsky 1980; Österlöf and Stolt 1982; Busse and Cofta 1986). The declines were significant, but not fatal for the species' existence. For example, according to the data from Denmark, numbers of trans-Saharan migrants decreased by 1.3% per year between 1976 and 2005 (Heldbjerg and Fox 2008). The main causes of population trends discussed in many publications (Busse et al. 1995; Berthold et al. 1998; Newton 2004, 2006; Vickery et al. 2014 and others)

were related to 3 main groups of factors: (1) anthropogenic impact, i.e. structural changes in forests, as well as environmental pollution at breeding sites and at stopovers and wintering sites, primarily due to the use of pesticides and herbicides, (2) climatic and weather factors, from the dynamics of cold and warm winters and springs to droughts in wintering areas in Africa, global warming including, and (3) intra-population factors, when due to competition and the "buffer effect", when a part of the population reproduces in poorer habitats and produces fewer offspring.

A series of publications by Leonid Sokolov and co-authors (Sokolov 1999; Sokolov et al. 2000, 2001) was devoted to the causes of fluctuations in the numbers of European passerine populations, where long-distance migrants were also discussed. The authors concluded that in different regions of Europe in the 1960s and 1980s there was a significant increase in the population size of many species, while in the 1970s and partly in the 1990s there was a significant decrease. Fluctuations in weather and climatic

factors were recognized as the reason for such long-term periods of increasing and decreasing numbers. The evidence was based on reliable links between the number of captured birds and April air temperatures, as well as on links between the number of birds, timing and effectiveness of their breeding.

In some cases, the results of the analysis of population trends were contradictory. Some publications reported dramatic population declines in several European species (Busse et al. 1995; Berthold et al. 1998). Others claimed that the abundance of the same species in the same years was stable (Marchant 1992; Sokolov 1999). A good example is the situation with the populations of Common Whitethroat (*Sylvia communis* Latham, 1787), which were the initial object of close attention to the changes in the numbers of European birds. This contradiction can only be explained by the fact that different populations may be subject to different external influences on the local scale.

As for the four bird species discussed here, the declines in their numbers were noted repeatedly by many researchers in different European regions. For example, a sharp decline in Wryneck population numbers was recorded in Germany (Moritz 1993; Berthold et al. 1999), Sweden (Pettersson 1997; Svensson 2000; Karlsson et al. 2002; Rytman 2003), Baltic countries (Payevsky 1991), and in the Leningrad region of Russia (Malchevsky and Pukinsky 1983). Among the other 3 species, the largest decline in numbers was found in the Red-backed Shrike, according to data from different countries and regions (Shapoval 1988; Busse 1994; Petterson 1997; Berthold et al. 1999; Sokolov et al. 2001; Karlsson et al. 2002). The degree of decline in the numbers of the Lesser Whitethroat and the Tree Pipit was varied across Europe (see Payevsky 2006 for a review).

Of all reasons for population declines discussed in the literature, the most probable is the influence of external factors during wintering on the African continent. In the Sahel, which is favourable for migrants in years with normal precipitation, the situation changes dramatically during dry periods. In catastrophic droughts, the quality of habitats deteriorates, and competition for food leads to an increase in the mortality rate of wintering birds (Newton 2004). The importance of weather and climatic conditions during arrival to African wintering grounds was exemplified by the of Lesser Whitethroats and Bonelli's Warbler (*Phylloscopus bonelli* Vieillot,

1819) migrating through Israel. Harsh conditions caused by heat and dryness of the environment, accompanied by the lack of adequate food, cause high bird mortality (Aloni et al. 2019).

It should be emphasized that all 4 bird species discussed here are not classified as vulnerable: "Despite the fact that the population trend appears to be decreasing, the decline is not believed to be sufficiently rapid to approach the thresholds for Vulnerable under the population trend criterion..." (BirdLife International 2021). However, it is still necessary to identify such declining populations and try to understand the reasons for their decline.

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REFERENCES

- Aloni I., Markman S. and Ziv Y. 2019.** Autumn temperatures at African wintering grounds affect body condition of two passerine species during spring migration. *PLoS ONE*, **14**(5): 1–15. <https://doi.org/10.1371/journal.pone.0217619>
- Berryman A.A. 2004.** Limiting factors and population regulation. *Oikos*, **105**: 667–670. <https://doi.org/10.1111/j.0030-1299.2004.13381.x>
- Berthold P. 1973.** Über starken Rückgang der Dorngrasmücke und anderer Singvogelarten im westlichen Europa. *Journal für Ornithologie*, **114**(3): 348–360. <https://doi.org/10.1007/BF01640341>
- Berthold P., Fiedler W., Schlenker R. and Querner U. 1998.** 25-year study of the population development of Central European songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften*, **85**: 350–353. <https://doi.org/10.1007/s001140050514>

- Berthold P., Fiedler W., Schlenker R. and Querne U. 1999.** Bestandsveränderungen mitteleuropäischer Kleinvögel: Abschlußbericht zum MRI-Programm. *Vogelwarte*, **40**: 1–10.
- BirdLife International 2021.** IUCN Red List for birds. Available from: <http://www.birdlife.org> (accessed 27 January 2021).
- Bolshakov C.V., Shapoval A.P. and Zelenova N.P. 2001.** Results of bird ringing by the Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. Part 1. *Avian Ecology and Behaviour*, Suppl. **1**: 1–126.
- Busse P. 1994.** Population trends of some migrants at the southern Baltic coast – autumn catching results 1961–1990. *The Ring*, **16** (1–2): 1–115.
- Busse P. 2018.** Migration patterns of individual populations a key requirement in studies on climate-caused changes of migration strategy. Conference: *A joint conference of the “Birds as Early Warning Systems” of the Poland–South Africa collaboration project, the Migrant Landbird Study Group, and the Polish Network of Bird Ringing Stations (KSSOP) Migrant birds as indicators of climate change* (13–16 December, Gdansk). The Polish Network of Bird Ringing Stations (KSSOP), Gdansk, Poland. <https://doi.org/10.13140/RG.2.2.23468.92804>
- Busse P., Baumanis J., Leivits A., Pakkala H., Payevsky V.A. and Ojanen M. 1995.** Population number dynamics 1961–1990 of *Sylvia* species caught during autumn migration at some North and Central European bird stations. *The Ring*, **17**: 12–30.
- Busse P. and Cofta T. 1986.** Population trends of migrants at the Polish Baltic coast and some new problems in the interpretation of migration counts. *Vår Fågelvärld, Supplement*, **11**: 27–31. <https://www.researchgate.net/publication/270276615>
- Calkins D.G., Becker E.F. and Pitcher K.W. 1998.** Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. *Marine Mammal Science*, **14**: 232–244. <https://doi.org/10.1111/j.1748-7692.1998.tb00713.x>
- Dolnik V.R. and Payevsky V.A. 1976.** Rybachy trap. In: V.D. Ilyichev (Ed.). Ringing in the study of avian migration in the USSR. Nauka, Moscow: 73–81. [In Russian].
- Dolnik V.R. and Payevsky V.A. 1980.** Dynamics of numbers in Baltic bird populations in 1960–1976. *Soviet Journal of Ecology*, **10**: 316–325.
- Green R.E. 1999.** Diagnosing the causes of bird population declines using comparative methods: The value of data from ringing. *Ringling & Migration*, **19** (Suppl. 1): 47–56. <https://doi.org/10.1080/03078698.1999.9674211>
- Heldbjerg H. and Fox T. 2008.** Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study*, **55**: 267–279. <https://doi.org/10.1080/00063650809461532>
- Karlsson L., Ehnbohm S., Persson K. and Walinder G. 2002.** Changes in numbers of migrating birds at Falsterbo, South Sweden, during 1980–1999, as reflected by ringing totals. *Ornis scandinavica*, **12**: 113–137.
- Lack D. 1954.** The natural regulation of animal numbers. Clarendon Press, Oxford, 343 p.
- Lack D. 1966.** Population studies of birds. Clarendon Press, Oxford, 343 p.
- Laidre K.L., Estes J.A., Tinker M.T., Bodkin J., Monson D. and Schneider K. 2006.** Patterns of growth and body condition in sea otters from the Aleutian archipelago before and after the recent population decline. *Journal of Animal Ecology*, **75**: 978–989. <https://doi.org/10.1111/j.1365-2656.2006.01117.x>
- Malchevsky A.S. and Pukinsky Y.B. 1983.** Birds of the Leningrad region and adjacent territories. Vol. 1. Leningrad University Publishing House, Leningrad, 480 p. [In Russian].
- Marchant J.H. 1992.** Recent trends in breeding populations of some common trans-Saharan migrant birds in Northern Europe. *Ibis*, **134** (1): 113–119. <https://doi.org/10.1111/j.1474-919X.1992.tb04741.x>
- Moritz D. 1993.** Long-term monitoring of Palaearctic-African migrants at Helgoland/German Bight, North Sea. *Annales of Royal Museum for Central Africa*, **268**: 579–586.
- Newton I. 2003.** Population regulation in birds: is there anything new since David Lack? *Avian Science*, **3**(2–3): 75–84.
- Newton I. 2004.** Population limitation in migrants. *Ibis*, **146** (2): 197–226. <https://doi.org/10.1111/j.1474-919X.2004.00293.x>
- Newton I. 2006.** Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology*, **147**: 146–166. <https://doi.org/10.1007/s10336-006-0058-4>
- Newton I. 2008.** The Migration Ecology of Birds. Academic Press, London, 976 p.
- Österlöf S. and Stolt B.O. 1982.** Population trends indicated by birds ringed in Sweden. *Ornis scandinavica*, **13** (2): 135–140. <https://doi.org/10.2307/3676200>
- Pavlova E.A. and Vysotsky V.G. 1989.** A new data on the Murgab pheasant *Phasianus colchicus principalis*. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, **197**: 98–104. [In Russian].
- Payevsky V.A. 1973.** Atlas of bird migration according to banding data at the Courland Spit. In: B.E. Bykhovskii (Ed.). Bird migration – ecological and physiological factors. Halstead Press of John Wiley and Sons, New York, 124 p.
- Payevsky V.A. 1985.** Avian demography. Nauka Press, Leningrad, 285 p. [In Russian].
- Payevsky V.A. 1991.** The extinct population of the Wryneck: its history and parameters. *Materialy 10 Vsesoyuznoy ornitologicheskoy konferentsii. Navuka i tekhnika, Minsk*, **2**: 132–134 [In Russian].

- Payevsky V.A. 1999.** Breeding biology, morphometrics, and population dynamics of *Sylvia* warblers in the Eastern Baltic. *Avian Ecology and Behaviour*, **2**: 19–50.
- Payevsky V.A. 2000.** Rybachy-type trap. In: P. Busse (Ed.). Bird Station Manual. Gdańsk University, Gdańsk, 20–24.
- Payevsky V.A. 2006.** Mechanisms of population dynamics in trans-Saharan migrant birds: a review. *Entomological Review*, **86**: S82–S94. <https://doi.org/10.1134/S001387380610006X>
- Payevsky V.A. 2009.** Songbird Demography. KMK Scientific Press, Moscow, 235 p.
- Payevsky V.A., Vysotsky V.G. and Zelenova N.P. 2003.** Extinction of a Barred Warbler *Sylvia nisoria* population: long-term monitoring, demography, and biometry. *Avian Ecology and Behaviour*, **11**: 89–105.
- Pettersson J. 1997.** Fågelräkning vid Ottenby 1996. Degerhamn, Naturvårdsverket. 31 p.
- Ryttman H. 2003.** Breeding success of Wryneck *Jynx torquilla* during the last 40 years in Sweden. *Ornis svecica*, **13**: 25–28.
- Shapoval A.P. 1988.** Some reproduction parameters of a declining population of Red-backed Shrike in the Courish Spit. Abstracts of 12th Baltic Ornithological Conference (15–18 November 1988, Palanga). Academy of Sciences of the Lithuanian SSR, Vilnius: 241–243. [In Russian].
- Sokolov L.V. 1999.** Population dynamics in 20 sedentary and migratory passerine species of the Courish Spit on the Baltic Sea. *Avian Ecology and Behaviour*, **3**: 23–50.
- Sokolov L.V., Yefremov V.D., Markovets M.Y., Shapoval A.P. and Shumakov M.E. 2000.** Monitoring of numbers in passage populations of passerines over 42 years (1958–1999) on the Courish Spit of the Baltic Sea. *Avian Ecology and Behaviour*, **4**: 31–53.
- Sokolov L.V., Baumanis A., Leivits A., Poluda A.M., Yefremov V.D., Markovets M.Yu., Morozov Y.Yu. and Shapoval P.P. 2001.** Comparative analysis of long-term monitoring data on numbers of passerines in nine European countries in the second half of the 20th century. *Avian Ecology and Behaviour*, **7**: 41–74.
- Svensson L. 1970.** Identification Guide to European Passerines 1st edition. Naturhistoriska Riksmuseet, Stockholm, 152 p.
- Svensson L. 1992.** Identification Guide to European Passerines. 4th edition. Stockholm. Naturhistoriska Riksmuseet, Stockholm, 368 p.
- Svensson S. 2000.** Övervakning av fåglars population-utveckling. Årsrapport för 1999. Ekologiska institutionen and Lunds universitet, Lund, 20 p.
- Vickery J.A., Ewing S.R., Smith K.W., Pain D.J., Bairlein F., Škorpilová J. and Gregory R.D. 2014.** The decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis*, **156**: 1–22. <https://doi.org/10.1111/ibi.12118>
- Vinogradova N.V., Dolnik V.R., Yefremov V.D., and Payevsky V.A. 1976.** Identification of Sex and age in passerine birds of the USSR. Nauka Press, Moscow, 192 p. [In Russian].