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# Three million ringed birds on the Curonian Spit (Baltic area) and ten thousand results on their migration routes: a brief overview, statistics and examples

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**ABSTRACT**

One of the mass migratory routes of birds in Europe is the White Sea-Baltic migration route, which runs through the eastern Baltic area. In order to study bird migration by ringing, Vogelwarte Rossitten, the world's first ornithological station, was founded on the Curonian Spit, the work of which was continued by the Rybachy Biological Station of the Zoological Institute of the Russian Academy of Sciences. The 3,214,217 birds of 202 species were ringed here during 1956–2020, and 10,165 reports of distant ring recoveries from 99 bird species were received. The paper provides a brief overview of these results. The main attention is paid to the following topics: a) the effectiveness of ringing in different bird species, including a decrease in the proportion of ring recoveries, b) the geographical distribution of migrants with an example of migration connectivity between geographical areas in different seasons, c) the possibilities of studying population dynamics based on annual trapping data, as well as d) various aspects of the demographic study of populations based on the results of ringing. Throughout the entire White Sea-Baltic migration route, the well-known interactive Eurasian-African Bird Migration Atlas (2022) includes the results of ringing from Finland, Estonia, Latvia, Lithuania, Belarus and Poland. However, for reasons unrelated to science, our aforementioned results were not included in this atlas. The article has been written in order to familiarize the international ornithological community with the results of bird ringing at the Rybachy Biological Station.

**Key words:** atlas, avian demography, birds, migration connectivity, migration routes, population dynamics, ringing

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# Три миллиона окольцованных птиц на Куршской косе (Прибалтика) и десять тысяч результатов о путях их миграций: краткий обзор, статистика и примеры

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**РЕЗЮМЕ**

Один из массовых пролётных путей птиц в Европе – Беломорско-Балтийская миграционная трасса, проходящая по восточной Прибалтике. С целью изучения перелетов птиц путем кольцевания на Куршской косе была основана первая в мире орнитологическая станция Vogelwarte Rossitten, работу которой продолжила Биологическая станция «Рыбачий» Зоологического института РАН. За 1956–2020 гг. в этом месте сотрудниками Биостанции было окольцовано 3 миллиона 214 тысяч 217 особей птиц 202 видов и получено 10165 сообщений о дальних находках колец у 99 видов птиц. В статье представлен краткий обзор этих результатов. Основное внимание уделено следующим темам: а) результативности кольцевания разных видов птиц, включая падение доли возврата колец, б) географическому распределению мигрантов с примером миграционной связности между географическими областями в разные сезоны, в) возможностям изучения динамики численности популяций на основе данных ежегодного отлова, а также г) разным аспектам демографического изучения популяций по результатам кольцевания. Статья написана с целью ознакомления международной орнитологической общественности с нашими результатами кольцевания птиц, не вошедшими (по причинам, не связанными с наукой) в известный международный интерактивный атлас миграций и веб-сайт по Евразийско-Африканскому пролётному пути птиц (2022 г.).

**Ключевые слова:** атлас, демография птиц, миграционная связность, миграции, динамика популяций, кольцевание

## INTRODUCTION

Research on bird migration remains very relevant today, as before, primarily due to the role of birds in the spread of arboviruses, as well as the study of problems of bird orientation and navigation, and a number of other problems (Spina 1998; Berthold 2001; Chernetsov 2012). In the study of bird migration, an event took place, that received great gratitude from the entire vast team of ornithologists and other biologists involved in the study of bird migration: an Interactive Migration Atlas and website for the Eurasian-African Flyway appeared (Spina et al. 2022). This project was implemented by an international team of 29 different specialists, coordinated by the European Union for Bird Ringing (EURING) together with the Max Planck Institute of Animal Behavior. The initial data on which this project is based was provided by more than 50 organizations engaged in bird ringing within Eurasia. This atlas details the ringing results of more than 300 bird species collected over more than 100 years, which in itself is the most important result of the activities of ornithologists. Unfortunately, not all ringing results are included in this atlas, and they will be discussed in this article.

One of the mass migratory routs of birds in Europe is the White Sea-Baltic migration route. It has been known for a very long time that the spring and autumn migration of many European bird species takes place in the Eastern Baltic area and, in particular, through the Curonian Spit separating the Curonian Lagoon from the Baltic Sea. The spit is elongated in the direction from northeast to southwest, which coincides with the main direction of bird migration in the Eastern Baltic (Thienemann 1928, 1931; Schüz 1930). It was here in 1901 that Johannes Thienemann founded the world's first ornithological station, Vogelwarte Rossitten, which operated until 1944. In 1956, the work of this station was continued by the Soviet, now Russian Rybachy Biological Station of the Zoological Institute of the Academy of Sciences (Fig. 1), which has been operating to this day. A new effective method of trapping migrating birds for ringing purposes has been developed here – the so-called Rybachy trap, which allows catching up to several thousand passing birds in one day.

Throughout the White Sea-Baltic migration route, the above-mentioned Eurasian-African Bird Migration Atlas includes the results of ringing by ornithologists from Finland, Estonia, Latvia, Lithuania, Belarus and Poland. However, for reasons unrelated to science, the thousands of results of bird ringing by the Rybachy Biological Station in the Curonian Spit are missing from this atlas. Many of these results have been previously published. In order to familiarize the international ornithological community with these results in the form of a brief overview, this paper has been written. The main attention is paid to the effectiveness of ringing in different bird species, the problems of studying population dynamics based on annual trapping data, examples of the migratory connectivity of birds between geographical areas in different

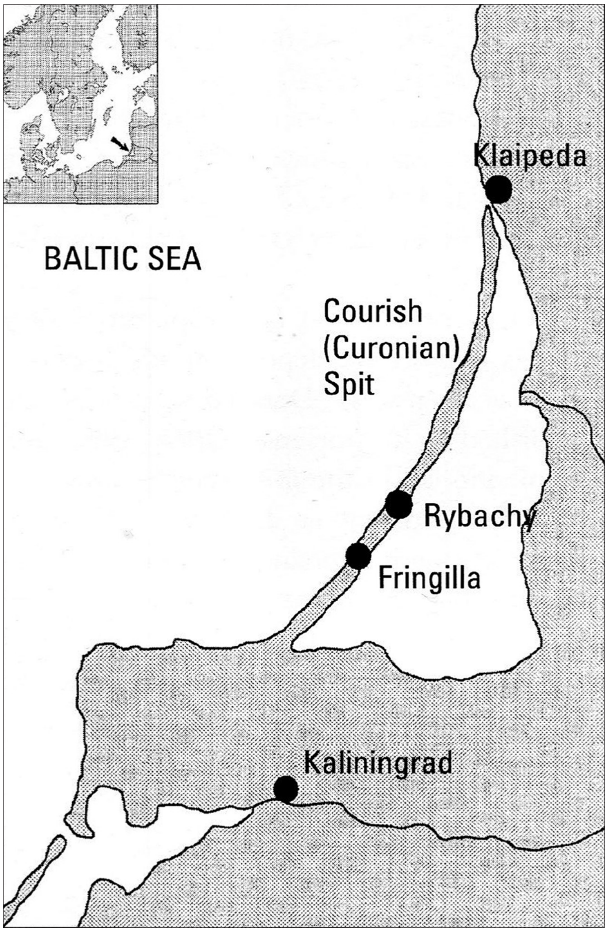


**Fig. 1.** Map of the Curonian Spit.

seasons, as well as the possibilities of demographic study of populations based on the results of ringing.

## MATERIAL AND METHODS

Trapping and ringing of birds by the staff of the Rybachy Biological Station of the Zoological Institute of the Russian Academy of Sciences has been carried out on the Curonian Spit (Eastern Baltic) since 1956 to the present. Trapping is carried out in two places: at the "Fringilla" field camp (55°05' N, 20°44' E) and at Rossitten Cape (55°09' N, 20°51' E). At the former site, birds are caught in the so-called Rybachy traps, at the latter site with mist nets. The detailed device of Rybachy traps has been described (Dolnik and Payevsky 1976). The traps operate for 7 months of the year, around the clock, from late March to early November. These traps differ sharply from the well-known Heligoland traps with their soft movable frame, absence of an arena for attracting birds, and huge size (height 12–15 m, length 70–100 m). Under optimal conditions of the autumn migration of birds, one such trap can catch up to 3–4 thousand migrating birds per day. It is significant that the Rybachy traps catch nocturnal migrants at their start, landing, and at night, and the number of nocturnal migrants in the traps is as large as the number of daytime migrants. In addition to migrants, local nesting birds fall into these traps in the summer. Many of them are repeatedly caught again in the same or subsequent years.

Trapping and ringing of birds of all species is accompanied by their lifetime examination, determination of sex and age, as well as standard measurements of wing length and body weight. In addition, the stage of the sexual cycle and the state of molting are also described (Vinogradova et al. 1976; Svensson 1992). Survival rate of birds was estimated from dead recoveries by the recent modifications of stochastic Brownie-type models (Brownie et al. 1985), included in the computer programme MARK, version 2.1 (White and Burnham 1999; Cooch and White 2001). Other statistical tests followed Sokal and Rohlf (1998).

The first results of work on ringing birds on the Curonian Spit were published more than 50 years ago in the form of an atlas of the spread of migratory birds across Europe and Africa (Payevsky 1973). Subsequently, a large number of new results of bird ringing accumulated, which were published as lists of the data obtained (Bolshakov et al. 1999 and in similar 17 papers in the same journal in subsequent years, 2000–2014), as well as Shapoval et al. 2017, and in similar 6 papers in the same journal in subsequent years, 2018–2022). In these publications, when reporting on ring recoveries, the coordinates of the location points, time elapsed since the day of the ringing, distance and azimuth are given. In addition, a number of analytical papers and books have been published over the years on studies of all bird movements, including maps of migration routes and wintering sites for individual species (Payevsky 1990; Vysotsky et al. 1990; Payevsky 1994; Shapoval 1994; Payevsky and Shapoval 1998; Payevsky 1999; Sokolov et al. 1999, 2002; Payevsky et al. 2004, 2005; Chernetsov et al. 2006; Sinelschikova et al. 2007; Payevsky 2010, 2012, 2013; Payevsky and Shapoval 2013; Payevsky, 2020 a, 2020 b, 2021a, 2021b; Payevsky and Shapoval 2022, 2023, 2024).

A total of 3,214,217 birds of 202 species have been ringed on the Curonian Spit in 65 years, from 1956 to 2020, of which 120 species belong to the order Passeriformes. By the end of 2023, 10,165 reports of ring recoveries from 99 bird species have been received, of which 69 are from passerines. In a number of the above-mentioned publications, a number of problems were investigated based on the materials of ringing and ring recoveries for 1956–1985, since these were the years with the largest number of birds caught and with the largest number of ring recoveries. In addition to research directly related to the migration routes of birds, other problems of ornithology are being investigated at the Rybachy Biological Station: population and demographic study of birds, physiological and biochemical foundations of the migratory state, as well as orientation and navigation of birds in space (Dolnik 1975; Payevsky 1985, 1998a, 1998b, 2009; Bolshakov and Chernetsov 2004; Markovets and Yosef 2005; Mukhin et al. 2005; Bolshakov et al. 2007; Bojarinova and Markovets 2007; Chernetsov 2016; Payevsky 2023; Tsvey 2023).

## RESULTS

### The effectiveness of bird ringing

The effectiveness of bird ringing, calculated as the percentage of distant ring recoveries obtained from the total number of ringed birds of each species for 1956–2020, is presented in Table 1 for non-passerines and in Table 2 for passerines. In non-passerines, this proportion varies from 0.1% in the Eurasian Wryneck to 17.2% in the Eurasian Woodcock, and in passerines from 0.1% in 25 different species to 6.7% in the Rook.

Analyses of passerines showed that the influence of bird species and year on the proportion of ring recoveries is very significant. The differences were found between Goldcrest and Garden Warbler, Common Chaffinch and Great Tit, Great Tit and Common Chaffinch. In three species, the proportion of ring recoveries decreased significantly over the years, on average from 0.8 to 0.2% in the Common Chaffinch, from 1.2 to 0.3% in the Eurasian Siskin, and from 2.0 to 1.0% in the Common Starling. Subsequent analysis

**Table 1.** The effectiveness of ringing of non-passerine birds on the Curonian spit, Eastern Baltic.

| Species | Number of ringed birds | Distant recoveries | |
|---|---|---|---|
| | | Number | Fraction, % |
| *Caprimulgus europaeus*, European Nightjar | 444 | 4 | 0.9 ± 0.4 |
| *Apus apus*, Common Swift | 698 | 2 | 0.3 ± 0.2 |
| *Cuculus canorus*, Common Cuckoo | 1707 | 15 | 0.9 ± 0.2 |
| *Columba palumbus*, Common Wood Pigeon | 70 | 4 | 5.7 ± 2.8 |
| *Streptopelia turtur*, European Turtle Dove | 126 | 3 | 2.4 ± 1.4 |
| *Streptopelia decaocto*, Eurasian Turtle Dove | 34 | 1 | 2.9 ± 1.7 |
| *Scolopax rusticola*, Eurasian Woodcock | 239 | 41 | 17.2 ± 2.4 |
| *Gallinago gallinago*, Common Snipe | 36 | 3 | 8.3 ± 4.6 |
| *Actitis hypoleucos*, Common Sandpiper | 45 | 2 | 4.4 ± 3.1 |
| *Ciconia ciconia*, White Stork | 364 | 9 | 2.5 ± 0.8 |
| *Ardea cinerea*, Grey Heron | 375 | 40 | 10.7 ± 1.6 |
| *Accipiter nisus*, Eurasian Sparrowhawk | 7749 | 334 | 4.3 ± 0.1 |
| *Accipiter gentilis*, Northern Goshawk | 52 | 4 | 7.7 ± 3.7 |
| *Circus cyaneus*, Hen Harrier | 71 | 2 | 2.8 ± 1.9 |
| *Aegolius funereus*, Boreal Owl | 355 | 4 | 1.1 ± 0.5 |
| *Asio otus*, Long-eared Owl | 3424 | 103 | 3.0 ± 0.3 |
| *Asio flammeus*, Short-eared Owl | 57 | 1 | 1.7 ± 1.7 |
| *Upupa epops*, Eurasian Hoopoe | 173 | 1 | 0.6 ± 0.5 |
| *Alcedo atthis*, Common Kingfisher | 268 | 2 | 0.7 ± 0.5 |
| *Jynx torquilla*, Eurasian Wryneck | 1218 | 1 | 0.1 ± 0.1 |
| *Dendrocopos major*, Great Spotted Woodpecker | 3883 | 11 | 0.3 ± 0.1 |

**Table 2.** The effectiveness of ringing of passerine birds on the Curonian spit, Eastern Baltic.

| Species | Number of ringed birds | Distant recoveries | |
|---|---|---|---|
| | | Number | Fraction, % |
| *Lanius collurio*, Red-backed Shrike | 3833 | 2 | 0.1 ± 0.05 |
| *Oriolus oriolus*, Eurasian Golden Oriole | 308 | 1 | 0.3 ± 0.03 |
| *Garrulus glandarius*, Eurasian Jay | 6770 | 156 | 2.3 ± 0.2 |
| *Pica pica*, Eurasian Magpie | 91 | 2 | 2.2 ± 1.5 |
| *Nucifraga caryocatactes*, Spotted Nutcracker | 476 | 18 | 3.8 ± 0.8 |
| *Coloeus monedula*, Western Jackdaw | 86 | 2 | 2.3 ± 1.6 |
| *Corvus frugilegus* Rook | 60 | 4 | 6.7 ± 3.2 |
| *Corvus cornix*, Hooded Crow | 76 | 5 | 6.6 ± 2.8 |
| *Bombycilla garrulus*, Bohemian Waxwing | 1355 | 26 | 1.9 ± 0.4 |
| *Periparus ater*, Coal Tit | 64773 | 209 | 0.3 ± 0.02 |
| *Poecile palustris*, Marsh Tit | 2763 | 2 | 0.1 ± 0.06 |
| *Poecile montanus*, Willow Tit | 2560 | 2 | 0.1 ± 0.06 |
| *Cyanestes caeruleus*, Eurasian Blue Tit | 118519 | 545 | 0.5 ± 0.02 |
| *Parus major*, Great Tit | 300335 | 881 | 0.3 ± 0.01 |
| *Remiz pendulinus*, Eurasian Penduline Tit | 1631 | 35 | 2.1 ± 0.3 |
| *Panurus biarmicus*, Bearded Reedling | 558 | 1 | 0.2 ± 0.01 |
| *Lullula arborea*, Woodlark | 4782 | 25 | 0.5 ± 0.1 |
| *Riparia riparia*, Sand Martin | 5127 | 13 | 0.3 ± 0.07 |
| *Hirundo rustica*, Barn Swallow | 12741 | 31 | 0.2 ± 0.04 |
| *Delichon urbicum*, Common House Martin | 8787 | 8 | 0.1 ± 0.03 |
| *Aegithalos caudatus*, Long-tailed Tit | 81248 | 277 | 0.3 ± 0.02 |
| *Phylloscopus sibilatrix*, Wood Warbler | 18127 | 10 | 0.1 ± 0.02 |
| *Phylloscopus trochilus*, Willow Warbler | 163452 | 116 | 0.1 ± 0.01 |
| *Phylloscopus collybita*, Common Chiffchaff | 13563 | 9 | 0.1 ± 0.03 |
| *Phylloscopus trochiloides*, Greenish Warbler | 132 | 1 | 0.8 ± 0.7 |
| *Acrocephalus arundinaceus*, Great Reed Warbler | 3664 | 21 | 0.6 ± 0.1 |
| *Acrocephalus schoenobaenus*, Sedge Warbler | 14063 | 32 | 0.2 ± 0.04 |
| *Acrocephalus dumetorum*, Blyth's Reed Warbler | 167 | 1 | 0.6 ± 0.05 |
| *Acrocephalus scirpaceus*, Common Reed Warbler | 23439 | 116 | 0.5 ± 0.04 |
| *Acrocephalus palustris*, Marsh Warbler | 7503 | 7 | 0.1 ± 0.03 |
| *Hippolais icterina*, Icterine Warbler | 12506 | 7 | 0.1 ± 0.02 |
| *Sylvia atricapilla*, Eurasian Blackcap | 31387 | 27 | 0.1 ± 0.02 |
| *Sylvia borin*, Garden Warbler | 25288 | 34 | 0.1 ± 0.02 |
| *Curruca nisoria*, Barred Warbler | 4029 | 7 | 0.2 ± 0.07 |
| *Curruca curruca*, Lesser Whitethroat | 20504 | 22 | 0.1 ± 0.02 |
| *Curruca communis*, Common Whitethroat | 14661 | 11 | 0.1 ± 0.03 |
| *Regulus ignicapillus*, Common Firecrest | 138 | 1 | 0.7 ± 0.7 |
| *Regulus regulus*, Goldcrest | 404965 | 254 | 0.1 ± 0.0 |
| *Troglodytes troglodytes*, Eurasian Wren | 15933 | 15 | 0.1 ± 0.02 |
| *Certhia familiaris*, Eurasian Treecreeper | 10175 | 5 | 0.1 ± 0.03 |
| *Sturnus vulgaris*, Common Starling | 116102 | 1232 | 1.1 ± 0.03 |
| *Turdus philomelos*, Song Thrush | 30382 | 433 | 1.4 ± 0.1 |
| *Turdus viscivorus*, Mistle Thrush | 318 | 5 | 1.6 ± 0.7 |
| *Turdus iliacus*, Redwing | 6328 | 106 | 1.7 ± 0.2 |
| *Turdus merula*, Common Blackbird | 16162 | 141 | 0.9 ± 0.1 |
| *Turdus pilaris*, Fieldfare | 2558 | 51 | 2.0 ± 0.3 |

**Table 2.** Ending.

| Species | Number of ringed birds | Distant recoveries | |
|---|---|---|---|
| | | Number | Fraction, % |
| *Muscicapa striata*, Spotted Flycatcher | 11124 | 15 | 0.1 ± 0.03 |
| *Erithacus rubecula*, European Robin | 205733 | 351 | 0.2 ± 0.01 |
| *Luscinia svecica*, Bluethroat | 231 | 1 | 0.4 ± 0.4 |
| *Luscinia luscinia*, Thrush Nightingale | 2806 | 9 | 0.3 ± 0.1 |
| *Ficedula hypoleuca*, European Pied Flycatcher | 30998 | 46 | 0.1 ± 0.02 |
| *Ficedula albicollis*, Collared Flycatcher | 31 | 2 | 6.4 ± 4.4 |
| *Phoenicurus ochruros*, Black Redstart | 1689 | 3 | 0.2 ± 0.01 |
| *Phoenicurus phoenicurus*, Common Redstart | 14439 | 17 | 0.1 ± 0.03 |
| *Saxicola rubetra*, Whinchat | 3399 | 3 | 0.1 ± 0.01 |
| *Passer domesticus*, House Sparrow | 1260 | 2 | 0.1 ± 0.09 |
| *Prunella modularis*, Dunnock | 7011 | 8 | 0.1 ± 0.04 |
| *Motacilla flava*, Western Yellow Wagtail | 2927 | 7 | 0.2 ± 0.08 |
| *Motacilla alba*, White Wagtail | 13801 | 16 | 0.1 ± 0.03 |
| *Anthus pratensis*, Meadow Pipit | 11051 | 96 | 0.8 ± 0.08 |
| *Anthus trivialis*, Tree Pipit | 6232 | 17 | 0.3 ± 0.07 |
| *Fringilla coelebs*, Common Chaffinch | 790253 | 2028 | 0.3 ± 0.01 |
| *Fringilla montifringilla*, Brambling | 76716 | 329 | 0.4 ± 0.02 |
| *Coccothraustes coccothraustes*, Hawfinch | 2037 | 13 | 0.6 ± 0.2 |
| *Pyrrhula pyrrhula*, Eurasian Bullfinch | 15693 | 36 | 0.2 ± 0.04 |
| *Carpodacus erythrinus*, Common Rosefinch | 7646 | 10 | 0.1 ± 0.04 |
| *Chloris chloris*, European Greenfinch | 8151 | 37 | 0.4 ± 0.07 |
| *Linaria cannabina*, Common Linnet | 1678 | 8 | 0.5 ± 0.03 |
| *Acanthis flammea*, Common Redpoll | 14768 | 29 | 0.2 ± 0.03 |
| *Loxia curvirostra*, Red Crossbill | 18876 | 53 | 0.3 ± 0.04 |
| *Carduelis carduelis*, European Goldfinch | 3222 | 25 | 0.8 ± 0.2 |
| *Serinus serinus*, European Serin | 492 | 5 | 1.0 ± 0.4 |
| *Spinus spinus*, Eurasian Siskin | 256724 | 1483 | 0.6 ± 0.01 |
| *Emberiza citrinella*, Yellowhammer | 5163 | 7 | 0.1 ± 0.05 |
| *Emberiza hortulana*, Ortolan Bunting | 517 | 2 | 0.4 ± 0.07 |
| *Emberiza schoeniclus*, Common Reed Bunting | 3138 | 12 | 0.4 ± 0.1 |

of possible reasons for the decrease in the proportion of ring recoveries was carried out on the ringing materials of 18 bird species with at least 50 recoveries. Statistical analysis of trends in the percentage of ring recoveries in individual species showed that in 14 of these species the trend was negative and highly significant (Table 3). This decrease occurred in the species of different systematic affiliation and different ecology. The analysis of all possible reasons for decline in the proportion of ring recoveries led to the conclusion that the main reason is the change in human behavior when detecting ringed birds over the past decades (Payevsky and Shapoval 1998, 2013).

## Dynamics of the numbers of migrating populations

The representativeness of captured bird samples for the long-term studying of their numbers has been repeatedly discussed. It is believed that only strict standardization of work on trapping birds can provide figures suitable for analysis (Berthold and Schlenker 1975). We also recognized the trapping method as a reliable way to record bird population dynamics only if a number of conditions are met, namely that trapping is carried out from year to year in the same place with the same traps, and under the

**Table 3.** The long-term trend in recovery rates of birds ringed on the Curonian Spit during 1956–2006.

| Species | Number of ringed birds | | Recoveries obtained | | | Spearman's rank correlation |
|---|---|---|---|---|---|---|
| | In total | Range by years | In total | Range by years | Total, % | |
| Eurasian Sparrowhawk | 6975 | 18–344 | 314 | 0–21 | 4.50 | −0.927 |
| Long-eared Owl | 3304 | 3–370 | 99 | 0–15 | 3.00 | −0.648 |
| Eurasian Jay | 6256 | 1–764 | 152 | 0–28 | 2.43 | −0.976 |
| Coal Tit | 54891 | 0–10051 | 191 | 0–69 | 0.35 | −0.212 |
| Eurasian Blue Tit | 85388 | 32–6654 | 383 | 0–43 | 0.45 | −0.188 |
| Great Tit | 215851 | 193–14188 | 913 | 1–60 | 0.42 | −0.794 |
| Willow Warbler | 151121 | 412–9237 | 106 | 0–10 | 0.07 | +0.351 |
| Goldcrest | 352436 | 3–37293 | 194 | 0–24 | 0.06 | −0.611 |
| Common Starling | 103075 | 148–8781 | 1178 | 0–194 | 1.14 | −0.963 |
| Song Thrush | 26265 | 29–2052 | 386 | 0–31 | 1.47 | −0.878 |
| Redwing | 5967 | 8–310 | 101 | 0–9 | 1.69 | −0.830 |
| Common Blackbird | 11803 | 25–1104 | 113 | 0–7 | 0.96 | −0.912 |
| Fieldfare | 2479 | 0–166 | 50 | 0–8 | 2.02 | −0.757 |
| European Robin | 158733 | 265–15110 | 261 | 0–18 | 0.16 | −0.866 |
| Meadow Pipit | 10954 | 0–1730 | 96 | 0–24 | 0.88 | −0.926 |
| Common Chaffinch | 733611 | 1936–46337 | 1944 | 1–151 | 0.26 | −0.976 |
| Brambling | 72119 | 27–4147 | 320 | 0–34 | 0.44 | −0.879 |
| Eurasian Siskin | 210882 | 28–14496 | 1350 | 0–227 | 0.64 | −0.939 |

same landscape conditions of the trapping site (Payevsky 1990; Sokolov et al. 2004).

Checking the possibility of objectively accounting of the number of migrating birds with permanent Rybachy traps has shown that the number of passerines caught can reliably reflect their annual fluctuations in numbers. Data on the annual number of captured Spotted Flycatchers on the Curonian Spit (Fig. 2) approximately demonstrate the overall picture of declining numbers of songbirds migrating there.

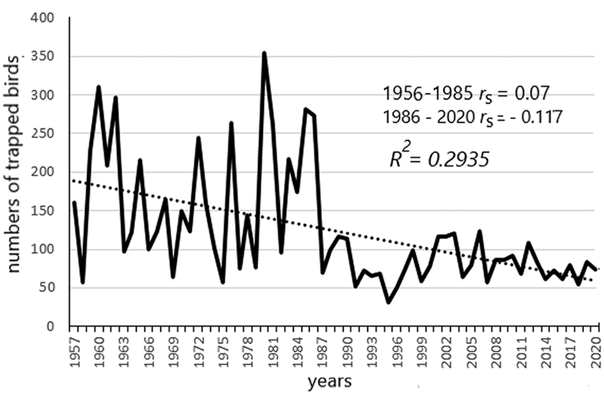


**Fig. 2.** Fluctuations in trapping numbers of Spotted Flycatcher at the "Fringilla" field station as an example of similar population trends of other passerines on the Curonian spit during 1956–2020. Numbers are presented on the unaligned annual totals curves.

Population studies of bird species breeding on the Curonian Spit and wintering in tropical Africa have shown that the cause of the most dramatic decline in numbers (Barred Warbler, Lesser Whitethroat, Tree Pipit, Red-backed Shrike) was not breeding disturbance, but a decrease in the survival rate of birds in wintering areas due to lack of precipitation, especially drought in the Sahel zone (Payevsky 2006, 2021a).

## Migration movements of birds ringed on the Curonian Spit

Population affiliation of migrants passing the Curonian spit can be traced by summer recoveries of individuals ringed during passage. These recoveries suggest that these birds belong to the populations of the Eastern Baltic, Finland, and north-western Russia, including Karelia, Vologda, Saint Petersburg and the Novgorod regions. However, some individuals belonged to populations of Scandinavia, the Urals, and Siberia. In autumn, after passing the Curonian Spit, the bulk of species migrate south-westwards (both those wintering in Europe and Africa), but some species are dispersed over a huge area between the Iberian Peninsula and the Caucasus. Long-distance recoveries of the birds ringed on the Curonian Spit have been reported from all over Western Europe and different regions of Africa.

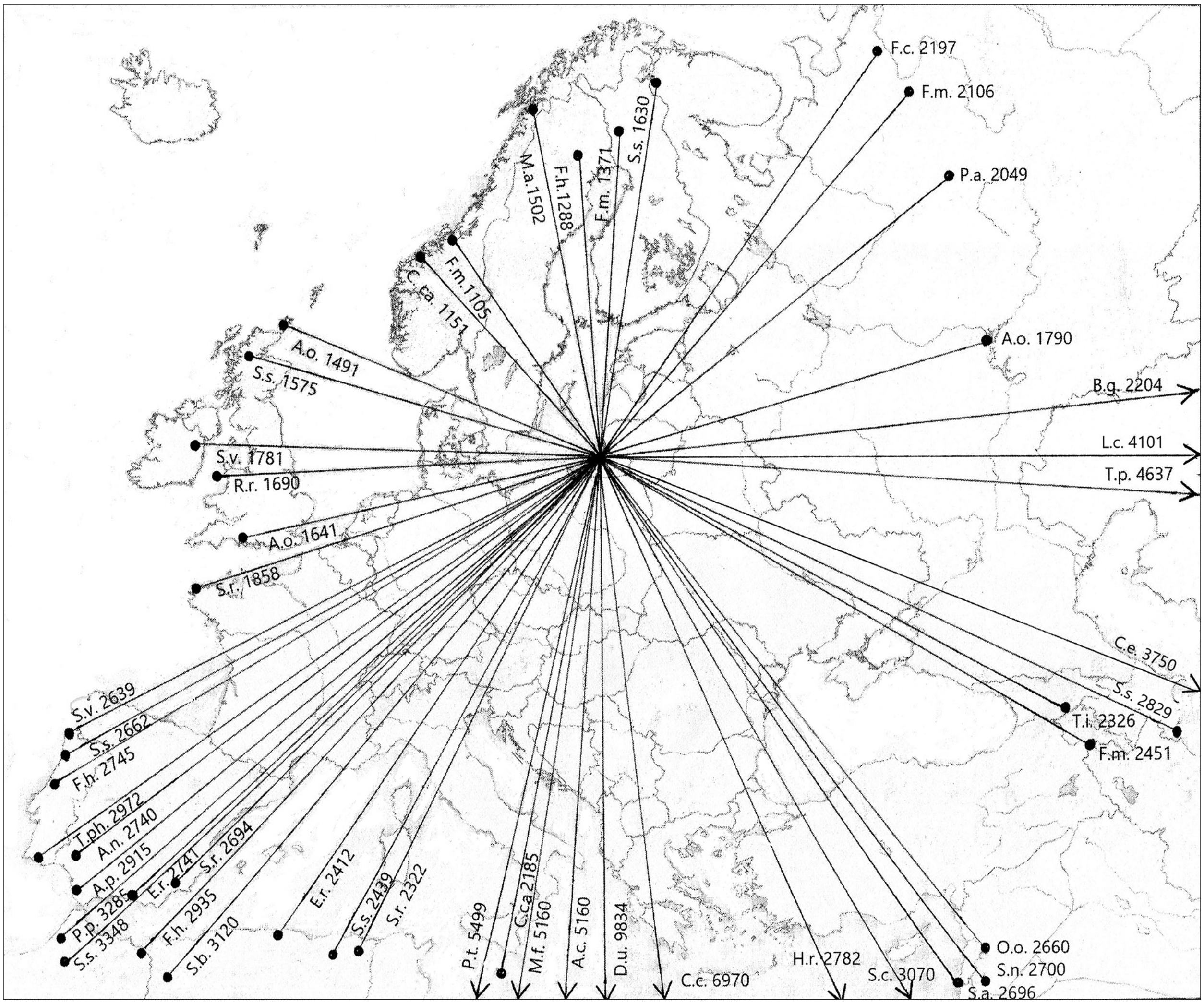


**Fig. 3.** Examples of the most distant ring recoveries of birds of 30 species, ringed on the Curonian Spit, according to different azimuths. Numbers indicate the number of kilometers from the place of ringing. *Symbols:* A.c. – *Ardea cinerea*, A.n. – *Accipiter nisus*, A.o. – *Asio otus*, A.p. – *Anthus pratensis*, B.g. – *Bombycilla garrulus*, C.c. – *Ciconia ciconia*, C.ca. – *Cuculus canorus*, C.e. – *Carpodacus erythrinus*, D.u. – *Delichon urbica*, E.r. – *Erithacus rubecula*, F.c. – *Fringilla coelebs*, F.h. – *Ficedula hypoleuca*, F.m. – *Fringilla montifringilla*, H.r. – *Hirundo rustica*, L.c. – *Loxia curvirostra*, M.a. – *Motacilla alba*, M.f. – *Motacilla flava*, O.o. – *Oriolus oriolus*, P.p. – *Phoenicurus phoenicurus*, P.t. – *Phylloscopus trochilus*, R.r. – *Regulus regulus*, S.a. – *Sylvia atricapilla*, S.b. – *Sylvia borin*, S.c. – *Curruca curruca*, S.n. – *Curruca nisoria*, S.r. – *Scolopax rusticola*, S.s. – *Spinus spinus*, T.i. – *Turdus iliacus*, T.p. – *Turdus pilaris*, T.ph. – *Turdus philomelos*.

Figure 3 shows the longest migration routes of birds of 30 species (straight line path lengths from 1105 to 9834 km), ringed on the Curonian Spit. This diagram is based on the principle of a wind rose, where the length of rays from the center of the diagram means the maximum migration distance. In addition to distance, the azimuths of some species indicate the diversity of their migratory paths, for example in Eurasian Siskin. After flying through the Curonian Spit, some Siskins flew southwest to Portugal and Morocco, another flew west to Scotland, and a third flew southeast and was discovered in southern Azerbaijan. Of course, the Siskin is not a long-lived species, and it cannot have improved migration behavior during its lifetime, as, for example, was found in the White Stork (Aikens et al. 2024). Nevertheless, the diversity of migration routes may indicate the search for the best destinations for the whole population, especially in the changing environmental conditions of the modern world.

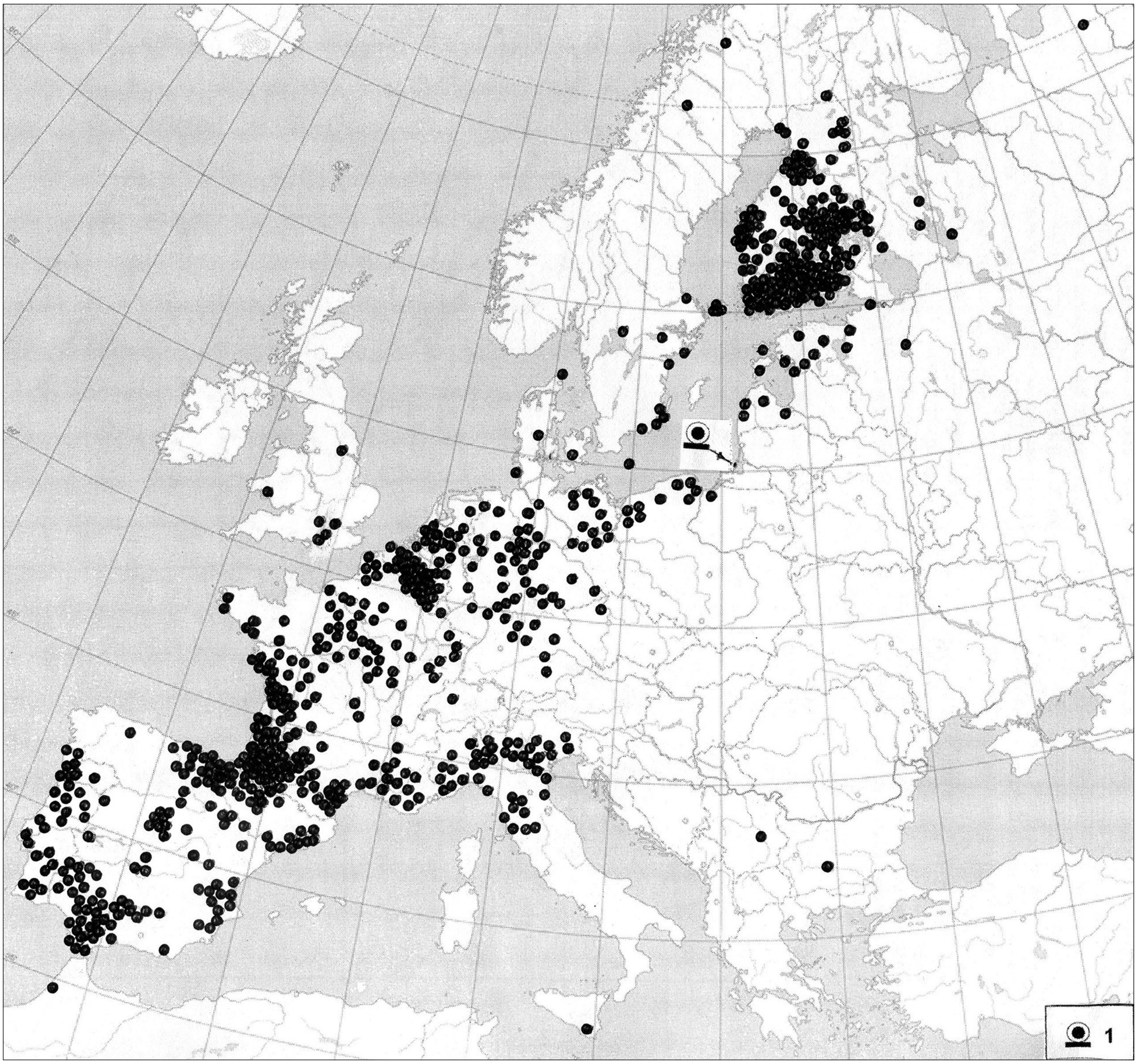


**Fig. 4.** Migrations of the Chaffinch (*Fringilla coelebs*) according to the data of ringing on the Curonian Spit for 65 years. Each point represents the location of one or more of the 2028 birds discovered. *Symbol:* 1 – the place of ringing.

Among all the migratory species on the Curonian Spit, the most numerous is the Common Chaffinch, which corresponds to its total abundance among the birds of Europe (Payevsky 2020b). Over 65 years, 790,253 finches have been ringed on the Curonian Spit and 2,028 ring recoveries have been received. The map compiled, based on these ring recoveries (Fig. 4), clearly indicates the migration routes and wintering grounds of the Common Chaffinches breeding northeast of the Curonian Spit. As is known, migratory connectivity is defined as the linkage among individuals between the periods and areas where they spend different phases of their annual life cycle (Ambrosini and Fattorini 2022). Among the Chaffinch ring recoveries received, the most numerous were those from Finland in spring and summer (557), from France in autumn and winter (472), and from Belgium and the Netherlands in autumn and spring (275). Consequently, Chaffinch populations from Finland and its neighbouring regions migrate south-westwards through the Baltic States, northern Poland, Germany, the Netherlands and Belgium on their way mainly to southwestern France, Spain and Portugal. This is clearly confirmed by the recoveries of rings from Chaffinches ringed in Finland itself (Valkama et al. 2014) and in another European atlas of bird migrations (Zink and Bairlein 1995).

## Speed of migration movements

The migration rate of birds was analyzed from ring recovery data, using those that meet known criteria (Hilden and Saurola 1982). The results show that the average speed varies between 10 and 880 km/day and the maximum speed varies between 30 and 1392 km/day, but the respective values for most species fall within the ranges of 20–100 and 40–360 km/day. Species of the family Turdidae migrate significantly faster than species of the family Fringillidae, and the latter migrate faster than the Paridae. No significant differences in migration speed have been revealed between the Sylviidae and Turdidae as well as between the Sylviidae and Motacillidae species. In many species, adult birds migrate significantly faster than juveniles, while male and female birds do not differ in this parameter. The average migration speed of passerines is significantly higher in nocturnal migrants departing early to long distances than in diurnal migrants departing late to short distances. In some species, the spring migration speed is much higher than the autumn speed (Payevsky 2013).

## Demographic studies of bird life based on ringing results

In order to investigate various aspects of demographic research, two types of initial data were analyzed: rings recoveries from birds that were ringed during migrations, and recaptures of birds on the Curonian Spit that were ringed there in previous breeding seasons. The main results are presented in the summary volume (Payevsky 2009) and in subsequent publications (Payevsky 2021b, 2023). First of all, the average annual survival rate of populations, both migrating and breeding, was determined. It ranged from 0.255 to 0.779 in different species, i.e. from 26 to 78% per year. One-year-olds, along with two-year-olds, made up the majority of population members in all studied species and populations – from 70 to 90%. They ranged from 66 to 80% in finches, from 67 to 82% in thrushes, from 75 to 91% in warblers, from 78 to 80% in wagtails, 73% in starlings, 80% in flycatchers, 81% in buntings and up to 90% in tits. The maximum life expectancy of the studied species ranged from 3 years in the Goldcrest to 13 years in the Song Thrush.

The analysis of the ring recoveries of Song Thrush showed the following (Payevsky and Vysotsky 2003). Of the 358 recoveries, 86% related to birds killed by hunters for gastronomic purposes. The largest number of birds killed during hunting and trapping was recorded in France, Italy, Spain and Portugal (73–93%), while in other countries there were only 28% of such birds. The probability of songbird survival, calculated for different time periods, ranged from 0.368 to 0.420 for young birds and from 0.561 to 0.633 for adults. In the British Isles, where the Song Thrush mainly lives all year round and is not a commercial bird, the survival rates of adult individuals did not differ from the values obtained for the Baltic populations, while the survival rate in the first year was slightly higher than that of the Baltic birds.

The ratio of adult males and females in natural population is a fundamental feature of population biology and a key factor in sexual selection. Analysis of published data on the tertiary sex ratio, i.e. in adult birds (Payevsky 2021b), showed that of the 308 estimates in 196 species, 76% of the ratio significantly differed from 0.5, i.e. equal. Most of them (82%) were biased towards males, 16–30% more than the proportion of females, varying significantly between different species and systematic groups. In most populations, the primary sex ratio (at fertilization and in egg clutches) is equal, and only in the course of later life the ratio disrupted by the influence of gender-specific mortality.

The sex ratio of birds at different ages was analyzed by ringing and re-trapping two numerous breeding species of the Eastern Baltic – the Common Chaffinch and the Willow Warbler. The excess of the proportion of males over females persisted at all ages in all years, starting with the acquisition of independence and slightly increasing with the age of birds. Higher survival rate of males compared to females was established based on our and published data on 62 bird species, but in many populations the differences did not reach the level of reliability, especially in tits (Payevsky 2021b). The most logical explanation for the multidirectional mortality in birds and mammals (increased in female birds and in male mammals) is genetic, namely, sex determination factor. In both sexes, mortality is higher in the heterogamous sex, but in birds females are heterogeneous (ZW), and in mammals, males (XY).

## Conclusions

The study of bird migrations by means of their ringing is in line with the fundamental problem of animal population biology about the mechanisms of self-maintenance of the optimal number of natural populations. In addition to the study of migration routes and wintering areas, bird ringing is absolutely necessary for various population studies. The age-sex structure of populations and survival rates of different age and sex cohorts are very important in order to investigate the array of extrinsic and intrinsic factors limiting population numbers during breeding, migratory, and wintering seasons. Ringing has been widely used all over the world for over 120 years and has yielded results that are of lasting value for many projects, not only for the study of bird migrations. Despite the current use of such high-tech methods of tracking bird movements as satellite telemetry, ringing has not lost its importance for many aspects of studying populations.

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