VLADIMIR PAYEVSKY

SONGBIRD
DEMOGRAPHY

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The population parameters of birds
have been studied for a period of over forty years

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Demographic structure, survival rates, and population dynamics of songbirds with particular reference to the birds of the Eastern Baltic

Russian Academy of Sciences
Zoological Institute

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Edited by
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This monograph summarizes the results of research into the age and sex structure, survival rate, longevity and the population dynamics of songbirds (passerines). The emphasis is on the demographic parameters of breeding and migrating birds of the Eastern Baltic, although population studies of songbirds from other parts of the world are also reviewed. Issues of terminology are especially considered, as well as the potential bias in data of importance to bird population studies through trapping and ringing methods. The history of dispersal and philopatry (site fidelity) research is presented. The annual and seasonal variation in age and sex in population structure and age-related aspects of territorial behaviour are discussed in detail. The results of a special analysis of sex-specific survival rates are presented. Demographic aspects of population studies of nine model species are analysed in detail. Problems of research into the mechanisms of population dynamics and the impact of global climate change on seasonal European-African migrants are reviewed.

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CONTENTS

To all ornithologists on the Courish Spit, from the past as well as the present, to all those who were lucky enough to enjoy watching and studying millions of tiny feathered vocalists on this sandy strip of land during their eternal struggle for life

PREFACE

The current growing intensity of population ecology research results from the need to understand the biological mechanisms underlying the development and dynamics of natural communities. This research is especially important in the light of accelerating anthropogenic impact on ecosystems. The study of demographic parameters and population ecology forms the basis for the sustainable use of natural resources and conservation, as well as for the development of methods to control animal numbers and their spatial distribution. Both conservation and control of populations primarily require a thorough and detailed understanding of the impact of environmental factors on population processes.

The direction of biological studies over the last quarter of a century has emphasised animal population dynamics and their structure under different environmental conditions (Pianka, 1978; Maximov, 1984; Begon et al., 1986; Hanski, 1990; Murdoch, 1994; Holmes & Sherry, 2001; Newton, 2004; 2008; Berthold & Fiedler, 2005, etc.). The knowledge of regulatory mechanisms for the maintenance of particular natural populations results from studies of fluctuating demographic parameters, i.e. fecundity, mortality, age and sex composition, emigration and immigration processes. Research into population and age structure is especially important in the light of the current global climate changes and increasing urbanisation.

A large number of studies of population dynamics have considered birds. These studies have resulted in the emergence of different theories on the control of population change and made important contributions to animal population ecology. A convenient model group for such studies are the songbirds (Oscines), a suborder within the order passerines (Passeriformes). Passerines occur throughout the globe. They dominate terrestrial ecosystems through their species diversity and numbers. They include over 5000 of the 8600 extant avian species. Many of these species are migratory and can be captured and ringed for the study of their migratory routes and seasons of migration as well as to estimate their survival rates and longevity. Ringing by aluminium rings and colour tagging make individual recognition during recaptures or resightings possible. Songbirds are also used as experimental models in the studies of biorhythms, bioenergetics, orientation and navigation, moult and other aspects of biology. Optimal ambient temperature for maximising productive processes (e.g. reproduction, growth and moult) is lower in passerines than in non-passerines. This allows them to have higher productive levels at moderate ambient temperatures (Gavrilov, 1999). During the previous quarter of a century important reviews on songbird population biology and ecology, bioenergetics, moult, ageing and sexing, territorial and spatial behaviour as well as migration have been published (Kovshar, 1981; Dolnik, 1982a; Busse, 1984; Zimin, 1988; Rymkevich, 1990; Sokolov, 1991a; Berthold, 1990; Blondel et al., 1990; Svensson, 1992; Ryabitsev, 1993; Jenni & Winkler, 1994; Ryzhanovsky, 1997; Boulet & Norris, 2006; Møller et al., 2006 etc.). However, many questions of songbird demography still remain unanswered.

Together with his colleagues, researchers of the Biological Station Rybachy of the Zoological Institute (Russian Academy of Sciences), the author has studied European songbirds on the Eastern Baltic coast, on the Courish (Curonian) Spit, for nearly forty years. This strip of land divides the Courish Lagoon from the Baltic Sea and extends from the north-east to the south-west, parallel to the main direction of bird migration in the Baltic area (White Sea – Baltic flyway). The Courish Spit is a site equal to few other places in Europe due to the abundance of migrating birds, especially small passerines. Here, in the village of Rybachy (Rossitten until WWII) the world's first bird observatory – Vogelwarte Rossitten operated from 1901-1944 (Thienemann, 1926; Schüz, 1938). It gained worldwide reputation mainly due to innovative large-scale scientific bird ringing. The research at Vogelwarte Rossitten laid the foundations for the study of many questions that still remain relevant today.

The Biological Station Rybachy was founded in 1956 with the objective of continuing the bird migration research established by the German ornithologists. The results of research by the team at the Biological Station Rybachy have been published as collections of papers and monographs (currently more than 1000 in various journals). The results of population ecology studies were published by the author in the monograph 'Avian Demography' (Payevsky, 1985a). In the years since this publication the study of birds, especially of passerines, has advanced, and the results are summarised in the current book. This book is based on the analysis of the results of capture and ringing, breeding studies of passerines, and on the analysis of the available literature on songbird population ecology and demography.

Many results have been only published in Russian. In writing this book, my intention is to present all the main results in English. This primarily concerns the studies of demographic structure, population dynamics and the causal relationships between natural mortality rates and productivity of avian populations under different environmental conditions. The analysis of these topics is in the framework of the fundamental problem of animal population biology and ecology and the natural mechanisms of population regulation. In addition, all studies in this field of songbird populations are reviewed in this book.

The first chapters of this monograph, detailing all methodology and techniques for the study of various aspects of avian biology, are rather substantial. The reason for this is probably due to the rather high diversity of study tools, as well as the importance of the topic of avian population research, unlike other more standardised ornithological techniques and more widely accepted theories.

Acknowledgements

A detailed study of avian populations and consequently the writing of this book would not have been possible without the joint activities of all the author's colleagues, members of the Biological Station Rybachy of the Zoological Institute and numerous volunteers who captured, measured and ringed the birds and studied their breeding biology on the Courish Spit over many years. Here the information on passerines from the database of the Biological Station from 1956-2000 is used. In total this database contains more than two million entries, on ringing and measurements of birds of 40 main study species, recorded by all the researchers. With deep gratitude I list here my colleagues who shared long-term, routine, but nevertheless most exciting work on mass trapping and ringing of birds, and the study of different aspects of their biology, with me. Apart from numerous temporary volunteers, my fellow workers in 1958-2000 were (in different years and to a varying degree) in alphabetical order:- ornithologists Alexander Bardin, Lev Belopolsky, Tatiana Blyumental, Casimir Bolshakov, Victor Bulyuk, Nikita Chernetsov, Inna Dobrynina, Tatiana Dolnik, Victor Dolnik, Valentina Dyachenko, Veino Erik, Vladimir Fedorov, Valery Gavrilov, Sergey Ilyin, Tatiana Ilyina, Vladislav Kosarev, Dina Lyuleeva, Mikhail Markovets, Andrey Mezhenny, Andrey Mukhin, Alexey Pogorelov, Roald Potapov, Anatoly Shapoval, Mark Shumakov, Alexandra Sinelschikova, Leonid Sokolov, Nikolay Titov, Arseny Tsvey, Natalia Vinogradova, Mikhail Yablonkevich, Vladislav Yefremov, Nadezhda Zelenova. The entire work on the study of demographic parameters of avian populations would not have been possible without constant attention and support by the directors of the Biological Station Lev Belopolsky, Victor Dolnik, Alexander Bardin and Casimir Bolshakov. I am most grateful to my numerous co-authors, and first of all to Victor Dolnik who had a decisive impact on my scientific development since our common undergraduate years. Over recent years a number of our joint population studies benefited from the convincing logic of Leonid Sokolov, the unfailing working capacity of Anatoly Shapoval, and the adherence to the modern modelling methods of Vadim Vysotsky. Data processing, analysis and understanding always took place in a stimulating atmosphere of fruitful argument and discussion. Over more than 40 years I have always enjoyed the constant attention and support in

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It is a pleasure to thank those who have helped in the preparation of this book. I express my appreciation to Nikita Chernetsov, who translated the book. I am deeply grateful for his advice, professional knowledge, innate linguistic ability and his exact rendering of the original Russian text. Martin Griffiths appreciated the high standard of the translation with the help it gave for his editing task. I am indebted to him for his valuable comments and recommendations as well as for his careful editing of the text.

Last but not the least, I always remember with much gratitude my first teacher in ornithology, Professor Alexey Malchevsky of St. Petersburg University, whose special admiration of songbirds shaped my choice and whose recommendation allowed me to begin my work on the Courish Spit.

Vladimir A. Payevsky

St. Petersburg, January 2009

Chapter 1

STUDY SITE, MATERIAL AND METHODS OF DATA COLLECTION

1.1. STUDY AREA

The location for the numerous studies summarised in this book is in the Kaliningrad Region of Russia (former Ostpreußen, East Prussia in Germany) on the Courish Spit[1] which is a narrow sandy strip of land 0.36 to 3.9 km wide and 98 km long that divides the Courish Lagoon from the Baltic Sea (Fig. 1). The southern part of the spit belongs to Russia and is currently the Curonian Spit National Park. A considerable part of the eastern (lagoon) coast is formed by huge bare sand dunes (plate 1), with the highest point 68 m a.s.l. Since the year 2000 the Courish (Curonian) Spit has been on the UNESCO's World Heritage List as an outstanding example of human interaction with an environment which has become vulnerable under the impact of irreversible change.

Specific natural conditions and changes of the spit landscape are mainly the result of the battle between wind erosion and sand deposition which drastically changed the appearance of the spit over centuries. Detailed studies of the vegetation on the Courish Spit were published by A. Nitsenko (1968, 1970) and many other botanists, whose papers are mentioned in the important monograph devoted to the description of the Courish Spit (Kulakov et al., 2008). Sand stabilisation began in the 19th century through planting mountain pine (*Pinus montana*) and black pine (*Pinus nigra*), lyme-grass (*Elymus arenarius*) and marram (*Ammophila arenaria*). Later Scots pine (*Pinus silvestris*), Siberian violet willow (*Salix acutifolia*) and mammoth wildrye (*Elymus giganteus*) were also planted. Subsequently natural growth of silver birch (*Betula pendula*), aspen (*Populus tremula*) and common alder (*Alnus glutinosa*) started to appear on the spit. At the present time major habitat change

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[1] The name Courish Spit comes from the name of Curonians, a Baltic tribe, and has many spellings in Russian, English, and other languages. The Lithuanian names Kuršiu Nerija and Kuršiu Neringa and the German name Kurische Nehrung are spelled as Kurshskaya, Kurishskaya or Kurskaya kosa in Russian, Curonian (the officially accepted name), Courish, Kursh, Kurland, or Courland Spit in English.

can be seen between the coasts along the east-west transect from bare sand dunes through fixed sand with young pine plantations and patches of deciduous and mixed forest (plates from 1 to 6) with undergrowth of common juniper (*Juniperus communis*), European dewberry (*Rubus caesius*) and redcurrant (*Ribes rubrum*). The herbaceous layer is formed by various plants, grey hair-grass (*Corynephorus canescens*), sheep scabious (*Jasione montana*), sand milk-vetch (*Astragalus arenarius*), common cow-wheat (*Melampyrum pratense*), upright hedge-bedstraw (*Galium erectum*), common bent (*Agrostis capillaris*), and woodland strawberry (*Fragaria vesca*) including. Most typical of the Courish Spit are the plantations of Scots pine of varying age, from 25-50 to 70-100 years.

Isolated patches of birch and alder forest alternating with low stands of mountain pine form long line of forest edges. Locally, old mature spruce and pine forests occur, as well as the stands of Norway spruce (*Picea abies*) and white spruce (*Picea glauca*). In the middle part of the spit that used to be an island in a geologically recent past, broad-leaved forests, a large meadow and a lake whose coasts are overgrown with reed (*Phragmites australis*) are situated. Extended reed stands also occur on Cape Rossitten near the village of Rybachy.

The climate is characteristically unstable, with mild winters and cool summers. Phenological events on the spit lag behind the mainland by 7-10 days. The particular location of the spit attracts breezy conditions during summer. Wind speeds are rather high (annual average 5.6 m·s^{-1}). The average annual precipitation is 665 mm. The long-term mean temperature for May, July and September is 12.0, 17.3 and 12.4°C, respectively.

The analysis of topics discussed in this monograph is based on capture data and the study of the breeding biology of birds at one of the permanent field sites of the Biological Station, the Frin-

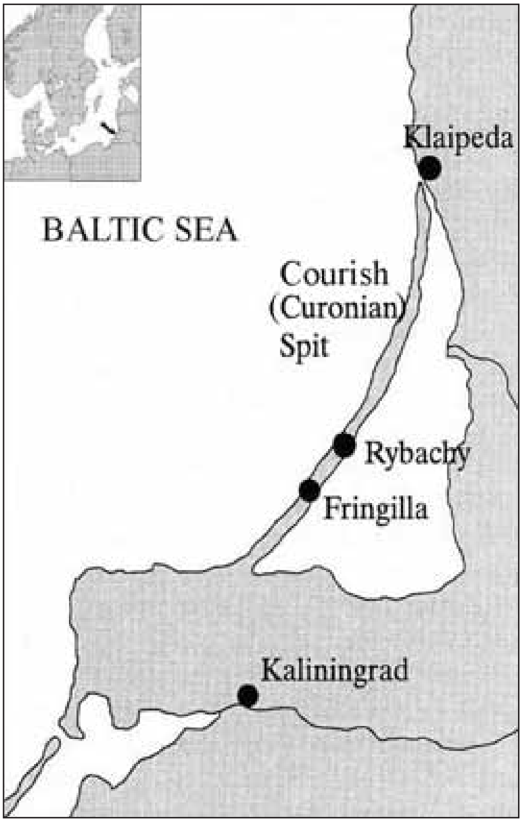

Fig. 1. Map of the Courish Spit.

gilla field station (Fig. 2). It is located at kilometre 22 of the Courish Spit (55º05' N, 20º 44' E), 11.5 km southwest of Rybachy. This field station has been in operation since 1957 when Rybachy-type stationary traps were first installed there.

1.2. CAPTURE METHODS

The Rybachy-type trap was constructed and installed in 1957 by the researcher Janis Jakšis at the Biological Station Rybachy together with Veino Erik and

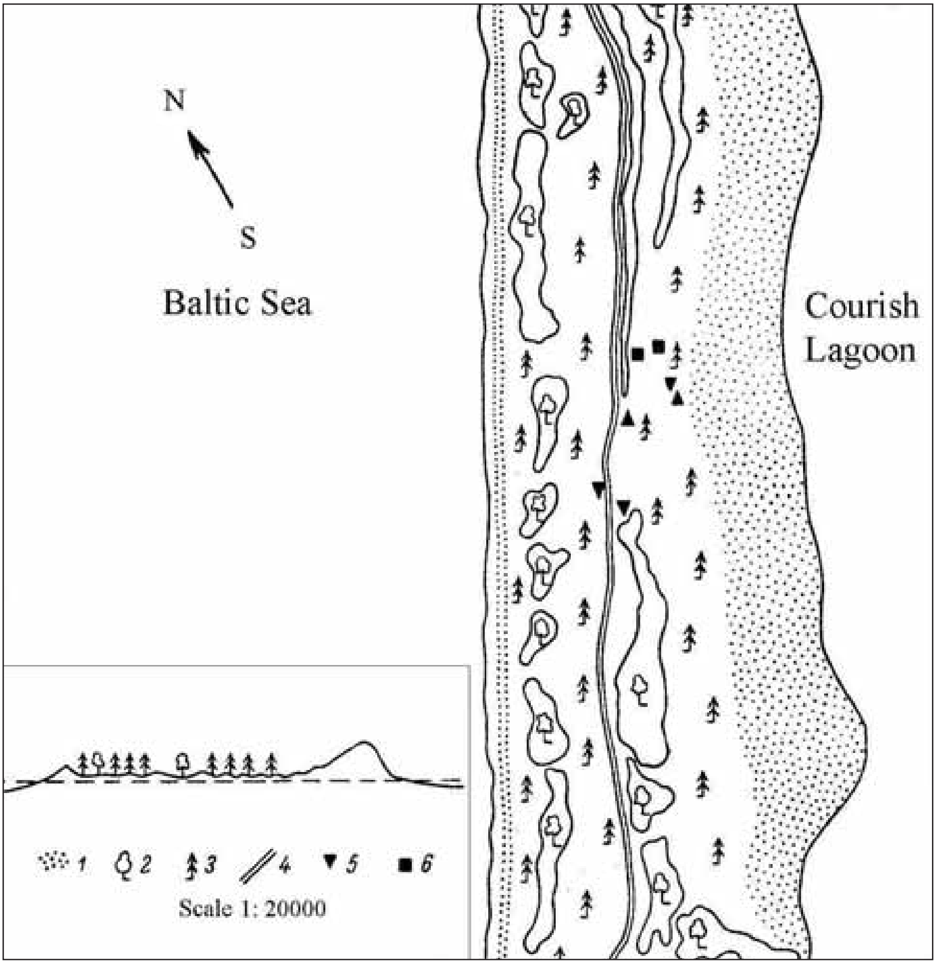

Fig. 2. Map of Fringilla field station on the Courish Spit. 1 – dunes, 2 – groups of deciduous trees, 3 – pine plantations, 4 – road, 5 – Rybachy-type traps, 6 – buildings.

Lev Belopolsky. A Rybachy-type trap looks like a giant trawl net made of cotton or nylon fishing net fixed on the ground and open towards the flow of low flying migrants or to the birds that move within the canopy (plates from 7 to 9). The birds enter the trap and arrive at the end chamber usually without being driven by man. They cannot leave the end chamber where they are captured by hand (plates from 10 to 14). The construction of a Rybachy-type trap has been described in the literature in detail (Dolnik & Payevsky, 1976b; Bub, 1969; 1991; Payevsky, 2000a), therefore only a general outline is given here.

Rybachy-type traps resemble Heligoland traps superficially (funnels traps first used on Heligoland) but differ by three important characteristics:

a) The very large size with 12 m high entrance gates, i.e. at the level of low flying migrants. Due to its huge size the trap is not seen by the birds as a danger, and do not avoid them, even the traps installed quite openly at an elevated site;
b) The non-rigid construction with the facility to erect and dismantle the net by a steel rope. The trap is stretched by the ropes between three pairs of poles, capable to be put it down quickly before an approaching gale (for safety reasons);
c) The absence of luring sites with food and water. This makes it possible to use such traps at the site of mass passage, even in the desert.

At Fringilla station several Rybachy-type traps were also installed with their funnels facing different directions to capture the birds flying towards the northeast and the southwest. The traps are in operation 24 hours per day, (plate 19) seven months per year (from late March until early November). They are primarily designed to capture small songbirds, (plates from 10 to 20) although non-passerines, such as the Long-eared Owl (*Asio otus*), Eurasian Sparrowhawk (*Accipiter nisus*), Greater Spotted Woodpecker (*Dendrocopos major*), and Common Cuckoo (*Cuculus canorus*) are frequently captured. The maximum daily total captured in three traps on the Courish Spit is 9,000 individuals. Between 23 and 108 thousand individuals are captured each year, with an average of 50,000. In summer, small numbers of birds are also captured at Fringilla by mist net which is globally the most widespread means of bird trapping. Since 1993, the birds have also been captured at Rybachy field station on Cape Rossitten on the Courish Spit in 7-m long fixed mist nets (total length over 800 m). More than 2.5 million birds of 197 species have been captured and marked by the Biological Station Rybachy at different places on the Courish Spit (Bolshakov et al., 1999-2005). More than 8,000 long-distance recoveries are recorded, and more than 65,000 individuals were recaptured at the marking sites. Many individual birds produced multiple recaptures. In addition, more than 6,000 birds ringed have been controlled on the Courish Spit from elsewhere.

In the former USSR the Rybachy-type traps have gained high popularity. Such traps have been used in Lithuania, Latvia, Estonia, Kazakhstan, Pskov Region, and at Ladoga Ornithological Station of St. Petersburg State University in Gumbaritsy. In the recent years similar traps were installed in southern Israel (Eilat), on the German Baltic island of Greifswalder Oie, and in Stora Fjaderagg in Sweden.

The high efficiency of the relatively bird-friendly and easily maintained traps, has brought them wide recognition. In all places where Rybachy-type traps are used they have been modified according to the local conditions of migration, logistics and the number of personnel available.

The working efficiency of the Rybachy-type traps often depends on wind direction, not only during passage but sometimes also in summer. At moderate opposing and side opposing wind the altitude of flying birds decreases, enabling migrating flocks to enter the trap entrance. In the ideal case the time lag between entering the funnel and reaching the end box is several seconds. Other weather factors, such as cloud cover, rain and fog, do not change numbers trapped in any season.

Apart from migrants, local breeding birds are captured in Rybachy-type traps during the summer. Many of them are captured repeatedly in the same year or in subsequent years. Some individuals are captured between 2 – 35 occasions in one summer. Eight birds have even bred in the bushes within the front part of a trap. This allows us to assume that local birds are regularly controlled in this natural environment on an individual basis which is most important in population ecology studies.

1.3. SPECIFIC COMPOSITION OF SONGBIRD POPULATIONS OF THE COURISH SPIT AND THE TRAPPING DATA

The study of avifauna of the Kaliningrad Region (former northern East Prussia) has a long tradition begun by renowned German zoologists (K.E. von Baer, F. Bock, F. Löffler, E. Hartert, F. Lindner, J. Thienemann, F. Tischler, E. Schüz). Subsequent to the last German reviews of local avifauna (Tischler, 1914, 1941) the new contributions did not begin to appear until the 1960s (Belopolsky & Erik, 1961; Lyuleeva, 1961; Payevsky, 1973a; Grishanov, 1986; Belyakov & Grishanov, 1986).

In addition to bird migration surveys on the Courish Spit, the data on various aspects of breeding biology have been collected by the members of the Biological Station Rybachy annually since 1958. Most data are collected in the same area around the Fringilla field station. Some 90 % of nests have been found within 2 km to the southwest and northeast from the field station. The overall area of all suitable breeding habitats within this area slightly exceeds 2 km^2 (Dolnik & Payevsky 1982). Other parts of the spit were visited less frequently, but the information on species composition and breeding density in those areas is near complete. It should be emphasized that the isolated position of the Courish Spit favours concentration of the birds and contributes to high breeding density.

In different years, the breeding data were collected by a variety of researchers and students. From 1974-1987, all data on open nesting birds were recorded in standard format. These data made it possible to analyse many aspects of breeding performance in different bird species.

According to our records and to historical data of German ornithologists (Tischler, 1941), the overall number of passerine species ever recorded on the Courish Spit is 127 (Table 1). A full list with the vernacular and scientific names and the status of each species is given together with the overall number of individuals captured on the Courish Spit in 1956-2000, the number of long-distance recoveries and the recaptures. These quantitative data give a general idea of numbers of each species. In total, 66 species of passerines currently breed on the Courish Spit, 28 species can only be encountered during migration and 31 species are vagrants. Two species (Lesser Grey Shrike and Crested Lark) have bred formerly and are now locally extinct. Since 1939, the Mistle Thrush and Sand Martin also ceased to breed but do occur during migration. Nine vagrant species are first recorded (trapped) by us: Orange-flanked Bush Robin (Bluetail), Red-rumped Wheatear, Subalpine Warbler, Pallas's Warbler, Firecrest, Penduline Tit, Short-toed Treecreeper, Indigo Bunting, and White-winged Crossbill. It should be added that in 1973, at least four Brambling pairs bred on the Courish Spit of 380 experimental birds that had been captured during spring migration and kept in captivity until early June (Shumakov et al., 1975). Finally, several *Fringilla coelebs* x *Fringilla montifringilla* hybrids and several so-called "*Parus pleskei*" (*Parus caeruleus* x *Parus cyanus* hybrids) have been captured.

Population affiliation of migrants passing the Courish 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, Leningrad and the Novgorod Regions. However, some individuals were from the populations of Norway, Sweden, the Urals, and Siberia. In autumn the bulk of species after passing the Courish Spit migrate towards the southwest (both those wintering in Europe and in Africa), but some species are dispersed over a huge area between Portugal and the Caucasus. Long-distance recoveries of the birds ringed on the Courish Spit have been reported from the whole of Western Europe (Payevsky, 1973a; Bolshakov et al., 1999-2005; 2001).

Table 1. Songbirds of the Courish Spit* and the trapping figures**

Species	Status ***	Overall ringing totals 1956-2000	Number of recoveries	Number of local recaptures
Red-backed Shrike *Lanius collurio*	B	2805	1	281
Lesser Grey Shrike *Lanius minor*	E	0		
Great Grey Shrike *Lanius excubitor*	M	104	0	7
Eurasian Golden Oriole *Oriolus oriolus*	B	271	1	3
Eurasian Jay *Garrulus glandarius*	B	5844	150	21
Common Magpie *Pica pica*	B	72	1	8
Eurasian Nutcracker *Nucifraga caryocatactes*	M	455	18	5
Eurasian Jackdaw *Corvus monedula*	B	73	1	0
Rook *Corvus frugilegus*	M	60	4	0
Hooded Crow *Corvus corone cornix*	B	67	5	3
Common Raven *Corvus corax*	B	4	0	0
Bohemian Waxwing *Bombycilla garrulus*	M	1168	24	9
Great Tit *Parus major*	B	171770	712	6224
Blue Tit *Parus caeruleus*	B	66759	292	3118
Coal Tit *Parus ater*	B	48542	186	393
Marsh Tit *Parus palustris*	B	1469	0	413
Willow Tit *Parus montanus*	B	1944	2	450
Crested Tit *Parus cristatus*	B	614	0	126
Penduline Tit *Remiz pendulinus*	M	761	12	120
Collared Sand Martin *Riparia riparia*	M	4637	12	4
Barn Swallow *Hirundo rustica*	B	8249	18	238
Northern House Martin *Delichon urbica*	B	8006	7	289
Long-tailed Tit *Aegithalos caudatus*	M	39329	116	963
Crested Lark *Galerida cristata*	E	0		
Woodlark *Lullula arborea*	B	4627	24	84
Eurasian Skylark *Alauda arvensis*	B	479	0	17
Horned Lark *Eremophila alpestris*	M	5	0	0
Lanceolated Warbler *Locustella lanceolata*	V	0		
Grasshopper Warbler *Locustella naevia*	B	526	0	27
River Warbler *Locustella fluviatilis*	M	115	0	9
Savi's Warbler *Locustella luscinioides*	M	59	0	20
Great Reed Warbler *Acrocephalus arundinaceus*	B	2158	6	372
Aquatic Warbler *Acrocephalus paludicola*	V	0		
Sedge Warbler *Acrocephalus schoenobaenus*	B	6813	13	1330
Paddyfield Warbler *Acrocephalus agricola*	V	5	0	0
Blyth's Reed Warbler *Acrocephalus dumetorum*	B	68	0	17
Eurasian Reed Warbler *Acrocephalus scirpaceus*	B	11955	37	3486

Species	**Status *****	**Overall ringing totals 1956-2000**	**Number of reco-veries**	**Number of local recap-tures**
Marsh Warbler *Acrocephalus palustris*	B	3690	3	1033
Booted Warbler *Iduna caligata*	V	5	0	0
Icterine Warbler *Hippolais icterina*	B	9509	6	1088
Willow Warbler *Phylloscopus trochilus*	B	137779	90	9421
Common Chiffchaff *Phylloscopus collybita*	B	8077	6	604
Wood Warbler *Phylloscopus sibilatrix*	B	13098	9	310
Dusky Warbler *Phylloscopus fuscatus*	V	1	0	0
Radde's Warbler *Phylloscopus schwarzi*	V	2	0	0
Pallas's Leaf Warbler *Phylloscopus proregulus*	V	20	0	3
Yellow-browed Warbler *Phylloscopus inornatus*	V	73	0	1
Greenish Warbler *Phylloscopus trochiloides*	B	65	0	11
Blackcap *Sylvia atricapilla*	B	14770	10	2576
Garden Warbler *Sylvia borin*	B	17826	24	1208
Barred Warbler *Sylvia nisoria*	B	3846	7	522
Lesser Whitethroat *Sylvia curruca*	B	14821	9	1985
Whitethroat *Sylvia communis*	B	9782	7	916
Subalpine Warbler *Sylvia cantillans*	V	3	0	0
Bearded Tit *Panurus biarmicus*	M	356	0	127
Firecrest *Regulus ignicapillus*	V	34	0	2
Goldcrest *Regulus regulus*	B	299666	164	6484
Winter Wren *Troglodytes troglodytes*	B	8091	3	2034
Eurasian Nuthatch *Sitta europaea*	B	204	0	31
Eurasian Treecreeper *Certhia familiaris*	B	4814	1	1250
Short-toed Treecreeper *Certhia brachydactyla*	V	7	0	0
Rose-coloured Starling *Sturnus roseus*	V	0		
European Starling *Sturnus vulgaris*	B	95999	1145	945
Ring Ouzel *Turdus torquatus*	V	11	0	0
Eurasian Blackbird *Turdus merula*	B	9121	95	956
Red-throated Thrush *Turdus ruficollis*	V	0		
Fieldfare *Turdus pilaris*	M	2316	48	3
Redwing *Turdus iliacus*	M	5496	97	80
Song Thrush *Turdus philomelos*	B	23295	355	408
Mistle Thrush *Turdus viscivorus*	M	285	4	1
European Robin *Erithacus rubecula*	B	117833	200	17157
Bluethroat *Luscinia svecica*	M	161	1	25
Thrush Nightingale *Luscinia luscinia*	B	1634	3	504
Orange-flanked Bush Robin *Luscinia cyanura*	V	1	0	0
Black Redstart *Phoenicurus ochruros*	B	988	0	19
Common Redstart *Phoenicurus phoenicurus*	B	11278	11	645

Species	Status ***	Overall ringing totals 1956-2000	Number of recoveries	Number of local recaptures
Whinchat *Saxicola rubetra*	B	2828	3	36
Common Stonechat *Saxicola torquatus*	V	2	0	0
Northern Wheatear *Oenanthe oenanthe*	B	807	0	8
Red-rumped Wheatear *Oenanthe xanthoprymna*	V	0		
Common Rock Thrush *Monticola saxatilis*	V	0		
Spotted Flycatcher *Muscicapa striata*	B	8467	14	265
Pied Flycatcher *Ficedula hypoleuca*	B	19542	33	1852
Collared Flycatcher *Ficedula albicollis*	V	16	1	0
Red-breasted Flycatcher *Ficedula parva*	B	809	0	52
White-throated Dipper *Cinclus cinclus*	V	1	0	0
House Sparrow *Passer domesticus*	B	453	1	18
Eurasian Tree Sparrow *Passer montanus*	B	249	0	0
Dunnock *Prunella modularis*	B	3932	6	794
Yellow Wagtail *Motacilla flava*	B	2616	7	34
Citrine Wagtail *Motacilla citreola*	M	1	0	0
Grey Wagtail *Motacilla cinerea*	M	6	0	0
White Wagtail *Motacilla alba*	B	9311	9	938
Richard's Pipit *Anthus richardi*	V	3	0	0
Tawny Pipit *Anthus campestris*	B	117	0	26
Meadow Pipit *Anthus pratensis*	M	10851	96	23
Tree Pipit *Anthus trivialis*	B	5261	17	310
Red-throated Pipit *Anthus cervinus*	M	0		
Rock Pipit *Anthus petrosus*	V	0		
Chaffinch *Fringilla coelebs*	B	683146	1891	11158
Brambling *Fringilla montifringilla*	M	68853	313	132
Serin *Serinus serinus*	B	378	5	4
European Greenfinch *Carduelis chloris*	B	6881	28	82
Eurasian Siskin *Carduelis spinus*	M	177281	1282	340
European Goldfinch *Carduelis carduelis*	B	2829	25	14
Common Redpoll *Carduelis flammea*	M	11298	23	368
Hoary Redpoll *Carduelis hornemanni*	M	18	0	0
Twite *Carduelis flavirostris*	M	32	0	0
Common Linnet *Carduelis cannabina*	B	1558	8	4
Common Rosefinch *Carpodacus erythrinus*	B	5645	5	965
Pine Grosbeak *Pinicola enucleator*	M	1	0	0
Parrot Crossbill *Loxia pytyopsittacus*	V	7	0	0
Red Crossbill *Loxia curvirostra*	M	6520	36	20
White-winged Crossbill *Loxia leucoptera*	V	9	0	0
Eurasian Bullfinch *Pyrrhula pyrrhula*	B	11511	27	798

Species	**Status *****	**Overall ringing totals 1956-2000**	**Number of recoveries**	**Number of local recaptures**
Hawfinch *Coccothraustes coccothraustes*	B	1238	8	43
Corn Bunting *Emberiza calandra*	V	8	0	0
Yellowhammer *Emberiza citrinella*	B	4225	7	471
Ortolan Bunting *Emberiza hortulana*	M	514	2	0
Little Bunting *Emberiza pusilla*	V	9	0	0
Rustic Bunting *Emberiza rustica*	V	9	0	2
Black-headed Bunting *Emberiza melanocephala*	V	1	0	0
Reed Bunting *Emberiza schoeniclus*	B	1951	7	279
Lapland Longspur *Calcarius lapponicus*	V	3	0	0
Snow Bunting *Plectrophenax nivalis*	V	1	0	0
Indigo Bunting *Passerina cyanea*	V	0		

The list of species follows Tischler, 1941; Payevsky, 1973a, 1994a; Shapoval, 1998, 2005; Bolshakov et al., 1999-2005. Bird names and the sequence of species follows Dickinson (2003).

** Ringing totals and results follow Bolshakov et al., 1999-2005.

*** B – breeding (and migratory), M – transient migrant, V – vagrant, E – extinct on the Courish Spit (as compared with the data from Tischler, 1941).

1.4. EXAMINATION AND MEASUREMENT OF CAPTURED BIRDS

Capture and ringing of birds is accompanied by taking biometrical information from them. The technique developed at the Biological Station Rybachy makes it possible to measure size (usually wing length), body mass, to estimate fat score, moult status and stage of the sexual cycle (Blyumental & Dolnik, 1962; Dolnik, 1976).

According to the specific aims of the study the number of biometrical parameters taken may vary. The data are digitised and are analysed when required. Thanks to taking biometrical parameters bird ringing has changed from an activity with low efficiency (as concerns reporting probability) into a high efficiency process gaining important data on the birds living under natural conditions. Standardised methods of capture and measurements yield the data on the timing of seasonal events in different sex and age classes, physical condition of migrants, timing of breeding, participation of different sexes in incubation, individual variation in times of different physiological states and plumage change.

Based on the measurement data of numerous birds of different species the team at the Biological Station Rybachy have compiled the Identification Guide of Sex and Age of Passerines of the USSR (Vinogradova et al., 1976). For many species, definite sexing and ageing criteria have been found. All details of measurement techniques, sexing and ageing are included. Apart from that particular book, other identification guides, primarily the standard one by Lars Svensson (1992, and all editions since the first one in 1970), and those by Busse (1984), Bub (1985), Rymkevich (1990), and Jenni & Winkler (1994) have been consulted. The data from specialist publications have also been consulted (Payevsky & Yefremov, 1972; Yefremov & Payevsky, 1973; Shapoval, 1981c, 1987; Chemyakin, 1988a; Markovets, 1991, 1992).

Chapter 2

TERMINOLOGY AND METHODOLOGY IN THE POPULATION STUDIES OF BIRDS

2.1. TERRITORIAL AND SPATIAL BEHAVIOUR TERMINOLOGY. STUDY OF DISPERSAL AND PHILOPATRY (SITE FIDELITY)

It is well known that confusion over terminology may cause serious difficulties in understanding. In the ornithological literature a certain variety in the use of terms exists in describing avian populations and their use of space and territory.

Population

In spite of everyday use of the term ‘population’ by nearly all biologists, it is quite difficult to give a clear, unambiguous definition suitable for this concept (as with the ‘species’ concept). The term ‘population’ entered biology from demography, as demography initially emerged as a part of medical statistics. It is self-evident that all animal species live and breed in groups, more or less isolated from other similar groups. However, no one can clearly say where and in which form the borders between such groups exist, i.e. to what degree they are isolated. The question whether it is in principle possible to study the degree of isolation of local animal populations remains an open one, because despite the objective character of the existence of populations they are usually not discrete (Pianka, 1978; Panov, 1983). Of course, it is in populations where processes relevant to such basic biological concepts as evolution, speciation, distribution of animal numbers and their spatiotemporal dynamics start and proceed. Evolutionary, genetic, ecological and to some extent ethological approaches to population studies may be lumped under the umbrella terms ‘population biology’ and ‘evolutionary ecology’, where the population is the specialisation of taxonomists (as a ‘chorological unit’), geneticists (as a ‘panmictic unit’-random mating according to Hardy-Weinberg rules), ecologists and ethologists (as a ‘structural organisation unit’). In many publications, notably those by David Lack, rules of demographic differences of fecundity, birth rate, mortality rate and dynamics of numbers of animal populations are placed among evolutionary ecology problems, i.e. studies of ecological mechanisms and factors of microevolution.

Many biologists have tried to define the term ‘population’. Most commonly, a population is defined as a panmictic aggregate of conspecifics that exists in an area with uniform physical conditions across a long period of time. Each population is a part of the natural community within which this population interacts with other biotic factors. Adaptations of populations that form a biocenosis to biotic and abiotic factors many play the decisive role in evolutionary change irrespective of co-adaptation of these populations. Within-species and within-population relationships of individuals are significant factors (Severtzov, 1998).

In ornithology, a group of species within certain areas may be called an avian community, an assembly of birds, ornithocenosis or ornithocomplex. None of these terms has a clear definition, as reviewed by N. Morozov (1992).

Many passerine species breeding on the Courish Spit are often assumed (Dolnik & Payevsky 1982, Sokolov, 1991a,b; Sokolov, 1997; Payevsky, 1999) to form distinct populations with a specific gene pool due to local recruitment across long periods of time. Such a group is a ‘local, or elementary population’ that is a part of an ‘ecological population’ which, in its turn, is a part of ‘geographic population’ (Shilov, 1977, 1995). The term ‘local population’ however, is related to a large array of dispersal-related problems, as discussed below. Usually autochthonous individuals, i.e. those born locally, and immigrants, i.e. birds of unknown origin that arrived from other populations, are distinguished within the local population.

Spatial movements

The problem of the spatial structure of migratory bird populations is much complicated by their high seasonal mobility. Alternation of sedentary and migratory periods in the annual cycle together with spatial concentration of migratory routes results in the mixing of different geographical groups of birds in different parts of their distribution range. Such mixing, as indicated by ring recovery data, occurs in many species on the Courish Spit where birds breeding in the Eastern Baltic, north-western European Russia and a part of Fennoscandia, mainly Finland, migrate in particular succession (Payevsky, 1967, 1973a, 1975). Therefore, in this book the term ‘passage populations’ is applied to a general geographic affiliation rather than a more specific definition of these various groups of migrants.

Terminology related to spatial movements of birds is very diverse. Some standard in English terminology related to avian territoriality and movements has been reviewed (Berndt & Sternberg, 1968; Greenwood, 1980; Greenwood & Harvey, 1982; Terrill & Able, 1988; Warkentin & James, 1990). German-language terminology for movements of juvenile songbirds has also been reviewed (Bauer, 1987). Russian terminology, however, cannot claim to be sufficiently standardised.

Some Russian terms accepted in ornithology do not fit the general biological terms (and sometimes differ from the exact meaning of similar English terms).

The term 'irruption' (occasionally 'invasion') in general biology means a process of range expansion in animal species and populations. In ornithology, this word denotes a dramatic increase in the numbers of migrating individuals, mainly juveniles, in those sedentary or nomadic species that otherwise occur at migratory sites in low numbers or do not occur at all (Lack, 1954; Svärdson, 1957; Formozov, 1965). In some so-called 'irruptive', or 'invasive', species some individuals may reach areas lying outside the usual distribution range. Some authors believe that only migratory movements that expand the distribution area beyond the usual breeding or wintering range may be called 'irruptions' (Noskov et al., 1975). As invasive individuals do not usually breed in these new areas, irruption cannot be equated to range expansion. Earlier it was commonly assumed that nearly all irruptive individuals perish (as occurs in e.g. lemmings, *Lemmus*), and that this type of mass movement is a mechanism of regulation of numbers by eliminating population surplus (Wynne-Edwards, 1962; Dolnik, 1975). Recently the view is gaining recognition that avian irruptions are not a special form of movement but rather a result of relatively strong annual fluctuation of migratory behaviour. This is because a considerable proportion of an irruptive population returns in spring to its breeding area (Bardin & Rezvyi, 1988; Alerstam, 1990; Sokolov et al., 2002). Unlike irruptive species that do not migrate annually, the so-called 'partial migrants' are the populations that either annually move for short distances or those where migratory movements are performed only by a proportion of individuals (Berthold, 1999).

Dispersal

The term 'dispersal' means the process of movement that causes dispersion of individuals in space. In addition to dispersal, the term 'spacing' is sometimes used that means movement induced either by the environment or by intra- or interspecies competition. A variant of spacing is 'intercepting' that occurs when at the final stages of return migration the birds are attracted ('intercepted') by a sexual partner and thus do not reach their migratory target (Fedorov, 1996). Unlike spacing, dispersal usually means voluntary movement from a natal site to the site of the first breeding (natal dispersal) or the movement of adults between breeding sites in successive years (breeding dispersal). The lack of a pronounced dispersal is called 'philopatry', separated into breeding philopatry of adults, i.e. returning to the site of the previous breeding, and natal philopatry of juveniles, i.e. returning to the natal site (Sokolov, 1991a). When a bird returns to the old place in the next breeding or wintering season, it is called 'site fidelity' or 'site tenacity'. A very detailed review on the dispersal and site-fidelity was recently given by I. Newton (2008).

The initial part of dispersal of juveniles, i.e. “postfledging (juvenile) dispersal” is sometimes called ‘juvenile settlement migration’ (Noskov et al., 1975; Noskov & Rymkevich, 2005). This term is only used by the authors affiliated with St. Petersburg State University and Karelian Research Centre of Russian Academy of Sciences. They assume that the timing and duration of this activity are controlled by an endogenous rhythm.

Apart from ‘juvenile settlement migration’, Russian ornithological literature can be noted for such terms as ‘breeding conservatism’ and ‘territorial relationships’ that exists in parallel with the broadly known philopatry, dispersal, and site fidelity. In the recent years, local survival rate in a population is sometimes called ‘remaining rate’. This term was suggested by A. Bardin (Bardin, 1988; Vysotsky et al., 1988). This was due to the lack of knowledge of true physical survival rate as just the proportion of animals from the previous year’s cohort can be measured for a local area. Local survival rate depends on the true survival rate and site fidelity (a bird that remained is the one that survived and returned). This parameter may be estimated by different methods if based on various assumptions. The most common assumptions are that re-capture probability of a ringed bird, its survival rate and site fidelity are year-independent and equal between different individuals (which is generally speaking not true).

These disagreements about terminology appear to reflect conceptual differences. A whole complex of spatial problems of birds may be reduced to dispersal. In Russian (Soviet) ornithology, two competing approaches to studying avian population ecology have existed, and these approaches are related to very different *a priori* concepts of mechanisms and distance of dispersal.

It started in the early and mid 20th century with the ideas of Howard (1920) who believed that all surviving birds return in spring to their natal area and breed there. A number of Russian authors (Isakov, 1949; Likhachev, 1955; Polivanov, 1957, 1984) supported the concept of local (elementary) populations, or micropopulations, of birds finely tuned to the local environmental conditions. It was assumed that the overwhelming majority of members of such populations, both adult and juvenile ones, in spring return to their area, thus supporting its genetic isolation and uniformity and enhancing adaptation to subtle local conditions. These views were obviously based on recaptures of the ringed birds at the sites of ringing in subsequent years. These recaptures mainly referred to songbirds, i.e. Starlings, Swallows, Pied Flycatchers, Great Tits. Understandably, the examples of the opposite cases when ringed birds were found breeding far from their natal sites were emphasized by the opponents of the micropopulation concept (Malchevsky, 1968, 1973, 1975, 1988; Danilov, 1983; Zimin, 1988). They insisted that these cases document the broad dispersal of birds, mainly juveniles, from their natal sites, the exchange of genes in birds, and the fact that each population is supported not only by its own offspring but by young birds emigrating from distant areas. As the proportion of birds found in the natal areas was very different in different avian species and population, a hypothesis of two types of evolution in birds, a conservative and a dispersed one, was forwarded (Malchevsky, 1968, 1988).

The researchers, who worked at the northern limits of the ranges of many passerine species under low population density, always maintained a separate opinion based on their long-term studies and large datasets. They believe that mortality rate in peripheral populations is considerably higher than in other parts of the species' range, and that these populations cannot exist without permanent immigration (Shutov, 1986; Zimin, 1988; Ryabitsev, 1993; Hoffmann & Blows, 1994; Ryzhanovsky, 1997; Thingstad et al., 2006). Some data suggest that return rate of passerines decreases in the tundra as compared with boreal forests (Shutov, 1989).[1]

Even though these conclusions may appear convincing, an obvious contradiction remains. If the views of long-distance dispersal of birds from their natal areas to breed in new summer habitats are true, it is impossible to explain the adaptive significance of complex and precise orientation and long-distance navigation mechanisms of many birds and other animals (e.g. diadromous fish, sea turtles). If breeding at any random site beyond the range of the local population is just as adaptive as returning home, one does not need to develop sophisticated means to return to a specific site on the globe.

As surviving yearlings (young birds of the previous year) return much less frequently than adults, it has been suggested that orientation abilities develop gradually during an individual's lifetime. From a number of species studied orientation based on astronomical cues is indeed not innate and they need to collect individual experience to develop their navigation abilities (Wiltschko, 1991). Perhaps those juveniles, whose ability to orientate or to memorise their future navigation target is impaired or develops later than in others, are the ones that transfer genes to other populations. If so, individual variation in navigation ability leading to philopatry may be a regular process supported by the selection.

The previous disagreements remain (see for example two recent publications expressing the opposing views: Sokolov, 1997; Zimin, 2002). The main source of conflict is the assumed fate of the birds that were never recaptured. Capture-mark-recapture studies in a limited area don't make it possible to estimate survival and return rates (or mortality and emigration rates) separately. Nearly all authors seem to realise that the proportion of ringed birds found at the ringing area in subsequent years is the product of the three parameters: survival rate, return probability of survivors and their detection (recapture or resighting) probability (which

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[1] It is worth noting that return rates of various species in the Subarctic Urals given in this publication show comparable dispersal rates at temperate and high latitudes (cf. review: Sokolov, 1991a).

is a function of the study area size). These disagreements basically depend on the methods for tackling this problem.

Many ornithologists assume that visual observations and capture efforts in a certain area allow them to detect the bulk of birds that survive and return. In fact, detection efficiency cannot reach 100 %, even in a population that breeds mainly in nestboxes or whose members are colour-ringed (even though such assumptions are occasionally made, e.g. Shutov, 1986). To roughly estimate this efficiency, or returning probability to the study area various logical constructions are occasionally used, including those based on the number of years when the birds were not captured but alive as they were captured in the subsequent years (Dolnik & Payevsky, 1982; Bardin, 1996). In other cases various stochastic models are used (Pollock et al., 1990; Bardin, 1990b). Stochasis means assumption or probability in Greek, and any stochastic method is a probabilistic one (to find the most probable vector from an array of random events). This is definitely also applicable to the study of dispersal.[2]

It remains unclear why dispersal discussions were so acute in Soviet/Russian ornithology. In international science, even though the idea of elementary populations was mainly accepted (Mayr, 1942), no such disagreements occurred, although it was recognised by many authors that dispersal problems were important and insufficiently studied (Bauer, 1987). Judging from the reviews, most ornithologists agree that, apart from several nomadic species, the bulk of survivors among adults return after wintering to the same population where they bred before (Sokolov, 1988, 1991a; Payne, 1991; Newton, 2003a; 2008). This is more pronounced in males than in females (Kovshar, 1981; Golovan, 1982; Chernyshov, 1986; Shutov, 1989; Newton, 2008). After a more successful breeding, more birds return (Shutov, 1986; Fedorov, 1996; Taillandier et al., 2003, Newton, 2003a, 2008; Sherry et al., 2006), and overwhelming majority of adult birds nested close to site where they bred during the previous years. Some authors distinguish between site fidelity (return to the population-specific area) and territory fidelity (return to breeding territory). Return rates are then very different, e.g. 85% and 33%, respectively, in Marsh Warblers in England (Kelsey, 1989) and 97% and 36%, respectively, in Eurasian Reed Warblers in France (Taillandier et al., 2003).

Sensitive period after fledging and dispersal

Juveniles hatched in a certain area return to their natal site much less frequently than adults. The first reason for this is their much higher mortality when compared with the adults, and the second is their likelihood of longer dispersal.

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[2] The expression ‘demographic stochasticity’ means random fate of individuals during population extinction (Legendre et al., 1999).

It is sometimes claimed that long-distance migrants show less pronounced site tenacity than short-distance migrants and sedentary species (Mouritsen, 2003), even though no data are given to support this claim. On average, breeding dispersal distance is one-half of natal dispersal distance, but in some species it may be just one-sixth of natal dispersal (Newton, 2003a, 2008). Females, especially the young ones, are less philopatric than males (Morton et al., 1991; Newton, 2008). Among 77 species, median natal dispersal distance varied between 0.03 km in the House Martin and 10 km in the Glaucous-winged Gull (*Larus glaucescens*), and the maximum natal dispersal distance between 1.3 km in the Magpie and 1305 km in the Great Horned Owl (*Bubo virginianus*). Most birds were concentrated close to their natal sites, and just a few settled far from it (Sutherland et al., 2000).

One obvious role of dispersal, to avoid inbreeding, has been frequently mentioned by both proponents and opponents of the hypothesis of strict genetic uniformity of populations (Bauer, 1987). Their views only differ in their estimate of dispersal distance necessary to prevent inbreeding. When the populations are spatially more isolated (insular effect) indeed both the proportion of philopatric juveniles and the occurrence of inbreeding cases increase (Zubtsovsky et al., 1989; Ryabitsev, 1993). However, there are many examples of rather high return rates of juveniles to their populations without obvious isolation (for a review see: Sokolov, 1991a; Newton, 2008).

The bonds with the future breeding areas (the so-called imprinting of the area) are formed in passerines during a special sensitive period 30-60 days after hatching, during juvenile dispersal (Sokolov, 1986, 1988, 1991a; Sokolov et al., 1984, 1987; Morton et al., 1991; Sokolov, 1997). As shown in *Phylloscopus* warblers on the Arctic Urals, the sensitive period may sometimes start slightly earlier, at the age of 26 days (Ryzhanovsky 1997). Juvenile dispersal with memorising the future breeding area may occur during the night, e.g. in Eurasian Reed Warblers on the Courish Spit at the age of 35-50 days (Bulyuk et al., 2000; Mukhin, 2004; Mukhin et al., 2005). If a bird is still close to its natal site at the age of one-two months, it will return there next spring. If during this period a bird has already moved to a distant area, it will show fidelity to this new site where it was during this age. This principle may be the key to the returning vs. the non-returning of the surviving juveniles.

Opportunistic breeders

Certainly, avian species differ in respect to site fidelity. Some passerine species are more prone to change living and breeding areas than others. This is especially true of irruptive species and generally of species with specialised foraging habits, e.g. Crossbills, Redpolls, Siskins and partly Coal Tits and Jays. They are capable not only of changing their sites of high concentration in different seasons depending on the abundance of their preferred food (Svärdson, 1957; Formozov, 1965), but also to start breeding in different places and at different times (Payevsky, 1970; Leonovich, 1976; Anderson, 1980; see also section 4.8). A similar behaviour is typical even of Goldfinches (Malchevsky, 1959). Such species are opportunistic, i.e. they are capable of quickly using a good opportunity, e.g. to breed. Some non-irruptive species, e.g. Common Rosefinch, may also show very low natal philopatry (Zimin, 1981; Sokolov, 1991a; see also section 4.9).

The proportions of juveniles that mainly perform gene exchange between the populations provide each population a source of genetic variation which is necessary for future adaptations. The proportion of gene flow depends on the features of the neighbouring populations and probably varies quite broadly among avian species and populations.

Ring recovery

Another specific ornithological term 'recovery' is closely related to this topic. In English-language literature it usually means an encounter with a ringed bird outside the area where it was marked. The corresponding Russian word may also mean a re-encounter at the site of ringing (i.e. a recapture, or control) in a subsequent year. The so-called 'return rate', i.e. the percentage of birds that returned to the study area of the total number of the birds marked, is still used by some authors as a proxy to site fidelity, even though its value is questionable. As mentioned above, this parameter is biased because it includes survival rate, and returning probability, and detection probability (i.e. is a function of searching effort). The inadequacy of return rate for studying spatial behaviour has been discussed repeatedly (Pollock et al., 1990; Bardin, 1993, 1996; Vysotsky, 2001 etc.). The authors who used return rate as a proxy to site fidelity have themselves clearly shown that different encounter techniques of locally ringed individuals yield different results (Zimin et al., 1983). Return rate cannot be used to estimate survival rate, as sometimes suggested based on the assumption that most surviving adult males are philopatric and their annual detection rate is close to 100%.

The only adequate use of return rate is by the comparison of ringing efficiency of different species and populations in a methodological framework (as shown in the following section).

2.2. RELATIVE EFFICIENCY OF BIRD RINGING IN RELATION TO SPECIES, SEX, AGE, SEASON, AND RINGING LOCATION

Over the century of scientific bird ringing this method of individual marking has contributed to significant progress in many fields of biology, especially in migration studies and demography. Measuring captured birds will yield potentially important datasets *per se* and need not be accompanied by ringing. If a bird is marked before release, this is done in order to obtain data on its subsequent fate. A number of questions will inevitably arise, related to the probability of obtaining meaningful results and the economic costs of the ringing activity. Production or purchase of tags by the ringing organisations, to say nothing of the whole trapping effort, inflicts considerable costs. Therefore, ringing efficiency should be calculated in advance. An analysis made by P. Saurola (1988) showed that 22% of all birds ringed in Finland were just two species, the Great Tit and the Pied Flycatcher, and that the cost of obtaining one Goldcrest ring recovery was 200 higher than one Goshawk (*Accipiter gentilis*) recovery.

However, currently only very limited information on ringing efficiently is broadly available. This information may be summarised as follows: recovery, or return, rate is much higher in large birds and especially in game species (e.g. ducks, geese) than in small songbirds, and much higher when migratory routes and wintering areas are densely populated by people in Europe and North America (Bub, 1969; Payevsky, 1973b). For example, among passerines 21 short- and medium-distance migrants had a recovery rate nearly three times higher than in 26 migrants to Africa (Shapoval, 1994).

The following analysis of ringing effort efficiency (Payevsky & Shapoval, 1998) is based on long-distance recoveries of birds ringed on the Courish Spit and re-encountered on migratory routes and in winter quarters. The analysis includes 10 species from 7 passerine families and for comparison birds of prey, shorebirds, cuckoos and owls (one species from each order). The choice of species was governed by the necessity to include birds with various ecology and different migratory habits. The linearity of the relationship between the number of marked individuals and the number of ringing recoveries was fitted by eye from the graphs of empirical regression y/x, where (x) is the number of ringed birds. Fitting applied in species with a high recovery rate (Eurasian Siskin, European Starling) showed that this relationship is a linear one. Therefore, coefficient of linear correlation was used. The uniformity of recovery rate variation among the species was tested by ANOVA, and variation of recovery rate among the countries by Friedman rank test. Within species, the annual fluctuation in recovery rates was analysed on the basis of coefficient of determination.

The above correlations were calculated on the basis of the annual data (1957-1984). To increase sample size, the original data were grouped into 24 half-month intervals. In all cases, recoveries not only in the current year, but also in all subsequent years were included.

The results are presented in Tables 2 and 3. The study species can be divided into two main groups by the mean recovery rate. The first group includes

Table 2. Correlations between ringing totals and number of recoveries from 1957 to 1984 in passerines and non-passerines

Species, sex, age	Number ringed	Number and percent of recoveries	Coefficient of correlation in different months							Annual variation
			IV	V	VI	VII	VIII	IX	X	
European Robin	35236	106(0.30)	0.56***	0.57***	-	-	-	0.71***	0.38*	-0.19-0.99
Song Thrush	13255	277(2.09)	0.41*	-	-	-	-	0.86***	0.69***	-0.49-0.99
Garden Warbler	6609	18(0.27)	-	-0.33	-0.10	-0.20	0.28	-	-	-0.09-0.99
Willow Warbler pooled	60250	37(0.06)	-	0.37**	-	-0.02	0.77***	0.67***	-	-0.22-0.50
♂♂	19651	11(0.06)	-	0.29	-	-	0.71***	0.63***	-	0.08-0.93
♀♀	13125	13(0.10)	-	-0.11	-	-	0.41*	0.45*	-	0.16-0.94
Goldcrest pooled	113846	82(0.07)	0.27*	-	-	-	-	0.78***	0.77***	0.02-0.89
♂♂	61723	41(0.07)	0.28	-	-	-	-	0.90**	0.85***	-
♀♀	46374	33(0.07)	0.42*	-	-	-	-	0.68**	0.71***	-
European Starling pooled	75415	1002(1.33)	0.79***	-	0.82***	0.79***	-	-	0.61***	-0.25-0.99
♂♂	21833	204(0.93)	0.49*	-	0.74*	0.97***	-	-	0.62**	-
♀♀	17768	147(0.83)	0.55*	-	0.74*	0.96***	-	-	0.68***	-
Great Tit pooled	83780	463(0.55)	0.69***	-	-	-	-	0.85***	0.61***	0.14-0.96
♂♂	32142	163(0.51)	0.67***	-	-	-	-	0.90***	0.60***	0.25-0.99
♀♀	47699	275(0.58)	0.73***	-	-	-	-	0.83***	0.61***	-0.29-0.83
♂♂ ad	4971	22(0.46)	0.53*	-	-	-	-	0.47	0.71***	-
♀♀ ad	6171	32(0.52)	0.53*	-	-	-	-	-0.14	0.53**	-
♂♂ sad	25507	125(0.49)	0.67***	-	-	-	-	0.89**	0.53**	-
♀♀ sad	38968	216(0.55)	0.77***	-	-	-	-	0.79**	0.54**	-

Species, sex, age	Number ringed	Number and percent of recoveries	Coefficient of correlation in different months							Annual variation
			IV	V	VI	VII	VIII	IX	X	
Chaffinch pooled	483838	1624(0.34)	0.76***	0.72***	0.170	0.28*	0.28*	0.78***	0.72***	0.51-0.98
♂♂	210302	759(0.36)	0.83***	0.38*	0.02	-0.09	-0.19	0.74***	0.74***	0.67-0.98
♀♀	219642	551(0.25)	0.79***	0.78***	0.38*	-0.10	-	0.79***	0.71***	0.46-0.99
♂♂ ad	71294	174(0.24)	0.91***	-0.04	0.35	-	-	0.87***	0.88***	-
♀♀ ad	72000	114(0.16)	0.81***	0.89***	0.30	-	-	0.93***	0.87***	-
♂♂ sad	69155	166(0.24)	0.47*	0.63**	-0.16	-0.07	-0.03	0.81***	0.80***	-
♀♀ sad	77903	126(0.16)	0.79***	0.65***	-0.17	-0.04	-	0.82***	0.78***	-
Eurasian Siskin pooled	134963	1094(0.81)	0.62***	0.48**	-	-	-	0.87***	0.79***	0.01-0.98
♂♂	70839	641(0.90)	0.,52***	0.24	-	-	-	0.87***	0.79***	-0.22-0.99
♀♀	64124	453(0.71)	0.45**	0.51***	-	-	-	0.86***	0.75***	0.14-0.99
Eurasian Jay	3990	128(3.21)	-	0.20	-	-	-	0.72**	0.75***	-0.38-0.99
Eurasian Sparrowhawk pooled										
♂♂	2647	162(6.12)	0.66***	0.09	-	-	0.81***	0.48***	0.55***	0.01-0.91
♀♀	1407	63(4.50)	0.40*	0.14	-	-	0.47	0.77***	0.68***	0.01-0.94
♂♂ ad	827	53(6.41)	0.39*	-	-	-	0.76**	0.39*	0.39*	-0.50-0.82
♀♀ ad	212	2(0.94)	0.84**	-	-	-	-	-	0.18	-
♂♂ sad	94	4(4.26)	0.79**	-	-	-	-	-0.13	-0.19	-
♀♀ sad	1123	53(4.72)	0.71**	-0.02	-	-	0.46	0.78**	0.70***	-
	696	45(6.47)	0.27	-	-	-	0.77**	0.39*	0.41*	-
Eurasian Woodcock	126	27(21.43)	-	-	-	-	-	-	0.80***	-
Common Cuckoo	949	12(1.26)	-	0.28	-	0.33	0.03	-	-	-
Long-eared Owl	1927	73(3.79)	-	-	-	-	-	-	0.95***	-

Note. Significance of correlation: * p≤0.05, ** p≤0.01, *** p≤0.001. Age codes: ad – adults (since the third calendar year), sad – yearlings (April - July) and juveniles hatched in this calendar year (August – October).

the species with recovery rates exceeding 1%, these are all non-passerines, i.e. the Long-eared Owl, Eurasian Sparrowhawk, Eurasian Woodcock (*Scolopax rusticola*) and Common Cuckoo, and the Eurasian Jay, Song Thrush and to some extent European Starling among passerines. The remaining passerines have recovery rates below 1%. The analysis of variation of recovery rates in birds of similar size (European Robin, Garden Warbler, Willow Warbler, Goldcrest, Great Tit, Chaffinch, and Eurasian Siskin) showed that both species and year were highly significant factors (($F = 5.3 > F_{st} = 2.0$ with df = 8 and $30.2 > 2.9$ with df = 6, respectively). A more detailed pairwise comparison of recovery rates in different species showed significant differences: Goldcrest vs. Garden Warbler, Chaffinch vs. Great Tit, Chaffinch vs. Garden Warbler, Great Tit vs. Siskin ($p < 0.001$ in all cases). In other pairs no significant difference was found (Willow Warbler vs. Goldcrest, Robin vs. Garden Warbler, Robin vs. Chaffinch).

Analysis of the annual variation of recovery rates in each species yielded quite interesting results (Table 3). Time series correlation in all species except

Table 3. Annual variation in recovery rate, from 1957 to 1984

Species	**Recovery rate, %**					
	lim	*x*	σ	*CV, %*	*r*	r^2
European Robin	0.0-1.0	0.3	0.2	66.7	-0.27	0.07
Song Thrush	0.0-7.2	2.6	1.6	61.5	-0.48	0.23
Garden Warbler	0.0-1.3	0.2	0.3	150.0	-0.22	0.05
Willow Warbler	0.0-0.2	0.06	0.05	83.4	0.24	0.06
Goldcrest	0.0-0.5	0.1	0.1	100.0	-0.09	0.01
Great Tit	0.0-1.4	0.7	0.3	42.9	-0.20	0.04
Chaffinch	0.1-0.8	0.4	0.2	50.0	-0.90	0.81
Eurasian Siskin	0.1-1.8	0.8	0.4	50.0	-0.83	0.69
European Starling	0.0-3.3	1.2	0.7	58.3	-0.56	0.31
Eurasian Jay	0.0-12.0	2.3	3.2	139.1	-0.29	0.08
Eurasian Sparrowhawk	0.0-17.3	7.7	5.3	68.8	-0.46	0.21
Common Cuckoo	0.0-8.7	1.3	2.1	161.5	-0.11	0.01
Eurasian Woodcock	0.0-33.3	18.2	34.3	114.3	-0.17	0.03
Long-eared Owl	0.0-11.1	4.5	6.2	137.8	-0.26	0.07

Notes:
lim – limits of annual values,
x – mean across the study period,
σ – mean quadratic deviation,
CV – coefficient of variation,
r – coefficient of correlation of time series,
r^2 – coefficient of determination,
Significant coefficients of correlation are underlined.

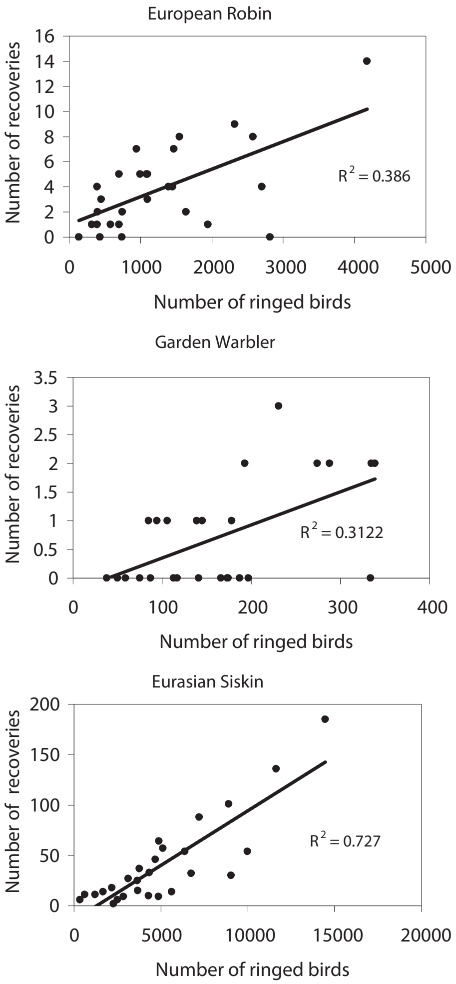


Fig. 3. Relationship between ringing numbers and recovery numbers in three songbird species.

for the Willow Warbler was negative, even though the trend was significant in the Chaffinch, Siskin and Starling only. This means that recovery rate in the latter three species declined over the 28 study years, in the Chaffinch from 0.8 to 0.2%, in the Siskin from 1.2 to 0.3%, in the Starling from 2.0 to 1.0%. It is noteworthy that coefficient of variation of recovery rate was within 50 – 58%, whereas in some other species it reached 140 – 160% (Table 3). The reasons for this should lie in some changes at migratory stopover sites and in winter quarters that influence the contacts between birds and people. It is possible that after the implementation of legislation limiting commercial bird fowling in some provinces of Italy, the fowlers ceased to report the rings they find (McCulloch et al., 1992). The same may apply to other countries, e.g. France where birds that pass through the Courish Spit spend their winter.

Annual variation of correlation coefficients between numbers ringed and numbers recovered is quite significant (Table 2, Fig. 3). Yearly coefficients vary between negative values and nearly +1. Monthly variation is much smaller. If only significant values are included, for most species correlations are weaker in spring months (April and May) than in autumn (September, October). The difference was significant in five species: Song Thrush (t = 3.68, df 76, $p<0.001$), Willow Warbler (t = 3.16, df 102, $p<0.01$), Goldcrest (t = 4.11, df 137, $p<0.001$), Great Tit (t = 2.08, df 111, $p<0.05$) and Siskin (t = 2.53, df 72, $p<0.05$). As for the age and sex variation in the coefficient under discussion, no clear trends emerged. Correlation value varied chaotically within each species. The lack of relationship between age and recovery rate can only be explained by the fact that juveniles were ringed on autumn passage when the period of elevated mortality of juveniles had already ended.

The lack of a clear linear positive relationship between the number of recoveries and ringing totals suggests that ringing efficiency strongly depends on the yearly fluctuation of environmental factors. The likely contributing factors are the weather and crops of the food plants in autumn and winter. Both factors may be closely associated with the probability of contacts between birds, dead or alive, and people.

Even though recovery data are widely used for compiling the maps of migratory routes and wintering areas, some doubt on the validity of the emerging patterns exists. The doubts are based on the obvious fact that recovery probability in a particular area strongly depends on local human population density, cultural traditions and hunting pressure. One of the strongest factors introducing bias in the distribution patterns of recoveries is the concentration of hunters and fowlers in some European countries and regions (Payevsky, 1973b; Perdeck, 1977; Busse, 2001).

National traditions for trapping migratory birds for food, songbirds included, result in increased numbers of birds captured and consequently a larger number of rings recovered in some countries and regions of Europe. Whether the density of recoveries reflects the genuine density of birds remains unknown. For example, an analysis of hunting intensity vs. recovery numbers in the Song Thrush showed that in many cases these parameters are not related. Moreover, even though in southern Italy where hunting pressure is strong and large concentrations of migratory thrushes occur, the number of recoveries declines towards the south of the country (Andreotti et al., 1999).

A particular question about the analysis of ringing efficiency is whether our data differ from the similar data from other countries and organisations. The first such comparison occurred over three decades ago (Payevsky, 1972). Now it is possible to compare recovery rate for the same species in other European countries with our data using a much larger dataset (Table 4). We selected seven species for comparisons where recovery rates were available for all 11 European regions included in the analysis. The results, first, confirmed the existence of species-specific variation in recovery rates ($\chi^2 = 128$, df = 6, $p<0.001$), and second, showed significant country-related variation ($\chi^2 = 13.5$, df = 4, $p = 0.01$). The latter result is somewhat unexpected, as many values in Table 4 are very similar or even identical. This outcome was probably due to a far higher percentage recovery rate for the UK: with the top 5 for all species and highest for 7 of the species. The reason is presumably because the UK has a higher proportion of resident or relatively sedentary populations for most of the species unlike other countries in the list.

Ringing of songbirds in North America yielded similar results: of a total of 17 million birds ringed over 30 years, just 0.4% were subsequently recovered, and only 26 species produced more than 500 recoveries (Francis, 1995).

The data described in these tables make it possible to conclude that the probability for obtaining information on the location of marked birds may be estimated

Table 4. Recovery rates (%) of birds ringed in different European countries

Species	**Countries**										
	UK	DK	EE	FI	DE-H	DE-R	NO	RU-R	RU-P	SE-F	ES
European Robin	1.5	0.3	0.2	0.8	0.4	0.6	0.6	0.3	0.1	0.5	0.2
Song Thrush	2.4	1.5	1.1	1.3	1.1	2.4	1.4	2.1	2.1	2.6	0.7
Garden Warbler	0.4	0.3	0.2	0.7	0.2	0.3	0.3	0.3	0.2	0.2	0.1
Willow Warbler	0.3	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.04	0.2	0.1
Goldcrest	0.3	0.1	0.1	0.03	0.2	0.1	0.1	0.1	0.1	0.1	-
Great Tit	0.9	0.4	1.2	2.5	0.6	0.5	1.2	0.6	0.5	0.8	0.0
European Starling	3.3	1.0	0.8	1.0	1.9	-	2.1	1.3	1.3	2.1	0.6
Chaffinch	0.8	0.3	0.3	1.0	0.8	0.5	0.8	0.3	0.1	0.4	0.1
Eurasian Siskin	2.5	0.3	0.3	0.9	1.4	0.9	1.0	0.8	0.3	0.9	0.1
Eurasian Jay	6.5	-	1.5	-	-	6.5	6.3	3.2	2.4	4.8	0.3
Eurasian Sparrowhawk	10.3	6.5	3.8	16.6	4.7	-	12.4	6.1	2.0	11.7	0.7
Eurasian Woodcock	7.8	11.1	8.1	-	6.6	-	7.5	21.4	22.9	-	4.0
Common Cuckoo	2.7	-	1.3	-	2.0	-	4.0	1.3	0.1	10.4	-
Long-eared Owl	7.3	7.4	1.7	-	9.7	-	4.0	3.8	1.4	10.1	0.5

Country codes:

UK – UK and Ireland, 1909-1990 (Mead & Clark, 1991)
DK – Denmark, Christiansø, 1928-1983 (Lyngs et al., 1990)
EE – Estonia, 1970-1992 (Kastepõld & Kastepõld, 1993)
FI – Finland, 1913-1962 (Nordström, 1963)
DE-H – Germany, Helgoland, 1900-1972 (Vauk-Hentzel, 1976; Zink & Bairlein, 1995)
DE-R – Germany, Radolfzell, 1947-1976 (Zink, 1969, 1973, 1981; Zink & Bairlein, 1995)
NO – Norway, 1914-1978 (Holgersen, 1978)
RU-R – Russia, Rybachy, 1957-1994
RU-P - Russia, Leningrad Region, 1955-1994 (Noskov & Rezvyi, 1995)
SE-F – Sweden, Falsterbo, 1947-1980 (Roos, 1984); ES – Spain, 1973-1991 (Cantos & Gomes-Manzaneque, 1992)

in advance depending on the species. A researcher studying autumn and winter spatial distribution of a Willow Warbler population should be prepared to mark at least 1600 individuals during two seasons to obtain a single recovery. His colleague working on Woodcocks has to ring just 6 birds to obtain a similar result. If the birds are migrating not to Europe but to Asia, where overall recovery rate for all avian species does not exceed 0.5% ringed (Gavrilov, 1979), the probability of obtaining information is too low to be incorporated into planning ringing projects.

2.3. ASSESSMENT OF HOW REPRESENTATIVE TRAPPING RESULTS ARE FOR THE POPULATIONS STUDIED

2.3.1. The adequacy of the sampling

The concern here is the adequacy of the samples obtained by trapping for tackling scientific problems. Trapping data obtained by Rybachy-type traps have been used for long-term population monitoring over 40 years. However, the question of how representative these data have been is only rarely raised. Bird numbers and estimates of their dynamics from captured data on the Courish Spit have been discussed repeatedly (Dolnik & Payevsky, 1976a, 1979; Payevsky, 1985a, 1990a,b; Sokolov, 1991b; Sokolov, 1999; Sokolov et al., 2000 etc.). In these studies capture method was assumed to be an adequate technique to study the dynamics of bird numbers only if a number of conditions were fulfilled: The trapping project was run annually at the same places in the same traps and with no habitat change at the capture site. The possibility that trapping numbers as a proxy for dynamics in numbers may contain a source of bias has been discussed before. It is assumed (Berthold & Schlenker, 1975; Pettersson & Hedenström, 1986) that only the strict standardisation of trapping methods makes it possible to obtain useful estimates. A comparison of different survey methods of birds showed that the highest annual variation was in visual counts, a lower variation in captures of migrants, and the most robust figures were yielded by breeding surveys (Svensson, 1978).

An undeniable advantage of the capture method is the full reliability of specific identification, sexing and ageing. At the same time this method is clearly only applicable for those species that are regularly captured, and the position of the traps governs the specific composition of the birds captured. Numbers of captured warblers, chats and thrushes greatly exceeds the numbers yielded by visual count. It would be an important advantage if Rybachy-type traps also captured nocturnal migrants at take-off, at landing, and sometimes at night, so that numbers of nocturnal migrants in the traps is just as high as the numbers of diurnal migrants (Shapoval, 1981a, 1982).

However, the observations have shown that only the lowest flying individuals can be captured. It remained unclear whether the numbers of their captures reflects the total numbers of passage. It was possible that captures did not cover some groups of migrants and that the samples obtained were not representative of the overall population of migrating birds. To resolve this question, special studies were required.

In 1977, the so-called 'Experiment' project was introduced on the Courish Spit led by V. Dolnik. The aim of this project was to test and compare five methods of surveying diurnal migration and seven methods of surveying nocturnal passage. One of the methods for both types of passage was the capture in Rybachy-type traps. It was shown (Shapoval, 1981b; Lyuleeva et al., 1981) that the correlation between daily ringing totals and the data of formalised visual observations during the whole day was reasonably high, r = 0.560 ± 0.010. The same value was obtained if only the 4 hours after sunrise were covered by observations.

This shows that captures of diurnal migrants in Rybachy-type traps generally reflect the pattern and dynamics of migration. The main factor introducing bias is the variation of flight altitude which is clearly dependent on wind direction and speed (Shapoval, 1981b). An interesting analysis showed an agreement of patterns of Great Tit passage (low flying birds) at different ornithological stations (Nowakowski, 2002). As for nocturnal migration, captures of nocturnal migrants on the next day were weakly correlated with estimates of migration traffic rate inferred from moon-watching data: r = 0.324 ± 0.176. However the correlation was much higher if the capture data on the day preceding nocturnal migration were used: r = 0.545 ± 0.156 (Bolshakov et al., 1981).

A study of the dynamics of passerine numbers on the basis of 42-years of captures on the Courish Spit (Sokolov et al., 2000) has found a significant positive relationship between the numbers of local and passage juveniles in 10 species out of the 12 studied. The correlations were highly significant for both intra-continental and long-distance migrants. Most species showed a significant negative relationship between the numbers at autumn passage and the time of breeding on the Courish Spit, i.e. the earlier the birds bred, the higher were their numbers in autumn. At the same time a comparison of numbers of autumn migrants and the spring mean monthly air temperatures in our region showed a significant positive relationship between the numbers and the April temperature in 11 species out of the 21 studied (Sokolov et al., 1999). This means that long-term dynamics of autumn numbers of passage passerine populations on the Courish Spit, as inferred from capture data, adequately reflect the fluctuation of numbers of the breeding populations that migrate in autumn through our study area. It can therefore be concluded that our samples of captured birds reflect the factors influencing the numbers of migrants. Moreover, as shown in section 3.1, age structures of local and passage populations of various species on the Courish Spit are very similar. This means that the results of trapping of migrants make it possible to estimate demographic parameters as efficiently as captures in the breeding area. Furthermore, these results seem to imply that trapping data at Rybachy reflect the breeding success covering a vast area of north-eastern Europe.

Despite the apparent adequacy of samples of captured passage migrants for population studies, one serious point contradicts this conclusion. This is the so-called ‘coastal effect’ which deserves special discussion.

2.3.2. “Coastal effect” problems

Migration studies of passerines in North America in the 1960s and 1970s showed that the proportion of first-year birds captured on the coasts of seas and large lakes is very high (80-95%) and significantly higher than at inland sites (65-75%). This applied only to nocturnal migrants; age ratio of diurnal migrants was normal (Drury & Keith, 1962; Murray, 1966, 1976; Ralph, 1971, 1978, 1981; Stewart et al., 1974; Dunn & Nol, 1980). This phenomenon was called “coastal effect” (Ralph, 1978). The hypotheses put forward by the above authors to explain this effect mainly referred to age-related differences during migratory flight and its termination.

In Europe, however, in spite of extensive study of bird migration and numerous trapping projects, coastal effect has until recently been mentioned in very few publications (Evans, 1968; Jenni, 1984). It has also been reported from the Courish Spit (Payevsky, 1982a, 1985a; Payevsky, 1998), on the shore of Kiev reservoir (Poluda, 1991) and to a smaller degree on the island of Barsakelmes in the Aral Sea (Shapoval et al., 1987).

For a more detailed analysis of coastal effect (Payevsky, 1998) when compared to the previous one cited above (Payevsky, 1985a) we selected 12 avian species, including 6 mainly diurnal and 6 mainly nocturnal migrants (Table 5). Special attention was paid to the method of calculating age and sex ratio. The problem is that age and sex structure changes according to spring and autumn passage, and capture numbers vary broadly over a different period; therefore the days of top captures bias the means towards the age and sex ratio of that period. To overcome this problem, seasonal means were calculated as second-order means of values averaged over 5-day period.

The mean age and sex ratios are given in Table 5, and the detailed annual data for 6 species in Fig. 4. Uniformity test showed that age ratio did not vary between years (χ^2 = 9.75, df =23, n.s.), whereas the species-related variation was highly significant (χ^2 = 233.6, df 11, $p < 0.001$). A clear difference between diurnal

Table 5. Mean proportion of adults (% ± SE) among migrating songbirds captured from 1972 to 1995. Range of annual values given in parenthesis. Seasons with less than 20 captures of each sex are excluded.

Species	**Trapping totals**	**Autumn**			**Spring**		
		Males	Females	Sexes pooled	Males	Females	Sexes pooled
Predominantly nocturnal migrants							
Willow Warbler	85990* (632-8649)	-	-	3.0 ± 0.2 (1.8-5.5)	-	-	-
Goldcrest	232240 (524-37324)	3.4 ± 0.4 (1.2-8.4)	4.3 ± 0.5 (1.7-8.6)	-	6.9 ± 0.8 (1.0-15.8)	7.6 ± 0.7 (4.6-16.9)	-
Common Redstart	1907*, ** (21-161)	6.1 ± 2.1 (3.0-10.6)	-	-	-	-	-
European Robin	40021 (600-4115)	-	-	8.2 ± 0.7 (2.4-13.7)	-	-	18.1 ± 0.8 (12.0-25.8)
Eurasian Blackbird	2955 (34-245)	11.9 ± 1.0 (3.7-22.7)	14.2 ± 1.4 (3.9-23.2)	-	31.8 ± 6.4 (4.3-52.0)	35.0 ± 3.7 (14.8-47.6)	-
Song Thrush	11544 (92-1496)			6.5 ± 0.7 (0.0-17.5)	-	-	19.2 ± 1.9 (0.0-33.8)
Predominantly diurnal migrants							
Blue Tit	41478* (109-5229)	8.9 ± 1.1 (1.6-22.0)	14.4 ± 1.2 (2.6-30.8)	-	-	-	-
Great Tit	116867 (1049-10455)	12.9 ± 1.6 (5.6-38.5)	13.3 ± 1.3 (6.5-33.5)	-	21.5 ± 2.2 (5.9-44.7)	16.3 ± 1.8 (6.5-36.2)	-
Chaffinch	385585 (3066-45641)	40.5 ± 1.9 (26.0-63.3)	42.9 ± 1.9 (28.3-63.2)	-	42.6 ± 1.9 (28.5-65.6)	43.4 ± 1.8 (28.4-64.9)	-
Brambling	17893** (38-1880)	35.2 ± 2.1 (18.7-58.5)	-	-	42.1 ± 2.6 (27.3-70.2)	-	-
Eurasian Siskin	87596 (722-10116)	22.4 ± 1.5 (8.9-37.7)	18.9 ± 1.2 (7.3-31.5)	-	32.2 ± 2.0 (15.1-59.6)	26.0 ± 1.9 (9.8-52.3)	-
Eurasian Bullfinch	3751* (57-571)	33.8 ± 4.3 (13.5-77.8)	21.0 ± 3.0 (9.9-50.8)	-	-	-	-

Notes: * - autumn only, ** - males only.

and nocturnal migrants in obvious in Fig. 5, where the data pooled across all species are given for each season.

The proportion of adults is significantly higher in diurnal migrants as compared with nocturnal migrants both in autumn (Fisher test: $F\varphi = 54366.4$, df 1, $p < 0.001$), and in spring ($F\varphi = 2047.9$, df 1, $p < 0.001$). Therefore, an elevated proportion of juveniles is typical of nocturnal migrants, unlike diurnal migrants, on the Courish Spit as in other coastal areas.

To compare the observed age ratio with breeding productivity of the populations under study, we estimated the average number of fledglings produced by a breeding pair per season (Table 6). These data show that only in the Chaffinch the proportion of juveniles on passage roughly fits population productivity. In all other species the data do not fit. As for nocturnal migrants, the proportion of juveniles (92-97%) found in the Willow Warbler, Goldcrest, Common Redstart and Song Thrush cannot be a realistic estimate of breeding results under any conditions. It should therefore be assumed that in these species adults are strongly underrepresented at coastal sites.

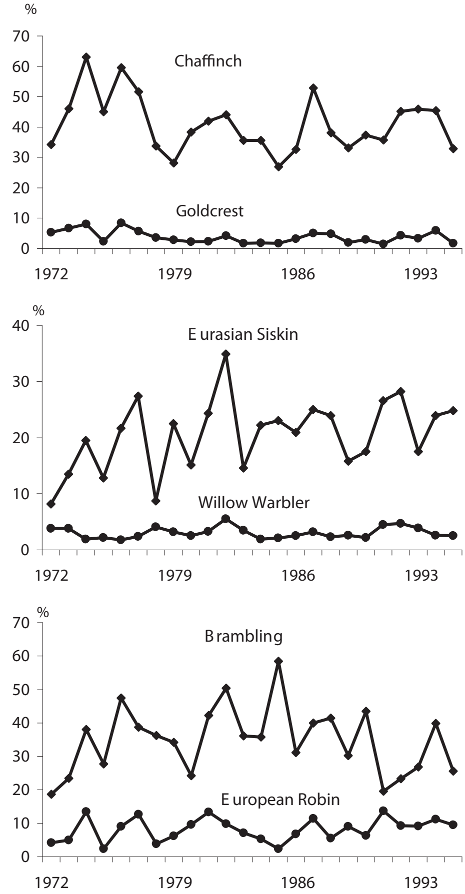


Fig. 4. Percentages of adults among diurnal and nocturnal avian migrants captured in autumns 1972 to 1995. Diurnal migrants are the Chaffinch, Brambling, Eurasian Siskin; nocturnal migrants are the Goldcrest, European Robin and Willow Warbler.

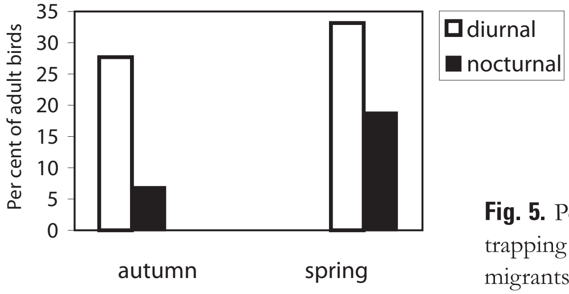


Fig. 5. Percentage of adults from the pooled trapping data in six diurnal and six nocturnal migrants in autumn and spring.

Table 6. Mean population productivity in some songbirds

Species, region	Percentage of double-brooded pairs	Size of the first clutch	Fledglings per egg laid	Source	Number of fledglings per pair per season*
Willow Warbler, Karelia	0	6.13	0.89	Lapshin, 2000	4.64
Goldcrest, Fennoscandia	~70	9.80	~0.64	Haftorn, 1978a, 1978b	8.39
Common Redstart, N Finland	0	6.42	0.77	Hildén et al., 1982	4.20
European Robin, Karelia	61	6.43	0.78	Zimin, 1988	6.39
Eurasian Blackbird, S Karelia	~20	4.31	0.53	Khokhlova, 1988	2.26
Song Thrush, Leningrad Region	~22	4.76	0.47	Malchevsky & Pukinsky, 1983	2.24
Blue Tit, Finland	12	10.00	0.92	Haartman, 1969; Hildén et al., 1982	8.62
Great Tit, Finland	20	9.90	0.81	Haartman, 1969	7.93
Great Tit, near St. Petersburg	28	11.00	0.71	Smirnov & Tyurin, 1981b	8.16
Chaffinch, S Karelia	0	4.86	0.65	Zimin, 1988	2.69

* The calculations are based on the following assumptions (Payevsky, 1985a): a) on average the size of the second clutch in passerines is 0.82 of the first clutch size; b) in 20 common songbird species, the mean breeding success rate calculated after Mayfield (1975) is 0.85 of the values obtained by the traditional method, i.e. as the number of fledglings per one egg laid.

The discussion of all hypotheses forwarded to explain the coastal effect yielded varying results (Drury & Keith, 1962; Murray, 1976; Ralph, 1978, 1981; Dunn & Nol, 1980). On the Courish Spit the most plausible explanation is that after a nocturnal flight over the sea juveniles touch down to the first land they see, whereas adults continue their flight inland (Payevsky, 1982a, 1985a; Shapoval, 1986; Payevsky, 1998). On Kiev water reservoir it was assumed that adults, unlike juveniles, cease any movements immediately after landing (Poluda, 1991).

The conclusion from all this should apparently be that using age ratio of nocturnal migrants captured in coastal areas for demographic analysis is not possible. However, by the example of the Goldcrest we have shown (Payevsky & Shapoval, 1990) that by using age ratio as a relative estimate, it is possible to analyse the following demographic factors. First, seasonal variation of age composition may be analysed: the proportion of adults in captures usually differs between the seasons, and this might be due to differential mortality. Second, sex-related difference in age ratio and its possible reasons may be studied. Finally, annual variation of these parameters exists and may be a most interesting topic for research.

2.4. RELIABILITY OF BREEDING PERFORMANCE ESTIMATES

Breeding success of passerines is usually understood as survival rate of eggs and nestlings until fledging. This is a parameter commonly estimated by ornithologists during their fixed site population studies. Together with clutch size and number of broods raised per breeding season, breeding success is one of the main parameters for estimating population productivity.

Breeding success is still sometimes estimated by the traditional method, i.e. as the proportion of fledged young to the number of eggs laid or just as a proportion of successful nests from all clutches started. As shown in much detail elsewhere (Payevsky, 1985a, 1985c), the method suggested by Mayfield (1975) yields better estimates. The idea of this method is to estimate the daily mortality rate of eggs and nestlings. Breeding success data on 20 passerine species of the Courish Spit (Payevsky, 1985a) made it possible to analyse many aspects by calculating these parameters. However, some questions remained. In particular, it was necessary to estimate whether individual researchers introduce bias into estimates of breeding performance (Payevsky, 1991a). The materials collected by the members of the Biological Station Rybachy are unique in this respect as they include data collected by different researchers on the same study species in the same area in the same seasons.

I analysed the data on 6 avian species collected in selected years in 1974-1987 by six ornithologists. The selection criterion was the number of controlled nests (at least 10 nests of one species with at least two visits) and participation of each observer during several years. The data on the Barred Warbler, Blackcap, Garden Warbler, Lesser Whitethroat, Chaffinch and Common Rosefinch were analysed. Daily mortality rate of eggs (q_e) and nestlings (q_p) were calculated as:

$q_e = \Sigma d_e / \Sigma tn_e$ and $q_p = \Sigma d_p / \Sigma tn_p$

where n_e is the number of eggs, n_p is the number of nestlings, d_e – number of unhatched eggs, d_p – number of dead nestlings, t – risk period in days. Egg survival probability during incubation (s_e) is $(1- q_e)^{ke}$, probability of survival of a nestling until (s_p) is $(1- q_p)^{kp}$, where k_e is incubation duration, k_p – time spent by nestlings in the nest. Survival probability from laying egg until hatching (s_b) is $s_e s_p = (1- q_e)^{ke} (1- q_p)^{kp}$. Standard errors of these parameters are calculated as standard errors of percentages.

The results are presented in Table 7. The data of individual observers are given in lines R_1, R_2 …R_6. Each researcher is denoted identically in all parts of the table. R without number means the remaining data pooled across the observers who checked less than 10 nests. The line 'pooled' includes the whole dataset of a particular year, i.e. $R + R_1 + \ldots R_6$, even if R is not given due to small sample size.

The significance of differences in breeding success parameters as estimated from the data collected by different persons was tested by t-test, as sample sizes did not differ more than 3-fold, and most proportions were within the 20-70% range. The results (Table 8) show that out of 37 pairwise tests, no significant difference was found between the observers in 8 cases only. In the remaining 29 cases the null hypothesis was rejected, in most cases with a high degree of confidence. This means that the estimates of breeding performance of the same population in the same season based on the data collected by different persons in most cases were different**.**

To find out the cause of these differences, it is necessary to perform further tests with the species of the largest sample size (the Chaffinch). Apart from the observer effect, the particular conditions of individual years have a major impact on breeding performance. I performed two-way ANOVA with year (1975-1978, 1986), i.e. environmental peculiarities, as one factor and observer (R_1 – R_6), i.e. sampling technique, as the other one. In our case it was a non-orthogonal matrix as not all researchers were active in the same years. The analysis showed that null hypothesis is rejected with 0.999 probability for each factor and their interaction. Impacts of year and sampling technique, and their interaction, were very significant. However, the proportion of variance explained by each factor was very small, but different (1.5% and 2.4%, respectively), whereas the interaction term explained 22.3%. Therefore, variation of breeding performance estimates was to some extent explained by the interaction of these factors. The residual variance is explained by some other factors not identified by the analysis.

Thus, our analysis showed that observer bias in breeding performance estimates is quite significant. Between-observer variation in this process is as large as individual variation in bird count results in the same area when it is impossible to decide which estimate is the correct one (Morozov, 1994).

The causes of difference in the collected datasets on breeding success apparently can be related to the following factors many of which are very difficult if not impossible to estimate: (a) different timing of data collection in relation to the full duration of the breeding season; (b) varying individual nest search efficiency

Table 7. Breeding success rate estimates on the same avian population at the Courish Spit, in the same season based on the data collected by different observers (for calculation methods and codes see text).

Species	**year**	**Observers**	**Number**						**Success rate, %**		
			Nests	Eggs and/or chicks	Egg·day	Egg lost	Chick· day	Dead chicks	Hatching	Nestling	Total
Barred Warbler	1974	Pooled	57	268	1351	28	901	9	72.7 ± 1.2	88.6 ± 1.1	64.4 ± 1.3
		R_4	31	141	968	19	508	2	73.9 ± 1.4	95.3 ± 0.9	70.4 ± 1.5
		R	26	127	383	9	393	7	70.5 ± 2.3	80.4 ± 2.0	56.7 ± 2.3
	1975	Pooled	43	204	1171	39	812	10	60.4 ± 1.4	83.5 ± 1.3	50.4 ± 1.4
		R_1	22	105	622	22	470	7	58.6 ± 2.0	83.4 ± 1.7	48.9 ± 2.0
		R	21	99	549	17	342	3	62.3 ± 2.1	89.7 ± 1.6	55.9 ± 2.1
	1976	Pooled	42	191	1888	24	761	6	82.2 ± 0.9	90.8 ± 1.0	74.6 ± 1.2
		R_1	28	129	1398	12	623	6	87.3 ± 0.9	88.6 ± 1.3	77.3 ± 1.4
		R	14	62	490	12	138	0	69.4 ± 2.1	99.9 ± 0.7	69.4 ± 2.1
	1977	Pooled	37	179	1290	32	888	4	70.1 ± 1.3	92.8 ± 0.9	65.1 ± 1.3
		R_1	14	66	483	22	321	0	49.3 ± 2.3	99.9 ± 0.3	49.3 ± 2.2
		R_2	10	55	149	5	277	4	59.6 ± 4.0	84.4 ± 2.2	50.3 ± 3.6
		R_6	10	48	549	3	240	0	92.8 ± 1.1	99.9 ± 0.4	92.8 ± 1.0
Blackcap	1986	Pooled	63	288	2563	54	1462	28	74.3 ± 0.9	79.4 ± 1.1	59.0 ± 1.1
		R_1	12	51	554	13	271	7	70.5 ± 1.9	72.9 ± 2.7	51.4 ± 2.4
		R_4	15	75	883	0	586	4	99.9 ± 0.1	91.9 ± 1.1	91.9 ± 3.1
		R_6	36	162	1126	41	605	17	59.8 ± 1.5	71.1 ± 1.8	42.5 ± 1.5
Garden Warbler	1986	Pooled	53	242	2270	38	1010	28	78.7 ± 0.9	73.1 ± 1.4	57.5 ± 1.3
		R_1	19	87	897	19	381	9	74.3 ± 1.5	76.5 ± 2.2	56.8 ± 2.0
		R_4	13	64	722	14	308	7	76.4 ± 1.6	74.4 ± 2.4	59.1 ± 2.2
		R_6	21	91	651	5	321	12	89.4 ± 1.3	66.0 ± 2.6	59.0 ± 2.5
Lesser Whitethroat	1976	Pooled	27	129	792	25	356	3	65.5 ± 1.7	92.3 ± 1.4	60.5 ± 1.8
		R_1	14	67	362	20	165	1	48.0 ± 2.6	94.2 ± 1.8	45.2 ± 2.6
		R	13	62	430	5	191	2	85.5 ± 1.7	90.4 ± 2.1	77.3 ± 2.4
	1977	Pooled	34	153	593	30	603	3	50.6 ± 2.1	95.1 ± 0.9	48.1 ± 2.0
		R_5	13	58	180	14	226	2	34.8 ± 3.6	91.4 ± 1.9	31.8 ± 3.5
		R	21	95	413	16	377	1	59.7 ± 2.4	97.0 ± 0.9	57.9 ± 2.4

Species	**year**	**Observers**	**Number**						**Success rate, %**		
			Nests	Eggs and/or chicks	Egg·day	Egg lost	Chick· day	Dead chicks	Hatching	Nestling	Total
Lesser Whitethroat	1986	Pooled	40	199	1345	30	979	25	74.9 ± 1.2	76.8 ± 1.3	57.5 ± 1.3
		R_1	15	69	372	19	329	2	50.6 ± 2.6	94.2 ± 1.3	47.7 ± 2.5
		R_6	13	70	454	2	303	14	94.9 ± 1.0	62.4 ± 2.8	59.2 ± 2.7
		R	12	60	519	9	347	9	80.0 ± 2.0	76.8 ± 2.8	61.4 ± 2.7
Chaffinch	1975	Pooled	117	452	2635	123	1733	39	51.0 ± 1.0	75.6 ± 1.0	38.6 ± 0.9
		R_1	21	77	486	28	298	4	43.3 ± 2.2	85.5 ± 2.0	37.0 ± 2.1
		R_3	32	129	1218	42	583	10	61.6 ± 1.4	81.4 ± 1.6	50.1 ± 1.5
		R_4	16	62	221	15	161	8	37.3 ± 3.3	54.0 ± 3.9	20.1 ± 2.3
		R_6	14	54	219	18	151	5	30.2 ± 3.1	66.8 ± 3.8	20.2 ± 2.6
	1976	Pooled	115	448	3002	200	1467	53	37.9 ± 0.9	64.4 ± 1.2	24.4 ± 0.8
		R_1	27	99	604	51	290	7	29.3 ± 1.9	74.7 ± 2.6	21.9 ± 1.6
		R_2	19	81	428	29	185	5	37.3 ± 2.3	72.0 ± 3.3	26.9 ± 2.1
		R_3	34	137	1299	71	570	26	45.3 ± 1.4	56.8 ± 2.1	25.7 ± 1.2
	1977	Pooled	161	704	4755	211	2981	77	53.3 ± 0.7	72.9 ± 0.8	38.9 ± 0.7
		R_1	58	244	1758	98	808	32	44.6 ± 1.2	61.3 ± 1.7	27.3 ± 1.1
		R_2	10	49	135	0	252	1	99.9 ± 0.8	95.3 ± 1.3	95.3 ± 1.5
		R_5	30	137	1116	30	849	14	68.2 ± 1.4	82.4 ± 1.3	56.2 ± 1.5
		R_6	20	94	711	23	424	14	63.4 ± 1.8	66.8 ± 2.3	42.4 ± 1.4
	1978	Pooled	307	1278	7964	332	4650	92	54.8 ± 0.6	78.5 ± 0.6	43.0 ± 0.6
		R_2	81	343	631	35	444	6	45.3 ± 2.0	84.4 ± 1.7	38.2 ± 1.8
		R_5	210	870	6674	277	3863	81	54.8 ± 0.6	77.5 ± 0.7	42.5 ± 0.6
	1986	Pooled	156	703	3492	206	2384	74	42.7 ± 0.8	64.3 ± 1.0	27.5 ± 0.7
		R_1	31	136	664	37	447	15	44.6 ±1.9	66.0 ± 2.2	29.4 ± 1.7
		R_4	20	93	341	28	254	5	30.2 ± 2.5	78.5 ± 2.6	23.7 ± 2.1
		R_6	44	204	1138	55	710	15	50.2 ± 1.5	77.5 ± 1.6	38.9 ± 1.4
Common Rosefinch	1986	Pooled	35	142	1176	20	636	12	78.7 ± 1.2	77.9 ± 1.6	61.3 ± 1.6
		R_6	15	64	517	10	277	7	76.4 ± 1.9	71.9 ± 2.7	54.9 ± 2.5
		R	20	78	659	10	359	5	81.0 ± 1.5	83.2 ± 2.1	67.4 ± 2.1

Table 8. Differences between breeding success estimates from the data of different observers (data from Table 7).

Observers	**Statistics, significance** (** p<0.01, *** p<0.001)
R_1 - R_2	1.9 n.s., 36.6***, 0.2 n.s.
R_1 - R_3	5.1***, 1.9 n.s.
R_1 - R_4	5.5***, 2.1*, 10.3***, 0.8 n.s.
R_1 – R_5	15.5***
R_1 – R_6	3.1**, 18.1*** , 0.7 n.s., 3.2**, 4.3***, 8.5***
R_1 - R	9.1***, 3.7***, 5.0***, 2.4*, 3.1**
R_2 – R_3	0.5 n.s.
R_2 – R_5	18.4***, 2.3 n.s.
R_2 – R_6	25.8***, 11.4***
R_3 - R_4	10.9***
R_3 - R_6	10.0***
R_4 – R_6	0.03 n.s., 0.03 n.s., 6.1***, 14.5***
R_5 – R_6	6.7***
R_5 – R	6.2***
R_6 - R	3.8***, 0.6 n.s.

and preferring different habitats when searching; (c) different number of visits to the nests found; (d) insufficient samples for comparisons. A detailed analysis of outliers showed that in only one case the biased estimated could be attributed to finding nests at late stages of breeding and only one monitoring visit after finding the nest. In all other cases no such causes were apparent. Therefore, the factors (a) and (c) cannot be treated as the leading ones.

Insufficient number of controlled nests is the most probable cause of the variation discussed, as outlying values of estimates were most typical of the datasets with small sample sizes. Varying experience of observers, and preference for different habitats when searching for nests is also a valid source of variation, as each researcher had his/her favourite routes and often bird species. Data in other areas and for other species were collected incidentally. It also cannot be ruled out that the breeding success of the population varied between different parts of the study area. To test for this hypothesis, I analysed the data collected by one person by dividing them randomly into two subsets: Chaffinch data by R_5 in 1978 and Blackcap data by R_6 in 1986. The results showed that when sample size was large (210 Chaffinch nests), estimates yielded from different subsets did not differ, whereas in the small Blackcap sample (36 nests), the estimates differed significantly ($p<0.01$).

This means that to obtain reliable estimates of breeding performance of a population it is necessary to have a sufficiently large number of nests under observation. What is the minimum number for open nesting species? This figure may be estimated from the formula for the contribution of alternative characters. With breeding success rate varying between 20 and 95%, 3% error of estimate (Δ) and confidence level of p = 0.95 (t = 1.96), the required sample (N_{min}) is roughly equal to:

$N_{min} = (t\sigma / \Delta)^2 = 96.0$ (eggs or nestlings).

As the average number of eggs or nestlings in the studied nests of all species was 4.7, the minimum number of nests necessary to obtain reliable estimates of breeding performance of passerines was roughly 20.

2.5. RESEARCH METHODS FOR THE POPULATION DYNAMICS AND ESTIMATES OF SURVIVAL RATES IN BIRDS

One of the main aims of population studies is to identify factors that influence the dynamics of numbers of natural animal populations. In most cases it is impossible to measure the absolute numbers of a population, so various proxies have to be used for estimates and comparing numbers. The reliability of these proxies is always a subject of discussion. Population number is a result of several population processes, i.e. birth rate, mortality rate, emigration and immigration, but it is rarely possible to study all these parameters in full. For each group of animals, there are certain advantages for different demographic methods, but there are also general principles that can be found in reviews (e.g. Williams et al., 2002).

Many methods of bird censusing belonging to the three main types that have been developed: transect count, point counts and territory mapping (Tomiałojć, 1980; Ralf & Scott, 1981; Verner, 1985; Priednieks et al., 1986; Bibby et al., 2000). In many countries traditional programmes of annual censuses of avian population exist (Christmas counts, Breeding Bird Surveys etc). In Russia, in spite of a large number of ornithologists who have systematically censused bird populations, no national system for surveying bird population or diversity exists (Bursky & Morozov, 1997). However, regional studies of this kind are rather numerous and their results may contain information for such monitoring.

From the demographic viewpoint, there are several approaches to bird census (Baillie & Peach, 1992). The first one is long-term study of breeding dynamics of a population when numbers and birth rate are annually inferred from census data, and mortality rate is inferred from individual marking data. The range of relevant environmental data is then correlated with population dynamics and demographic parameters. The second approach is the experimental one when breeding density is manipulated in well-studied populations. The third approach to the study of population processes is the analysis of annual trapping totals at ringing stations and search for relationships with the ambient factors. The longest, 50-year, series of trapping data of migrating and breeding birds is available for the Courish Spit.

An important problem in the study of populations is the question of key factors. Their analysis is designed to identify the stage of the annual cycle that is most responsible for the dynamics of populations. Of the ambient factors that are believed to exercise an influence on the timing of seasonal movements of birds and on their survival rate in different parts of the annual cycle the following are the most frequently included the analysis: air temperature, precipitation and the NAO (North Atlantic Oscillation) index. Weather and climate in Eurasia are to a large extent regulated by the atmospheric circulation over the North Atlantic and therefore the monthly NAO index values are used to estimate the meteorological situation. NAOI is calculated as the difference of the normalised sea-level pressures between the centre of high pressure localised near the Azores (Azores maximum) and the centre of low atmospheric pressure near Iceland (Iceland minimum). Negative NAOI values are typical of weak westerly winds and thus low air temperatures and insignificant precipitation. Positive values indicate situations of large-scale air movement from the Atlantic and thus higher air temperatures and intensive precipitation (Hurrell et al., 2001).

An important problem with using comparative analysis for studying the causal factors in population dynamics is whether it is necessary to estimate other demographic parameters. Theoretically, the relationship between the observed change in numbers and the dynamics of the ambient factors may be sufficient to decide on the causal relationships without additional data. However, several possible factors have demonstrated (Green, 1999) the use for demographic parameter estimates when using comparative methods.

Firstly, it cannot be ruled out that the correlation obtained is an incidental one and that the factor analysed, even though it varies in parallel with the declining bird numbers, may not be the genuine cause of the decline. In that case the data on breeding performance and survival rate may provide an alternative solution and a demographic mechanism of influence may be determined. Secondly, long-term data on the numbers ringed from a population could provide an additional index to the existing indices based on counts of breeding individuals. For example, the British Trust for Ornithology has developed population size indices based on standardised ringing totals (Peach et al., 1998). Thirdly, ringing results make it possible, not only to calculate annual survival rates with the help of special programmes, but also to estimate productivity, as the share of juveniles in autumn captures at ringing station may be treated as a productivity index (Green, 1999; Payevsky & Shapoval, 2002).

The study of one of the components of population dynamics, namely annual survival rate, as a fundamental dimensionless population parameter, may give deeper insights into population dynamics compared with the study of population in the form of relative abundance estimates. The reliable survival rate estimates are necessary to understand the processes that define population numbers and their dynamics

(Lebreton et al., 1992). The accuracy of estimates depends on the quality of the original data, usually bird ringing data, and the strategy for their analysis, i.e. calculation techniques (Anderson & Burnham, 1999 ; Horton~~, C.E.~~ & Letcher, ~~B.H.~~, 2008).

The methods of bird survival analysis have made great progress in the 20th century. Nearly all of them are based on documenting the fate of individually marked birds. It started with the work of M. Nice (1937) who estimated the mortality rate of Song Sparrows (*Melospiza melodia*). For a long time, mortality, or demographic tables were used that yield survival rate estimates averaged across several years. These were mainly the variations of the original methods by D. Lack (1951) and J.B.S. Haldane (1955). The model for these tables assumed that both survival rate and the proportion ('norm') of recoveries depend only on the age of birds. Influence of annual variation of the weather, habitats etc. was ignored. As this assumption is biologically unrealistic, this method has been later shown to yield quite biased estimates (Lebreton, 2001). It should however be noted that in some cases, the estimates of mean annual survival rate on the basis of the same dataset analysed by different methods (mortality tables and stochastic models) was very similar, within the limits of statistical error (Payevsky, 1981a; 1985a). This is probably good evidence of the high reliability on the original dataset.

Stochastic mathematical models that replaced demographic tables made it possible to obtain a reliable estimate of survival rate for each year and take into account the annual variation of the environmental factors. Formation principles of the observed population structure in relation to the main environmental variables are especially important for forecasting the change in numbers. One of the most authoritative handbooks on the methods for the detailed analysis of ringing results for obtaining population parameter estimates is the monograph by C. Brownie et al. (1985). This handbook (the first edition was published in 1978) contains recommendations for using various calculation models and software (e.g. the once popular ESTIMATE and BROWNIE software). All models were developed for the waterfowl case studies. For waterfowl, high recovery rates are typical, therefore many models suggested these were not applicable for songbirds because of the small sample sizes. For instance, recoveries from 17 million songbirds ringed in North America make it possible to obtain satisfactory/exact estimates of adult survival rates in only four of the 26 species with >500 recoveries (Francis, 1995).

During the past two decades the number of computer programmes available for analysing data on marked animals expanded greatly (SURVIV: White, 1983; JOLLY, JOLLYAGE: Pollock et al. 1990; SURGE: Lebreton et al., 1992; Cooch et al., 1997, from: Cooch, 2001). Software SURGE (Survival Generalized Estimation), in the opinion of E. Cooch (2001), is a fundamental step forward in the principles of analysis of any data from marked individuals, even though it was originally designed only for recapture analysis. The logical extension of its principles was programme MARK developed by G. White (White & Burnham, 1999; Cooch & White, 2006). Programme MARK includes the best possible variants of stochastic models, it is a freeware, and is currently most frequently used for estimating annual survival rates. It allows the researcher to estimate survival rate from recoveries (true physical survival rate, denoted as S_i) and from recaptures in an annually surveyed breeding population (local survival rate, denoted as phi or φ, which includes the returning probability). In conformity with the aims of the study, several alternative models are fitted, starting from the global (time-dependent) model. The final selection of the most adequate model is made on the basis of Akaike's Information Criterion. Both survival rate and recovery rate (reporting rate) are estimated (Lebreton et al., 1992; White & Burnham, 1999; Cooch & White, 2006). The advantages of MARK certainly do not invalidate the results obtained with the help of other software. In this book survival rate estimates made by different programmes in various years, not MARK alone, are used.

Capture-mark-recapture has been used for many years to estimate population size. Several approaches to this problem for different population models that may be potentially important can explain the causes of a population decline (e.g. Aebischer, 1986; Huggins 1991; Norris & Pollock 1996). When a significant correlation is found between population dynamics and an environmental variable, doubts often remain as to whether the factor indicated could alone cause a significant decline (Green, 1999). To resolve any doubts, it is possible to test the relationships observed by simulation models to estimate their contribution or impact (Potts & Aebischer, 1995).

Chapter 3

SURVIVAL RATE, AGE AND SEX STRUCTURE OF SONGBIRD POPULATIONS

3.1. AGE DISTRIBUTION OF POPULATIONS INFERRED FROM RINGING DATA

The main population parameters, primarily mortality and reproduction rates, are reflected in the age structure of populations. In a theoretical ideal population with constant numbers, mortality and instantaneous reproduction once a year, the age structure is by definition balanced. In natural populations in the real world, with resources always limited, age structure undergoes fluctuations, especially non-periodic fluctuations that may influence birth rate and survival rate. Differences in age structure also depend on many species and population specific factors that may influence birth rate and survival rate such as the age of maturity, duration of the breeding period and the number of broods raised during this period, as well as by the overall type of population dynamics (Pianka, 1978; Solbrig & Solbrig, 1979; Payevsky, 1985a; Begon et al., 1986; Alimov & Kazantseva, 2004).

The dynamics of age structure are often studied by the use of models. Averaged long-term empirical data may also yield simple population models of age distribution. For avian populations whose age structure may be studied by capture-mark-recapture, it is possible to estimate an age structure averaged across a number of consecutive years. Prevalence of short-term research projects significantly limits the likelihood of obtaining representative estimates of population age structure (i.e. estimates averaged across a number of years). The materials reported below are based on more than 30 years of data collection which indicates their reliability for representing the age structure of birds on the Courish Spit.

For relatively stable populations, the proportion of yearlings needs to be similar to the annual death rate. This is especially true of songbirds as they start breeding in the spring following their birth. To establish the age structure in various species and to estimate population stability, ringing data on the birds that breed and migrate on the Courish Spit in 1958-1992 were analysed. These data include 9245 recoveries of 21 species that have been partly published with regard to age structure (Payevsky & Shapoval, 2000a, b). The list of study species, sample sizes and the resulting parameters are given in Table 9 (31 datasets for 21 avian species).

We analysed datasets of two types: (1) recoveries of birds ringed on the Courish Spit during migration; and (2) recaptures on the Courish Spit of the birds ringed here during the preceding breeding seasons. In all cases, the analysis was based on the annual cycles of the birds rather than on calendar seasons. A bird ringed in August as a juvenile and recaptured in May of the following year was treated as a yearling, i.e. 1 year old. A bird ringed during autumn passage as an immature (= 'subadult', i.e. hatched during the previous summer, fully grown and moulted) and found dead during the subsequent winter (starting from January) was treated as a yearling. If it was found during the following autumn, it was treated as a 2 year old individual. Mortality rate of first-winter passerines, starting from their first January, does not exceed the mortality rate of other adults (Payevsky, 1985a). Therefore the recoveries of juveniles found before their first January were excluded from the analysis. In all cases the first year of life, used in this analysis, was the first year of adult life which started when a bird became twelve months old.

Age structure was calculated from the empirical data on the basis of all ringing data available. It is possible to calculate the stable age distribution from the death rate estimates and the calculated reproduction rate. However, empirical data were preferred because all species included in this analysis were long-term and with large sample sizes. When analysis was based on recovery data, the number of birds of each age class was recalculated to include each dead bird into all junior age classes as alive.

We assumed the following for the populations studied during the breeding period: The birds were believed to be local breeders if they had been captured at least twice during breeding periods. They were assumed to be dead when seven years elapsed after the last capture. The year of the last capture was assumed to be the year of death. The maximum age of each bird was included with the number of the birds alive at that age. Then we recalculated the data so that each individual was included in all junior age classes as alive (because it was a part of the breeding population until the last year of its life). By this method we obtained the numbers of a conventional average population across the years of the study whose age distribution was the best possible approximation to the actual one. Sometimes it was decided to use the data on birds whose exact age at ringing was unknown (e.g. ringed as adults). Such data were calculated separately. We first calculated the number of yearlings from the proportion of first- and second-year birds among the individuals with the known age at ringing. Then we recalculated the data to obtain a conventional population as specified above.

The mean annual survival rates of these populations, both passage and breeding birds, have been estimated for previous publications (see Section 3.4;

Table 9. Some population parameters of migrating and breeding birds used in calculations and interpretation of age structure from capture data from 1960 to 1992 (see text).

Species, sex	Status (m - migrants, b - breeders)	Number of recoveries or recaptures	Mean annual adult survival rate	Percentage of yearlings	Percentage of 2-year-old birds	Maximum lifespan (years)
Meadow Pipit	m	41	0.388	61.0	19.4	5
White Wagtail	b	103	0.453	54.8	23.6	7
European Starling, ♂♂	m	217	0.501	40.7	28.1	12
♀♀	m	133	0.478	47.0	29.7	9
Eurasian Jay	m	63	0.496	50.4	20.8	8
Icterine Warbler	b	301	0.409	59.6	24.1	10
Sylvia warblers	b	64-303	0.401-0.502	53.5-60.1	21.2-23.2	6-9
Willow Warbler, ♂♂	b	816	0.331	68.2	20.8	6
♀♀	b	409	0.255	70.5	20.7	6
Goldcrest, ♂♂	m	28	0.365	75.0	22.7	3
♀♀	m	21	0.265	69.7	27.3	3
Pied Flycatcher	b	200	0.312	52.0	28.0	5
European Robin	m	82	0.419	58.5	23.2	6
Turdus thrushes	m	38-165	0.469-0.779	47.4-54.1	19.5-24.8	6-13
Great Tit, ♂♂	m	127	0.380	61.4	28.8	5
♀♀	m	203	0.380	55.5	31.5	6
Chaffinch, ♂♂	b	1609	0.498	45.0	24.7	11
♀♀	b	1254	0.482	48.0	24.1	9
♂♂	m	834	0.562	38.2	27.3	10
♀♀	m	644	0.523	39.6	27.4	9
Brambling, ♂♂	m	147	0.471	43.7	27.7	11
♀♀	m	93	0.430	44.5	29.8	10
Siskin, ♂♂	m	407	0.488	46.5	30.4	12
♀♀	m	283	0.370	47.6	32.3	11
Common Rosefinch	b	284	0.504	49.8	28.1	7
Yellowhammer	b	143	0.468	53.5	27.4	7

Payevsky, 1985a; Payevsky et al. 1997; Vysotsky & Payevsky, 2002; Payevsky & Vysotsky, 2002; Payevsky et al, 2004), and are presented in Table 9 where these survival rates are shown to vary in different species between 0.255 and 0.779, i.e. between 26 and 78% per annum, with the proportions of yearlings and two-year-old birds in populations also included in the Table. The full age distributions in the form of modified age pyramids are presented in Figures 6 and 7. Yearlings together with two-year-olds formed the bulk of breeding populations (70 to 90%) in all species and populations studied. The proportion was 66-80% in finches, 67-82% in thrushes, 75-91% in warblers, 78-80% in wagtails and pipits, 73% in the European Starling, 80% in the Pied Flycatcher, 81% in the Yellowhammer and up to 90% in the Great Tit. The maximum lifespan varied between 3 years in the Goldcrest and 13 years in the Song Thrush.

The proportion of yearlings was smaller than the proportion of older birds only in finches, thrushes, and the Starlings, i.e. in 6 species out of the 21 studied (both breeding and passage populations). This suggests a longer lifespan in the populations of these species. The reasons for this are unknown, but data from other populations of some finches support our findings. For example, the proportion of yearlings among breeding Chaffinch males in Voronezh nature reserve was as low as 28% (Vengerov, 2001), and among breeding Great Rosefinches (*Carpodacus rubicilla rubicilla*) in the Caucasus the proportion of yearlings did not exceed 40% (Loskot, 1991). In the Common Rosefinch age distribution broadly varied between different breeding populations (see section 4.9) but generally the proportion of yearlings did not exceed 20%. It is worth noting that in African songbirds an opposite pattern is observed. The mean expected lifespan of African insectivorous and nectarivorous birds (3.1 years) is nearly twice as long as in African granivores (1.6 years). This is explained by the unpredictable precipitation regimen in Africa that governs seed crops and may seriously influence survival prospects (Peach et al., 2001). In the same paper it was found that the mean life expectancy of European insectivores is nearly one-half of that found in African members of the same families. The difference in insectivores is believed to be due to smaller clutch size in African species as compared with the European ones, as fecundity is generally known to be inversely related to survival rate (Payevsky, 1985a; Sæther, 1988).

Similarity between age structures of different species may be measured by the coefficient of variation of proportions of birds of each age. To do so, we calculated the age distribution averaged across the study species. Subsequently, species-related variation in each age class was analysed (Fig. 8). Coefficient of variation showed a significant trend to increase from the age class of yearlings to the class of 10 years ($r = 0.84$, df 8, $p = 0.002$). The smallest variation was shown by the proportion of two-year-olds, and the largest one by the 8-year-olds.

We compared the proportion of yearlings with the mean mortality rate (i.e. 1 – survival rate) for 27 datasets. The expected match, i.e. lack of significant difference, was found in the 19 cases of 27. In eight cases the proportion of yearlings was significantly lower than the calculated mean mortality rate: in Pied Flycatchers ($p<0.001$), in the Chaffinch for all datasets under varying levels of significance (from $p<0.05$ to $p<0.001$), in female Bramblings ($p<0.05$), in female Siskins ($p<0.001$) and in male Starlings ($p<0.05$). We found no relationship with sex. We have no reasons to assume that these eight populations were undergoing considerable change in their numbers, especially because in these three species the difference was only significant in one gender. The precision of mean annual mortality rate estimates is not always very high. In some cases only rough figures are available, which is more or less satisfactory for comparisons of population parameters.

Despite the observed fluctuations of numbers, most populations studied remained roughly at the same level over the 35 years of study. Numbers of one of the species, the Barred Warbler, declined dramatically so that it became locally extinct (see section 4.3). However, age structure of this population was only estimated for 1967-1976 when the numbers were high and stable enough to fulfil the model assumptions.

The minimum species-related variation in the age class of two-year-olds is worth noting (Fig. 8). This means that the proportion of two-year-old birds (3rd calendar year of life) was most similar across the species and populations studied. It is possible that these birds form the 'strongest and healthiest' part of the population as they are already experienced and competitive enough. Probably two-year old passerines are the core of the population in which the population's adaptability is concentrated.

All age distributions of different passerine species obtained for either passage and breeding populations and both sexes were very similar (Figs 6 and 7). All of them reflect typical survival curves that are evidence of similar age-related mortality rate, at least starting from yearlings that breed for the first time. On a logarithmic scale, some of these curves are roughly equivalent to the diagonal straight line, i.e. the survival curve observed at age-independent mortality rate. Even though the theory of constant rate of mortality of adults has been criticised (Botkin & Miller 1974), it may be considered acceptable. In all cases when datasets were large and the number of age classes was at least seven, the tendency of the mortality rate to remain constant was observed in intermediate age classes (Payevsky, 1985a). When comparing free-living and captive birds it was found that age-related mortality component did not differ. This allowed the assumption that the age-related mortality depends on intrinsic factors (diseases, genetic burden) and is independent of the events in the environment (Ricklefs, 2000). As a result, if the probability of incidental death does not increase with age, even in advanced age the birds remain physically fit.

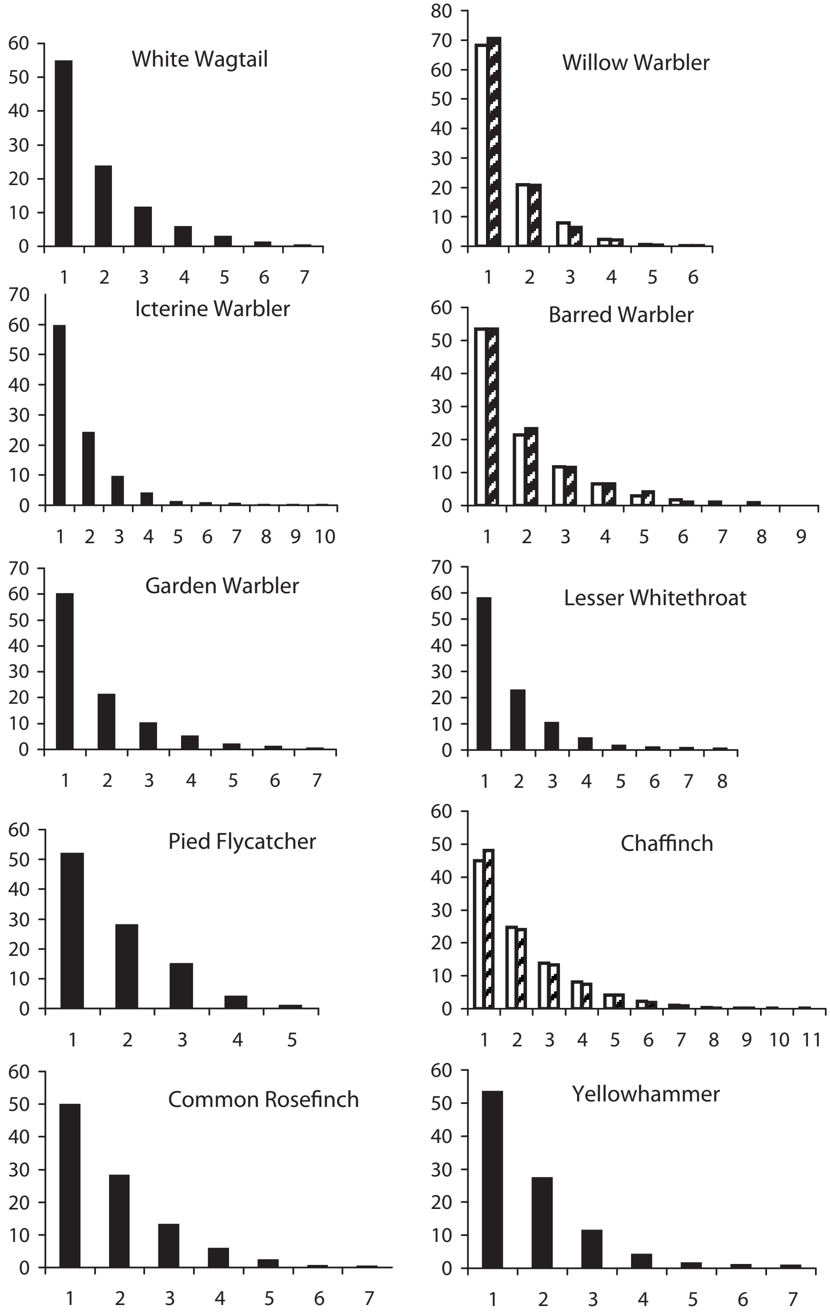


Fig. 6. Age composition in the birds of the local population on the Courish Spit. X axis – years of life. Hatched bars – females, open bars – males, black bars – both sexes pooled. Y axis shows the percentage in an age class.

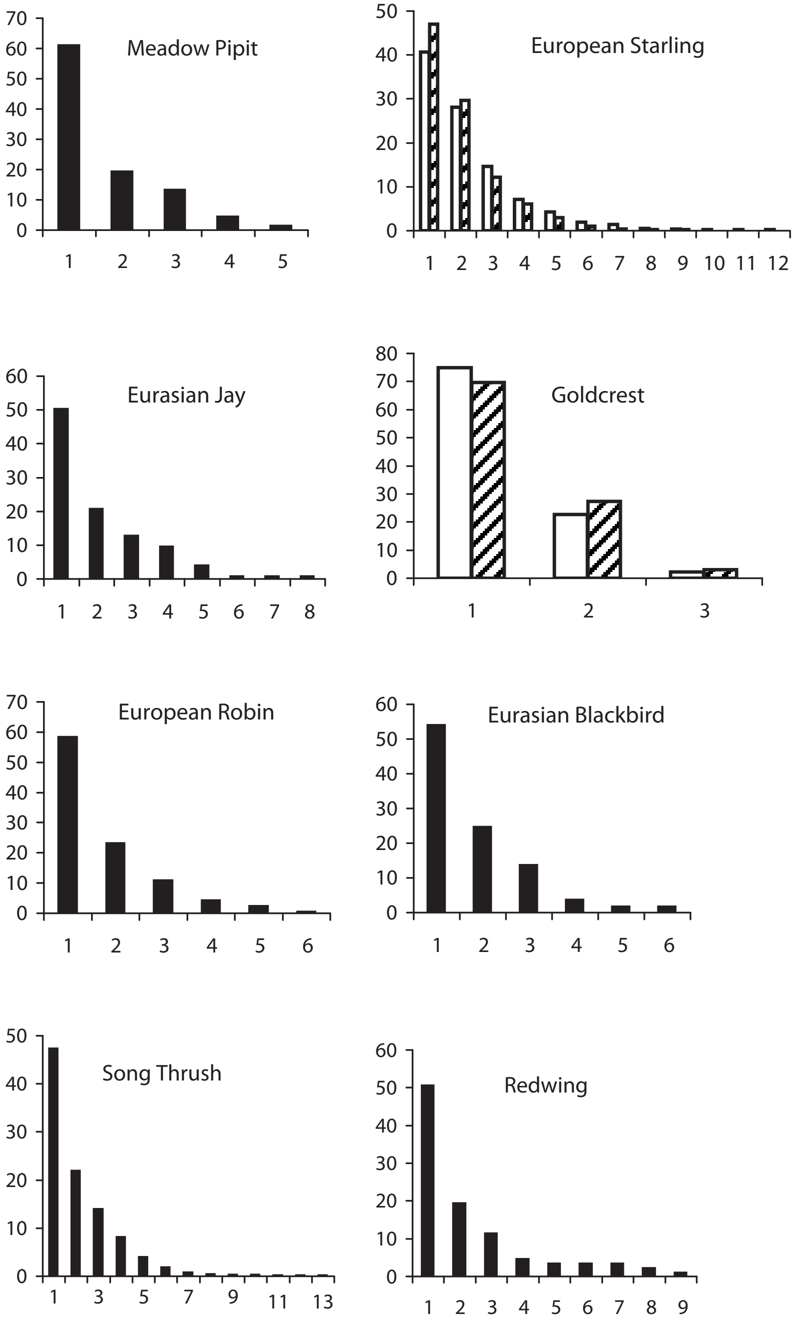


Fig. 7. Age composition in migrants on the Courish Spit. Symbols as in Fig. 6.

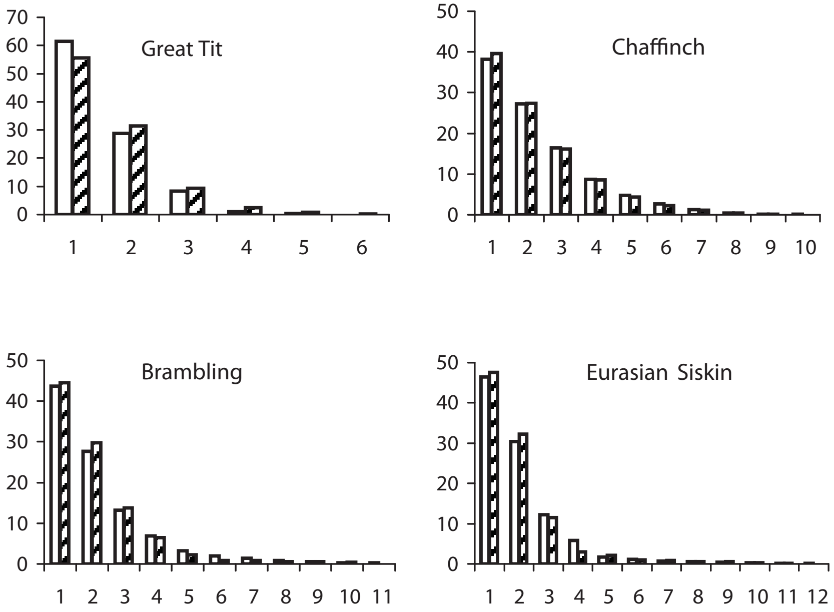


Fig. 7. Continued.

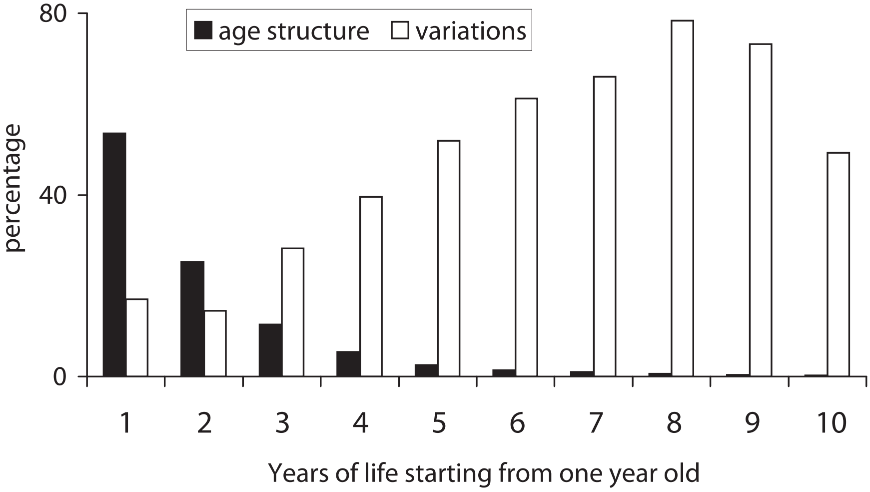


Fig. 8. Age structure in passerines averaged from 31 datasets from 21 species. Variation represents dispersion of species-specifics values in each age class.

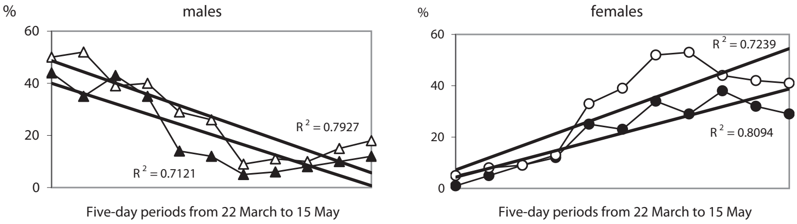
3.2. CHANGES IN THE OF AGE AND SEX STRUCTURE OF MIGRATORY POPULATIONS THROUGH SPRING AND AUTUMN PASSAGE

The distribution of birds recorded of both sexes and of different age on migratory routes and the schedule of their movements have been discussed over many years. Many aspects of this phenomenon, usually called 'differential migration', are well known but studies into this topic still continue (Ketterson & Nolan, 1979; Payevsky, 1976, 1985a; Chernyshov, 1986; Francis & Cooke, 1986; Chandler & Mulvihill, 1990; Otahal, 1995; Cristol et al., 1999; Newton, 2008). In the case of passerines, the most common event is the earlier arrival of males compared with females, often by several days to a fortnight. This is called protandry as opposed to protogyny, i.e. earlier arrival of females in species with reverse sexual roles. Among the hypotheses forwarded to explain earlier arrival of males, two are most common. The first is the 'rank advantage hypothesis' suggesting that competition for breeding territories between the males drives the selection for early arrival. The second is the 'mate opportunity hypothesis' that is based on sexual selection and suggests that early arrival improves for chances of mating to a greater extent for males than for females. A special test of these two hypotheses based on modelling protandry or protogyny evolution supports the second hypothesis (Kokko et al., 2006).

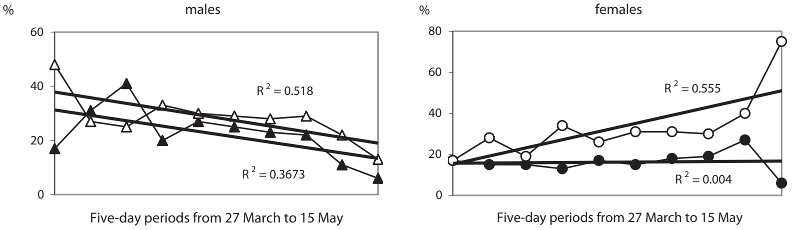
Increased application of individual marking over recent decades and progress in sexing and ageing techniques of captured birds has allowed a more detailed study of the migration sequence of sex and age groups of songbirds. In spite of some general characteristics, species and even population-specific features of differential migration were revealed (Gistsov & Gavrilov, 1983; Shapoval et al., 1987).

Larger datasets compared with those used in the previous analysis of differential migration on the Courish Spit (Payevsky, 1985a) make it possible to perform a detailed analysis of the most common passerine migrants of the Eastern Baltic. This analysis is based on 838499 captures of the most common species, the Great Tit, Chaffinch, Brambling, Siskin, Goldcrest and Willow Warbler, in 1978-2000. The results pooled across this period are presented in Fig. 9 for spring passage and in Fig. 10 for autumn passage.

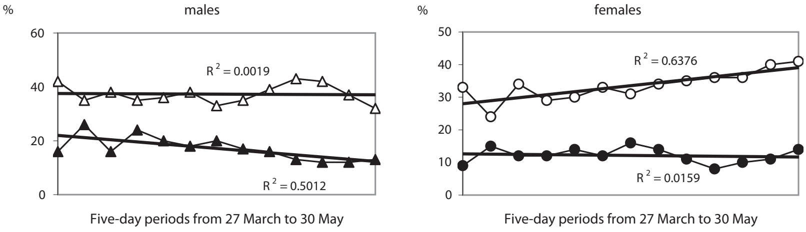
The graphs illustrate the sequence of spring migration (Fig. 9) confirming the well-known rules of sex-related differential migration. The proportion of males in the stream of migrants decreases, and the proportion of females increases with the progress of the season. However, in the Great Tit and to some extent in the Siskin this trend is not so obvious. The proportion of adult males among migrants decreased with the progress of spring in all species except of the Great Tit. The proportion of adult females increased only in the Chaffinch. It should be noted that the study of the schedule of spring migration in 12 North



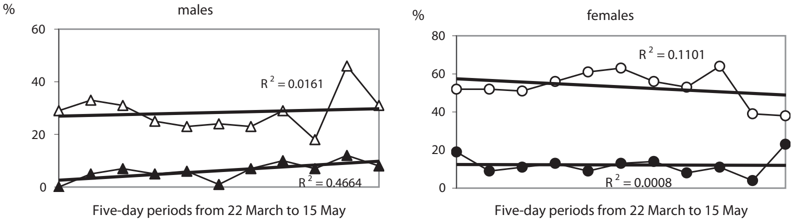
Chaffinch, n = 84483



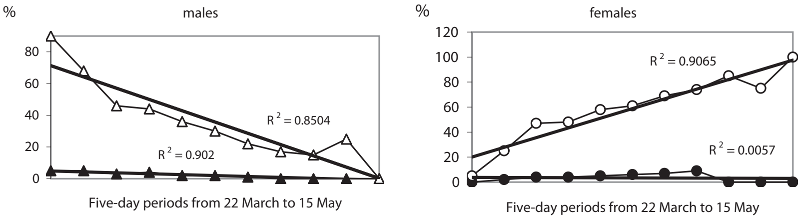
Brambling, n = 4260



Eurasian Siskin, n = 19797

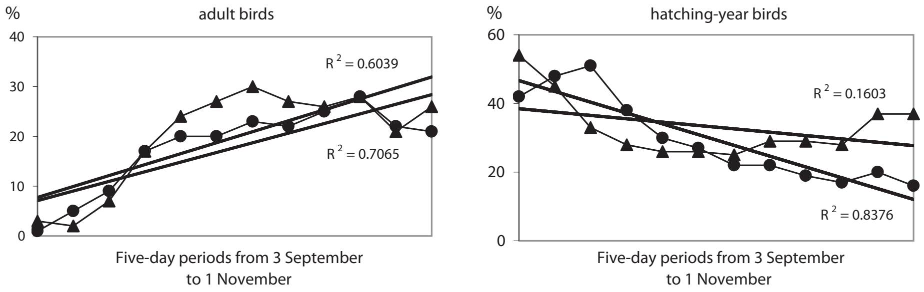


Great Tit, n = 7078

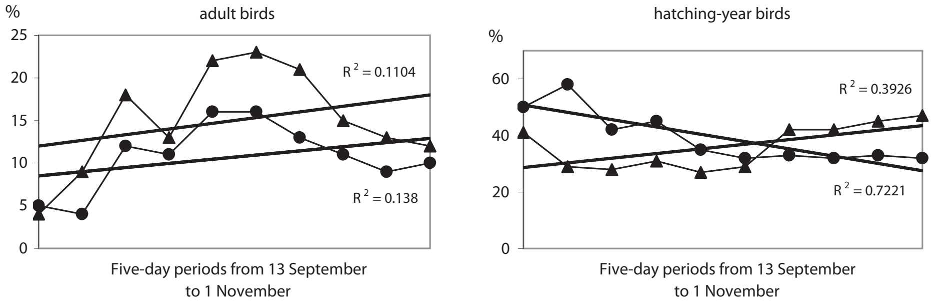


Goldcrest, n = 7956

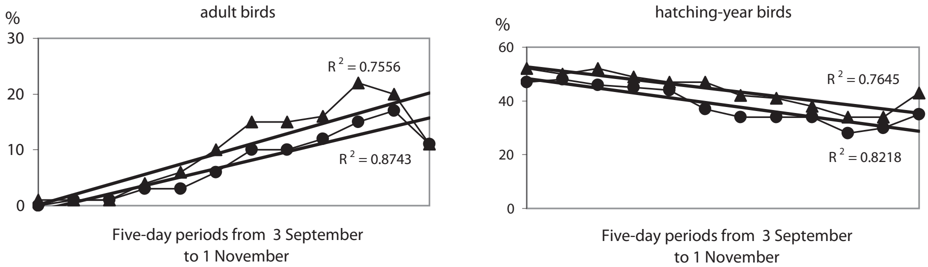
Fig. 9. Trends in age and sex structure of migrating populations of five species in spring inferred from the averaged trapping data over 23 years (1978 to 2000). The values for adults are shown by closed symbols, for yearlings by open symbols. Y axis shows the percentage in an age class.



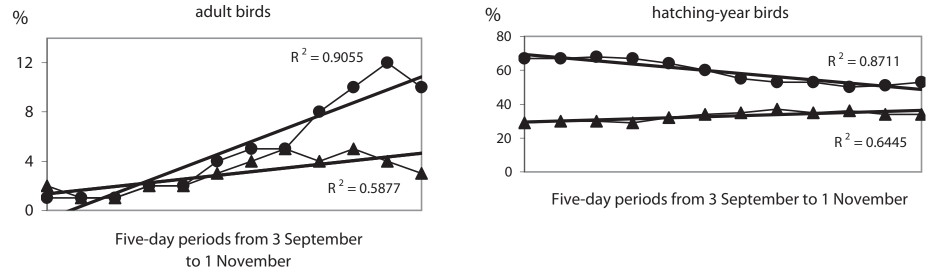
Chaffinch, n = 243311



Brambling, n = 24847

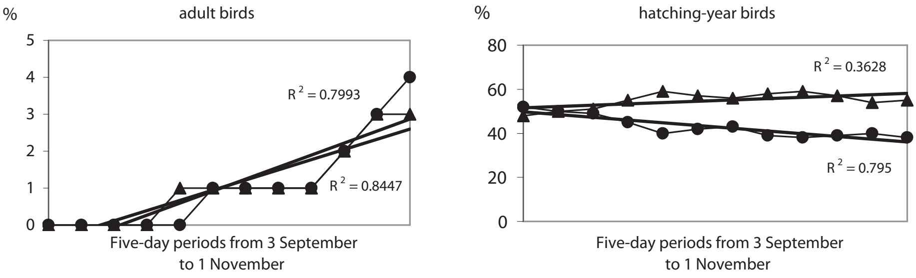


Eurasian Siskin, n = 46633

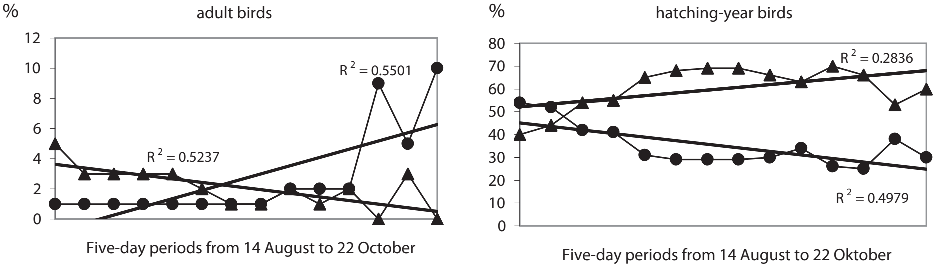


Great Tit, n = 95973

Fig. 10. Trends in age and sex structure of migrating populations of six species in autumn inferred from the averaged trapping data over 23 years (1978 to 2000). Triangles show males, dots show females. Y axis shows the percentage in a sex class.



Goldcrest, n = 233510



Willow Warbler, n = 70640

Fig. 10. Continued.

American passerines allowed the authors to conclude that the average time lag between the arrival dates of adults and yearlings was significantly larger in males than in females (Stewart et al., 2002). The authors suggest that factors that govern the delayed arrival of yearling males may also influence females but apparently do so to a smaller extent.

During autumn migration (Fig. 10), the proportion of adults, both males and females, in most species studied either increases with the progress of the season, or (in the Brambling) peaks in the middle of the migratory season. Consequently, the proportion of juveniles slightly decreases along the season of autumn passage, even though juveniles form the majority of migrants in each 5-day period in all species. Another sequence of age groups during autumn migration was found in the Baraba forest steppe (West Siberia) in wetland passerines: *Acrocephalus* warblers, wagtails, the Bluethroat, buntings. In these species adults were the first to migrate, whereas the passage of juveniles occured later and was more protracted (Chernyshov, 1986). In three *Acrocephalus* warbler species on the Courish Spit (the Eurasian Reed Warbler, Marsh Warbler, and Sedge Warbler) adults also depart earlier than juveniles (Chernetsov, 1999). A similar picture was established in the same three species and in Great Reed Warbler in the Western Ukraine (Zakala, 2008). This feature might be typical of all *Acrocephalus* warbler populations.

Annual variation in the sequence of migration of age groups was analysed for the most common species, the Chaffinch. In both seasons, annual variation was sometimes rather pronounced (Fig. 11). Nevertheless, the data for each particular year clearly support the previous general remarks for most species studied on the Courish Spit. This sequence of passage of age and sex groups of some species may be treated as a regular event in the Baltic area, as it occurs annually.

A more detailed analysis of the whole pattern of migration in respect to of age and sex is only possible when the total numerical ratio of different age and sex groups is analysed in parallel. The further analysis is presented below.

3.3. SEX RATIO IN AVIAN POPULATIONS AND ITS VARIATION

The question of sex ratio which is important for a number of aspects of natural selection was considered in the 1930s – 1960s. In most sexual organisms the primary sex ratio (at fertilisation) is governed by the combination of sexual chromosomes and is 1:1, whereas secondary (among juveniles) and tertiary (among adults) sex ratios depend on sex-related mortality rates controlled by natural selection (Fisher, 1958; Leigh, 1970; Maynard-Smith, 1978; Pianka, 1978). Subsequent studies showed that sex structure of animal populations is quite variable and reflects both genetic and ontogenetic influences and ‘biogeocenosis’ involvement (Bolshakov & Kubantsev, 1984; Yablokov, 1987; Poethke, 1988; Breitwisch, 1989).

In birds, sex ratio in natural populations has been a frequent subject of study (Larionov, 1927; Mayr, 1939; Lack, 1954; Witschi, 1961; Payevsky, 1969, 1993; Chemyakin, 1988b; Breitwisch, 1989; Vysotsky & Sokolov, 1998; Sokolov & Vysotsky, 2000; Donald, 2007). All published data clearly show (with rare exceptions, see Chemyakin, 1988b) that in nestlings the sex ratio is 1:1 or slightly female-biased, while sex ratios of adults are male-biased. The data of various surveys and captures usually are male-biased with a notable exception of game species where females may be more numerous due to male-biased hunting. Doubts in the validity of the data on adult sex ratio are usually raised by apparent methodological problems, i.e. that males are more obvious due to their coloration, singing and higher mobility, so that they occur more frequently in survey results, scientific collections and hunting bags.

Sex ratio on the breeding grounds may be influenced by the situation in winter quarters. For example, American Redstarts (*Setophaga ruticilla*) are known to exhibit age-specific segregation in the breeding area and sex-specific segregation in the wintering area. As winter is the season limiting the total population numbers in this species, and males display dominant behaviour, numbers of females drop

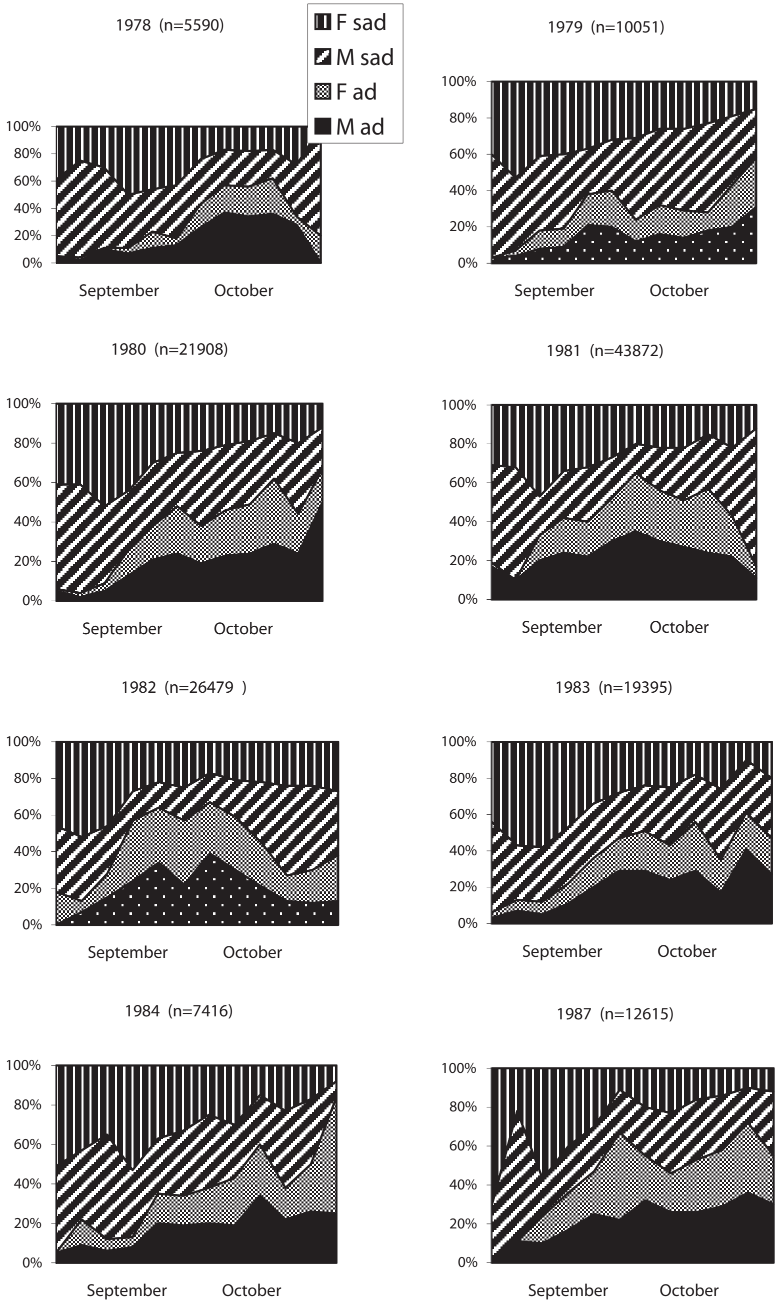


Fig. 11. Annual variation in the sequence of autumn passage of age and sex groups of the Chaffinch from 1978 to 1987. F sad – first-autumn females, M sad – first-autumn males, F ad – adult females, M ad – adult males.

in winter to a greater extent than the numbers of males, resulting in a shortage of females during breeding (Marra & Holmes, 2001; Runge & Marra, 2005).

A comparative analysis of sex ratio in passerines that breed on the Courish Spit and pass through in autumn and spring is based on capture data from 1957-2000 using two datasets: 1957-1988 and 1978-2000. The number of years included in the first dataset varies between the species, because species-specific methods of reliable age and sex determination were not found for all species simultaneously. The mean sex ratio was calculated by the same method that was used for age and sex distribution (see section 2.3.2).

The data for 1957-1988 are given in Table 10. Among the 15 songbird species studied for sex ratio, the data on just two species referred to the breeding period, and in two other species the data refers to the period of postbreeding and postfledging movements. In the remaining species all data referred to spring and autumn migratory periods. During the period of breeding, sex ratio was significantly male-biased in both adult and yearling Chaffinches and Yellowhammers. During the postbreeding and postfledging movements, sex ratio was significantly male-biased in both adult and juvenile Starlings and in juvenile, but not adult, Crossbills.

During autumn passage, males significantly outnumber females in adult birds of 6 species and in juveniles of 8 species. The females outnumber males only in the Great Tit and Bullfinches. During spring migration, significantly more males than females are captured in the Blackcap, Willow Warbler and Siskin, irrespective of age and only in the Great Tit the opposite trend is found. In the Blackbird sex ratio in spring does not differ from 1:1, unlike autumn. In general, across all the species studied on the Courish Spit the percentage of males varied between 52-78%, on average 58.0 ± 1.5 % for all species pooled.

I analysed year-specific sex ratio on the basis of the data pooled across 23 years (1978-2000) by calculating the relationship between number of sex and age groups of birds and the timing of their passage during spring and autumn migration (Table 11). The results supported the main conclusions concerning the schedule of passage of sex and age groups for sex ratio (section 3.2, Figs 9 and 10). In autumn, in all species the females are more common at the initial stages of migration, and the proportion of males increases towards the end of passage, but the degree of significance varies between the species.

Sex ratio estimate for the Goldcrest in spring (on average 38% of males, unlike 56% in autumn) is not reliable, as not the whole period of spring movements is covered by captures. The movements start in mid March, sometimes even earlier, whereas captures do not commence until late March or, more frequently, early April. It is logical to assume that the males are more common during the first part of migration not covered by captures. Spring trapping figures form just ~3% of the overall totals in this species. A similar relationship between autumn

Table 10. Sex ratio in captures of songbirds

Species	years	Season	Number of birds with identified		Proportion of males, %								
					Adults			Juveniles (yearling in spring)			Pooled		
			sex	sex and age	lim	m	χ^2	lim	m	χ^2	lim	m	χ^2
European Starling	1963-1982	SW	34864	28716	34.8-58,0	55.0 ± 0.9	61.3 ***	36.4-55.2	54.1 ± 0.4	193.0 ***	35.3-56.8	54.9 ± 0.3	334.7 ***
Blackcap	1969-1988	AM	836	804	-	-	-	46.0-70.6	56.8 ± 1.8	9.8 **	45.7-71.0	55.2 ± 1.7	5.9 *
«» «»	«» «»	SM	917	294	-	-	-	-	-	-	38.2-72.4	56.6 ± 1.6	16.0 ***
Willow Warbler	1972-1983	AM	24618	24618	51.9-85.2	68.9 ± 1.5	204.9 ***	50.2-71.7	60.7 ± 0.3	1083 ***	50.8-78.6	59.6 ± 0.3	907.3 ***
«» «»	«» «»	SM	4267	-	-	-	-	-	-	-	55.3-92.1	78.2 ± 0.6	1356 ***
Goldcrest	1963-1988	AM	134666	131943	41.9-54.7	50.1 ± 1.0	0.0	51.7-60.3	55.9 ± 0.3	1783 ***	51.2-63.0	55.7 ± 0.4	1750 ***
Common Redstart	1958-1988	AM	6120	2697	-	-	-	-	-	-	45.9-69.1	55.8 ± 0.6	82.4 ***
Eurasian Blackbird	1973-1988	AM	1523	1516	41.5-46.8	44.4 ± 3.4	2.4	48.1-64.1	56.2 ± 1.4	18.2 ***	46.6-68.4	55.5 ± 1.3	18.2 ***
«» «»	«» «»	SM	632	627	37.7-56.9	48.7 ± 3.5	0.1	47.9-53.4	50.1 ± 2.4	0.0	38.8-58.3	50.2 ± 2.0	0.0
Great Tit	1969-1988	AM	90947	90760	28.1-52.3	42.7 ± 0.5	243.2 ***	33.2-43.1	38.7 ± 0.2	4053 ***	33.3-43.8	39.7 ± 0.2	3851 ***
«» «»	«» «»	SM	7714	7555	29.9-49.4	37.7 ± 1.3	118.9 ***	19.3-46.5	34.1 ± 0.6	612.4 ***	26.1-56.2	37.6 ± 0.6	624.3 ***
Chaffinch	1957-1980	AM	295685	127572	49.2-60.0	51.1 ± 0.2	26.8 ***	48.4-61.7	52.0 ± 0.2	115.8 ***	44.0-62.1	51.8 ± 0.1	383.2 ***

Species	**years**	**Season**	**Number of birds with identified**		**Proportion of males, %**								
					Adults			Juveniles (yearling in spring)			Pooled		
			sex	sex and age	lim	m	χ^2	lim	m	χ^2	lim	m	χ^2
«» «»	1958-1980	B	5138	5138	53.0-59.3	55.9 ± 0.9	46.9 ***	52,8-66.2	56.2 ± 1.2	27.0 ***	52.4-63.8	55.4 ± 0.7	59.7 ***
Brambling	1957-1988	AM	54418	26746	-	-	-	-	-	-	47.5-63.7	51.8 ± 0.2	70.6 ***
European Greenfinch	1969-1988	AM	2521	2385	37.5-75.0	59.1 ± 1.8	16.6 ***	39.8-56.6	47.6 ± 1.2	3.3	38.3-57.1	51.0 ± 1.0	0.3
Eurasian Siskin	1972-1987	AM	57631	57614	51.3-68.8	59.7 ± 0.5	2169 ***	47.6-54.3	52.2 ± 0.2	111.2 ***	49.9-56.6	53.2 ± 0.2	237.4 ***
«» «»	«» «»	SM	18266	18250	44.3-65.9	58.8 ± 0.7	564.4 ***	45.7-58.4	52.2 ± 0.4	35.4 ***	45.1-59.4	55.5 ± 0.4	220.9 ***
European Goldfinch	1969-1988	AM	516	445	-	69.2 ± 4.5	15.7 ***	53.0-60.9	55.5 ± 2.7	1.7	-	57.9 ± 2.2	13.0 ***
Red Crossbill	1983	SW	822	822	-	53.1 ± 2.9	1.8	-	55.8 ± 2.2	4.4 *	47.3-62.5	54.8 ±1.7	7.4 **
Eurasian Bullfinch	1969-1988	AM	2590	2282	38.5-56.8	49.4 ± 1.9	0.1	22.7-42.1	35.2 ± 1.2	136.9 ***	24.4-49.1	39.9 ± 1.0	110.1 ***
Yellowhammer	1957-1988	B	386	202	-	58.7 ± 3.6	5.6 *	-	58.9 ± 3.5	6.4 *	-	58.8 ± 2.5	12.0 ***
«» «»	1969-1988	AM	746	697	-	43.1 ± 4.7	2.1	37.5-65.5	52.4 ± 2.1	1.3	35.4-62.6	50.5 ± 1.8	0.1

Notes: SM – spring migration, SW – summer movements, AM – autumn migration, B – breeding period; lim – range of annual values, m – mean annual value.

Significance of correlation: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Table 11. Relationship between trapping totals of age and sex groups and timing of their passage during spring and autumn migration using data from 1978 to 2000 (Spearman's rank correlation: * $p<0.05$; ** $p<0.01$).

Species and sex and age groups	Coefficients of correlation	
	spring	autumn
Great Tit		
♂♂ ad	0.782*	0.767*
♀♀ ad	-0.096	0.977**
♂♂ sad	-0.050	0.736*
♀♀ sad	-0.073	-0.915**
Chaffinch		
♂♂ ad	-0.781*	0.642*
♀♀ ad	0.870**	0.828**
♂♂ sad	-0.818**	-0.158
♀♀ sad	0.827**	-0.949**
Brambling		
♂♂ ad	-0.527	0.255
♀♀ ad	0.203	0.195
♂♂ sad	0.553	0.683*
♀♀ sad	0.790*	-0.868**
Goldcrest		
♂♂ ad	-0.963**	0.944**
♀♀ ad	-0.103	0.946**
♂♂ sad	-0.946**	0.457
♀♀ sad	0.999**	-0.889**
Eurasian Siskin		
♂♂ ad	-0.699*	0.878**
♀♀ ad	-0.175	0.953**
♂♂ sad	-0.031	-0.879**
♀♀ sad	0.836**	-0.873**
Willow Warbler		
♂♂ ad	-	-0.706**
♀♀ ad	-	0.893**
♂♂ sad	-	0.394
♀♀ sad	-	-0.619*

Notes. ad – adults (starting from the third calendar year), sad – yearlings (second calendar year) in spring, and juveniles (first calendar year) in autumn.

and spring Goldcrest trapping figures is reported from Heligoland in the North Sea where just 10% of all Goldcrests are captured in spring (Heiber, 1987). This author assumes that the small spring trapping totals are due to very high mortality rate in winter months. It seems however a more likely explanation is the incomplete coverage of spring migrants, as males form just 42,5% among Goldcrests on Heligoland in spring. This suggestion is supported by the data from Poland (Busse & Machalska, 1969). In spring just 21,6% of all Goldcrests are trapped there (33454 birds in 6 years), with females forming in different years 36 to 63% of the first wave of passage, and 74 – 89% in the second wave. The overall percentage of males in spring was just 35%. The authors explained this by different population origin of migrants with different sex ratio. The same strong sex bias in Goldcrest flocks was reported from the Isle of Man (UK, Thorpe & Sapsford, 1992). At both sites differential migration of males and females is probably very strict. This means that under-representation of early spring migrants due to lack of trapping may seriously bias estimates of sex ratio and winter mortality rate. The small number of spring migrants as compared with autumn is unlikely to be fully explained by winter mortality. The data from Poland would yield winter mortality rate estimates of ca. 57%, Heligoland data would result in 80%, and our data for the same years 93% mortality, which cannot be treated as a realistic estimate. Such a high mortality rate may only occur in the sedentary part of the Goldcrest population (Österlöf, 1966; von Haartman, 1968; Hanssen, 1981), and probably only in very severe winters. The mortality rate between early November and March for Goldcrests wintering in Finland is estimated on the basis of multiple surveys at ~ 70% (Hildén, 1982b, 1988).

Sex ratio data in seven passerine species collected at different European sites, for comparison with the data from the Courish Spit, are given in Table 12. Among juveniles and adults males are usually more common, even though their proportion in different species and at different sites varies between 32 and 87%. The data reported in the literature are not always reliable. Most caution should be exercised in respect to the surveys done during seasonal movements due to the widespread differential migration discussed above. Nevertheless, in two data-

Table 12. Range of sex ratios in juvenile and adult birds in different parts of Europe (data from the review: Payevsky, 1993)

Species	**Range of the proportion of males, %**	
	Juveniles	Adults*
European Starling	48.0 – 54.1	53.0 – 60.4
Blackcap	54.4 – 56.8	51.4 – 59.6
Willow Warbler	49.0 – 60.7	59.0 – 78.2
Goldcrest	54.5 – 55.9	50.1 – 64.0
Eurasian Blackbird	50.1 – 73.1	44.4 – 58.7
Great Tit	31.6 – 62.9	37.7 – 76.5
Chaffinch	48.2 – 56.2	42.0 – 87.0

Note: * - including ‘full grown’, i.e. independent birds of unknown age.

sets, from the Courish Spit and from other European sites, sex ratio is mainly male-biased; in general agreement with results of earlier reviews (Lack, 1954; Breitwisch, 1989; Payevsky, 1993; Donald, 2007). Significantly female-biased sex ratios in Great Tits and Bullfinches migrating through the Courish Spit is probably explained by the fact that in these short-distance migrants, the part of the population better adapted to survive severe winter conditions, i.e. adults and males, more often winter in the northern parts of the range than females.

What explanation is there for the slight but constant male-biased sex ratio in avian populations? To answer this question, it helps to analyse the available data on sex-specific survival rates which is done in the following section.

3.4. SEX-SPECIFIC SURVIVAL RATE IN BIRDS: DIFFERENCES FROM OTHER ANIMALS

Shorter lifespans of males, when compared with females, are generally known for most animals (Comfort, 1964; Trivers & Willard, 1973; Case, 1978; Geodakyan, 1974, 1985). It has also been generally assumed that higher mortality rate of males at all ages is typical of very different animal taxa, from insects to mammals, and is supported for humans by the vast datasets of medical statistics (Smith, 1989). The general nature of this phenomenon has however been questioned first for the birds (Payevsky, 1985a; Curio, 1989), and then for some other groups of animals (Gavrilov & Gavrilova, 1991). Among mammals, for instance, mortality rate of females exceeds that of males in some insectivores: bats, rodents and carnivores (Bolshakov & Kubantsev, 1984). Most data on sex ratios in avian populations show that they are significantly male-biased (see the previous section). The unequal secondary and tertiary sex ratios may be due to sex-specific survival. The first attempts at comparison resulted in proposing the theory of higher survival rates of bird males when compared with females (Payevsky, 1985a).

Do the birds indeed differ from other animals by this character? To answer this question, we proposed a special study (Payevsky et al., 1997) that consisted of two parts: (1) estimates of sex-specific survival rates from the ringing data on the Courish Spit; (2) analysis of the published sex-specific survival rates of birds.

In the first part of the study, we used two different independent ringing results: (1) Recovery data from wintering areas and/or migratory routes and (2) recapture data from the local breeding populations of the Courish Spit. We analysed a total of 4508 re-encounters of 784733 ringed individuals. Only the species where sex and age identification was reliable were included in the analysis. Dead recovery data were analysed using the stochastic methods of Brownie et al. (1985) by the programme ESTIMATE. To fulfil the formal requirement of the models demanding that sampling periods must be much shorter than inter-sampling intervals, we only included the recoveries of birds ringed in September and October. Survival rates were estimated for those treated as full grown individuals, i.e. for independent birds in fresh autumn plumage. They included both adults and first-autumn individuals, as the survival rate of birds is usually age-independent after the initial period of low survival during the first months of independent life (Haldane, 1955; Payevsky, 1985a).

Recapture data were analysed following Cormack-Jolly-Seber models and using the programme JOLLY (Pollock et al., 1990). Presence of transients (migrating individuals) in the breeding population could cause a problem. To exclude the effect of transients on the survival rate of local individuals, we only included birds that were captured at least twice during the breeding season and were first captured as juveniles. Also, in most cases only the birds that produced more than one recapture were included in the analysis.

As the software used in our analysis could not accommodate capture histories exceeding 20 capture events, the long-term data were divided into two roughly equal parts, and the mean of the obtained estimates was calculated. To test the null hypothesis of sex-independent survival rates vs. the alternative hypothesis of higher survival rate of males we used Z-test (Brownie et al., 1985); the null hypothesis was only rejected if $Z > 1.645$.

Estimates of survival rates of males and females based on dead recoveries are given in Table 13, based on recaptures in Table 14. Survival rate of males was significantly higher than in females in just two cases, in the local breeding populations of the Willow Warbler and Pied Flycatcher. In all other species sex-related difference in survival rates was not significant, even though males survived better always except for the Great Tit where survival rates of both sexes were equal. In some cases the difference was significant in some portions of the total dataset (e.g. in some periods male Chaffinches survived significantly better than females), but in general, this was not significant. The most important result is that survival rate in females was never significantly higher than in males.

In the second part of our study (Payevsky et al., 1997) we analysed the literature data on sex-specific survival rates in different avian taxa, including 31 species of 11 non-passerine orders and 40 species of passerines. Some of these data are given in Fig. 12: species- and sex-specific survival rates in 27 European passerine species (for some species, the estimates are averaged across several populations).

A total of 109 pairs of survival rates reported by various authors were analysed (for many species, data for several populations were available). Even though not all published survival rate estimates are reliable, especially those extracted from old sources, the data show that higher survival rate of males (80 cases out of 109) occurs more often than the opposite trend (19 cases). This is significantly more than 50% (the expected number is 49.5), 10 pairs are ignored, one-way sign test: Z

Table 13. Estimates of sex-specific annual survival rates (S) of migrating adults from dead recoveries.

Species, sex	**Years of ringing**	**Recovery number / ringing total**	**Model # from ESTIMATE programme**	**Survival rate (S) and standard error (se)**		**Significance of difference between sexes**	
				S	se	Z	p
European Starling, males	1980-1988	84 / 10112	3	0.501	0.040	0.371	> 0.05
European Starling, females	«» «»	62 / 8036	3	0.478	0.047		
Goldcrest, males	1980-1993	53 / 105546	3	0.365	0.073	1.016	>0.05
Goldcrest, females	«» «»	40 / 76549	3	0.265	0.066		
Great Tit, males	1962-1988	188 / 38382	3	0.380	0.029	0.000	>0.05
Great Tit, females	«» «»	298 / 57287	3	0.380	0.022		
Chaffinch, males	1962-1989	727 / 201078	0	0.562	0.034	0.620	>0.05
Chaffinch, females	«» «»	528 / 186925	0	0.523	0.053		
Brambling, males	1962-1971	78 / 10188	0	0.471	0.164	0.192	>0.05
Brambling, females	«» «»	72 / 9186	0	0.430	0.136		
Eurasian Siskin, males	1962-1976	405 / 36239	0	0.488	0.082	1.230	>0.05
Eurasian Siskin, females	«» «»	300 / 33458	0	0.370	0.049		

Table 14. Estimates of sex-specific adult annual survival rates (Phi) from recaptures of breeding birds

Species, sex	**Years of ringing**	**Recapture number / ringing total**	**Model # from JOLLY programme**	**Capture proba-bility**	**Survival rate (Phi) and standard error (se)**		**Significance of difference between sexes**	
					Phi	se	Z	p
Barred Warbler, males	1967-1976	59 / 420	D	0.16	0.502	0.041	0.14	>0.05
Barred Warbler, females	«» «»	22 / 273	D	0.09	0.491	0.065		
Willow Warbler, males	1976-1995	172 / 1259	D	0.30	0.331	0.019	2.51	<0.05
Willow Warbler, females	«» «»	78 / 678	D	0.35	0.255	0.023		
Pied Flycatcher, males	1984-1991	163 / 449	A	0.89	0.349	0.026	2.50	<0.05
Pied Flycatcher, females	«» «»	82 / 507	A	0.63	0.238	0.036		
Chaffinch, males	1960-1995	591 / 2804	A	0.29	0.498	0.022	0.45	>0.05
Chaffinch, females	«» «»	378 / 2290	A	0.23	0.482	0.028		

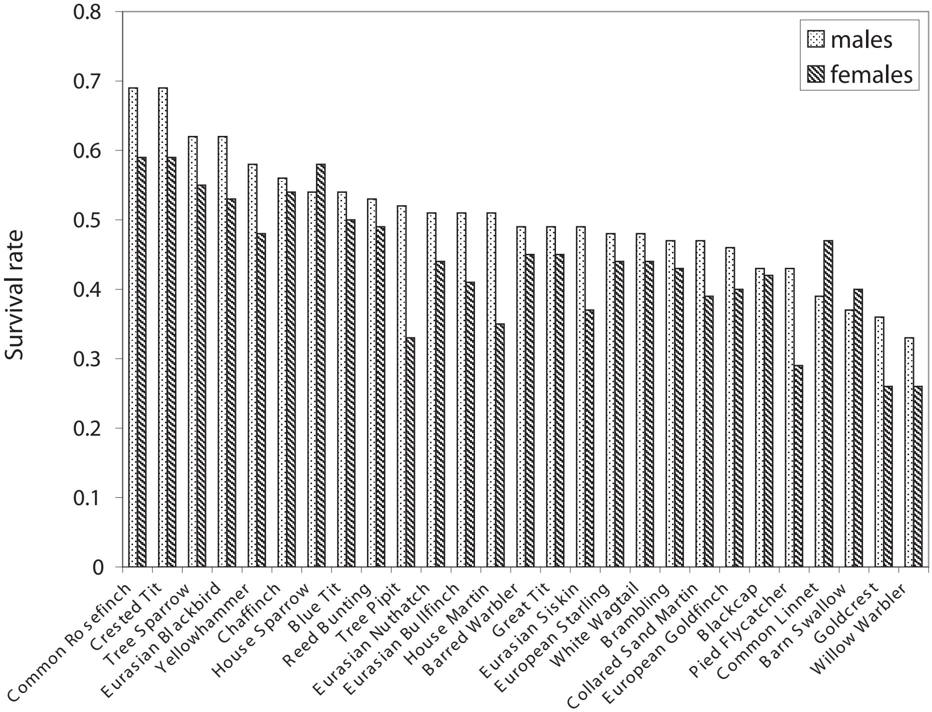


Fig. 12. Species- and sex-related survival rates in 27 European passerines from the literature data (Payevsky et al., 1997). In some species the values from several populations are averaged.

= 6.03, p = 0.000008). The Kolmogorov-Smirnov test shows a significant difference between the frequency distributions of survival rate estimates of males and females ($\lambda = 1.83$, $p = 0.002$). We found also a significant relationship between the lag between male and female rates and survival rate value ($r = -0.420$, $p < 0.01$): the higher was species-specific survival, the smaller was the difference between sexes.

These analyses show that avian populations of the Courish Spit, and numerous populations from other countries studied by other authors, show a persistent trend towards higher annual survival rate of males in comparison with females. This trend becomes apparent when all data concerning many species are compared, whereas for each particular population the pattern is often insignificant. It should be emphasized that higher survival rate of females occurs much less frequently. The same results were obtained on the basis of extensive dataset on songbird ringing in Britain (Siriwardena et al., 1998). Survival rate of adult males was higher than survival of adult females or equal to it in 10 out of 15 species, whereas survival rate of females was higher in just one species. As with our study, in most species the sex-related difference in survival rates was not significant.

It should be noted that in different titmice species no sex-related differences in survival rates has been found in many populations. For example, it was not found in Great Tits on the Courish Spit (Table 13), in Finland (Orell & Ojanen, 1979), Germany (Winkel & Frantzen, 1989), or near Oxford, UK (Clobert et al., 1988); in Belgian Blue Tits (Dhondt et al., 1990) and German Coal Tits (Dietrich et al., 2003). Female Blue Tits survived slightly better on Corsica, and males in Provence (Blondel et al., 1992). However, in some Great Tit populations male survival was higher than in females, e.g. in the Netherlands (Kluijver, 1951) and in England (Siriwardena et al., 1998). Only in Estonia female Great Tits survived significantly better than males (Hõrak & Lebreton, 1998). Even though female Great Tits cover longer distances than males during both natal and breeding dispersal (section 4.1, see also Andreu & Barba, 2006), no evidence is currently available suggesting that this may influence their survival.

From these results we may confidently conclude that the broadly accepted theory of the increased mortality of males in all animals is not supported by the data on birds. What is the cause of birds being different in this respect, first of all from the mammals? Several hypotheses have been suggested seeking to explain the increased mortality of male mammals (Trivers & Willard, 1973; Clutton-Brock et al., 1985; Clutton-Brock, 1986; Dobson, 1987). First, it has been suggested that the heterogametic gender (the one carrying the Y chromosome) is less resistant to environmental factors. Second, parental investment in daughters was thought to be greater than in sons. Third, sex-related size dimorphism and higher vulnerability of the larger gender to starvation was thought to play a role. Finally, sex-related natal dispersal distance was inferred to explain the results. These explanations are not mutually exclusive, so the observed sex-related survival might result from a combination of factors. Let us examine these with respect to birds.

Several ways of genetic sex determination exist in animals, and in different taxa any gender may be heterogametic (XY, XZ) or homogametic (XX). Avian females are heterogametic (XZ), like mammal males (XY). As the sex chromosome Y (analogous to Z chromosome of birds) is believed to be responsible for increased mortality, the same relationship may be expected to exist in birds. The previous results are in agreement with this theory. It should however be noted that no evidence of longer lifespans in males of many butterflies (Lepidoptera) exists, even though the females are also heterogametic in this order.

Differential parental investment in offspring of different sex has not been studied in birds. R. Fisher (1958) forwarded a theory of evolution of sex ratio in animals. He suggested that parental investment, i.e. energy costs of raising offspring, are equally distributed between individuals of both sexes, and primary sex ratio (at fertilisation) may shift until the sum of costs of raising males and females becomes equal. As a result, in sexually dimorphic species individuals of the smaller (i.e. energetically cheaper) sex may outnumber the other sex. In most birds males are larger than females, so they are more expensive to grow; therefore males should be rarer. However, sex ratio in nestlings seldom differs from the equality (Clutton-Brock, 1986; Breitwisch, 1989; see also section 3.3). No relationship was found between sex ratio and egg mass, sequence of laying, age of the mother, habitat quality etc., but sometimes there is a relationship with birth date and the proportion of males in broods (Dijkstra et al., 1990). A study of the impact of various factors on the survival of the Serin showed a very weak relationship between mortality rate and environmental factors, but a significant correlation with body mass, especially in young birds (Conroy et al., 2002).

A study of the sex ratio in Coal Tits in Germany by molecular sexing and estimates of survival rate of juveniles until their first breeding season showed equal sex ratio and sex-independent survival rates (Dietrich et al., 2003). Males and females did not differ in their site fidelity and the distance of natal dispersal.

In conclusion it should be emphasized that most data available at the moment suggest that male birds survive better than females, resulting in prevalence of males in avian populations. The unequal sex ratio may make intraspecific competition during the breeding season more acute, probably enhancing behavioural and physiological variability of populations.

3.5. ANNUAL AND SEASONAL VARIATION OF AGE AND SEX STRUCTURE OF MIGRATING SONGBIRD POPULATIONS

An interesting, but insufficiently studied, problem of demography of migrating birds is the annual variation of age structure and difference between autumn and spring seasons, and between males and females. As shown above (section 2.3.1), capture data provides a good opportunity for the analysis of age and sex structure of passage populations of diurnal migrants. In nocturnal migrants captures at coastal sites, age structure parameters may only be used as relative indices (section 2.3.2) due to the coastal effect, i.e. the strongly biased proportion of juveniles.

We analysed capture data over 25 years (1971-1995) for the six most common species, the European Robin, Willow Warbler, Goldcrest, Great Tit, Chaffinch, and Siskin to study annual and seasonal variation of age and sex structure (Payevsky & Shapoval, 2002). The pooled data are presented in Table 5, and the detailed data for each year for all species are given in Fig. 13. The proportion of adults varied in relation to year, season, and species, being on average between 3 and 43%.

The variation of the proportion of adults (annual, species, season and sex-related variation) among all captured birds was analysed as follows. It is known that very large samples always helps to improve the possibility for finding significant

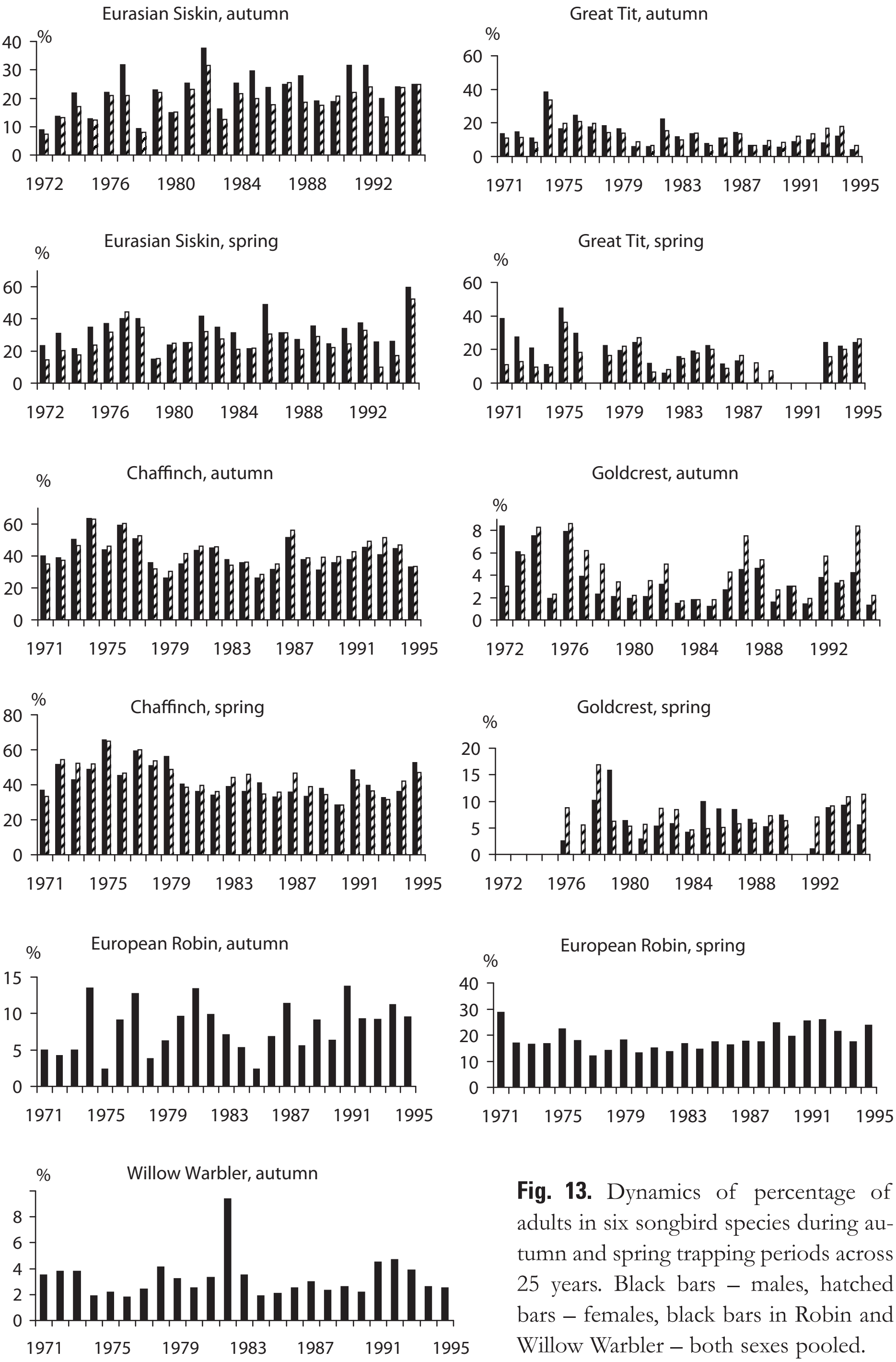


Fig. 13. Dynamics of percentage of adults in six songbird species during autumn and spring trapping periods across 25 years. Black bars – males, hatched bars – females, black bars in Robin and Willow Warbler – both sexes pooled.

differences even if the difference is negligibly small (Fleiss, 1986). Our samples pooled across 25 years are just such large samples (tens and hundreds thousands). Therefore the first step of analysis was to calculate the proportion of adults in each individual season, as shown in Fig. 11. This value varied broadly on the annual basis. To test for the significance of this variation, we compared proportions from several independent samples (Fleiss, 1986) using the formula:

$\chi^2 = 1/pq \sum n_i (p_i - p)^2$,

where p_i is the proportion in each year, $q = 1 - p$, p is the proportion averaged across the years of study, n_i is the sample size in each year.

In all species studied, both in spring and in autumn, annual variation of the proportion of adults was always highly significant (χ^2 values [df. 24 and 23] varied between 2031.4 in the Goldcrest and 5329.6 in the Chaffinch in autumn). Annual variation of age structure as shown by the coefficient of variation was the strongest in the Goldcrest (40-63%) and the Great Tit (45-58%), and the weakest in the Chaffinch (21 – 23% in all combinations of sex and season). Due to very strong annual variation, general trends of significance of age composition were estimated by the sign test.

Table 15 shows the results of comparing the annual proportions of adults. A significant difference was recorded in both diurnal and nocturnal migrants. However, autumn samples of Willow Warbler and Goldcrests contained identical proportions of adults. A significant difference among the sexes in the proportion of adults was found in Siskins and Great Tits in spring and in Siskins, Goldcrests and Chaffinches in autumn. The proportion of adults was significantly higher in spring than in autumn in all species except of the Chaffinch. No correlation was found between the proportions of adults in autumn and the next spring (Spearman's coefficient of correlated varied between 0.15 and 0.42 and was not significant in any case). This means that the relationship between these values varied randomly.

Thus, the expected significant among-species variation was found in 8 cases out of 9 (due to coastal effect, species-specific proportion of adults was compared only within the groups of nocturnal and diurnal migrants). The difference in the mean proportion of adults between Goldcrests (3.8%) and Willow Warblers (3.1%) in autumn was not significant. As the true proportion of adults cannot be determined in these species of nocturnal migrants, it may be assumed that they have similar mechanisms of behaviour of migrating populations after nocturnal flights over water surfaces when the bulk of birds on the coasts consist of juveniles.

Annual variation of the age composition may be mainly related to varying population productivity. For instance, juvenile : adult ratio in October Bullfinch captures near Oxford, thought to be a proxy for population productivity, varied from 2.8 to 5.5 between the years. It was clearly related to the known breeding performance (Newton, 1999). Annual variation in the age structure obtained by

Table 15. Comparison of species-, season- and sex-specific variation in the proportion of adults by sign test (annual seasonal samples of capture data from 1971 to 1995)

Categories of difference and samples compared *	Significance of difference with n = 25 and 24		
	Z test statistics	Calculated number of signs	Significance level
Species-specific difference			
European Robin A – Willow Warbler A	4.4	1	<0.01
Willow Warbler A – Goldcrest A	0.2	11	n.s.
Goldcrest A – European Robin A	2.8	5	<0.01
Chaffinch A – Siskin A	4.4	1	<0.01
Chaffinch S – Siskin S	3.6	3	<0.01
Chaffinch A – Great Tit A	4.8	0	<0.1
Chaffinch S – Great Tit S	3.4	2	<0.01
Siskin A – Great Tit A	2.8	5	<0.1
Siskin S – Great Tit S	2.0	5	<0.05
Seasonal difference			
European Robin A – European Robin S	4.4	1	<0.01
Goldcrest AM – Goldcrest SM	3.1	2	<0.01
Goldcrest AF – Goldcrest SF	3.2	2	<0.1
Great Tit AM – Great Tit SM	2.9	3	<0.01
Great Tit AF – Great Tit SF	2.3	5	<0.05
Chaffinch AM – Chaffinch SM	0.0	12	n.s.
Chaffinch AF – Chaffinch SF	0.0	12	n.s.
Siskin AM – Siskin SM	2.7	5	<0.05
Siskin AF – Siskin SF	3.1	4	<0.01
Sex-specific difference			
Goldcrest AM – Goldcrest AF	3.6	2	<0.01
Goldcrest SM – Goldcrest SF	0.7	7	n.s.
Great Tit AM – Great Tit AF	0.0	12	n.s.
Great Tit SM – Great Tit SF	2.0	5	<0.5
Chaffinch AM – Chaffinch AF	2.0	7	<0.05
Chaffinch SM – Chaffinch SF	0.0	12	n.s.
Siskin AM – Siskin AF	3.3	3	<0.01
Siskin SM – Siskin SF	2.8	4	<0.01

*Notes: A – autumn, S – spring, M – males, F – females.

us (Table 5, Fig. 13), analysed from this viewpoint, suggests that Goldcrests and Great Tits display a much higher variability in annual breeding performance than Chaffinch and Brambling.

In spring, as expected, the proportion of adults in most species is higher than in autumn, probably due to higher winter mortality of juveniles when compared with adults. The difference was the largest in European Robins: 8.1% in autumn, 18.5% in spring (2.3-fold higher); in the Goldcrest, Siskin and Great Tit the difference was smaller, 1.2 – 1.9-fold. Only in the Chaffinch was the proportion of adults nearly identical in autumn and in spring: 40.8 and 42.5% in males and 42.7 and 43.6% in females, respectively. The reason could be in the sampling procedure in spring and in autumn: in some years the first spring flocks, mainly consisting of adult, oldest males, pass the Courish Spit before the traps start operation. However, this explanation cannot be valid for females, because the period of their passage is completely covered by trapping times. There are no reasons to assume that mortality rate of Chaffinches is equal between adults and juveniles, unlike all other birds (Payevsky, 1985a). It is therefore necessary to study the sex difference between age ratios, i.e. in which gender and in which seasons the proportion of adults is higher.

Sex-related difference in age ratio is species-dependent: in Goldcrests and Chaffinches the proportion of adults in autumn is higher among females, whereas in the Great Tit in spring and in the Siskin in both seasons the proportion of adults is higher in males (Tables 5, 15). Assuming the equal sex ratio at hatching, and sex-independent mortality, a higher proportion of adults among females may result from the more sedentary habits of males, so that a proportion of them do not migrate. This might be applicable to Goldcrests and Siskins, but male survival in these species, like in many others, is higher than female survival (see the previous section), so the initial assumption is not acceptable. Nevertheless, seasonal sex-related variation of age ratio in Goldcrests and Chaffinches, i.e. transition from higher proportion of adults among males in autumn to similar age ratio in both sexes in spring may indicate a lower winter survival rate in the females.

It may be concluded that season-related variations in age composition of migrating populations mainly result from age and sex-related variation in winter survival rates: mortality rates of juveniles is higher than in adults, and higher in females than in males.

3.6. DIFFERENTIAL WINTERING AND SURVIVAL OF AGE AND SEX GROUPS

Age and sex-related differences in migration distance and in habitat use are known in many avian species (Gauthreaux, 1982; Ketterson & Nolan, 1983; Payevsky, 1985a; Ornat & Greenberg, 1990; Newton, 2008). Females and first-winter birds of both sexes are believed to winter further south than males and all adults. An analysis of the literature data with a particular reference to passerines (King et al., 1965; Myers, 1981; Rising, 1988; Prescott & Middleton, 1990) shows that this phenomenon has been statistically tested in only a few species. Age and sex distribution in winter quarters should be related to the optimal survival prospects taking into account all factors that influence a bird in winter.

In this study age and sex-related differences in migration distance were analysed in relation to the survival rate in three common finch species, the Chaffinch, Brambling, and Eurasian Siskin (Payevsky, 1995). These birds migrate through the Courish Spit from breeding sites in Finland, north-western Russia and the Baltic countries to winter in Western Europe (Payevsky, 1973a). The analysis included 1042 recoveries of 585459 ringed Chaffinches, 292 recoveries of 60787 ringed Bramblings and 977 recoveries of 156310 ringed Siskins. The similarity of autumn and winter distribution between years (only the data with the largest datasets were included) was tested by the Friedmann test for randomised blocks (Hollander & Wolfe, 1973). With no significant annual variation found, the data were pooled for analysis. Migration distance was calculated according to M. Beklova (1978), and the mean directions of migratory movements of age and sex groups were compared by the Mardia-Watson-Wheeler test (Batschelet, 1981). Significance of variation in migratory distance was tested by the two-way ANOVA and the Wilcoxon test.

In those cases where comparison reveals no significant difference between the mean recovery distance in each autumn and winter month then those birds may be regarded as having reached their winter locations over that period. For Chaffinch and Brambling such periods included November, December, January and February, and for the Siskin, only December and January. The mean distances and directions of movements for different periods (autumn migration, wintering, and spring migration) are presented in Table 16.

The direction of movement does not vary with sex or age in any of the species (F values vary between 1.3 and 2.6, n.s.). Males and females and juveniles and adults migrate in autumn towards the same south-westerly direction, on average 236° for the Chaffinch, 232° for the Brambling and 224° for the Siskin. With migratory distance, two-way ANOVA rejects null hypothesis with P = 0.99 in the Chaffinch ($F_1 = 14.2 > F' = 9.3$ и $F_2 = 21.9 > F' = 9.3$) and P = 0.95 in the Brambling ($F_1 = 6.3 > F' = 4.8$ и $F_2 = 7.5 > F' = 4.8$) in respect to both factors, i.e. sex and age. This means that age and sex-related variation of migratory distance is significant in these two species. In the Siskin the difference was not significant ($F_1 = 5.8 < F' = 7.7$ и $F_2 = 6.2 < F' = 7.7$), in spite of large difference in the mean values of both sexes.

The difference was studied in more detail during the period of wintering proper (Table 17). Lack of sex and age-related variation in the migratory distance in the Siskin compared with the clear differences in the Chaffinch and the Brambling is confirmed. Adult and juvenile females spend their winter on average further south than males, and somewhat unexpectedly the adult males spend winter further south than juvenile males. Unlike males, females showed no age-related difference.

Tables 16. Mean distance (D ± se, km) and direction (α ± s, degrees) of movements of age and sex groups of finches recovered at different times of the year

Species, sex, age	**October (October and November for Siskins)**		**November – February (December – January for Siskins)**		**March (February – March for Siskins)**	
	D ± se	α ± s	D ± se	α ± s	D ± se	α ± s
Chaffinch						
♂♂	1410 ± 45	236 ± 16	1654 ± 27	238 ± 25	1415 ± 73	237 ± 22
♀♀	1497 ± 48	237 ± 12	1852 ± 34	233 ± 23	1722 ± 84	234 ± 20
♂♂ ad	1459 ± 72	235 ± 11	1748 ± 37	234 ± 28	1517 ± 89	235 ± 25
♂♂ juv	1346 ± 82	224 ± 14	1375 ± 77	235 ± 19	1230 ± 141	237 ± 18
♀♀ ad	1580 ± 68	236 ± 10	1896 ± 43	233 ± 16	1898 ± 117	230 ± 13
♀♀ juv	1386 ±133	230 ± 8	1841 ± 107	235 ± 11	1318 ± 149	236 ± 9
Brambling						
♂♂	1142 ± 52	227 ± 28	1269 ± 36	229 ± 19	1007 ± 75	229 ± 21
♀♀	1207 ± 46	226 ± 16	1416 ± 52	227 ± 18	1225 ± 88	226 ± 19
♂♂ ad	1137 ± 64	227 ± 31	1296 ± 40	229 ± 16	1277 ± 104	232 ± 5
♂♂ juv	1176 ± 115	216 ± 13	1012 ± 91	240 ± 28	1011 ± 83	246 ± 13
♀♀ ad	1194 ± 66	221 ± 14	1414 ± 61	222 ± 23	1248 ± 103	233 ± 21
♀♀ juv	1257 ± 58	224 ± 14	1294 ± 98	221 ± 17	1115 ± 127	197 ± 18
Eurasian Siskin						
♂♂	1354 ± 21	219 ± 18	1601 ± 56	227 ± 28	1424 ± 70	230 ± 24
♀♀	1313 ± 23	218 ± 21	1485 ± 59	224 ± 19	1327 ± 63	224 ± 17
♂♂ ad	1343 ± 36	219 ± 14	1689 ± 95	224 ± 11	1457 ± 98	220 ± 17
♂♂ juv	1280 ± 55	220 ± 22	1667 ± 112	229 ± 10	1315 ±104	239 ± 14
♀♀ ad	1331 ± 35	213 ± 18	1434 ± 85	217 ± 7	1340 ± 98	218 ±14
♀♀ juv	1202 ± 49	219 ± 9	1322 ± 87	229 ± 12	1329 ± 97	232 ± 4

Table 17. Differences in distance to wintering areas for age and sex groups of finches (data from Table 16).

Groups compared	**Species and Wilcoxon statistics t_w under different levels of significance**					
	Chaffinch		Brambling		Eurasian Siskin	
	t_w	*p*	t_w	*p*	t_w	*p*
♂♂ ad - ♀♀ ad	2.78	<0.01	1.36	<0.05	0.78	n.s.
♂♂ ad - ♂♂ juv	1.81	<0.01	1.60	<0.01	0.11	n.s.
♂♂ juv - ♀♀ juv	1.86	<0.01	1.29	<0.05	0.98	n.s.
♀♀ ad - ♀♀ juv	0.00	n.s.	0.11	n.s.	0.14	n.s.

When considering the results it should be taken into account that winter areas for sex and age groups are not strictly separate in any species. In any part of the winter range birds of any sex and age can occur, and the differences only indicate trends in the different group concentrations. Winter ecology of the species studied is also of importance. The Brambling is a more specialised species; in Western Europe it feeds on beech mast. The Siskin mainly feeds in the trees on alder, birch, and conifer seeds, whereas the Chaffinch is a generalist in the contribution of different plant species as food, but only takes seeds from the ground. These features of foraging ecology undoubtedly influence the intensity of winter movements in relation to crops and snow cover.

Three main hypotheses have been proposed to explain the intra-species variation in winter distribution (Ketterson & Nolan, 1976, 1979, 1983; Gauthreaux, 1982; Marra, 2000; Runge & Marra, 2005; Newton, 2008). The 'Social Dominance Hypothesis' suggests that males and adults of both sexes dominate females and juveniles and displace them to poorer wintering areas to avoid competition in the optimal areas. The 'Body Size Hypothesis' assumed that males may winter in colder and more unpredictable regions, i.e. further north, than females, because they are larger and stronger. The 'Arrival Time Hypothesis' suggests that selection favours wintering of males closer to the breeding areas than is necessary for females, because males need to occupy breeding territories in spring as soon as possible. These hypotheses are not mutually exclusive, and it cannot be ruled out that in different species a combination of these potential explanations can determine winter distribution.

The above hypotheses are only partly supported by our results for the Chaffinch and the Brambling. More southern winter quarters of adult, not juvenile, males on first glance contradict both the body size hypothesis and the arrival time hypothesis. The same pattern has been reported in the Dark-eyed Junco (*Junco hyemalis*) and the American Goldfinch (*Carduelis tristis*) where adult males spend their winter further south than juveniles (Ketterson & Nolan, 1982; Prescott & Middleton, 1990). Mortality rate has been suggested to be related to migratory distance:

the longer the migratory period, the higher is mortality risk, but the further south winter quarters are, the lower is the risk. Therefore, mortality rate is similar in birds that winter in the south and in the north. Since males suffer lower mortality than females do (section 3.4), and adult males spend their winter further south than juveniles but still north of females of any age, the observed pattern is in agreement with social dominance hypothesis and arrival time hypothesis.

Our results for the Chaffinch and the Brambling indicate that the winter quarters of adult males are located optimally: That is not too far from the breeding area but not in the coldest parts of the winter range. Apparently, inexperienced juveniles suffer greater competition in the best areas than in other places, and juveniles may benefit, relatively by staying in suboptimal areas through reduced competition from adult males.

3.7. AGE-RELATED ASPECTS OF SPATIAL BEHAVIOUR IN THE BREEDING AREA

Spatial distribution of birds in the breeding season takes several main forms. In songbirds, breeding territory that is defended against other individuals is usually distinguished from a larger home range which is utilised but apparently not defended. Most authors treat the adaptive significance of territoriality as a necessary condition of normal reproduction. The space is always divided into functional blocks that are used to different degrees (Ivanitsky, 1989, 1990). Non-breeding floaters that have no territory freely move within their home ranges that usually overlap with home ranges of several other individuals.

Any spatial distribution of birds is a result of individual habitat selection under varying population density. Two models of habitat selection exist. The first one, called 'Ideal Free Distribution', assumes that the birds are free to select the available habitats under low population density. This results in equal fitness within the habitat. The other model, called 'Ideal Despotic Distribution', assumes a buffer mechanism when individuals who settle first, displace others from high and middle-quality areas under medium and high population density. The result is the higher fitness achieved in high-density habitats (Brown, 1969; Weidinger, 2000). Studies in different passerine species usually support both models of territorial distribution. Some passerine (and other avian) species breed in compact group settlements, the so-called 'parcellar groups', within uniform habitats (for a review see Ryabitsev, 1993). This has been reported in many passerines, but most often in the Yellow-browed Warbler. Apart from the obvious benefit of alerting each other, which is given by any breeding aggregation, social stimulation of breeding synchronisation has been discussed as one important explanation (Marova, 1990).

In the context of these ideas it is interesting to analyse territorial behaviour of the Willow Warbler and the Chaffinch on the Courish Spit during the breeding season. In particular the question of whether the birds are freely distributed within some area, or do they remain within some limited home ranges. A usual method to study this is to record display sites of individually marked males. Home range size may be estimated from maximum and mean distances between display sites. However, home range size may also be estimated from the number of multiple captures of birds at different sites within an area occupied by breeding populations.

Ringing and recapture data on Willow Warblers and Chaffinches were collected over 20 years, 1962-1981 at the Fringilla field station. I analysed multiple captures when at least one capture occurred between 1 May and 9 August. Even though in early May some captured birds of both species were transient migrants, most adult males from local breeding populations are already in the study area. In 1962-1967, two Rybachy-type traps were operated in summer, in 1968-1976, three traps, and in 1977-1981, four traps. In the Chaffinch, a total of 1678 within-season recaptures and 1672 between-season recaptures were recorded during these years. In the Willow Warbler, the corresponding figures were 1550 and 404. Recaptures of individuals ringed as nestlings were only included after their first recapture in the traps as juveniles or adults.

During the analysis, two types of recaptures were distinguished: (a) those in the same trap or (b) those in a different trap. If a bird was captured several times in different traps, the baseline trap was the one in which most captures occurred. The analysis was done separately for males and females of three age categories: in their first calendar year, yearlings (in the second calendar year) and adults (two year old and older).

In order to decide whether data pooling is justified, the annual variation was tested for homogeneity. I used the one-sided sign test for the 8 years with the largest number of recaptures. Three groups were selected for tests: 1) number of within-season recaptures of adults; 2) number of within-season juveniles; (3) the number of between-season recaptures. The null hypothesis was that captures in the same trap should occur in roughly one-half of all cases. The null hypothesis was rejected in all three groups ($n = 8$, $df = 14$, $p < 0.05$). This means that the data for all years may be pooled for analysis, as the pattern of their annual variation was similar.

The results in detail are given in Tables 18 and 19, and in graphic summary in Fig. 14. Within one season, the proportion of recaptures of adults and yearlings of both species in the same trap is significantly higher than in different traps. In juvenile Willow Warblers, conversely, the proportion of recaptures in different traps is significantly higher. In juvenile Chaffinches the same tendency was observed, but the difference was not statistically significant. Among between-season recaptures, the proportion of captures in the same trap was significantly higher in

Table 18. Age and sex difference in the number of recaptures of Chaffinches in the same trap and in different traps in summer seasons from 1962 to 1981.

Age and sex group	**Number of recaptures**		**Proportion of recaptures in the same trap**	**χ^2 statistics**
	Same trap	Different traps		p
Within the same summer season				
Adult males				
2-year-old and older	179	41	81.4 ± 2.6	<0.001
Yearlings	196	95	67.4 ± 2.7	<0.001
Non-juveniles pooled	506	189	72.8 ± 1.7	<0.001
Adult females				
2-year-old and older	110	32	77.5 ± 3.5	<0.001
Yearlings	104	60	63.4 ± 3.8	<0.001
Non-juveniles pooled	318	137	69.9 ± 2.2	<0.001
Juveniles males	138	162	46.0 ± 2.9	n.s.
Juvenile females	108	120	47.4 ± 3.3	n.s.
In subsequent summer seasons				
Males				
2-year-old and older	383	331	53.6 ± 1.9	n.s.
Yearlings	97	174	35.8 ± 2.9	<0.001
All males	480	505	48.7 ± 1.6	<0.05
Females				
2-year-old and older	259	221	54.0 ± 2.3	n.s.
Yearlings	89	118	43.0 ± 3.4	<0.05
All females	348	339	50.7 ± 1.9	n.s.

adults of both species, whereas in yearlings the opposite trend was significant. No sex-related difference in the behaviour studied was recorded.

The graphical representation of these results in Fig. 14 shows that the observed patterns were identical for both study species. The proportion of birds recaptured in the same trap, declines from adults to yearlings: within season in male Chaffinches and Willow Warblers ($\chi^2 = 12.6$, $p < 0.001$ and $\chi^2 = 16.3$, $p < 0.001$, respectively); in female Chaffinches ($\chi^2 = 7.1$, $p < 0.01$); between season, in male Chaffinches ($\chi^2 = 25.1$, $p < 0.001$); in female Chaffinches ($\chi^2 = 6.7$, $p < 0.01$), in male Willow Warblers ($\chi^2 = 13.6$, $p < 0.001$). A similar decline of the proportion of captures in the same trap was found from yearlings to juveniles in male Chaffinches ($\chi^2 = 27.3$, $p < 0.001$), in female Chaffinches ($\chi^2 = 9.8$, $p <.0.01$), in male Willow Warblers ($\chi^2 = 13.6$, $p < 0.001$), and in female Willow Warblers ($\chi^2 = 4.7$, $p < 0.05$).

All results show that the older a bird is, the more often it is captured in the same trap. This pattern is equally apparent in both study species and in both sexes. Each capture may be treated as evidence of the presence of a bird in the area of

Table 19. Age and sex difference in the number of recaptures of Willow Warblers in the same trap and in different traps in summer seasons from 1962 to 1981.

Age and sex group	**Number of recaptures**		**Proportion of recaptures in the same trap**	**χ^2 statistics**
	Same trap	Different traps		p
Within the same summer season				
Adult males				
2-year-old and older	68	9	88.3 ± 3.7	<0.001
Yearlings	82	50	62.1 ± 4.2	<0.01
Non-juveniles pooled	296	89	76.9 ± 2.1	<0.001
Adult females				
2-year-old and older	15	2	88.2 ± 7.8	n.s.
Yearlings	13	6	68.4 ± 10.7	n.s.
Non-juveniles pooled	103	26	79.8 ± 3.5	<0.001
Juveniles males	279	349	44.4 ± 2.0	<0.01
Juvenile females	175	233	42.9 ± 2.5	<0.01
In subsequent summer seasons				
Males				
2-year-old and older	83	52	61.5 ± 4.2	<0.01
Yearlings	59	104	36.2 ± 3.8	<0.001
All males	142	156	47.7 ± 2.9	n.s.
Females				
2-year-old and older	22	18	55.0 ± 7.9	n.s.
Yearlings	30	36	45.5 ± 6.1	n.s.
All females	52	54	49.1 ± 4.9	n.s.

the trap during some period of time. These results show age-related variation in territorial and spatial behaviour of the birds. The older a bird is, the smaller is its home area during the summer season. It should be emphasized that this area is very limited: the distance between the traps varied between 160 and 220 m.

Assuming that during the summer period, the birds mainly remain within their breeding territories, we are forced to conclude that many of the captured individuals were non-breeding floaters that freely moved in the area near the traps. However, the studies of breeding biology of the Chaffinch (Payevsky, 1982b) and the Willow Warbler (Payevsky, 2000b) on the Courish Spit showed that breeding density in the habitats near the stationary traps was up to 250 pairs·km^{-2} in the Chaffinch and from 80 pairs·km^{-2} in the Willow Warbler. This means that in the plot near the traps with an area of ca. 0.5 km^{-2}, a maximum of 125 Chaffinch pairs and 40 Willow Warbler pairs could breed. However, at least 400 Chaffinches and 200 Willow Warblers are captured in the traps in the middle of the breeding period annually. Many of the trapped birds had very clear signs of breeding: incubation

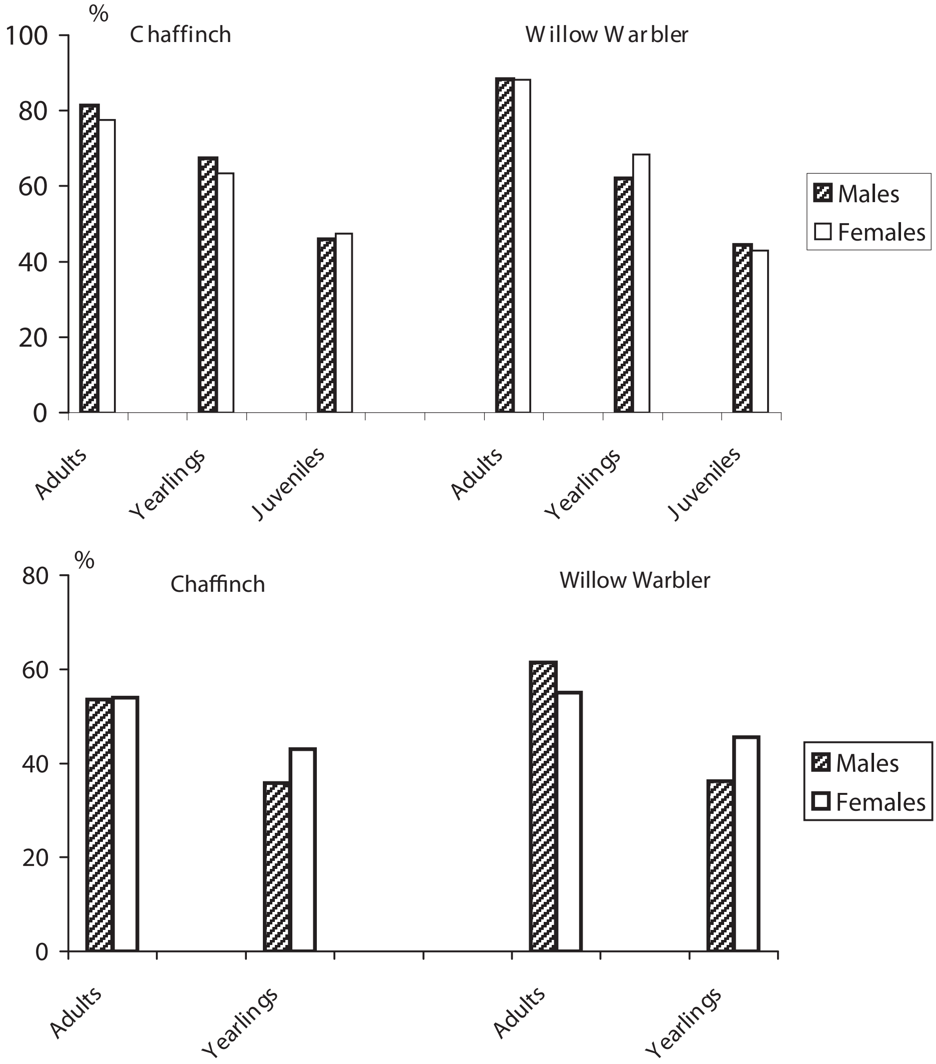


Fig. 14. Percentage of recaptures in the same trap within a single summer season (above) and between different summer seasons (below).

patches in females and enlarged cloacal protuberances in males. Thus it becomes apparent that breeding individuals of these species do not remain only within their breeding territories but have somewhat larger home ranges, but stay in the same area from one to several years.

As shown in a review (Martin, 1986), most populations in avian communities have sub-maximum density so that not all habitat available is divided between breeding territories. In England, the larger Chaffinch territories are, the less actively they are defended. When collecting food for the young, parents regularly visit neighbour territories (Marler, 1956).

Increasingly with age the tendency is to remain in a certain area which is larger than the breeding territory proper which may be advantageous only if in this habitat a bird maximises its fitness by selecting optimal (micro) habitats for reproduction and foraging. We may therefore assume that the study area was equally optimal for the Chaffinch and the Willow Warbler.

3.8. SURVIVAL RATES AND LIFESPAN OF BIRDS: THE RELATIONSHIP

Relationships between population parameters of animals (clutch or litter size, age structure, survival rate, observed maximum lifespan etc.) and especially covariation of these parameters and body size have been a subject of intensive research (Lindstedt & Calder, 1976; Sacher, 1978; Prinzinger, 1979; Dolnik, 1982b; Calder, 1984; Payevsky, 1985a; 1991b; Golikov, 1985; Zammuto, 1986; Krementz et al., 1989).

Among population parameters, the maximum lifespan is the least clearly defined, similarly the species-specific maximum lifespan. Firstly, maximum lifespan will always increase with increasing number of observations. Secondly, theoretically the assumption of the existence of the maximum possible age means that after reaching this age, the probability of death must be equal to 1, which never occurs in practice (Gavrilov & Gavrilova, 1991).

Nevertheless, the maximum lifespan is not infrequently used in comparative studies. Indeed, to find out the causes of variation of a number of demographic parameters between species and populations, some measure of longevity is needed. Apart from the anecdotal records of maximum age reached by some individuals, an age reached by a small proportion of the population, e.g. by 1% of simultaneously born individuals, should be used. This parameter may be called population-specific maximum lifespan.

Whether longevity is related to the process of ageing, and thus to survival rate, is virtually unstudied (Ricklefs, 2000). In North American waterfowl maximum lifespan is not significantly related to annual survival (Krementz et al., 2000). This conclusion seems doubtful. Theoretically, adult survival rate and population age structure, and thus maximum age, must be directly related.

We tested empirical relationships between annual survival and maximum lifespan of birds (Payevsky & Shapoval, 1999, 2000b) in two datasets: ringing results of passerines on the Courish Spit and literature data on 130 species from 13 avian orders. The data on passerines are given in Table 20.

Table 20. Mean annual survival rate and maximum lifespan of songbirds from the ringing data in different parts of the world (for sources see reviews: Payevsky, 1974, 1985a; Payevsky et al., 1997)

Species	Survival rate	Maximum lifespan, years
Barn Swallow	0.30	16
Meadow Pipit	0.39	5
White Wagtail	0.45	7
	0.52	10
Red-backed Shrike	0.33	12
European Starling	0.49	12
	0.47	12
Eurasian Jay	0.50	8
	0.74	18
Blue Jay (*Cyanocitta cristata*)	0.55	14
Common Magpie	0.43	15
Eurasian Jackdaw	0.65	14
Rook	0.74	20
Hooded Crow	0.53	14
House Wren (*Troglodytes aedon*)	0.32	5
Icterine Warbler	0.41	10
Barred Warbler	0.50	9
Garden Warbler	0.40	7
Lesser Whitethroat	0.48	8
Willow Warbler	0.29	6
Goldcrest	0.32	3
Pied Flycatcher	0.31	5
	0.45	7
	0.41	7
Common Redstart	0.38	7
European Robin	0.42	6
Eurasian Blackbird	0.58	13
	0.49	6
	0.31	7
	0.34	10
Redwing	0.43	18
	0.52	9
Song Thrush	0.53	13
	0.55	13
American Robin (*Turdus migratorius*)	0.48	11
Black-capped Chickadee (*Parus atricapillus*)	0.60	10
Blue Tit	0.46	8
	0.28	7
Great Tit	0.38	6
	0.54	9
	0.51	7

Species	Survival rate	Maximum lifespan, years
Ovenbird (*Seiurus aurocapillus*)	0.55	7
Red-winged Blackbird (*Agelaius phoeniceus*)	0.53	14
Brown-headed Cowbird (*Molothrus ater*)	0.44	8
Common Grackle (*Quiscalus quiscula*)	0.51	16
Red-billed Firefinch (*Lagonosticta senegala*)	0.27	7
House Sparrow	0.58	13
Eurasian Tree Sparrow	0.38	10
Chaffinch	0.49 0.54	11 10
Brambling	0.45	11
European Greenfinch	0.57	10
Eurasian Siskin	0.43 0.34	12 11
Common Redpoll	0.39	6
Common Rosefinch	0.50	7
Purple Finch (*Carpodacus purpureus*)	0.54	9
Eurasian Bullfinch	0.53	8
Evening Grosbeak (*Hesperiphona vespertina*)	0.58	14
Yellowhammer	0.47	7
Song Sparrow	0.55	7
Indigo Bunting	0.42	6

Two indicators of maximum longevity were used: 1) maximum recorded age; 2) population-specific maximum lifespan, as defined above. The results show (Fig. 15) that annual survival rate of Baltic passerines is positively and significantly related to maximum longevity in four possible combinations:

- Survival estimated from capture-mark-recapture stochastic statistics;
- Survival estimated from the proportion of yearlings in the population;
- Maximum recorded age;
- Population-specific maximum lifespan.

Correlation coefficients vary between 0.63 and 0.78 with df 29 и $p < 0.001$. The analysis of the literature data (156 datasets from 130 species of 13 orders) also results in highly significant correlation between maximum longevity and mean annual survival rate: $r = 0.77$, df 154, $p < 0.001$ (Fig. 15).

All the results therefore indicate that mean annual survival rate is significantly related to the maximum longevity in the same populations. Significant correlations were obtained in all five dataset variants. What is the reason for the discrepancy between our results and the conclusions of Krementz et al. (1989) that failed to find a correlation between maximum lifespan and survival rate? A possible reason is the specificity of the group studied by Krementz and co-authors: it included 16

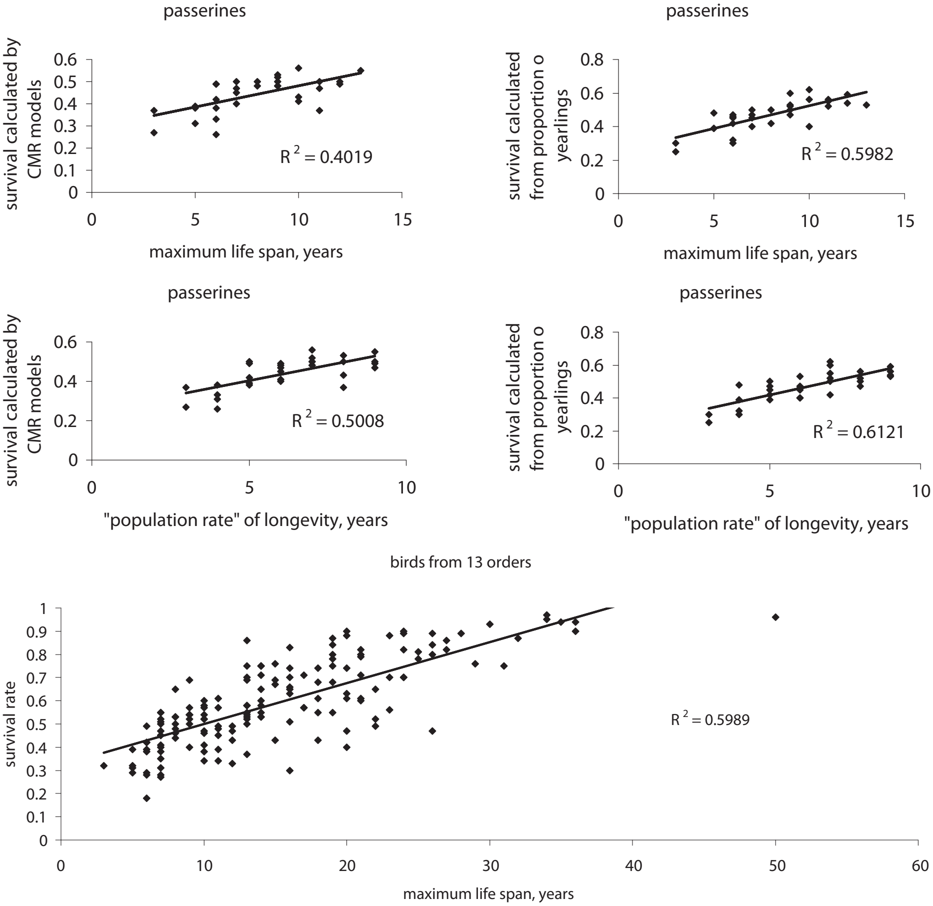


Fig. 15. The relationship between the maximum longevity and the mean annual survival rate in Baltic passerines based on four different variants of these parameters (above) and in 130 bird species from 13 orders from literature (below).

species of North American waterfowl with just 2-fold difference between minimum and maximum values of potential longevity.

In spite of this, it is possible to support the view that the observed maximum longevity significantly depends on the sample size, length of the study period and annual variation in data distribution (Calder, 1984; Krementz et al., 1989). Besides, it has been noted (Payevsky, 1974), that maximum age reached in captivity exceeds than that reached in nature, thus the longevity observed in nature is not a 'physiological limit of lifespan', as often assumed. Nevertheless, maximum longevity is a function of survival rate, so a significant relationship between these parameters can be *a priori* expected.

In summary: In spite of the lack of clear species-specific limits to lifespan, mean annual survival rate of adult birds and their potential longevity are significantly positively related.

3.9. PASSERINE AND NON-PASSERINE DEMOGRAPHY: COMPARATIVE ASPECTS

Demographic parameters are known to vary broadly between populations in different places and habitats, and within populations in relation to season and year. In spite of that, a comparative analysis of demographic parameters is possible not only at the population level, but also at the level of species, genus, family, and order. D. Lack (1954, 1968) was the first author to analyse the nature of avian evolutionary adaptations in relation to the variation of demographic parameters in populations and species; the best known case is the clutch size analysis. It has been subsequently demonstrated that fitness, which in each individual is apparent in the optimal distribution of time and resources, defines all individual demographic parameters in a population in relation to the environmental factors (Cody, 1966).

In the literature, many evolutionary ecological explanations of different demographic parameters have been suggested. For instance, latitudinal variation of clutch size was analysed in relation to population density, age of birds, biome zonality, ambient temperature, day: night ratio, food availability, predation pressure etc. (Stearns, 1980; Kovshar, 1981; Ricklefs, 1983, Payevsky, 1985a). Most comparative demographic studies relate various population parameters to body size of animals. In birds, relationships between body mass (sometimes size) and such parameters as annual survival rate, maximum age, maturity age, clutch size, duration of incubation and feeding the young, and covariation of these factors have been studied. The results are usually presented (Table 21) as allometric functions $y = ax^b$, which can be transformed to the linear relationship by logarithmic transformation: $\lg y = \lg a + b \lg x$; b is the slope of the equation.

In birds, demographic parameters are generally allometrically related to body mass (see Payevsky, 1991b for a review). A positive relationship with body mass was found in mean and maximum longevity, annual survival, age of the first breeding, duration of incubation and feeding the young. A negative relationship was found in the clutch size, but not in all cases. Clutch size is the parameter most independent of body size. Different demographic parameters co-vary, e.g. age of the first breeding is positively related to adult annual survival. Clutch size is inversely related to maturity age, annual survival, and maximum age. Partial correlation analysis showed that these relationships are not just a reflection of body mass variation: with constant body mass correlations persist, even though coefficients become smaller.

Table 21. Relationships between demographic parameters and body mass in passerines and non-passerines as empirical allometric equations.

Variable	**Group of birds**	**a and b coefficients in equations $y = aM^b$, where M is body mass**		**Source**
		a	*b*	
Mean expected longevity	Passerines, 29 species[1]	0.81	0.16	Payevsky, 1985a
	Non-passerines, 57 species[1]	0.85	0.21	« «
	All birds, 86 species[1]	0.64	0.25	« «
	All birds, 114 species		0.29	Lebreton et al., 1987; Gaillard et al., 1987
Maximum lifespan	Non-passerines, 81 species[2]	16.6	0.18	Lindstedt & Calder, 1976
	Passerines, 71 species[2]	21.6	0.26	« «
	All birds, 90 species[3]	1202.0	0.23	Prinzinger, 1979
	All birds, 25 species[4]	0.05	1.3	Golikov, 1985
	Non-passerines, 57 species[1]	8.28	0.13	Payevsky, 1985a
	Passerines, 29 species[1]	7.65	0.14	« «
Maturity age	All birds, 40 species[1]	2.33	0.23	Western & Ssemakula, 1982
Clutch size	Passerines, 66 genera[5]	7.08	-0.08	Saether, 1985
	Birds of Europe, 148 genera[5]	1.81	0.20	Saether, 1987
	Birds of Europe, 191 genera[5]	7.68	-0.11	« «
Duration of incubation	Passerines, 60 genera[5]	11.35	0.07	Saether, 1985
	Birds of Europe, 180 genera[5]	9.79	0.17	Saether, 1987
	All birds, 176 species[6]	9.11	0.16	Blueweiss et al., 1978
Duration of feeding the young	Birds of Europe, 147 genera[5]	17.39	0.21	Saether, 1987
	All birds, 42 species[1]	0.97	0.16	Western & Ssemakula, 1982

Notes. 1 – mass in g, age in years; 2 – mass in kg, age in years; 3 – mass in g, age in days; 4 – size in cm, age in years; 5 – calculated from regression equation; 6 – mass in g, incubation period in days.

General relationships found in the groups composed of birds of different orders, remain, first, in more taxonomically limited groups, e.g. among passerines; second, in ecological groups (e.g. open nesting or hole breeding passerines).

Regression slopes varying between 0.16 and 0.30 often occur in allometric equations of duration of various physiological processes and thermoconductivity on body mass (Dolnik, 1982b). In birds the relationships between mean longevity and maturity age on body mass indeed usually have the slopes varying between 0.20 – 0.29. The relationship between some anatomical and physiological parameters and longevity shows that brain mass and body mass are a reliable indicator for such analysis (Sacher, 1978). Species-specific growth rate is better predicted by brain mass than by body mass. Brain size related to body mass in praecocial birds is just one-half that value in altricial birds, and their growth rate is much higher (Western & Ssemakula, 1982). In different phylogenetic clades of animals the longest lifespan is found in evolutionary advanced taxa with the most developed brain, but not the largest body size. This means that maximum longevity is typical of the most adapted genotypes that may be smaller than ancestral forms within the same taxa (Golikov, 1985). The example of praecocial and altricial birds supports these conclusions: lifespan of the larger praecocial birds is on average much shorter than in evolutionary more advanced altricial birds, passerines included.

Chapter 4

DETAILS OF DEMOGRAPHIC PARAMETERS AND THEIR DYNAMICS FOR SELECTED SPECIES

4.1. SURVIVAL RATE AND POPULATION REGULATION IN THE GREAT TIT

The Great Tit is one of the world's most studied avian species, probably due to its widespread availability for the study of reproductive processes as a hole nester (by individual marking and recapture of individuals breeding in artificial nest boxes). Over recent decades, detailed studies of all population aspects have been investigated in many areas within the species' breeding range. They have shown that the Great Tit (plate 21), alongside the Pied Flycatcher (plate 37), remains the perfect model species in Palaearctic ornithology. The studies carried out in different Great Tit populations and including the demographic aspects (Payevsky, 2006b) is reviewed here in the framework of population reproduction.

The question of juvenile survival in the Great Tit appeared to be most directly related to the general problem of population density regulation in breeding populations. Lack (1966) concluded on the basis of a long-term study of the Great Tit population near Oxford that the population size is mainly governed by factors acting outside the breeding season, in particular by the mortality rate of juveniles during the first months after fledging. He suggested that survival rate of juveniles before winter mainly depends on foraging conditions, but not on population density, and that all birds that survive until spring gain a territory and breed. This was confirmed by Krebs (1970) who re-analysed the same data. Conversely, Klyuver (1971) suggested on the basis of an equally solid long-term dataset from the Netherlands that the disappearance of Great Tits in the fall is mainly due to emigration caused by territorial behaviour under increasing density. Later studies showed that both proponents were right to some extent (Drent, 1984). Juvenile mortality is indeed a decisive factor which influences the subsequent population density (Perrins, 1980b). Juvenile dispersal whose importance was underestimated by Lack also plays in important role. In early studies estimates of local survival of fledglings were assumed to represent the actual survival of juveniles. In reality, during 1-1.5 months after fledging an explosive dispersal of juveniles takes place, and the data based on recaptures at a single site caused biased estimates. Postfledging dispersal for longer distances results from the years of high population density in further natal dispersal, i.e. birds settle further from their natal sites (Greenwood et al., 1979). However, dispersal distance has no hereditary component in its variation (van Noordwijk, 1983).

To study mortality factors and the relationship between mortality and juvenile dispersal it is necessary to distinguish between three different post-fledging periods, as shown by a study of the Great Tit populations near Groningen and Arnhem in the Netherlands (Drent, 1984). These are the dependent period, critical period, and independent period. During the dependent period (14-20 days after fledging) when fledglings remain in broods with their parents, the first phase of dispersal takes place. During this period and that directly following it the critical period (up to two weeks long) fledgling survival mainly depends on the quality of their parents. If food is in short supply, the parents prolong the dependent period. During the critical period, i.e. during the transition to independence from parents, in many birds their body mass declined by approx. 10% as compared to fledgling mass. Local survival rate of juvenile Great Tits until 1 September in the Netherlands, the number of potential emigrants taken into account, was approx. 42% in males and 35% in females (Drent, 1984).

To estimate the true survival rate of juveniles together with the actual emigration rate A. Dhondt (1979) captured Great Tits in Sweden at their natal site and in adjacent forests. The author confirmed sex-biased dispersal pattern (longer dispersal in females than in males) which had been reported from a Belgian population (Dhondt & Hublé, 1968). Sex-related dispersal was also confirmed by the sex ratio: among locally hatched birds, males were more common, and immigrants included more females. In adults, sex-biased dispersal persists: in a Spanish Great Tit population distance of breeding dispersal was longer for females, even though the tendency to disperse was independent of sex (Andreu & Barba, 2006). A recent follow-up study of Great Tit dispersal in Belgium showed a significant influence of landscape structure of forest plots on dispersal distance (Matthysen & Adriaensen, 2006).

For the Great Tit during the whole autumn and winter period the average weekly mortality rate was ca. 13%, with brood size and fledging date being no significant predictors of mortality (Dhondt, 1979). Mortality rates during the first five weeks after fledging (~ 48%) and the subsequent five weeks (~ 51%) were roughly the same in males but significantly different in females (~ 43 and ~ 61%, respectively). This difference, however, could be due to the females' greater tendency to undergo dispersal. In southern Sweden only ~ 22% of fledged young survive to the beginning of September. Drent (1984) reports a 40% survival rate until early

September in Dutch populations, and Perrins (1980b) states that in England 0.16 – 2.0 juveniles per 1 adult survive until autumn (with 5.6 fledglings per adult). This means up to 35.7% survival rate until autumn.

No clear evidence exists that individuals that undergo dispersal suffer greater mortality that those that do not disperse. In the biogeographic framework, any dispersal has significant consequences. The biological significance of dispersal is the potential range expansion and spatial redistribution of individuals to decrease the risk of inbreeding. This could also be the reason behind the sex-biased dispersal patterns.

Post-fledging survival of juveniles has also been studied in much detail in order to estimate the most productive clutch size. For this reason, recaptures of Great Tits aged more than 3 months were analyzed, and it was found that broods with the average number of fledglings were the most productive ones (Lack, 1958; Klomp, 1980). Other authors did not always confirm this relationship.

A. Dhondt (1979) compared his data with the results from other populations (Dhondt, 1971; Kluyver, 1971) and concluded that generally just 15% of fledged western European Great Tits survive until the next breeding season. This roughly corresponds to one bird per 6 fledglings, and is sufficient to keep the population stable assuming a 50% annual survival rate of adults. It is noteworthy that even though Dhondt (1979) did not find a relationship between brood size and juvenile survival rate, such a correlation was found in a Great Tit population on Gotland where experimental increase of the brood size compromised overwinter survival rate of juveniles (Linden, 1990).

Several studies have shown that large Great Tit fledglings have a greater chance to survive until the next breeding season and to be recruited into the breeding population than their smaller conspecifics (Drent, 1984; Tinbergen & Boerlijst, 1990, Perrins & McCleery, 1999). Larger fledglings grew into larger adults which potentially influenced their chance to gain a territory in spring (Perrins & McCleery, 1999). Females laying large eggs constantly produce more recruits into the breeding population, independently from the simultaneous effect of clutch size and time of breeding. On the other hand, clutch size in the Great Tit is known to have a hereditary component (van Noordwijk et al., 1981), with all size characters (Hõrak et al., 1995). However, body size, egg size and clutch size are all dependent on nutritional conditions experienced by the individual as nestling (e.g. in good or in poor years), i.e. on non-hereditary factors (Hõrak, 1994). Growth conditions also influence immunocompetence of chicks and as a result their subsequent survival (Hõrak et al., 1999a).

Individual morphophysiological characteristics, including width of the ventral black band, body size and mass play an important role in maintaining social status of Great Tits in different seasons and consequently are crucial for winter survival rate and breeding performance (Kerimov et al., 1994).

Sex-related difference in survival rates is usually manifested in higher mortality of females. However, nearly all authors raise doubts in the validity of these results due to the females' longer dispersal distance. Ringing data from different parts of England suggest that juveniles survived better in the years with low population density, but the difference was significant in females only (O'Connor, 1980).

It may be concluded that the mean survival rates of juvenile Great Tits between fledging and the onset of the next breeding season are generally rather similar across different populations, with annual variation within each population taken into account. This value is 13.2% in the Netherlands (Kluijver, 1951), 15 % in southern Sweden, Belgium and the Netherlands (Dhondt, 1979), 18-22% in the UK (Perrins, 1980a,b), 21.9% near Oulu, Finland (Orell & Ojanen, 1979), 11.7-25.7% in the Oka nature reserve, central Russia (Numerov, 1987) and up to 35% in Tomsk, Western Siberia (Moskvitin & Gashkov, 2000). Averaged across the populations studied, survival rate of juvenile Great Tits until the new reproductive season is approx. 15-20%.

Adult survival rates in different populations were estimated by different methods. For comparison, the data available in the literature are given in Table 22, but it should be taken into consideration that the accuracy of estimates varied. Estimates from different populations varied broadly, from 30 to 60%. The former figure seems to be seriously biased. Errors in estimation are often caused by too small a sample size in older age groups, but in the Great Tit they may be additionally introduced through high immigration rate. However, if 6-8 fledglings are produced per breeding pair (Perrins, 1980a; Orell & Ojanen, 1983; Smirnov & Noskov, 1975) and the mean annual survival rate of juveniles is ~ 15-20% (see above), adult survival rate should vary between 28-46% to keep population numbers stable. At least for north-western Russia the mortality rate of adults equal to 69.8% is corroborated by the same proportion of yearlings during spring pre-breeding period (69.7%) and a similar proportion of yearlings at the onset of breeding (73.1%, Smirnov & Noskov, 1975; Smirnov & Tyurin, 1981a).

It is very difficult to estimate variation of mortality rates in different seasons. Few estimates of survival rates of adults during summer have been made. In a Dutch population survival rate of adults between the breeding season and the beginning of September varies between 67–88% in males and 53–66% in females (Drent, 1984). Near Göttingen in Germany the mortality rate of breeding females reaches 32% (Winkel, 1981). Outside the breeding season mortality rate peaks in mid-winter, as mentioned earlier. Ring recovery data from western Russia on the Courish Spit (Payevsky, 1985a) show that frequency of dead recoveries varies between months: they are least common in September (1.1%), uncommon in summer (4.6%), and most common in October – February: 34.5-37.9 %. In March to May this proportion is 21.9%, but a thorough analysis shows that the

Table 22. Survival rate estimates of adult Great Tit in different populations

Study region	Annual survival rate in descending order			Source
	Sexes pooled	Males	Females	
UK	-	0.65	0.57	Dobson, 1987
Belgium	0.60	-	-	Huble & Dhondt, 1973
S Finland	0.56	-	-	Haukioja, 1969
Switzerland	0.536	-	-	Plattner & Sutter, 1947
Finland near Helsinki	0.527	0.553	0.502	Hildén, 1982a
The Netherlands	0.51	0.55	0.48	Kluijver, 1951
England near Oxford	0.500	0.524-0.560	0.466-0.480	Bulmer & Perrins, 1973; Perrins, 1980a; Perrins & McCleery, 1985
Russia, Oka nature reserve	0.484	-	-	Numerov, 1987
France	0.48	-	-	Dejonghe & Czajkowski, 1983
Finland near Oulu	0.444	0.451	0.448	Orell & Ojanen, 1979
England near Oxford	-	0.440	0.410	Clobert et al., 1988
Czech Republic	0.423	-	-	Beklova, 1972
Germany, Braunschweig	0.417	0.429	0.405	Winkel & Frantzen, 1989
W Russia, migrants	0.38	0.38	0.38	Payevsky et al., 1997
Russia, Pskov Region	~0.37	-	-	Bardin, 1988
Estonia: rural population		0.26	0.38	Hõrak & Lebreton, 1998
urban population		0.34	0.47	
Spain	0.36-0.67			Belda et al., 1999
Russia, Siberia, Tomsk	0.302-0.354			Moskvitin & Gashkov, 2000; Gashkov & Moskvitin, 2000
Russia near St. Petersburg	0.302	0.259	0.350	Smirnov & Tyurin, 1981a

real mortality rate of Great Tits in spring, before the onset of breeding, is higher. Generally it contributes a substantial proportion of annual mortality (Slagsvold, 1975; Payevsky, 1985a).

Sex-specific survival rates could be estimated in 9 populations out of 17; in 7 cases males survived better than females (Table 22). Male survival rate has estimated to be lower than for in the opposite sex in just one population (Hõrak & Lebreton, 1998). Indirect data suggest that mortality rate of females was also higher than in males in the population near Paris (Migot & Malher, 1978).

Many authors have discussed the seasonal dynamics of sex and age structure and have suggested that it could be due to differential mortality of different sex and age groups (e.g. Bardin, 1990a; Grishchenko, 1995). In the population of riparian woods of the Ural River females are more numerous among juveniles, but males are more common among adults. This difference is explained by high mortality of females during the breeding period (Levin, 1986). A similar explanation is suggested for a higher proportion of males in winter in southern Finland (Hildén, 1978), but here the reason is probably the higher occurrence of sedentary behaviour in males than in females.

During breeding, broods were more often abandoned by females in better nutritional condition, i.e. individual variation exists in the readiness of females to compromise their own survival in order to reproduce. Nutritional status of males was not related to abandoning broods (Hõrak et al., 1999b). This paper discussed the general problem of energy costs of reproduction vs. survival of adults. Annual mortality rates and clutch size are known to show a close direct relationship (Payevsky, 1985a; Sæther, 1988). A study of this relationship in titmice showed a significant inverse correlation between breeding productivity (number of fledglings per female per season), but not initial fecundity (number of eggs per pair per season), and annual adult survival rate in several Great Tit and Blue Tit populations (Dhondt, 2001). It is appropriate at this point to cite the opinion of Bennett and Owens (2002): "A good example is provided by field manipulations of different species of passerine birds that aim to test a central assumption of life history theory that an increase in fecundity leads to a reduction in survival… Some studies appear to support the assumption while others refute it… Demonstrating a trade-off between survival and reproduction in a single population at a particular time does not mean that this trade-off occurs in all species, or even that the trade-off occurs in all populations of the original species."(p. 8).

Is there a difference in survival rates of adults of different age? Most studies of Great Tit demography do not discuss this issue, because the sample size of older age groups is very small and insufficient for drawing conclusions. It is generally assumed that survival rate of Great Tits, like that of many other passerines, does not change after they become sexually mature, i.e. after the age of one year, except a slight increase until 4 years old and then a decrease afterwards (Bulmer & Perrins, 1973; Perrins & Moss, 1974; Perrins, 1980b). The data from Denmark suggest that annual mortality rate until 3 years old was lower than in older birds (Frederiksen & Larsen, 1980).

Unlike the low survival rate of juveniles that significantly influences the numbers of the breeding population, the adult survival rate seems to be lower and less crucial. This was shown in a correlation analysis of different demographic parameters of Belgian populations (Dhondt & Eyckerman, 1980). Other studies, however, did not yield significant relationships between juvenile survival and the subsequent breeding numbers (Drent, 1984; Tinbergen et al., 1985).

The survival rate of the Great Tits is mainly governed by food and temperature and is positively correlated with tree seed crops and negatively – with the number of frosty days in winter (Tinbergen et al., 1985). Numerous studies of western European populations show that survival rates of broods in oak (*Quercus robur*) forests are considerably higher than in other forest types. Towards the end of summer the attractiveness of oaks as foraging substrate decreases, and speed of dispersal from this habitat increases (Drent, 1984). During the following autumn and winter period, survival of western European juvenile tits is greatly dependent on beech mast which ripens in late September (van Balen, 1980). European beech (*Fagus silvatica*) shapes the winter life of Great Tits to a large degree. Dutch data (Perdeck et al., 2000) show that in the years of poor beech mast crops, providing sunflower seeds in winter increases survival chances of Great Tits. However, beech mast crops do not influence breeding performance during the subsequent summer.

The data derived from different parts of the range show that breeding conditions in urban habitats are poorer than in the country forests, while urban areas are better for wintering due to higher air temperature and additional food (Hõrak, 1993; Hõrak & Lebreton, 1998). In north-western Russia late hatched Great Tits also spend their first winter mainly in urban habitats making use of their richer food supply. However, the proportion of late-hatched birds drops with the progress of winter probably due to mortality (Bojarinova et al., 2002b). In the same populations it was shown that Great Tits from second broods start autumn migration at a younger age (age of commencing migration decreases with hatching date) than the birds from first broods (Bojarinova et al., 2002a). It is possible that starting autumn movements at a younger age compromises survival of late-hatched individuals.

Winter mortality of Great Tits sharply increases with decreasing air temperature, and this occurs not only in especially cold winters (O'Connor, 1980; Zang, 1988). The cold February 1978 decreased the number of Great Tits wintering in the Netherlands by 80%, and breeding numbers by 46%. The subsequent very cold and snowy winter 1978/1979 decreased breeding numbers by 24% (van Balen, 1980). Near Göttingen in Germany that same winter resulted in a threefold reduction of breeding numbers (Winkel, 1981). In the Carpathians the winter 1984/1985 was characterized by low temperatures and deep snow cover. Dead Great Tits were already found in November, and mortality peaked in early January (Guziy, 1988).

The studies in Karelia showed that years of population decline alternate with peak years due to an increased proportion of pairs raising second broods. This means of population regulation is typical of potentially double- or triple-brooded species (Zimin, 1988).

In the Great Tit populations studied, the maximum recorded age was 7 – 15 years (Table 23). The same table contains data on the mean life expectancy of yearlings. This parameter is estimated on the assumption that age-specific mortality rate remains unchanged during the lifetime of the current generation. For the birds in the youngest of age classes, in our case for yearlings, the mean life expectancy equals life expectancy for the whole cohort studied. Young birds that have survived to the beginning of the next breeding season are expected to live on average 11 – 23 months more in different populations studied. Certainly, life expectancy of fledglings is much lower, e.g. in Danish Great Tit populations it is 7.5 months (Frederiksen & Larsen, 1980).

Unlike life expectancy, the mean age is calculated from the number of live individuals in each age class. The mean age of a Great Tit population studied near Oulu, Finland, is 1.8 years, whereas their life expectancy is 1.3 years (Orell & Ojanen, 1979). In a population near St. Petersburg, Russia, the mean age is 1.4 years, and life expectancy is 0.93 years (Smirnov & Tyurin, 1981). Near Oxford in England the mean age of females is 1.91 years, of males 2.47 years, and the mean life expectancy is 1.5 years (Perrins, 1980b).

A relationship between age composition of breeding pairs, their stability and breeding performance is very interesting. As in other avian species, yearling Great Tits perform poorer than older individuals in all aspects of reproductive activity (Perrins & Moss, 1974; Winkel, 1975). However, the relationship between age of breeding pairs and their contribution to population reproduction is not straightforward: During increasing population pairs of old individuals reproduce more, whereas during population decline young individuals perform better. Pairs formed by birds of the same age are significantly more frequent than uneven marriages (Vilbaste & Leivits, 1986). The existence of this mechanism is complicated by considerable emigration and immigration rates, and by frequent separations. Estonian data suggest a stability of pair bonds in the Great Tit (Vilbaste, 1975), but a separation rate of 33% in pairs with both members surviving to the next breeding season was reported in England (Perrins & McCleery, 1985).

Table 23. Longevity of Great Tits

Study region and source	**Lifespan (years)**					
	Maximum			Mean expectation		
	Sex unknown	Male	Female	Sex unknown	Male	Female
Germany (Rydzewski, 1978)	15					
UK (Spencer, 1962)	10					
France (Dejonghe & Czajkowski, 1983)	10			1.4		
England (Keen, 1972)			10			
The Netherlands (Kluijver, 1951)	9			1.5		
France (Crousaz, 1959)	9					
Czech Republic (Beklova, 1972)	8			1.2		
Switzerland (Rydzewski, 1978)	8					
Data from the USSR (Rydzewski, 1978)	8					
The Netherlands (van Balen et al., 1987)			8		1.9	1.7
Germany (Winkel & Frantzen, 1989)			8			
Russia, Pskov region (Bardin, 1988)	8					
England (Greenwood et al., 1979)		8	7			
W Russia (Payevsky, 1985a)			7	0.9		
England (Bulmer & Perrins, 1973)					1.8	1.4
Finland (Haukioja, 1969)				1.7		
Finland (Orell & Ojanen, 1979)					1.3	1.3
Russia near St. Petersburg (Smirnov & Tyurin, 1981b)		5	6	0.9	0.8	1.0

Extra-pair paternity was found in 28-44% of Great Tit broods, and 5 to 9% of all nestlings studied carried the genes of fathers other than social partners of their mothers. However, no difference in recruitment rate between extra-pair young and 'legitimate' young was found (Lubjuhn, 1999). Extra-pair paternity seems to be shaped by some factors other than the genetic quality of biological fathers. It seems that factors other than genetic quality of males play a role in the occurrence of extra-pair paternity, even though the two main hypotheses suggested to explain involvement of females in extra-pair copulations are the "good genes hypothesis" and "assortative genes hypothesis". Recent studies have failed to support the good genes hypothesis, but it was found that nestlings from certain assortative combinations of pairs had higher chances to father extra-pair young than nestlings from disassortative pairs (van Oers et al., 2006).

In spite of the tendency to form pair bonds between individuals of the same age or between an older male and a younger female (Greenwood et al., 1979; Kerimov & Ivankina, 1991; Saitou, 1991), instability of pair composition from one breeding season to the next one greatly hampers the study of the age-related breeding performance. Nevertheless, in British populations the breeding performance was shown to peak at the age of 2-4 years and to decrease progressively from the age of 5 years (Perrins & Moss, 1974; Perrins, 1980b). Roughly the same pattern was shown in Belgian populations where the largest and most valuable territories were occupied by 3-5-year-old males, whereas older males had smaller territories of poorer quality. In the females from the age of 5 years onwards all reproductive parameters were lower than in 2-3-year-olds (Dhondt, 1987).

In a Dutch study the lifetime reproductive success of Great Tits was studied, i.e. number of recruits into the breeding population produced during the lifetime (van Balen et al., 1987). Of the five components of lifetime reproductive success (longevity of parents, number of breeding attempts per season, clutch size, number of fledglings per egg laid, proportion of recruits per fledgling), the most important were the proportion of recruits per fledgling and longevity of parents. A most interesting result of this study is that nearly one-half of females in the population do not produce any recruits into the breeding population. One-half of recruits are produced by 11% of breeding females. It is also noteworthy that most recruits are produced during the first breeding season of an adult.

In conclusion I construct the parameters of a hypothetical average Great Tit population. Let the birth rate (as number of female fledglings per breeding female) be 3.6, the average value from different populations, and adult survival rate 47.0%. Let us assume that juvenile survival rate, the demographic parameter showing most within-population variation, vary between 10 and 26%, and that birth rate and adult survival are the same in different age cohorts of adults. Then the net reproduction rate R_o, i.e. the expected number of surviving female offspring, is equal to $\Sigma \ell_x m_x$, where ℓ_x is survival, and m_x is birth rate, will vary between 0.673 and 1.761. This corresponds to a declining (under 0.673), stable (under 1.027), or growing (under 1.761) population. In all three populations, the most input into reproduction will be made by females aged between 1 year (yearlings) and 3 years. The net annual growth rate (λ) of the populations is equal to $R_o^{1/T}$, where $T = \Sigma x \ell_x m_x / \Sigma \ell_x m_x$, i.e. the mean generation time. Growth rate will be 1.014 which corresponds to a practically stable population, under the 85% juvenile mortality rate. Under the juvenile mortality rate of 74% the population can grow by 35% per annum ($\lambda = 1.353$), and if this parameter equals to 90%, the population will decline by 19% per annum ($\lambda = 0.806$).

4.2. POPULATION PARAMETERS OF THE LESSER WHITETHROAT

The Lesser Whitethroat is a common warbler species in the Baltic area (plate 22). It reaches a very high breeding density on the Courish Spit, in some years up to 60 pairs per km^2 in optimal habitats of loose young Mountain pine and Scots pine plantations (Vinogradova, 1983; Payevsky, 1999a).

The population ecology of this species on the Courish Spit has been studied over many years (Vinogradova, 1983; Payevsky, 1992a; Payevsky, 1999a). Population trends of Lesser Whitethroats, along with other species have also been discussed by several authors (Dolnik & Payevsky, 1979; Payevsky, 1990a; Sokolov, 1999a; Sokolov, 1999). From 1959 to 1974, their numbers were increasing significantly, and in subsequent years they remained stable, unlike other *Sylvia* warblers. An analysis of trends from 1974 to 1990 for local breeding adult and juveniles and numbers captured on the Courish Spit, together with trends in numbers of Lesser Whitethroat nests found on the Courish Spit, showed that the numbers of this species have remained reasonably stable (Fig. 16, Table 24). Similar trends derived from these different datasets are supportive.

The full clutch size of Lesser Whitethroats from 1959 to 1995 varied between 3 and 6 eggs, on average 5.13. The proportion of clutches with the maximum number of eggs in this species (19.6%) was significantly higher than in other *Sylvia* species (1-11%). This may be an indirect indication of the demographic stability of local population. Mean clutch size declines with the breeding season from 5.50 ± 0.15 in mid May to 4.46 ± 0.28 in early July ($r = -0.975$, $p < 0.001$).

Clutch size and breeding performance were separately analysed for the 1960s, 1970s, and 1980s. In the 1960s clutch size was significantly ($p < 0.05$)

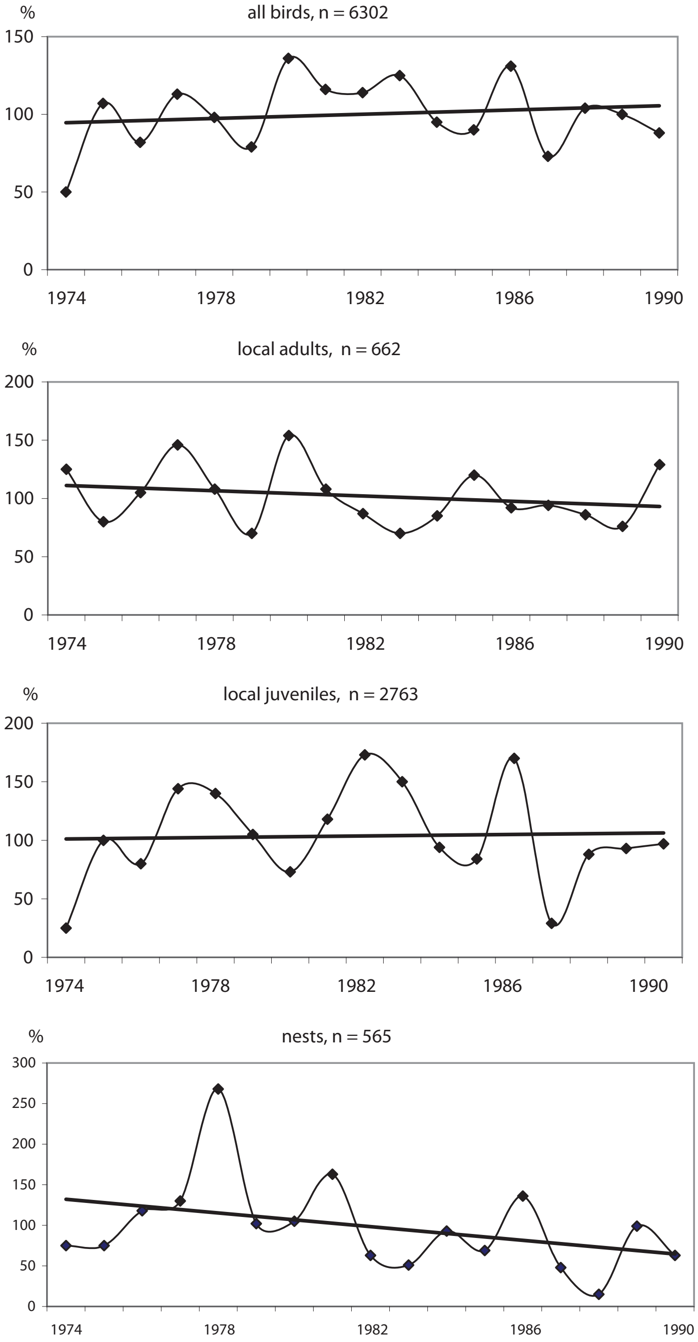


Fig. 16. Trends of numbers in different classes of Lesser Whitethroats in the breeding season based on trapping data and nest search data from 1974 to1990.

Table 24. Population trends of the Lesser Whitethroat in 1974-1990, from capture data and nest records, Kendall rank correlation (τ).

Variable	Value	Significance
Trapping total	6302	
Annual range	177-493	
Mean	371	
τ	+ 0.022	n.s.
Local individuals		
Adults, total	662	
Annual range	25-35	
Mean	39	
τ	- 0.111	n.s.
Juveniles, total	2763	
Annual range	35-268	
Mean	162	
τ	+ 0.044	n.s.
Nests found, total	565	
Annual range	5-99	
Mean	33	
τ	- 0.274	n.s.

larger than in the 1970s (5.25 vs. 5.06), whereas the values obtained in the 1970s and the 1980s showed no significant change. This could be explained by the population growth from 1959-1974. However, breeding success rate calculated according to Mayfield (1975) showed no significant difference in these decades, varying between 61.7 and 66.5% (43.8% to 74.0% in particular years). Each breeding pair produced on average 4.3 fledglings. It is worth noting that very similar breeding success rate (64.2%) was reported for this species from the southern Lake Ladoga coast (Muzaev, 1981).

To estimate survival rate in the study population, ringing results over 32 years (1957-1988) were used. A total 8980 Lesser Whitethroats were captured and 1160 individuals produced a total of 1677 recaptures (both within and between seasons). We used Jolly-Seber model in the modification of Pollock et al. (1990). The model assumed that 1) capture events occurred at the same time each year, i.e. in summer; 2) both survival and capture probability were age- and time-dependent; 3) the population was open, i.e. immigration and emigration occurred. The results are presented in Table 25.

Annual capture probability of adults varied between 1.1 and 6.2%, on average 2.6%. This is a low value, because local birds *sensu stricto* and other breeders were not distinguished, therefore this capture probability is an average across approximately 1400 individuals of the potential study population. The size of the

Table 25. Demographic parameters of the Lesser Whitethroat population estimated by Cormack-Jolly-Seber model after Pollock et al. (1990)

Year	N_i	M_i	f_i	SE_f	φ_i	SE_φ
1968	2808	54	0.011	0.008	0.724	0.366
1969	1271	113	0.025	0.012	(1.026)	0.728
1970	2767	200	0.014	0.009	0.278	0.191
1971	2182	77	0.016	0.010	0.428	0.205
1972	952	68	0.027	0.010	0.134	0.066
1973	207	30	0.062	0.025	(2.289)	1.801
1974	2161	190	0.013	0.010	0.114	0.108
1975	318	31	0.033	0.022	0.794	0.370
1976	2349	54	0.011	0.008	0.122	0.064
1977	210	17	0.050	0.021	0.729	0.266
1978	1318	62	0.024	0.012	0.965	0.433
1979	621	138	0.040	0.019	0.838	0.419
1980	1462	145	0.030	0.011	0.591	0.258
1981	2400	150	0.021	0.009	(1.106)	0.703
1982	1487	282	0.020	0.012	0.280	0.226
1983	418	92	0.033	0.019	0.275	0.220
1984	502	38	0.028	0.016	0.364	0.257
1985	729	36	0.022	0.013	0.487	0.338
1986	1100	55	0.018	0.011	0.413	0.295
1987	2248	62	0.013	0.008	0.571	0.490
Mean	1376	95	0.026	0.003	0.477	0.071

Notes: N_i – population size in year *i*, M_i – number of marked individuals recorded in year *i* that have been captured and ringed before year *i*, f_i – capture probability, φ_i – probability of survival from *i* to *i* + 1, *SE* – standard errors.

controlled population was on average 1376 with annual variation between 210 and 2808. Such a broad range is unexpected and unlikely to be realistic, as no accompanying breeding success fluctuation was recorded.

Annual survival rate of adults varied between 11.4 and 100% (with three biologically invalid values exceeding 100%); omitting the latter values yields an average of 47.7%. The range of annual fluctuation is too broad to be treated as realistic. However, the mean value is an expected one and rather similar with the survival rate (43.5%) of adult Lesser Whitethroats reported from Lincolnshire (England; Boddy, 1994).

Comparing the survival rate estimate with other demographic parameters reveals that to support stable populations, with a 48% adult annual survival rate and a production of 4.3 fledglings per breeding pair, mortality rate of juvenile Lesser Whitethroats from fledging to the onset of the subsequent breeding season needs to be about 76%.

4.3. ANALYSIS OF THE CAUSES OF THE BARRED WARBLER POPULATION COLLAPSE

Among avian species monitored on the Courish Spit, the most rapid population decline resulting in local extinction occurred in the Barred Warbler (Vinogradova, 1988; Payevsky, 1999a). To understand the causes of this population collapse, it was necessary to study all demographic parameters and biometric features of adults and juveniles. The analysis of trends in number, survival rate, and body size was based on the data collected over 41 years, from 1960 to 2000 (Payevsky et al., 2003). The main aims of the analysis were to identify the numbers of surviving adults and the recruitment into the breeding population in different periods of time, and to find out whether the decline in numbers was accompanied by changing productivity or physical condition of the birds.

Over the study period, 2342 Barred Warblers were captured (plate 23), including 1949 local breeders (1230 adults and 719 juveniles). A total of 566 nests were found, of them 371 nests with clutches or nestlings. It was assumed that the permanently operating Rybachy-type traps would control the same local population each year, and that trapping figures are a proxy for population numbers (even though estimates from capture-mark-recapture models make it possible to analyse the change in numbers more reliably than trapping figures alone). For analysis of body size of juveniles, birds captured in June – August at the age of 24 – 49 days were selected. Median body mass in both adults and juveniles showed no significant variation with the time of day (one-way Kruskal-Wallis test).

The following demographic parameters were estimated (Pradel, 1996; Nichols et al., 2000; Cooch & White, 2006): Annual apparent survival rate φ_i, population growth rate $\lambda_i = N_{i+1}/N_i$, where N_i is the population size during sampling event i; and seniority γ_i which is the probability that an individual alive and in the population during sampling event i was alive and in the population during sampling event i-1. Seniority estimate (Nichols et al., 2000) makes it possible to obtain information on the relative contributions of two demographic parameters for population growth: Adults surviving since the previous breeding season and recruits ($1- \gamma$) due for reproduction and/or immigration. All these parameters were modelled as time-dependent. Programme MARK (see section 2.5) was used for computations with subprogrammes “Pradel Survival and Lambda” and “Pradel Recruitment Only”. Model selection was on the basis of Akaike’s Information Criterion (AIC, Burnham & Anderson, 2002). A total of 1158 recaptures of 1046 individuals were analysed.

Population trends were analysed by Spearman’ rank correlation, where one variable was year, and the other one – trapping figures, adults and juveniles separately. For comparison, the annual number of nests found was also analysed (Fig. 17). In the first years of study, numbers of trapped Barred Warblers were growing,

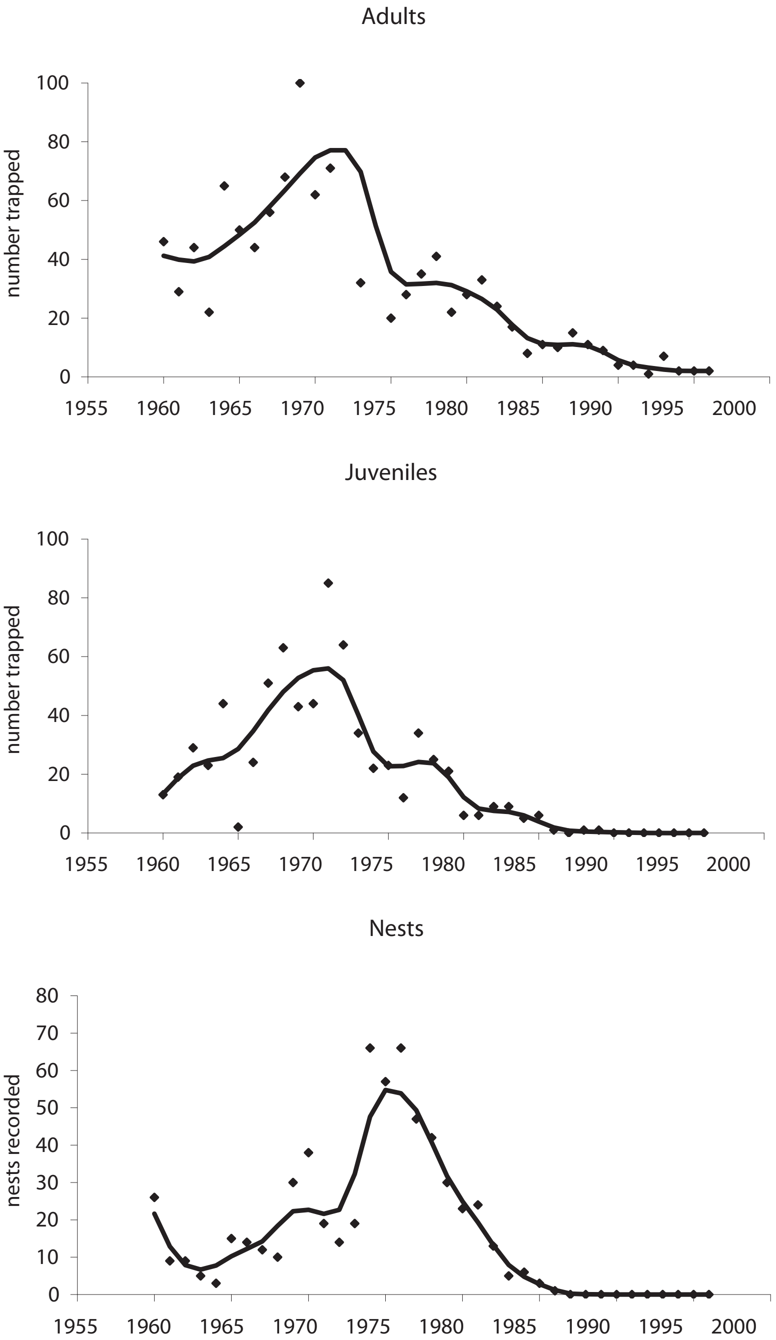


Fig. 17. Changes in Barred Warbler numbers in the breeding season based on capture data and nest search data from 1960 to 2000.

and then they declined sharply. The maximum annual number was the transition between these two periods. During the period of decline, coefficient of correlation was -0.945 for juvenile numbers, -0.939 for adult numbers, and -0.884 for number of nests. The peak number of nests found in 1974-1976 coincided with the onset of the period of population decline, as shown by trapping figures, and was due to more intensive nest searches across the whole study area.

Clutch size and breeding success were studied separately for 1959-1970, 1971-1980, and 1981-1986. The mean clutch size in the 1960s (4.96 ± 0.05) was significantly larger ($t = 2.2$, $p < 0.05$) than in the 1970s (4.83 ± 0,04), but did not differ from the value recorded in the 1980s (4.94 ± 0.09). Breeding success, as a percentage of successful nests amongst all monitored nests, was higher in the 1970s (67.6% ± 0.6) than in the 1960s (59.5% ± 1.2; $\chi^2 = 8.3$, df =1, $p < 0.01$). In the 1980s it was roughly the same (67.0% ± 1.6) as in the 1970s ($\chi^2 = 0.1$, df = 1, n.s.). No clear explanation could be found for the decline in numbers. The juvenile to adult ratio varied without a definite trend over these years, and only in 1986 did it drop to zero (Fig. 18).

Body mass of adult males and females did not show significant annual variation (Kruskall-Wallis test, males: 40.53, $p = 0.12$; females: 25.04, $p = 0.67$), unlike body mass of juveniles (41.60, $p = 0.007$). However, the range of annual variation of mean body mass was too small (< 3% of the mean) to be biologically meaningful. Fat score varied significantly between the years in juveniles (Kruskall-Wallis test, 95.48, $p < 0.0001$) and in adult males (61.65, $p < 0.0001$), but not in adult females (39.62, $p = 0.07$). Most importantly, in the years directly preceding extinction fat scores were not below average. The analysis of wing length data did not show any significant change during the period of population decline, either.

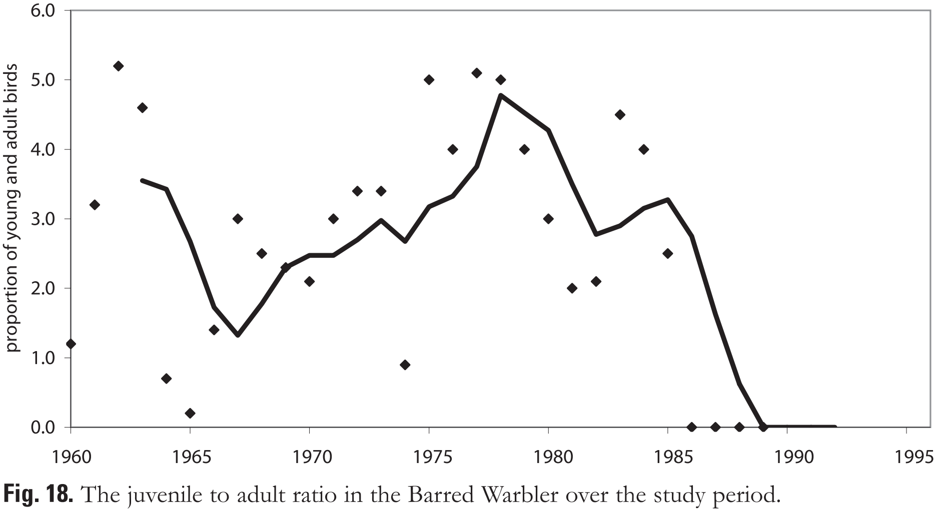


Fig. 18. The juvenile to adult ratio in the Barred Warbler over the study period.

Annual survival rate estimates showed that survival constantly declined and dropped practically to zero by 1983 (Fig. 19). Since then, Barred Warblers ceased to return to the population, and only some immigrants bred on the Courish Spit. After 1983, solitary Barred Warbler individuals were occasionally recorded in the area where a large population had once bred, but no nests were found.

The analysis shows that no productivity parameter (clutch size, breeding success, juvenile : adult ratio) changed before extinction, even though these parameters did fluctuate in some decades. Body size, mass and fat score showed no significant trends. It suggests that breeding conditions of this population remained normal. The only parameter that dropped to zero was local survival rate of adult birds, suggesting that the cause of extinction was some factor acting outside the summer range.

Numbers of some other European Barred Warbler populations varied considerably. This has been reported from Sweden, Germany, Czech Republic (Cramp, 1992), Austria and Finland (Shirihai et al., 2001). The West Berlin population be-

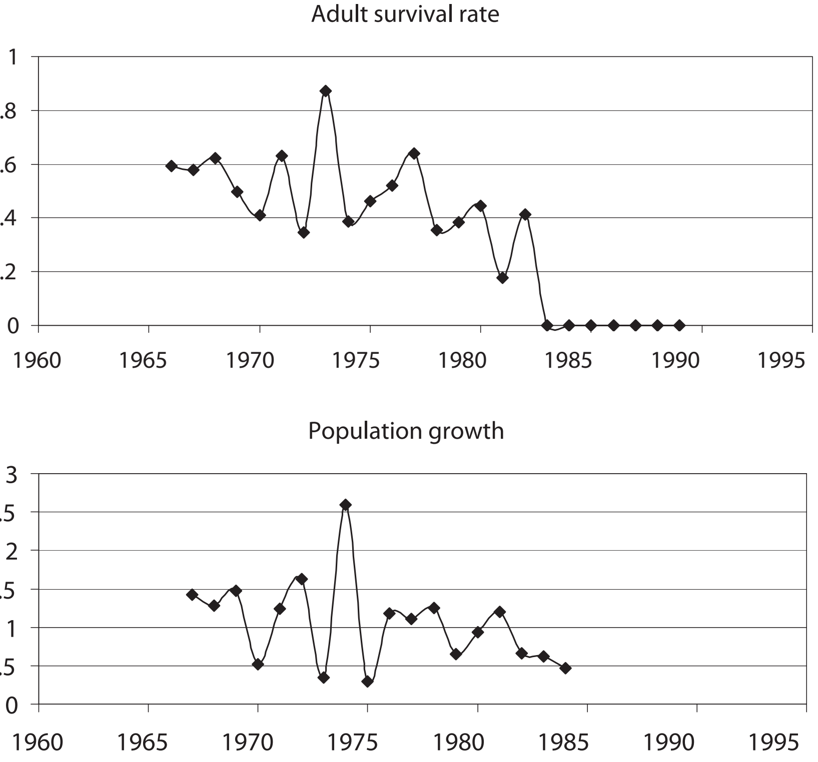


Fig. 19. Annual variation in adult survival rate and population growth rate in the Barred Warbler.

came extinct (Cramp, 1992). The reason for the decline was believed to have been climatic and habitat change (Wassmann, 1986). The overall very rough estimate of Barred Warbler numbers in European Russia is 250 – 650 thousand pairs, with an unknown trend (Mischenko, 2004). In the late 20th century the status of this species was defined as comparatively safe but in need of attention (Tucker & Dixon, 1997; Kondratiev, 2000). However in some regions, e.g. in East Fennoscandia, the Barred Warbler is treated as potentially vulnerable (Kotiranta et al., 1998). An unexpected arrival of Barred Warblers was recorded between mid August – mid September 2002 at many coastal sites in Norway (Solbakken, 2003).

An analysis of capture data of five *Sylvia* species from six European bird observatories made by P. Busse (Busse et al., 1995) suggested that all species suffered significant declines at all sites. However, in my opinion, the data on each species at different sites do not always warrant such a conclusion. Concerning the Barred Warbler, the dynamics of this species presented by P. Busse was similar to our data because it was mainly based on trapping figures from the Courish Spit and Sweden.

Some publications have presented a detailed description of the Barred Warbler population under study (Vinogradova, 1986, 1988; Payevsky, 1999a). The latter two papers discuss the possible causes of population decline and emphasize the importance of habitat change: growth of the pine forest, cutting down the scrub, change of structure of grass layer, and competition between *Sylvia* species. However, other possible reasons cannot be ruled out.

Dynamics of Barred Warbler numbers similar to the one recorded on the Courish Spit mirror capture data at Ottenby ornithological station in Sweden (Pettersson, 1997) and in Kabli (Estonia; unpublished data kindly provided by A. Leivits; Fig. 20). Similar trends in different countries suggest action of some factors that act across broad areas either on the breeding grounds, or at migratory stopovers or in the wintering area. The global climate change is a likely candidate.

These trends or patterns that may result from negative factors acting outside the breeding season may similarly influence other Baltic populations. Population declines in several Palaearctic migrants are known to be caused by severe droughts in their African winter quarters (Hjort & Lindholm, 1978; Den Held, 1981; Svensson, 1985; Jones, 1986; Peach et al., 1991). The Barred Warbler winters within a relatively limited area in East Africa, mainly in Kenya and in East Uganda and North Tanzania (Cramp, 1992, Shirihai et al., 2001). Apart from these areas, the birds have been recorded in winter in other parts of Africa (Shirihai et al., 2001). It remains unknown where exactly Baltic Barred Warblers spend their winter, because solitary recoveries of Finland and Baltic-ringed birds are only available from the intermediate staging area, from Syria and Lebanon (Bolshakov et al., 2001).

The main wintering area of the Barred Warbler in Kenya is subject to severe droughts. The data on mean monthly precipitation and air temperature in Kenya

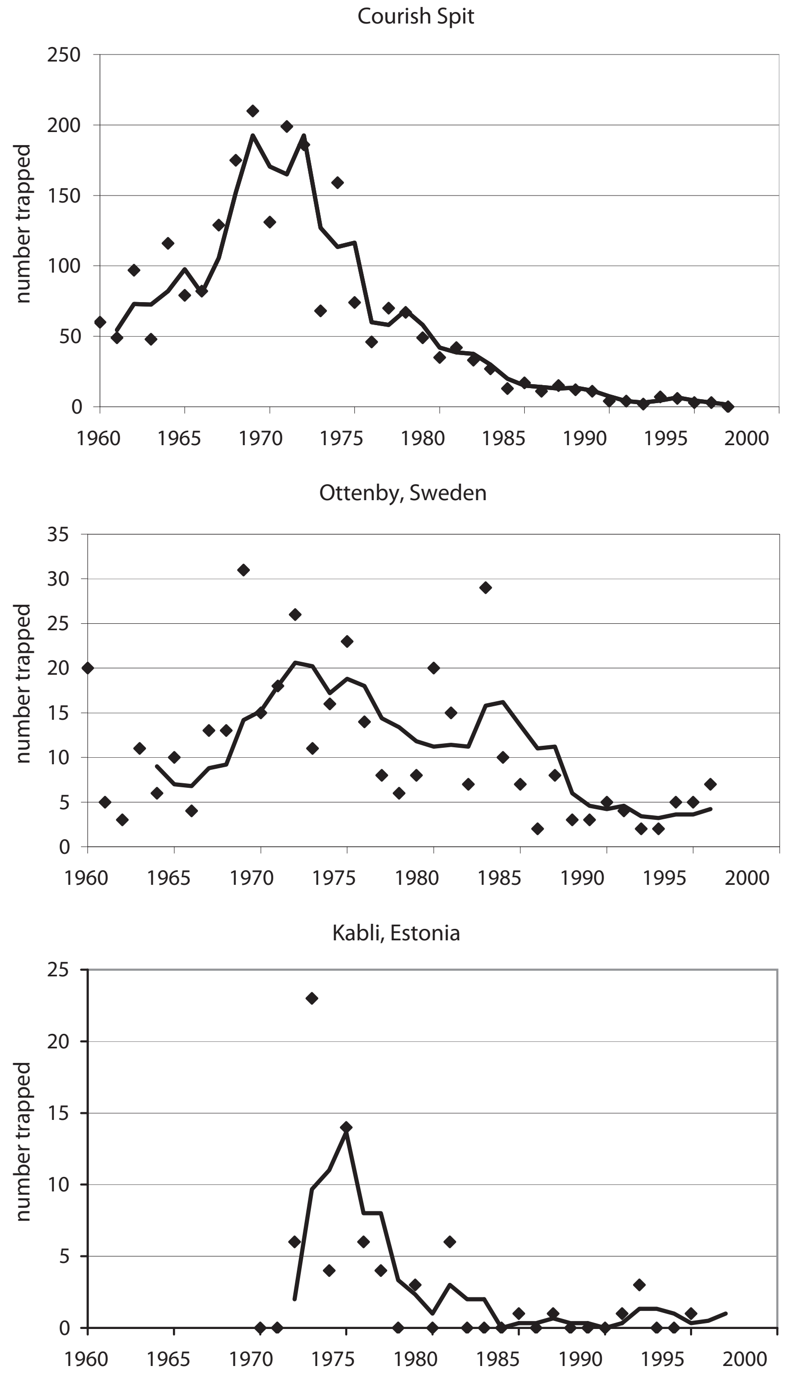


Fig. 20. Changes in Barred Warbler numbers inferred from trapping data from different Baltic sites.

in January and February (Mitchell et al., 2002) show that the years when our study population was becoming extinct (the early 1980s) were the years with abnormally low precipitation and high air temperature. The combination of these factors probably sharply increased the mortality rate of wintering Barred Warblers. Population growth in the 1960s (Fig. 17) coincided with a wet period in winter quarters.

A comparison of the main African wintering areas of the five *Sylvia* species common in North and Central Europe shows that the Barred Warbler has the smallest winter range which is located in the area subject to extreme droughts. The most severe drought in Africa during the recent decades was recorded in December – January 1982-1983 (Dai et al., 1998). This is exactly the time when our study population became extinct. In 1983 and 1984, the number of trans-Sahara migrants captured at the Swedish Falsterbo bird observatory also declined sharply (Karlsson et al., 2002).

The resulting facts allow us to assume that droughts in Africa were the main factor causing changes in the dynamics of Barred Warbler numbers in the Eastern Baltic.

4.4. ASPECTS OF THE WILLOW WARBLER DEMOGRAPHY

The Willow Warbler (plate 25) is one of the most common songbirds across its vast Eurasian range. The Willow Warbler in second only to the Chaffinch in abundance amongst the avian species occurring in the East European plain (Ravkin & Ravkin, 2005). Its territorial behaviour, breeding biology, moult and migration in north-western Russia and Eastern Baltic are rather well studied. The dynamics of its numbers in this region has been analysed in a number of publications (Dolnik & Payevsky, 1979; Payevsky, 1985a; 1990a; Sokolov, 1999; Sokolov et al., 2000). Over 40 years, from 1957-1996, a large dataset that allows us to estimate demographic parameters of the Willow Warbler population has been collected on the Courish Spit (Payevsky, 1991c, 1994б; Payevsky, 2000b).

From 1957 to 1996, a total of 122879 Willow Warblers (including recaptures) were caught at Fringilla, three thousand per year on average. The percentage of recaptures of local birds in the subsequent years is 6.7% among adults, 7.9% among juveniles, and 7.3% among birds ringed as nestlings (Sokolov, 1991a). Compared with the data from the northern part of Tyumen Region (Shutov, 1986), this is three-fold more in juveniles but three-fold less in adults.

All habitats suitable for the Willow Warbler were in the study area of about 1.5 km^2, centred at the field station. Breeding density of the Willow Warbler was calculated by two methods. The first method was based on capture probability. Stochastic models run by programme JOLLY (Pollock et al., 1990) estimate capture probability as 0.30 for males and 0.35 for females. Capture probability can also be estimated empirically from the number of summer seasons when the birds were not captured but were alive, as they were captured in subsequent seasons (Dolnik & Payevsky, 1982). In this case the same estimate 0.30 was obtained for the males.

Breeding density was calculated as follows:

During the 10 years from 1972 to 1983 (except for 1974 and 1980 when spring passage moved towards a later time), 650 males were captured in the breeding period (21 May – 29 July), on average 65 males annually. Taking into account capture probability of 0.30, this means that the number of pairs in the monitored 1.5 km^2 area was 217, or 145 pairs per 1 km^2. One can check whether this figure was realistic by comparing it with the number of Willow Warbler nests found at different search intensity. In the most searched area near the stationary traps 3-6 nests were found when no special attention to the Willow Warbler was made and up to 26 nests if special efforts were made. This means that over the whole study area approximately one-sixth of the Willow Warbler nests were found. In 1984-1989, 113 nests were found, i.e. 19 nests per season. This means that the real density was minimum 114 pairs per 1.5 km^2, or 76 pairs per 1 km^2.

Thus it can be concluded that breeding density of the Willow Warbler population studied varied approximately between 80 and 150 pairs·km^{-2}. These figures are close to the data reported from the most densely populated habitats of Poland (120-200 pairs·km^{-2}; Tomiałojć & Stawarczyk, 2003), Swedish Lapland (108-157 pairs·km^{-2}; Arvidson & Nilsson, 1983), south Finland (71 pairs·km^{-2}; Tiainen et al., 1983), southeast Lake Ladoga coast (180-320, on average 112 pairs·km^{-2}; Noskov et al., 1981; Lapshin, 2000), the Yamal Peninsula (102 pairs·km^{-2}; Danilov et al., 1984), the Subarctic Urals (70 pairs·km^{-2}; Shutov, 1990a).

Most Willow Warblers formed monogamous pairs, and both parents fed the young. However, of the 50 nests that were closely observed, in 11 the males were never recorded either during incubation or when feeding the young. Special studies of mating relationships in the Willow Warbler on the Courish Spit with marked individuals (Ilyina, 1991) showed that polygamy was recorded in three cases out of 24. In one case a yearling male attracted a secondary female when the nestlings in his first nest were 11 days old. This male helped feeding in both nests. In another case a yearling male successfully bred with a two-year-old female, and in the next year the same pair was found at their old breeding place as a part of a polygamous quartet. When two-years old, this male was consecutive trigamous: He paired with a three-year old female, then with a two-year-old female, and then with the female with which he bred the previous year (she was three-year old by now). Breeding of the first two females was successful from the first attempt, and of the third female only from the second attempt. The male fed the nestlings only in this first nest. In the next year this male (he was three-year-old by then) returned to his territory and simultaneously mated two females: one yearling one and one with which he bred each year (she was four-year-old now). When both females were incubating, the male tried to attract the third female, but without success. Breeding was successful in both females, and the male fed the young in both nests, but devoted more efforts to the first one.

These facts show, first, the potential constancy of pair bonds, in spite of the very small probability of simultaneous survival of both birds until the next breeding season, and second, a small but regular level of polygyny in the Willow Warbler. The main stimulus is probably territory fidelity and not personal bonds. The males are more faithful to their old breeding territory than females. This has been reported from different parts of the Willow Warbler range, from Finland (Tiainen, 1983a) to England (Pratt & Peach, 1991). This sex-biased site fidelity is formed during postfledging movements when females disperse at younger age and further (Norman, 1994). However, site fidelity of male Willow Warblers significantly differs between sites, probably due to varying habitat quality (Lawn, 1994).

Facultative polygyny has been reported also from other parts of the Willow Warbler range. In the Arctic Urals in some years up to 50% of males were bigamous (Shutov, 1990b), and in Karelia polygyny was reported in 10% of males from long-term data (Lapshin, 1983). In southern England in 172 breeding territories 11 bigamous males were recorded, five of them had secondary territories (Lawn, 1982). Polygyny also exists in other *Phylloscopus* warblers, the Wood Warbler and the Chiffchaff; the annual proportion of bigamous males in optimal habitats varies strongly, between 0 and 40% (Wesołowski, 1987).

In many avian species facultative polygyny is known to be more typical of adult males than of yearlings (Payevsky, 1985a). The existence of yearling polygynous males in the Willow Warbler means that this form of mating relationships is a regular event in the population, and maybe typical of the species as a whole, rather than an incidental occurrence. The biological advantage of the polygyny in the described form is to maximise the number of offspring from the most active and the fittest individuals. This is supported by their relatively long lives. The bulk of the population consists of yearlings and two-year-old birds (see section 3.1); nevertheless, older birds, in spite of their scarceness, make a significant contribution to the population reproduction. However, the polygyny may have ambiguous consequences for the population. As secondary females raise their young alone, in the years with adverse weather and foraging conditions the young from such nests may suffer increased mortality already after fledging. This is supported by their complete absence in the subsequent breeding seasons and generally indicates the diverse impacts of polygyny on the population numbers in relation to extrinsic factors (Shutov, 1990b).

The full Willow Warbler clutch on the Courish Spit contains 4 to 7 eggs, on average 6.11 ± 0.08 (n = 94). The mean varies between 5.00 and 6.50 between different 5-day periods, but shows no calendar trend (Spearman rank correlation, $r_s = 0.48$, n = 6, n.s.). Brood size was mainly recorded when ringing, i.e. at the age of 7 – 12 days, and varied between 2 and 7 nestlings, on average 5.55 ± 0.13 (n = 89). Breeding success rate was calculated after Mayfield (1975) was 62.4 ± 2.6%.

The overall population productivity could only be estimated when the number of repeat breeding attempts after the failed ones is known. Presumably repeat breeding attempts more often occur after a clutch loss or desertion than after a brood loss. If one assumes a complete clutch size of 6.11 and the probability of survival until fledging of 62.4%, one breeding pair produces on average 3.81 fledglings, or 1.91 fledglings per adult bird. This value is higher than the 1.4 fledglings per adult reported from southern Finland (Tiainen, 1983b).

Sexing of captured Willow Warblers is possible not only during breeding by cloacal protuberance of males and incubation patch of females, but also in other seasons by size. The easiest to measure size indicator is wing length. Sex-related difference in wing length makes it possible to identify sex reliably in most Willow Warblers, even though the range of size variation in different age and sex groups somewhat differs as reported by different authors (Niemeyer, 1969a; Fonstad & Hogstad, 1981; Schönfeld, 1982; Tynjälä et al., 1994; Lapshin, 1998). Sexing reliability in the Willow Warblers captured on the Courish Spit was tested by post mortem made on 192 birds killed by raptors and Jays in traps in 1959-1980. Outside the breeding season wing length (in mm) of adult males was 65-74, on average 69.4 ± 0.2, young males 65-73, on average 68.5 ± 0.2, adult females 61-67, on average 64.0 ± 0.3, young females 59-67, on average 63.2 ± 0.3 (Fig. 21). This means that all Willow Warblers with wing length exceeding 67 mm are males, and all birds with wings shorter than 65 mm are females. In the overlap zone (65-67 mm) remain 4 to 24, on average 12% of adults, and 21 to 32, on average 25% of juveniles. The frequencies of the theoretical Gaussian distribution give us the most probable percentage of birds of different sex and age for each wing length value in the overlap zone. Birds with the wing length of 65 mm include 6.5% of adult males and 12.1 % of juvenile males, with the wing length of 66 mm – 25.6% and 50,8.%, respectively, and with the wing length of 67 mm – 63.2% and 84.8%, respectively.

Is it possible to ignore the birds with the wing length values in the overlap zone when calculating sex ratio? To answer this question, it is necessary to find out whether sex ratios in the birds with wing lengths within the overlap zone and outside this zone differ. For this analysis, we used Willow Warbler capture data for 1980, when due to late migration sufficient numbers of birds were captured in each calendar period. We calculated the proportion of males with wing lengths

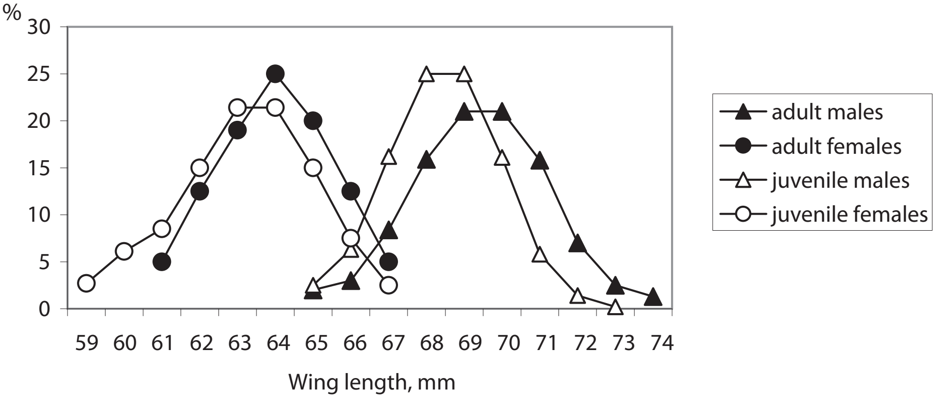


Fig. 21. Wing lengths in sex and age groups of the Willow Warbler, based on measurements of 4956 individuals captured in 1980.

within and outside the overlap zone in different 10-day periods of the year. In only one case (the last 10-day period of May) the difference was marginally significant (t = 1.96, df = 656, p = 0.05). In all other 10-day periods it was not significant, thus sex ratio in the Willow Warbler may be estimated by ignoring the birds in the overlap zone and assuming that all birds with wing length >67 mm are males and all birds with wing length <65 mm are females.

Sex ratio was estimated from the 12 years of capture data, 1972-1983, when trapping figures in different periods of the year were most representative. The first step had to be the estimation of annual variation in the dataset. Each sex and age cohort had significant annual heterogeneity of variation as shown by the Bartlett test. However, pairwise comparisons of all annual samples showed a positive relationship between numbers of Willow Warblers captured in the same 10-day periods in different years (coefficient of correlation was not below 0.7 in all cases). This allowed the pooling of the long-term data for analysis.

The proportion of males among Willow Warblers across the twenty 10-day periods when these birds are present in our study area varied very widely among adults, between 13 and 92%, and less widely among juveniles, between 46 and 67% (Table 26). During the breeding season, the males outnumber females until the beginning of the second 10-day period of July, but then, during the rest of July, the females become more numerous. Later, during the postbreeding movements, males again outnumber the opposite sex among adults. The average proportion of males in the period between the appearance of the independent young until the end of passage is 58.9 ± 1.4%.

Recaptures of Willow Warblers ringed as nestlings make it possible to estimate the sex ratio of pulli. In only one nest all nestlings were subsequently re-

Table 26. Sex ratio in the Willow Warbler in different 10-day periods of the year after capture. Data from1972 to 1983.

10-day periods	**Number of adults**			**Proportion of males, %**	**Significance of proportion**	**Number of juveniles**			**Proportion of males, %**	**Significance of proportion**
	males	females	not sexed			males	females	not sexed		
11-20 IV	16	2	1	-	-	-	-	-	-	-
21-30 IV	267	23	28	92.1 ± 1.6	<0.001	-	-	-	-	-
1-10 V	1355	122	198	91.7 ± 0.7	<0.001	-	-	-	-	-
11-20 V	1137	409	325	73.5 ± 1.1	<0.001	-	-	-	-	-
21-30 V	518	418	222	55.3 ± 1.6	<0.001	-	-	-	-	-
31 V-9 VI	157	104	54	60.2 ± 3.0	<0.001	-	-	-	-	-
10-19 VI	97	24	5	80.2 ± 3.6	<0.001	-	-	-	-	-
20-29 VI	126	64	7	67.9 ± 3.4	<0.001	-	-	-	-	-
30 VI-9 VII	79	61	7	56.4 ± 4.2	n.s.	123	101	106	54.9 ± 3.3	n.s.
10-19 VII	19	32	6	37.3 ± 6.8	n.s.	698	805	568	46.4 ± 1.3	<0.01
20-29 VII	3	20	2	13.0 ± 7.0	n.s.	1166	1298	770	47.3 ± 1.0	<0.01
30 VII-8 VIII	39	26	15	60.0 ± 6.1	n.s.	1131	970	647	53.8 ± 1.1	<0.001
9-18 VIII	109	19	15	85.2 ± 3.1	<0.001	1049	1039	658	50.2 ± 1.1	n.s.
19-28 VIII	180	38	19	82.6 ± 2.6	<0.001	2985	2704	2055	52.5 ± 0.7	<0.001
29 VIII-7 IX	247	78	50	76.0 ± 2.4	<0.001	5140	3266	2865	61.1 ± 0.5	<0.001
8-17 IX	55	38	29	59.1 ± 5.1	n.s.	2092	1005	939	67.5 ± 0.8	<0.001
18-27 IX	40	37	9	51.9 ± 5.7	n.s.	1239	542	525	69.6 ± 1.1	<0.001
28 IX-7 X	31	15	9	67.4 ± 6.9	<0.05	291	115	138	71.7 ± 2.2	<0.001
8-17 X	1	7	2	-	-	43	30	20	58.9 ± 5.8	n.s.
18-27 X	1	1	1	-	-	10	5	4	-	-

captured: the brood included two males and four females. The sex ratio was equal among subsequent recaptures of nestlings from different nests. Chromosome sexing of 1-3 days old nestlings made by Sokolov & Vysotsky (2000) showed that 212 nestlings from 43 nests included 98 males and 114 females, i.e. the sex ratio did not significantly differ from the equal one ($\chi^2 = 1.21$, n.s.).

Among juveniles during the beginning of postfledging movements the females are significantly more common than males (53%). This may be due to the known higher mobility of females after fledging (Norman, 1994). Later in summer and autumn, the males are significantly more numerous, and this trend is maintained until early October. In total, males comprise 57.6 ± 0.3% of juveniles. On the island of Heligoland in the North Sea the sex ratio of juveniles was equal; and among the adults, the males prevailed (59 ± 9%; Niemeyer, 1969b).

Annual survival rate of adult Willow Warblers in 1976-1995 estimated from model D from the programme JOLLY was 0.331 ± 0.019 in males and 0.255 ± 0.023 in females (Payevsky et al., 1997; see section 3.4, Table 14). As capture-recapture dataset on males is much larger and more reliable, we may assume that the mean annual survival rate of adult Willow Warblers is roughly 33%. In other parts of the range survival rates were somewhat higher: 41 % in southern Finland (Tiainen, 1983b), in England 37% (Peach et al., 1995) and 34-41% (Lawn, 1994). Only in western Poland was the survival rate of male Willow Warbler very similar to the estimate from the Courish Spit, 34% (Czarnecki, 1979). It should however be emphasized that different authors used very different methods to estimate survival rates.

To estimate the mean expected lifespan after reaching maturity, e_x, one can use the simple equation $e_x = 2 - q/2q$, where q is the mean annual mortality of adults. With the annual survival rate of 0.33, i.e. mortality rate of 0.67, the mean expected lifespan of Willow Warblers that survived until the summer season following their natal year is 361 days, i.e. one year. The maximum lifespan is equal to 6 years and was reached by one male and one female that exceeded the mean expectation 3-fold. The same maximum lifespan was recorded from ringing data in Finland (Saurola, 1980), but ringing results from the German Hiddensee station indicated that one Willow Warbler reached 10 years and 3 months old (Staav, 1998).

With reference to the survival rate of juveniles, this can only be estimated indirectly. If the population growth rate across a number of years is on average zero, birth rate and mortality rate should be equal. This means that net reproduction rate, R_o, which is a sum of products $s_x \cdot b_x$, where x is the time interval (one year in our case), s is annual survival rate and b is production rate (number of fledglings produced per one breeding individual), should be equal to 1. In this case the mortality rate of juveniles, q_o, is calculated as $q_o = 1 - s_1 / \sum s_x \cdot b_x$, with x from 1 to max. Assuming that the survival and reproduction rate after reaching maturity are age-independent, this equation can be substituted by a simple one, $s_o = n_1q / n_2$, where s_o is the desired survival rate of juveniles, q is the mean annual mortality of adults, n_1 is the number of breeding birds, and n_2 is the number of fledged young. The n_1/n_2 proportion may be estimated from a sample mean, and the simplest estimate is the mean brood size at fledging. With the above calculated population productivity rate, i.e. 3.81 fledglings per breeding pair and mean annual mortality of adults of 0.67, survival rate of juveniles until the subsequent breeding seasons appears to be the same as in the adults. This is questionable, even though the same result was obtained for a south Finnish population (Tiainen, 1983b). Survival rate of juvenile Willow Warblers, like in other species, should be expected to be below the correspondent value for adults. The fact that calculations do not support this is probably due to the underestimation of breeding attempts in the population.

In previous publications, different significant trends of local and passage population numbers in the Willow Warbler on the Courish Spit were reported, with both decline and population growth (Payevsky, 1990a; Sokolov, 1991b; Sokolov, 1999; Sokolov et al., 2000). In spite of annual and often considerable fluctuations of trapping figures, generally Willow Warbler numbers showed no significant trend across 40 years, 1957-1996 (Fig. 22). Spearman's correlation coefficient varied between -0.098 and -0.342 and was not significant in any case.

Surveys of Willow Warblers at different European sites yield very variable patterns. May and June surveys in southern Sweden showed very stable numbers across 1972-1980 (Nilsson, 1986). Trapping figures of migrants at Ottenby bird observatory in Sweden were related to precipitation in Africa and were found to be positively correlated (Hjort & Pettersson, 1989; Pettersson & Hedenström, 1986). The fluctuation pattern of autumn trapping numbers at Ottenby (Pettersson, 1990) is similar to the pattern from the Courish Spit, but the correlation between two time series is not significant (Sokolov et al., 2000). The European Breeding Bird Atlas (Hagemeijer & Blair, 1997) reports stable Willow Warbler populations in most countries until the 1980s, unlike many other species, especially fellow long-distance migrants. It seemed that this species was immune to severe African droughts, because its main winter quarters are further south of the Sahel as compared with other species. However, later the situation has changed. The data from Britain and Ireland (Peach et al., 1995; Balmer & Peach, 1998) suggest that until the late 1980s, the Willow Warbler was the species with one of the most stable numbers on the British Isles, but in 1983-1995 its population significantly declines, as indicated by both adult and juvenile numbers. A significant decline of breeding numbers in the early 1990s, especially in the southern Britain, is thought to be due to poorer winter survival in Africa (adult survival rate in southern Britain dropped from 45% in 1988 to 24% in 1992). A similar drop was recorded in 1991 and 1992 in the Netherlands

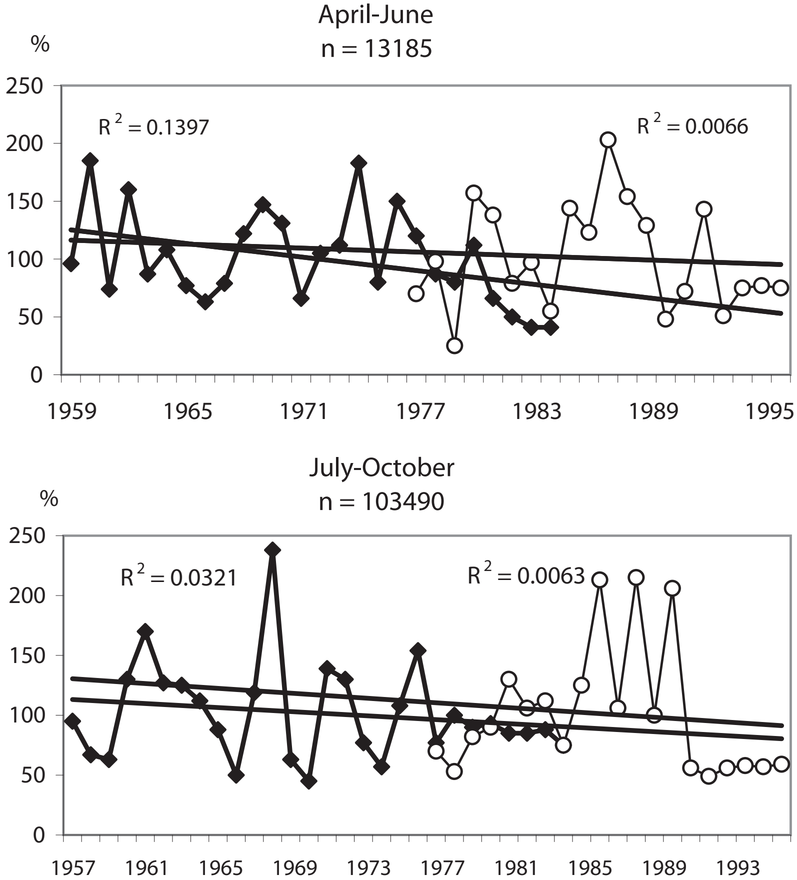


Fig. 22. Population dynamics of the Willow Warbler in spring and autumn based on captures in three standard Rybachy-type traps from 1959 to 1984 (dots) and in two standard Rybachy-type traps from 1977 to 1996 (circles). Y axis represents the proportion of the annual mean.

(Foppen & Reijnen, 1996). For the data on the Willow Warbler in relation to the conditions in African winter quarters see also in sections 5.2.1 and 5.2.2.

The analyses of Willow Warbler population dynamics on the basis of trapping figures from European ornithological stations (Busse & Marova, 1993; Busse, 1994) show that both negative and positive trends were recorded in different areas. However, the authors assume that on average, the numbers declined. Fluctuations of Willow Warbler numbers at the Tauvo station in Finland showed no significant trends, and no correlation between Finnish and other European data (Tynjälä et al., 1995). These authors support the view that Willow Warbler population dynamics in different parts of its range are weakly related.

4.5. DEMOGRAPHY OF THE CHAFFINCH

The Chaffinch is one of the commonest and most healthy songbird species across all of its Eurasian range. It is the absolute champion among all birds of the East European plain, reaching 12% of all birds' abundance (Ravkin & Ravkin, 2005). At the Biological Station Rybachy the Chaffinch (plate 24) has always been one of the most popular model species in all research projects (including orientation, bioenergetics, photoperiodism, endocrinology, circadian and circannual rhythms, demography and reproduction ecology). Detailed studies in the Chaffinch population ecology resulted in the writing of a monograph on this species by composite authors (Dolnik, 1982a). The demographic parameters of the Chaffinch have been studied in much detail (Payevsky, 1981b, 1982b, Payevsky, 1985a). After these publications, the demographic studies of breeding and migrating Chaffinches were continued (Payevsky, 1986, 1992b, 1995; Bardin, 1990б; Payevsky et al., 1997; Vysotsky & Payevsky, 2002). Below are presented some aspects of these follow-up studies.

As shown in section 3.3, the proportion of male Chaffinches is significantly higher than 50 % in both breeders and transient migrants. The number of Chaffinches captured during the breeding season on the Courish Spit was sufficient to analyse sex ratio in different parts of the season and for different ages. The dataset analysed was collected in 1958-1980. Juvenile Chaffinches can be reliably sexed by plumage and wing length from 30-40 days old. In most years, juveniles reached this age in early or mid July. Sex ratio of nestlings was determined on the basis of the data on the birds taken into captivity and hand-raised. Chaffinch nestlings were hand-raised until full independence and released into the wild by the members of the Biological Station Rybachy in the framework of studies of territory imprinting (Sokolov et al., 1984), and moult patterns in the birds from the first and second broods. Furthermore, all members of five broods were recaptured at an age that allowed reliable sex identification. The equality of sex ratio was tested by the Fisher's test.

The sex ratio in nestlings between 7-12 days old was determined in 93 individuals from 23 broods. Sex ratio of individual broods varied broadly, from broods consisting exclusively of females, to broods comprised only of males. In total, 47 birds were males and 46 females, i.e. the proportion of males was 50.5 ± 5.2% which is does not differ significantly from equality.

The sex ratio of juvenile Chaffinches in their natal summer season was estimated in three subsamples: (1) captures of all juveniles; (2) recaptures of juveniles ringed as nestlings; (3) recaptures of juveniles earlier captured in stationary traps (Table 27). Within the first group, the proportion of males varied between different 10-day periods of the season without a clear trend between 50.0 and 56.5%, on average 53.8 ± 0.8%. In the second and the third groups the proportion of males

Table 27. Sex ratio in first-year Chaffinches from capture data

10-day periods	**Bird cohorts**								
	Captured in traps*			Recaptured** after ringing as:					
				nestlings			juveniles		
	n	Proportion of males, %	p	n	Proportion of males, %	p	n	Proportion of males, %	p
30 VI-9VII	-	-	-	459	55.1 ± 2.3	<0.01	58	53.4 ± 6.6	n.s.
10-19 VII	464	53.7 ± 2.3	<0.05	428	56.5 ± 2.4	<0.001	190	53.7 ± 3.6	n.s.
20-29 VII	565	54.9 ± 2.1	<0.001	317	57.7 ± 2.8	<0.001	310	54.5 ± 2.8	<0.05
30 VII-8 VIII	790	56.5 ± 1.8	<0.001	214	60.3 ± 3.3	<0.001	349	56.5 ± 2.7	<0.001
9-18 VIII	401	54.6 ± 2.5	<0.01	134	60.4 ± 4.2	<0.001	263	58.6 ± 3.0	<0.001
19-28 VIII	595	52.8 ± 2.0	n.s.	105	70.5 ± 4.5	<0.001	229	59.4 ± 3.2	<0.001
29 VIII-7 IX	871	50.0 ± 1.7	n.s.	74	66.2 ± 5.5	<0.001	178	59.0 ± 3.7	<0.001
On average		53.8 ± 0.8	-		61.0 ± 1.4	-		56.4 ± 1.5	-

Notes. * data collected from 1972 to 1980, ** data collected from 1958 to 1979. Each bird included into every 10-day period since ringing until last recapture.

significantly increased from early July towards late August from 55.1 to 70.5% in the birds ringed as nestlings, and from 53.4 to 59.4% in the birds earlier captured in the traps. Correlation of the time series was significant in both cases: $r = 0.89$, $df = 5$, $p < 0.01$, and $r = 0.96$, $df = 5$, $p < 0.01$, respectively.

The sex ratio of adult Chaffinches of various ages was determined on the basis of recaptures of birds ringed as nestlings and first-autumn birds, ringed as yearlings and as adults of unknown exact age (Table 28). The proportion of males varied at different ages from 54 to 59 % and was on average 55.9 ± 0.9% (the mean of significant values). In the bulk of breeders, i.e. birds from one to three years old, the proportion of males was 55.1 ± 0.8%.

All these data suggest that from the age of one month, male Chaffinches are consistently in the majority and comprise 54-55% of the birds which means 1.2 males per 1 female. At the age of 7-12 days the sex ratio is equal. One may assume that subsequently the 'mechanism of sex-related mortality rate' is switched on and the females suffer greater mortality than males. Apparently the increased mortality is typical of female Chaffinches immediately after fledging from the age of 12 days. There are some arguments supporting this assumption. First a significantly increasing proportion of males in the trapped juvenile birds may result from the increased hyperactivity of females which forces them to leave their natal sites earlier than males. It has been reported earlier that males remain at the natal site longer than females (Sokolov, 1982). Young females that show higher activity in the first weeks after fledging may suffer greater mortality. This however contrasts with the data from several passerine species in West Murman where a higher proportion of males among captured juveniles was attributed to their greater mobility (Chemyakin, 1988b).

As mentioned earlier (section 3.4), lower robustness of females might be due to their different sex characteristics. In that section we showed that even though survival rate of males was always higher than in the females, in general it was not significantly so. Only in some years male survival rate significantly exceeded the survival rate of the opposite sex.

Therefore the question arises whether survival rate of such a flourishing species as the Chaffinch remains stable between the years. Our analysis of annual survival rate of the Chaffinch (Vysotsky & Payevsky, 2002) was based on the ringing data on the Courish Spit from 1957 to 1996. We used 1281 dead recoveries of Chaffinches within Europe obtained from birds ringed in September and October. As the same dataset has been earlier shown to have no sex-related difference in the survival rate (Payevsky et al., 1997, see section 3.4., Table 13), both sexes were pooled for analysis. We used the programme MARK, model selected was done on the bases of Akaike's Information Criterion values. The best model included constant annual survival of $S = 0.556 \pm 0.011$. The model structure showed constant survival rate without any temporal trend. For further analysis on the basis of the

Table 28. Sex ratio in adult Chaffinches of different age from recapture data

Year of life[1]	**Ringed as:**								
	nestlings and juveniles before juvenile moult[2]			moulted juveniles (August – October) and yearlings (April – July)[3]			«adults», exact age unknown[4]		
	n	Proportion of males, %	*p*	*n*	Proportion of males, %	*p*	*n*	Proportion of males, %	*p*
1	1195	53.8 ± 1.4	<0.001	453	54.4 ± 1.6	<0.001	957	54.4 ± 1.6	<0.001
2	498	55.6 ± 2.2	<0.001	279	55.6 ± 2.9	<0.01	530	55.1 ± 2.2	<0.001
3	274	55.8 ± 3.0	<0.01	165	55.8 ± 3.9	<0.05	311	55.6 ± 2.8	<0.01
4	150	52.0 ± 4.1	n.s.	102	54.9 ± 4.9	n.s.	190	56.3 ± 3.6	<0.05
5	96	50.0 ± 5.1	n.s.	52			108	59.3 ± 4.7	<0.01
6	42			19	59.0 ± 5.4	n.s	59		
7	24			9	(from four last values)		23	53.1 ± 5.0	n.s.
8	9	52.6 ± 5.6	n.s.	3			10	(from five last values)	
9	4	(from six last values)					5		
10	1						1		
11	1								
Mean		53.0 ± 1.6	-		56.0 ± 1.8	-		55.6 ± 1.4	-

Notes: [1] – The first year of adult life starts in the summer season following the year of birth (second calendar year), [2] – Data from 1958 to1979, [3] – Data from 1964 to 1979, [4] – Data from 1958 to 1972.

global model we estimated survival rate for each year and obtained a time series of 40 annual values for 1957-1996. This is sufficient to identify cycles with a period of up to 11 years. To study the structure of this time series we removed the mean to obtain stationarity – the relation between variables does not depend on time – which is a necessary condition for further analysis (Fig. 23).

Of the studied time series chaotic fluctuation around the mean is typical, with fluctuations of a very large range at the end of the series. The reason for this is the declining accuracy of estimates due to the much more scarce data in these years (reporting rate of dead recoveries of Chaffinches has a very clear downward trend, see Section 2.2). An attempt of non-linear median smoothing by five values did not yield any regularity. As the values of the time series are satisfactorily well approximated by the normal distribution (Shapiro-Wilks normality test, W = 0.956, p = 0.17), the further analysis is based on parametric procedures. Regression analysis failed to detect a trend ($F_{1,38} = 0.07$, p = 0.77). Three tests sensitive to different types of randomness violations (median test, series test and Box-Pearce statistics) made it possible to conclude that the data points were a random series. No autocorrelation was found, no inner relationships between the elements.

Therefore, in spite of the very long period included into the analysis, 40 years, the Chaffinch survival rate remained statistically unchanged across the whole study period, and this is apparently due to the stable numbers of this common songbird species. The results obtained may be treated as a special case of the well-known law of population dynamics ‘that constant survival rate permits stable population numbers’. This situation is typical at least for the Chaffinches of the Eastern Baltic, Finland and northwest Russia, i.e. of the regions of origin of the birds analysed.

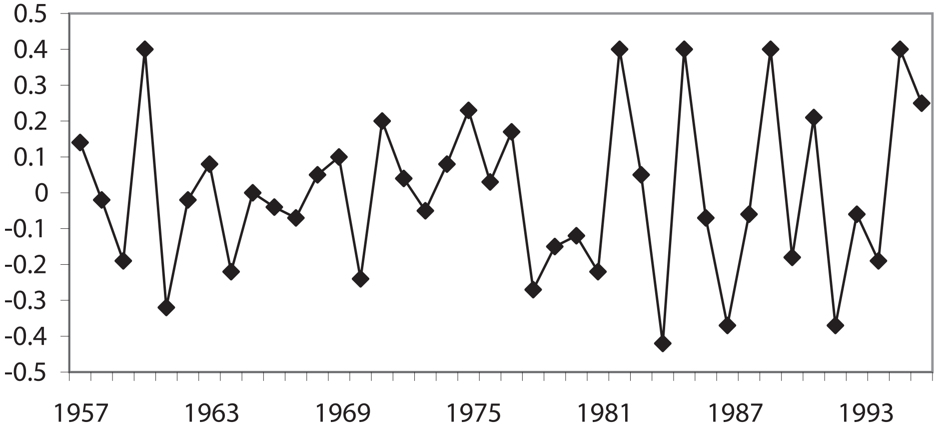


Fig. 23. Chaffinch time series of 40 annual survival rates based on migrant recovery data from 1957 to 1996. Y axis represents the residuals of the arithmetic mean.

We can compare the values of the mean annual survival rate of Chaffinches from these populations derived from different sources. Survival rate estimates of adult birds are based on different time periods and are obtained by different methods (Payevsky, 1982b; 1985a; Bardin, 1990b; Vysotsky & Payevsky, 2002). For the local breeding population of the Courish Spit and for transient populations they yielded the following figures: 0.501 ± 0.012; 0.524 ± 0.017; 0.544 ± 0.031, 0.555 ± 0.013, 0.556 ± 0.011, 0.562 ± 0.015, 0.571 ± 0.033. The range of variation is the same as the annual variation in both transient populations (Fig. 23) and the local population of the Courish Spit: annual local survival rate varied between 0.22 and 1.00. It is worth noting that for ornithologists who were involved in studying this Chaffinch population across many years such broad variation of the local survival rate seems unlikely, as it would have resulted in the variation of annual numbers. However, no apparent variation in either breeding numbers or in their breeding performance across the study years was recorded (at least at the level of general impressions, to say nothing of the detailed survey work). In this framework, long-term mean values of survival rate, even though they are a certain abstraction, seem to be much more realistic than some apparently biased annual values. In British and Irish Chaffinch populations the mean annual survival rate of adults was 0.489 ± 0.131 (Balmer & Peach, 1998). Taking into account the broad confidence interval the survival rate of British Chaffinches may be considered similar to the value obtained by us for the Baltic birds.

The reproduction rate of the Courish Chaffinch population was on average 3.08 fledglings per breeding pair; the mean annual survival rate of adults was 0.499, and the survival rate of juveniles until the subsequent breeding season was 0.325 (Payevsky, 1982b). These mean demographic parameters, and the monthly distribution of the non-surviving Chaffinches made it possible to calculate and present the seasonal dynamics of population numbers (Fig. 24) under the (unrealistic) assumption of the closed population (no emigration and immigration). In general similar curves of the seasonal dynamics of numbers are probably also typical of many other songbird species. It is however not possible to test this, because only in the Chaffinch was the dataset large enough to build such a curve.

4.6. POPULATION DYNAMICS, AGE AND SEX STRUCTURE OF THE NOMADIC EUROPEAN STARLINGS

Numbers of European Starling (plate 26) populations have recently undergone serious changes. The causes have been discussed by many authors but remained obscure. The Finnish population increased greatly by 1952-1963 as compared by 1936-1949 (Järvinen & Väisänen, 1978a,b), but later its numbers started to decline and dropped dramatically by 1977 (Haartman, 1978). A later publication

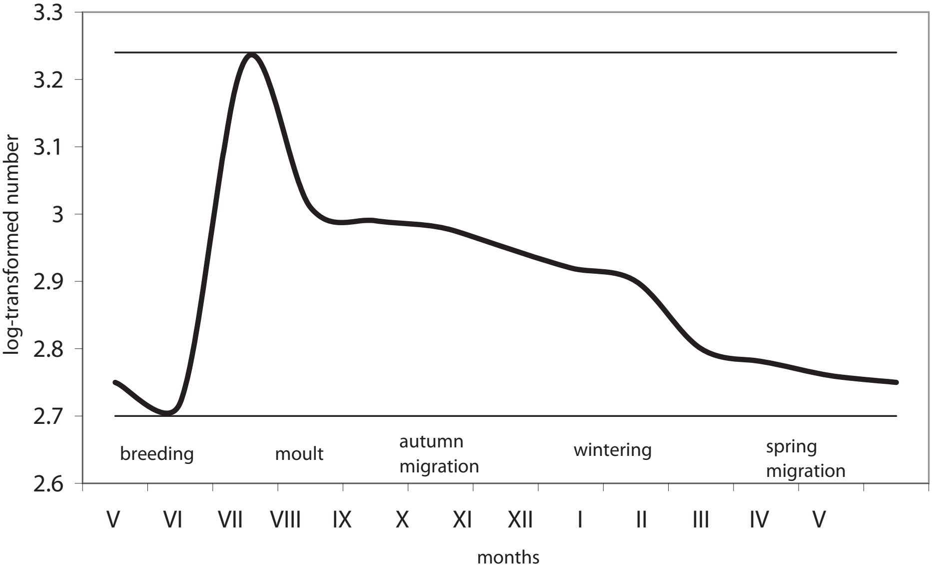


Fig. 24. Seasonal dynamics in the Chaffinch population. Based on the averaged demographic parameters and monthly distribution of dead recoveries.

(Rintala et al., 2003) reported that the Finnish Starling population was generally stable in 1952-1970, and the decline that started in the 1970s wiped out 90% of the population by 1985. The data collected at the Falsterbo bird observatory in southern Sweden showed that the numbers of migrating Starlings significantly declined in 1980-1999 (Karlsson et al., 2002), as did the total Swedish breeding numbers of this species (Svensson, 2002). The same is true of southern Germany over the recent 50 years (Berthold, 2003).

The British Starling population was rather stable in 1962-1991 but started to decline in 1992-1994 (Siriwardena et al., 1998). Other data suggest that the numbers of European Starlings in Britain had declined since the late 1960s, and by 1988 the population numbered 50-67 % of the numbers of the mid 1960s (Feare, 1996). In the 1990s, a new decline began, so that by 1994 the numbers comprised ca. 25% of the 1980s level. The same author suggested that the decline of Starling numbers was typical not only of western Europe, as the numbers at their Israel winter quarters declined from 15 million in 1970 to 1 million in the 1990s (Feare, 1996).[1] This review reported that European Starling range and numbers in the British Isles underwent very significant changes during the 18th and 19th century,

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[1] Generally speaking, this is probably due to more mass wintering in northern regions because of global climate change.

varying from extinction to new mass colonisation. As with the recent changes, the reasons behind these events remain unknown.

One of the first recent hypotheses that sought to explain the decline of the Starling populations was the method of the direct mass extermination of wintering Starlings that are vineyard pests in Western Europe (Orell & Ojanen, 1980). However, it appears that numbers started to decline earlier than these control measures were implemented. The suggestion that the breeding habitat change causes an increased mortality rate of nestlings was to some extant supported for some local populations in Finland (see Rintala et al. [2003] for a detailed discussion). However, this hypothesis cannot be tested for other parts of the Starling range, because no comparable habitat change occurred there (Solonen et al., 1991).

The dynamics of Starling numbers on the Courish Spit, as shown by standardised captures in two Rybachy-type traps are shown in Fig. 25. By comparing spring and summer data, two periods may be distinguished: the period of constant decline in 1961-1973 (Kendall correlation: $\tau = -0.46$, $n = 13$, $p = 0.03$) and the period of relatively stable low numbers in 1974-1985 ($\tau = -0.06$, $n = 12$, $p = 0.78$). As practically no adult Starlings occur in summer captures (see below), the adult to juvenile ratio gives no indication of the productivity of the Baltic Starling populations. However, theoretical reasons allow us to assume declining productivity of the populations studied. Let us consider survival rate of these Starlings using MARK programme (see section 2.5) and Freeman-Morgan age-dependent model (Vysotsky, 2005). The survival rate of young Starlings during the period of declining numbers in 1961-1973 was somewhat higher (0.417) than during the period of low numbers 1974-2002 (0,339). Adult survival rate, conversely, was lower during the decline (0.250) than in the other period (0.594). However, the difference was not significant in either age group, and the survival rate across the whole study period (1961-2002) is best characterised by the model with constant survival rate. This means that the downward trend in the Baltic Starling numbers cannot be attributed to declining survival rate. Conversely, the demographic analysis of the British Starling populations showed that their declining numbers are most probably due to the decreased survival rate of juveniles during their first autumn and winter (Freeman et al., 2007).

During the postfledging movements of Starlings on the Courish Spit, from mid or late June until the beginning of the second 10-day period of August, adults make up a very insignificant proportion of each flock. The proportion of adults (one-year-old and older birds) is on average 2.8% of males and 3.4% of females, with daily variation between 0 and 5.4-16.3 %. In just one day the proportion of adults was 73.6%. During this period, sometimes small flocks may be observed that consist only of adult birds. However, such flocks are rare. The vast majority of flocks contain nearly exclusively juveniles, and in the period of high numbers

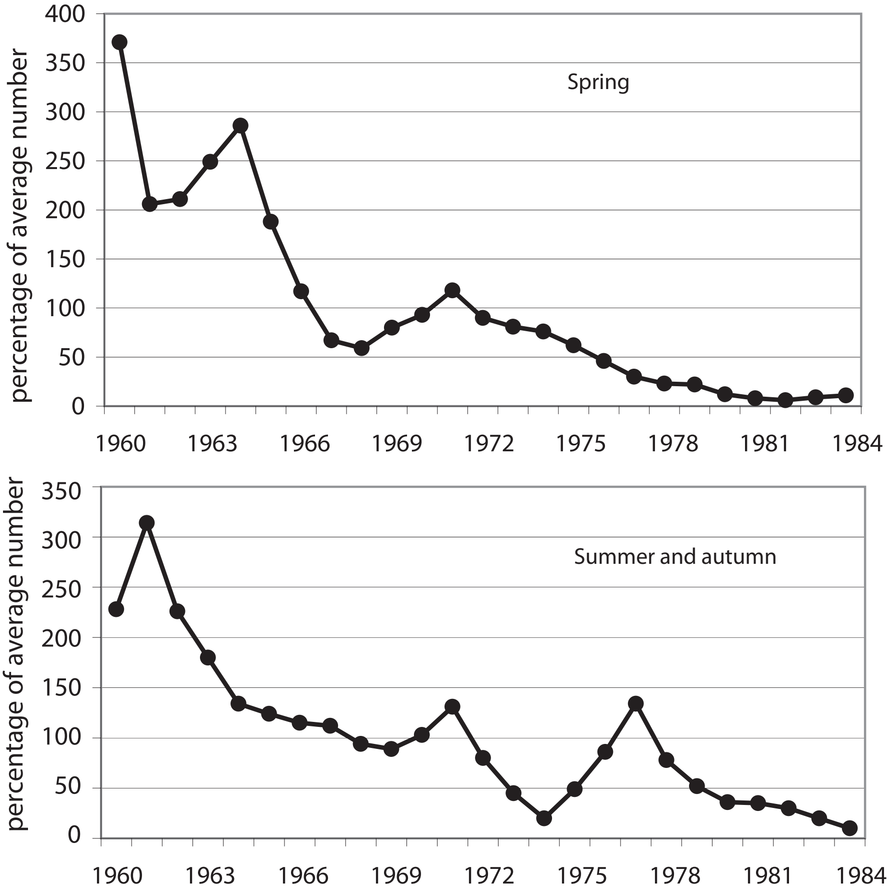

Fig. 25. Variation in European Starling numbers inferred from capture data from 1960 to 1985 (total sample size 42173 birds). The curve is a smoothed mean.

such flocks could reach a huge size (sometimes up to five thousand Starlings were captured in two Rybachy-type traps simultaneously). The flocks move both towards the southeast and towards the northwest. At Ladoga ornithological station in 1980-1981 also only juveniles participated in postfledging movements from late July (Vysotsky, 1983).

During all seasons of Starling captures on the Courish Spit the sex ratio was male-biased: in spring the proportion of adults was on average 57%, during postfledging movements it was 52-55% and in October it was 55%. Sexing of these birds, especially of juveniles, is not always error-free, however the bias is likely to result in overestimating the numbers of females, not males (Payevsky & Yefremov, 1972). Therefore, male-biased sex ratio is reliable.

Age ratio of Starlings captured during postfledging and postbreeding movements obviously does not reflect population productivity and suggests that some age segregation occurs. The overall breeding productivity of the Starling in Europe (both first and second clutches included) in 1951-1958 was 4.75 to 5.83 on average 5.18 fledglings per pair (the data from Germany, Czechoslovakia, Switzerland, the Netherlands and Belgium; calculated from the data of Schneider [1972]). In 1970-1978, the mean reproduction productivity per breeding pair was 2.5-4.7, on average 3.57 fledglings, as suggested by the data from Finland and the Netherlands (Korpimäki, 1978), northern Poland (Gromadzki, 1980) and southwest Germany (Hund & Prinzinger, 1981).

On the Courish Spit in 1959-1977 with one clutch per season, of mean clutch size of 4.8 eggs and breeding success rate of 78.8%, a breeding pair produced on average 3.8 fledglings. This means that the number of juveniles should be roughly double the number of adults. Even assuming 5 fledglings per nest and some mortality of adults during this period, the proportion of adults should be at least 30%. As the flocks contained 96% of juveniles, we are forced to conclude that adult and juvenile Starlings behave differently or live in different habitats/areas.

4.7. DEMOGRAPHIC PARAMETERS OF SONG THRUSH POPULATIONS HUNTED IN WESTERN EUROPE

Demographic studies have special aspects for the game species. The existence of the tradition to hunt songbirds in some European countries since historic times attracts special attention of many environmentalist NGOs and of Birdlife International. *Turdus* thrushes are among the most activity hunted passerine species (Ghigi, 1958; Spina, 1986; McCulloch et al., 1992). The main migratory routes of several thrush species from the populations of northwest Russia and Finland run through the Eastern Baltic (Gromadzki, 1964; Payevsky, 1973; Busse & Maksalon, 1986; Bolshakov et al., 2002; Sinelschikova & Sokolov, 2004). Currently a large pool of ring recoveries is available, especially for the Song Thrush (plate 27), which makes it possible to analyse the distribution of thrushes on their migratory routes in Europe (Payevsky et al., 2005), to identify countries and regions with the strongest hunting pressure, and to determine the age composition of thrushes in the hunting bag as well as to calculate their annual survival rates (Payevsky & Vysotsky, 2003; Payevsky et al., 2004).

In the analysis of recovery distance and directions, direct and indirect recoveries were pooled, as the mean azimuths and distances of both types of recoveries did not differ: χ^2 values varied between 1.0 and 1.8. For more convenient analyses, all recoveries were pooled by 20-day periods of recovery dates. The data from different years were pooled for analysis, as no significant annual variation was found: Song Thrush recoveries grouped by years and geographic latitude of recovery, showed no significant variation ($\chi^2 = 0.86$, df = 4, p = 0.93). For testing the differences between samples in the mean direction and directional scatter, we used the methods of circular statistics: test B of Mardia-Watson-Wheeler when $n \leq 17$ and χ^2 if $n > 17$ (Batschelet, 1981). When comparing median recovery distances, Kruskall-Wallace and Mann-Whitney tests were used.

As mentioned before, the decline in the number of rings reported from Italy from the north to the south of the country is more likely due not to low numbers of wintering thrushes in southern Italy but to reluctance of fowlers and hunters to report the rings after the introduction of the ban on commercial hunting of songbirds (McCulloch et al., 1992; Andreotti et al., 1999).

Song Thrushes showed no variation in the direction of movements in different parts of autumn and winter. Even in the periods when median recovery distances were significantly different, the mean directions were essentially the same: 225° and 224° in one case and 223° and 222° in the other one ($\chi^2 = 1.2$ and 1.7, df = 2, p = 0.32, n.s.). These data suggest that after reaching the main winter quarters by late November, Song Thrushes continue to move during the winter and reach the most distant area; over 2000 km from the Courish Spit, in January – early February, and in March they again appear in the areas they occupied in November. The distance of movements by adults (on average 1959 km ± 41 km, median 1880 km from the Courish Spit, n = 140) did not significantly differ from the respective figure in first-winter birds (on average 1862 ± 41 km, median 1815 km, n = 111; p = 0.09, n.s.). The mean directions did not differ, either (the mean azimuth 223° in both groups, $\chi^2 = 1.1$, df = 2, n.s.).

Across all the years of study, just 30 cases were recorded when Song Thrushes ringed in autumn in the same day of September or October and thus assumed to belong to the same population (a total of 92 individuals) were killed in the subsequent months of the same season. In five cases the birds were killed in three different countries, in 15 cases in two different countries, and in 10 cases in the same country. This means that just 33.3% of birds ringed in the same day were subsequently recovered in the same country, and therefore the assumed members of the same population spend their winter in Europe in totally different areas.

The above assumption is also supported by the winter distribution of thrushes from the breeding populations of the Courish Spit. Song Thrushes ringed in different years as nestlings, and adults ringed in early May, were killed in France, Italy, Spain, and Portugal. In the Leningrad Region all thrush species have dispersed in different directions already during the postfledging movements, and the thrushes wintering in Bulgaria have a very unstable composition and regularly mix (Nankinov, 1970). These results confirm a very broad distribution of members of the same population of thrushes on migratory routes and in winter quarters, without using population-specific areas, is a regular event that occurs annually.

The Song Thrush, along with other thrush and many other songbird species, is a traditional hunting quarry in Western Europe, especially in Italy and France. In the latter countries the proportion of hunters in the total population is the highest among European countries, up to 4.4% (Spina, 1986). A total of 77 to 144 million thrushes are killed in Europe annually (Ricci, 2001). Of the 601 recoveries obtained from the five species of thrushes ringed by the Biological Station Rybachy, 398 (66%) were shot by hunters. It is possible that many birds reported as 'trapped, further fate unknown' and 'capture method unknown' were also victims of hunters and fowlers. This assumption is based on the popular method in Western Europe of netting the migrating birds for food, especially in Italy (Ghigi, 1958; Spina, 1986). Probably 80% of all thrushes reported to the ringing centre were killed by hunters and fowlers. The season of thrush hunt is from the last 10-day period of September until 10 March, and the peak of this activity falls between the second half of October and late December.

Differential hunting pressure in different countries is clearly demonstrated by the proportion of killed birds among the recoveries. This proportion is the highest in France, Italy, Spain, and Portugal (70-90%), therefore it may be concluded that in these countries the thrushes are subject to the strongest hunting pressure. The difference from other European countries where the proportion of killed birds is just 18.6%, is highly significant ($\chi^2 = 196.3$, df = 1, $p < 0.001$). This difference is in the general form shown in the diagram (Fig. 26).

As the Song Thrush is a predominantly nocturnal migrant, the problem of the coastal effect (section 2.3.2) is relevant. The analysis of Song Thrush captures on the Courish Spit in 1972-1005 showed that in some years, no adults were captured at all: of the 11544 Song Thrushes, the mean proportion of adults was 6.5% in autumn and 19.2% in spring (Payevsky, 1998).

When calculating the age distribution of thrushes killed by hunters we first calculated separate distributions for the birds with the age known and age

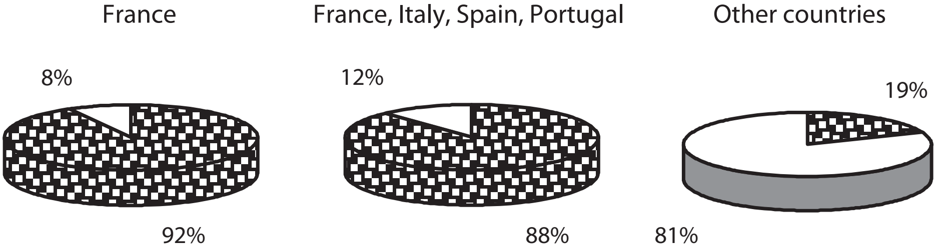

Fig. 26. Variation in the hunting pressure on thrushes in different countries. The proportion of killed birds is hatched.

unknown at ringing. A similarity of these distributions convincingly shows that among all Song Thrushes identified in autumn as full grown, 93% were juveniles. Therefore pooling of both distributions is legitimate. The resulting pooled age distribution of Song Thrushes in the hunting bag is shown in Fig. 27. The proportion of first-winter Song Thrushes in the hunting bag exceeded the proportion of adults by a factor of 1.6.

In spite of these calculations, some doubts still existed whether the obtained age distribution was a realistic one, because mainly first-autumn birds are ringed. If only the ringing season is included and age-independent probability to be killed by hunter is assumed, the fate of adults remains unknown to us simply because they are very rarely ringed. Probably, the age distribution is realistic from the age of two years and older. It may however be hypothesised that due to their naivety the juveniles are killed more often.

The published data on the breeding biology of the Song Thrush (Haartman, 1969; Malchevsky & Pukinsky, 1983; Payevsky, 1985a) shows that population production rate of this species in northwest Russia and Finland on average does not exceed 3 juveniles per breeding pair per season. This is a rough estimate based on

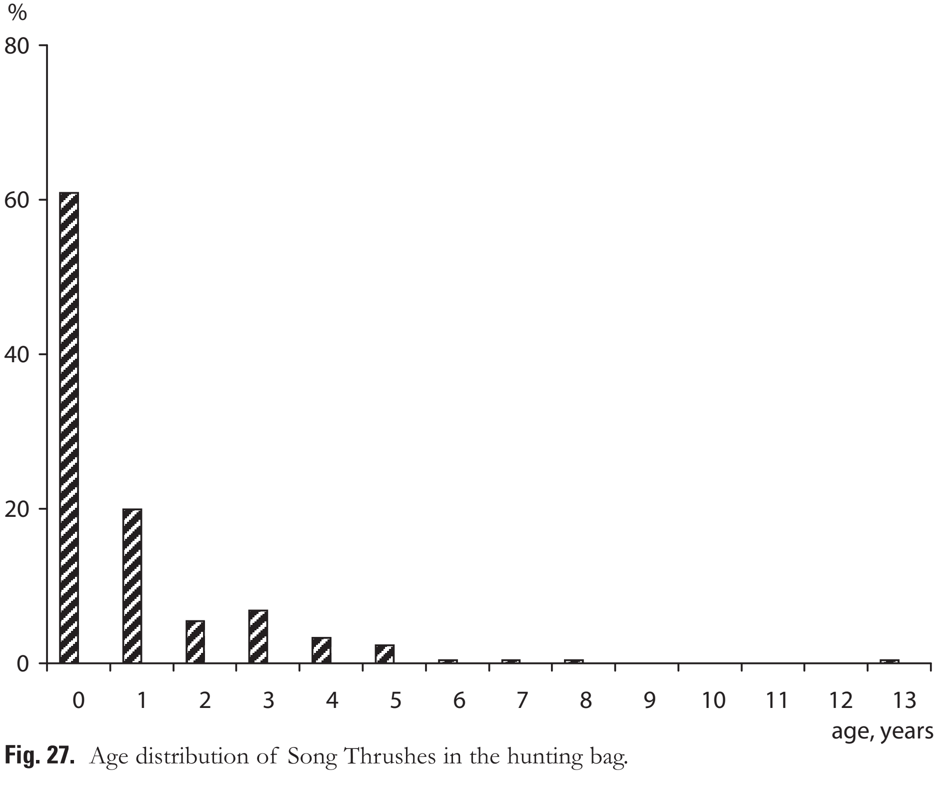

Fig. 27. Age distribution of Song Thrushes in the hunting bag.

the clutch size of 4.3 – 5.2; breeding success rate of 42–61% and 10-20% of pairs engaging in second clutches after successfully raising the first one. Therefore, the juvenile: adult ratio in the wild in autumn should be ca. 1.5: 1. This is very close to the ratio 1.6: 1 in the hunting bag.

Under the pressure of environmentalist NGOs and Birdlife International a number of European countries legally restricted songbird hunting in 1979 (McCulloch et al., 1992). It would be interesting to compare the survival rates of Song Thrushes that winter in continental Europe and on the Mediterranean islands with the published data from the British Isles in the comparable time periods (Siriwardena et al., 1998; Thomson et al., 1997; 1999). Most British Song Thrushes are year-round residents, and just a proportion of birds from southern England migrate to France and Spain (Ashmole, 1992; Cramp, 1988). The main difference is that on the British Isles the thrushes are not hunted.

The survival rate of thrushes was estimated from dead recoveries by stochastic BROWNIE models (Brownie et al., 1985) implemented in the programme MARK (section 2.5). Only birds ringed in September and October were included to maintain the formal requirement of the models of sampling events to be much shorter than intersampling intervals. We fitted age-dependent models (Freeman & Morgan, 1992) by MARK and separately estimated survival rates of juveniles and adults (Payevsky & Vysotsky, 2003).

In Table 29 survival rates of first-winter and adult Song Thrushes on the continent and in the British Isles are presented. Annual survival rates of adult birds were roughly the same across all time periods and regions, i.e. no difference exists between Baltic and British Song Thrushes in this respect.

In some studies, e.g. in the Willow Ptarmigan (*Lagopus lagopus*) a significant decline in survival rate was shown in the areas with a strong hunting pressure

Table 29. Annual survival rate of the Song Thrush on the European continent (with strong hunting pressure) and on the British Isles (without hunting).

Region and time period	**Annual survival rate**		**Source**
	Juveniles (first year of life)	Adults	
Continent			
1958-1978	0.368 ± 0.051	0.593 ± 0.059	Section 4.7; Payevsky et al., 2004
1962-1975	0.411 ± 0.065	0.561 ± 0.085	« «
Before 1968	0.460 ± 0.061		Haukioja, 1969
British Isles			
1962-1975	0.484 ± 0.020	0.573 ± 0.011	Thomson et al., 1997
1962-1993	0.450 ± 0.014	0.571 ± 0.009	« «
1962-1994	0.463 ± 0.011	0.563 ± 0.007	Siriwardena et al., 1998
1975-1993	0.405 ± 0.022	0.568 ± 0.013	Thomson et al., 1997

(Smith & Willebrand, 1999). Decreasing survival rates in British Blackbirds, Song and Mistle Thrushes were recorded in the years of population decline. In the Song Thrush this was only in first-winter birds due to severe weather conditions (Baillie, 1990; Thomson et al., 1997; Wernham et al., 1998).

Other studies, especially in ducks, indicated long ago that natural and exploitation mortality, i.e. mortality due to natural causes and due to hunting, mutually compensate (Anderson & Burnham, 1976; Mihelsons et al., 1985). This implies that hunting mortality is not additive to the natural one unless it does not exceed a certain threshold. Fecundity and survival rates start to compensate one another on the basis of density-dependent mechanisms.

The results of our studies of survival rate in Song Thrush populations in different regions in winter and in different years show that hunting does not cause an increased mortality in adult Song Thrushes. It would appear that decline due to hunting is compensated by increased reproduction rate. In any case, the Baltic populations showed no signs of trouble. The numbers of the Baltic thrush populations varied slightly in 1960-1986, within a small range and without significant trends (Payevsky, 1985a, 1990a).

Legal limitations of songbird hunting introduced in 1979 seem to have had a very limited effect on the size of the hunting bag. A downward trend in the number of ring recoveries, as suggested by many authors, is due not to the decreasing hunting pressure but rather to reluctance to report the rings because of possible sanctions (McCulloch et al., 1992).

One can only guess what population mechanisms enable higher productivity of Baltic populations as compared with British ones. The published data on thrush breeding biology (Haartman, 1969; Malchevsky & Pukinsky, 1983; Cramp, 1988) show no significant difference in either clutch size or brood size. The parameter most difficult to estimate in any field studies is the proportion of normal second clutches after successfully raising the first brood, because second clutches are very difficult to separate from the repeat ones. The only possible supposition is that in Baltic Song Thrush populations subject to a strong hunting pressure, a higher proportion of pairs are annually double-brooded than in other populations of this species.

4.8. SPECIFIC FEATURES OF POPULATION STRUCTURE AND MIGRATIONS OF EURASIAN SISKINS

In most parts of its range the Eurasian Siskin (plate 30) behaves as a nomadic and migratory species. It is sometimes treated as an irruptive species, because Siskin movements are often dependent on foraging conditions and thus their timing and number of participating birds vary between the years. One of very specific features of the migratory behaviour of the Siskin is the mass summer movement of adults with the benefits of a completed breeding cycle together with juveniles. These summer migrations within Europe in different directions are a specific event calling for a special analysis.

On the Courish Spit the migratory movements of Siskins take place annually. Most birds spend their winter in the Mediterranean region, via northern Italy, broadly scattering across the whole of Europe on the way along the south European mountain ranges and even reaching North Africa (Mezhenny, 1963; Payevsky, 1970; Payevsky, 1973a). Age and sex structure of migrating Siskin flocks has been mentioned in sections 2.3.2, 3.3, 3.5 and 3.6 (Tables 5, 10, 11, 15). More detailed information on this subject is given in Table 30. These data show that, first, young birds (yearlings in spring) predominate throughout the year, and second, sex ratio is male-biased (on average 51 to 60% of males) across all age categories of migrating Siskins. The same age and sex distribution was reported from the Ladoga ornithological station in south-eastern Ladoga area (Iovchenko & Noskov, 1983).

It has been shown (section 3.6) that unlike the Chaffinch and the Brambling, the Siskin has no significant sex and age-related variation in the migratory distance. A more detailed analysis of the mean recovery distances from the Courish Spit (the ringing site) in different months (Fig. 28) showed that in some periods (December, January and March) males are found farther from the ringing place than females. Whether this distribution is related to any ecological difference between age and sex groups, remains open.

The phenomenon of summer migration of Siskins that seems to involve two breeding cycles in different parts of Europe has been reported repeatedly

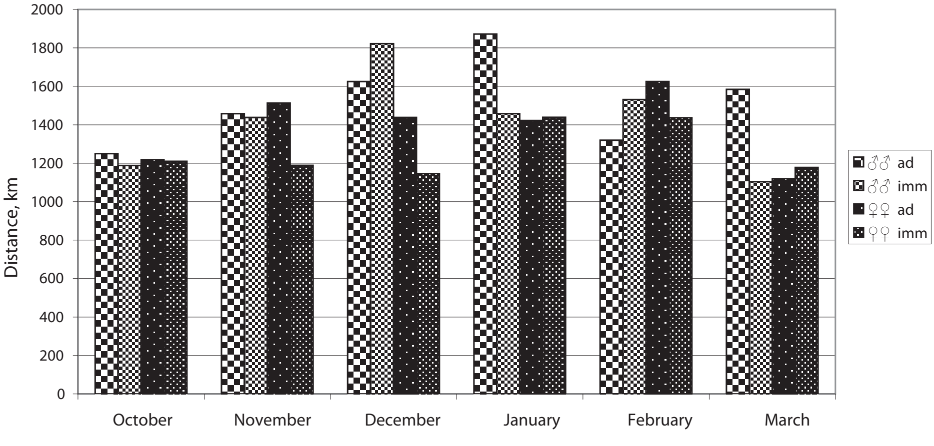

Fig. 28. The mean distance between ringing site (Courish Spit) and recovery sites of Eurasian Siskins of different age and sex in different months from 1957 to 1989.

Table 30. Age and sex structure of migrating Eurasian Siskins for 16-years of capture data from 1972 to 1987.

Months	**Ringing totals**		**Proportion of adults, %**				**Proportion of males, %**					
	Total	limits	Among males		Among females		Among adults		Among yearling in spring and juveniles in autumn		Among non-moulted juveniles in summer	
			M	limits	M	limits	M	limits	M	limits	M	limits
April – May	18250	165-3569	30.9 ± 0.5	15.5-42.9	26.1 ± 0.5	14.6-44.2	58.8 ±0.7	44.3-65.9	52.2±0.4	45.7-58.4	-	-
June – August	2717	4-824	-	-	-	-	-	-	-	-	53.2 ± 0.9	48.5-55.7
September – October	57614	201-9167	21.3 ±0.2	8.9-37.7	18.1 ±0.2	7.3-31.5	59.7 ±0.5	51.3-68.8	52.2 ±0.2	47.6-54.3	-	-

Notes: limits – range of annual values, M – annual mean.

(Weber, 1959; Mezhenny, 1963; Payevsky, 1970; Payevsky 1973a, 1994c; Newton, 2003a; Shapoval et al., 2006). On the Courish Spit summer movements are sometimes directed towards the south, but generally the flocks migrate towards the north. Most interesting is the simultaneous presence in these flocks of adults with the signs of a completed breeding cycle and first-summer birds of juvenile plumage. The earliest captures of females with incubation patches, at the stages corresponding to the completed breeding, occur in early April. In April, just one-quarter of the trapped females have incubation patches, and from June – nearly all of them. In 1984-1987, the proportion of adult females with incubation patches varied between 22.6 and 90.7% in different years, and of yearling females between 34.7 and 85.9%.

Trapping data show that juvenile Siskins do not appear during summer movements together with the adults every year. For example, in 1959-1968, they were recorded in 1959, 1961, 1963, 1965, and 1967, and the most massive summer movements in 1959-2000 were recorded in 1965, 1972, 1974, 1979, 1981, 1990, 1995, and 1997. This recurrence may indicate that mass summer movements are a result of increased population density after successful spring breeding in the mountains of southern Europe. The only direct support of this hypothesis is the capture in July 1959 of a juvenile male that had been ringed 25 days earlier 760 km to the southwest of the recovery site, in Germany. The supposition that the Siskins may breed for the second time in more northern parts of Europe (Mezhenny, 1963; Payevsky, 1973a; Iovchenko & Noskov, 1983) has support. It cannot be ruled out that Eurasian Siskins in this respect are similar to Red Crossbills (plate 29) that not only may breed in winter and early spring, but also both adults and juveniles move in different directions within the species' range. On the Courish Spit such Red Crossbill movements are recorded regularly, but the total numbers and the proportion of juveniles varies broadly, like in Siskins.

4.9. RANGE EXPANSION AND DEMOGRAPHIC PARAMETERS OF THE COMMON ROSEFINCH

The Common Rosefinch (plate 28) is of special interest for a demographic study due to its three peculiarities. First, this species intensively expands its range towards the northwest and west; second, it shows population and sex-related variation in the proportion of yearlings participating in breeding; and third, it shows a very low degree of natal philopatry. Theoretically, these three features may be related, as natal site infidelity may enable a quick colonisation of the new areas, where the age composition of the populations may differ from the composition in the ancestral range. Let us analyse these parameters in more detail.

The onset of range expansion of the Common Rosefinch towards the west of its previous range was recorded nearly two centuries ago. The first stage of expansion started in the beginning of the 19th century when the range of the Common Rosefinch reached southeastern Finland, eastern Germany, Czechoslovakia and Austria. In the newly colonised areas the Common Rosefinch for a long time remained a rare species and its breeding was only occasionally recorded there. In southeast Finland, east and southeast Poland it bred sporadically in solitary pairs until early 20th century. In the southwest part of the range Common Rosefinch numbers were increasing from the last decade of the 18th century until the mid 19th century. The southern border of the breeding range in this part of Europe ran across the upper region of the Bug and the Dniestr rivers, southern slopes of the Tatra Mts. and across southern Silesia. However in 1880-1930, the Common Rosefinch disappeared from many areas and the southern border of its range retreated to Pomerania and Masuren area (Józefik, 1960; Bozhko, 1980; Jung, 1983).

The second wave of range expansion began in the 1930s and peaked in the 1960s – 1970s. In the current Leningrad Region the Common Rosefinch was common already at the end of the 19th century, but in the 1940s – 1950s its numbers increased sharply, especially in suburban and city parks. Simultaneously its numbers increased in Finland, Sweden, Karelia and many parts of the European USSR (Osterlöf & Stolt, 1982; Malchevsky & Pukinsky, 1983). In the subsequent years the numbers continued to increase and the range was expanding further to the north, reaching the White Sea coast and 64°N in Finland. In Sweden the numbers recorded increased from 30 in 1959 to 1400 in 1974. Currently the breeding range of the Common Rosefinch in Scandinavia has crossed the Arctic Circle, reached 67°N on the Swedish-Finnish border, and includes most of Sweden and southern Norway (Stjernberg, 1985; Cramp & Perrins, 1994; Isenmann, 1994).

Range expansion towards the west mainly proceeded along the Baltic and North Sea coasts. The first breeding record from the Netherlands dates back to 1987 and in Scotland to 1982. The main wave of expansion to the British Isles started in spring 1992 along the whole east coast, resulting in the first breeding records in England in the same year (Wallace, 1999).

Several hypotheses have sought to explain the causes and mechanisms of the Common Rosefinch expansion (Bozhko, 1980; Stjernberg, 1985). The main ones implicate quick population growth caused by landscape and climate change. In the late 19th and 20th centuries major landscape changes occurred in the European USSR, Finland, and Sweden that facilitated a broad occurrence of suitable habitats: lumbering and cutting in the contiguous forests, growing popularity of suburban settlements, and growing of secondary forests. Furthermore, in the years preceding the second expansion wave May and June air temperatures were higher than in the preceding years, thus vegetation development was accelerated. Breeding success rate of the Common Rosefinch is directly dependent on the concealed location of its rather conspicuous nest, and early foliage growth provides better shelter from predators.

The high productivity of Common Rosefinch populations in the 1930s forced juveniles to settle in more open habitats, and their offspring imprinted such habitats and went further west where such habitats were abundant. Natal philopatry is less typical of Common Rosefinches than of other birds and spring settlement of yearlings in novel areas is more likely. At the same time high air temperatures, both during postfledging dispersal and during spring migration stimulate young birds to disperse further and to settle in new areas (Stjernberg, 1985).

In spite of a large numbers of studies of Common Rosefinch biology in different regions of Europe and Asia (Kovshar, 1979; Bozhko, 1980; Zimin, 1981; Payevsky, 1981c, 1985a; Iovchenko, 1986; Cramp & Perrins, 1994), a controversy still remains concerning the participation of yearling males in breeding. The difficulty of distinguishing between yearling males and females and clear separation of yearling and older males by plumage dictate the necessity of long-term stationary observations at nests. Yearling males may breed alongside with adults, but the percentage of their involvement in the breeding apparently varies broadly between the populations. At the same time, all yearling females captured during the breeding season in Karelia (Zimin, 1981) and on the Courish Spit had incubation patches. Such sex-related bias in the participation of yearlings in the breeding has been reported among European songbirds with the Starling.

The percentage of yearling males in the breeding population of Common Rosefinches greatly varies on an annual basis and between the regions. In southern Finland the ratio of adult males (with red plumage) to yearling males (with grey plumage) varied between 7:2 and 10:0 in different years. On average, there were 7.1 adults per breeding yearling; in Sweden this ratio was on average 6:1 (Bozhko, 1980). At another Finnish site 9 adults were recorded per one breeding yearling (Stjernberg, 1979), in Karelia this figures varied between 1.2 and 4.2, on average 2 (Zimin, 1981). In Tien Shan at one site 4 adults bred per one yearlings (Kovshar, 1979), and another site the ratio was 5:1 (Iovchenko, 1986). These ratios probably do not reflect the true proportions of breeding adults and yearlings, because yearlings are known to occur at the nests of old males, sometimes to help, and sometimes their number exceeds one (Nankinov, 1974; Bozhko, 1980; Cramp & Perrins, 1994). However, yearling males do breed, like adults, in monogamous pairs, even though rare cases of polygyny have been reported for adults. A competition for mates exists among males, but mate choice by the female is neutral towards the characteristics of the male, and no females remain unmated (Stjernberg, 1979; Björklund, 1990).

On the Courish Spit breeding biology of the Common Rosefinch was studied across 33 years in 1959-1995, except of 1961, 1967, 1988, and 1993. A total of 269 Common Rosefinch nests were found, of them 258 with eggs or nestlings. Nest fate was followed in 190 pairs, and in 119 pairs the breeding was successful (at least at the moment of ringing the young at the age of 7-11 days). In order to test for the possible difference between the decades, the breeding data were pooled into three groups: 1959-1971, 1972-1982, and 1983-1995. The mean clutch size did not change across the study period and was 4.6, 4.7, and 4.6 eggs, respectively. The proportion of successful breeding attempts also did not change between the periods: it was 71.4% in 1959-1971, 63.1% in 1972-1982, and 60.6% in 1983-1995 ($\chi^2 = 0.106$-0.487, n.s.).

Age of males in the breeding pairs was determined in 45 cases. At 26 nests the males were old, with red plumage, and in 19 they were yearling, with grey plumage (42.2%). Breeding performance of adult and yearling males was determined for 18 nests of adults and 13 nests of yearlings. Clutch size was on average 4.88 eggs in the nests of old males and 4.54 in the nests of yearlings, but breeding success rate estimated by the Mayfield (1975) method was somewhat higher in the latter group: 56.0% vs. 50.8% in adults. However, the difference was not significant ($\chi^2 = 0.25$, df 1, n.s.). Thus, no significant variation in the breeding performance was found either in the temporal aspect or in relation to the age of breeding males.

It might be expected that due to range expansion young birds and yearlings, in particular yearling males, would occur more frequently in the novel habitats and generally in north-western and western populations of the species. However, the geographic distribution of adult to yearling male ratios does not follow this logic. It may be assumed that range expansion of Common Rosefinches took place by gradual settlement of the young birds in the novel areas, and that their breeding performance was sufficiently high and stable for a part of their offspring to continue this process.

Chapter 5

POPULATION DYNAMICS OF SONGBIRD POPULATIONS

5.1. KEY ISSUES IN THE STUDY OF THE MECHANISMS OF POPULATION DYNAMICS

Since the last century's fundamental contributions to population studies especially by Andrewartha & Birch (1954); Nicholson (1954); Lack (1954; 1966); Elton (1958) 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. Studies of the impact of limiting factors on the populations are necessary to solve theoretical questions about the natural mechanisms for maintaining population stability and for developing practical measures aimed at conservation of the qualitative and quantitative faunal structure.

5.1.1. The concept of density-dependent regulation of numbers

The development of various theories and concepts forwarded to explain the causes of the dynamics of animal numbers, steered towards two traditional directions based on *a priori* assumptions accepted by the researchers. Some authors tended to relate all fluctuations of numbers to extrinsic, environmental factors and their permanent instability, whereas others emphasized the role of intrinsic factors acting within populations (Payevsky, 1983). Most popular has been the concept of regulation by density-dependent or independent factor, where density is the number of individuals per unit area. Even though density-dependence is one of the oldest topics in population ecology, it still remains the most controversial one. The debate is ongoing for more than a half of the century and has intensified in the recent years. The polemics in the recent publications (Murray, 1999; Turchin, 1999; White, 2001) has grown very emotional. One of participants (Wolda, 1995) suggested that the disagreements on whether animal population numbers are regulated should be "quietly buried and quickly forgotten", because, as he suggests, "no one has been able to prove beyond doubt that one side or the other was right and the other wrong". Other authors, e.g. T.C.R.White (2001), wrote that in the face of the impossibility of showing the existence of regulation, "many ecologists hold the belief that populations *must* be regulated and continue to seek evidence for this" (p. 148). Originally D. Lack (1966) and T. Royama (1977) wrote that the idea of density-dependence is *a priori* correct, and that it needs no empirical proof. They believed that the concept of density-dependent regulation springs from one main assumption of stability of natural populations. Even though the concept of population homeostasis is rather widely accepted, for a long time no evidence of homeostatic self-regulation was available.

What is the essence of this controversy and where lies (or should lie) regulation of population numbers? It is well known that numbers of most species are relatively constant, and if they change, they do so either gradually or cyclically. This means that a certain balance between birth and mortality rates should explain it. Population density-independent factors are extrinsic factors such as climatic and weather, anthropogenic such as human-induced disasters and habitat change, and astronomic ones, especially the cycles of solar activity. Mortality caused by such factors, e.g. by extreme weather or by fires, does not depend on animal numbers, and no dynamic feedback exists between each factor and population density. Conversely, intrinsic factors have a dynamic feedback that influences population numbers. Population density-dependent factors are mainly the biotic ones, primarily food and food-related intraspecific competition, predation and disease. Mortality induced by these factors, e.g. by food shortage, directly depends on population density. Under high density high mortality rate and/or low birth rate must be expected, and under low density – low mortality rate and/or high birth rate. Therefore, a population can exist if its growth rate is inversely related to population density. Competition is then one of mechanisms of natural selection. This impact of competition on population growth rate is density-dependent. The regulation mechanism works so that the numbers are stabilised before the level when biotic resources are exhausted. The main unit in population regulation is population change realised per one individual (per capita), defined as $r_t = N_t / N_{t-1}$, where N_t is population density at time t (Turchin, 1999).

The alternative hypothesis is the population limitation supposition (some erroneously call it 'the hypothesis of density-independent regulation'). It the most extreme form it was formulated by T.C.R. White (2001) as follows: "…the abundance of animals is passively limited by the inability of the environment to support them all. …it is the resultant struggle to survive in this hostile and inadequate world which generates the ferocious inter- and intra-specific interactions that ecologists observe. These interactions are responsible for the evolution of life as it is today, but they do not regulate its abundance." (p. 148).

Some terminological inconsistency related to these problems should be noticed. If 'population limitation' is treated by some biologists as an alternative to 'population regulation', in many papers of regulation advocates 'population limitation' is treated as the limit to population growth just in the process of regulation.

Many researchers equally accept the dependence of animal numbers on both extrinsic physical factors and biotic factors whose action may be steered by population density. The relative importance of these factors may vary broadly under different living conditions of animals, and some factors may be density-dependent or independent under different circumstances (Bendell, 1972; Ricklefs, 1976). Nevertheless, pessimistic estimates prevail in respect to the possibility of creating a "theory of everything", i.e. to develop a general theoretical explanation of the causes of cyclic variation of animal numbers (Maximov, 1984).

It should be emphasized that in the ornithological community no such acute debate existed on the problem of density-dependence, as in other biological disciplines. This might be due to the great authority of David Lack, who believed density-dependent regulation to be an appropriate natural phenomenon. The views of Lack on population regulation were expressed in two monographs (Lack, 1954, 1966). A special analysis of the development of Lack's ideas has been recently published by I. Newton (2003b). As stated, D. Lack summarised his ideas: (1) The reproductive rate, evolved through natural selection, is that which results in the greatest number of surviving offspring per pair; (2) Population density is regulated by density dependent mortality, in most species by food shortage outside the breeding season. I. Newton (2003b) wrote that these two firm statements we may now recognize as partly correct, but in need of considerable modification. This mainly refers to the role of density-dependent processes in the population dynamics and the role of territorial behaviour in the regulation of breeding density of birds.

5.1.2. The evidence of density-dependent regulation of avian populations

For birds, as with other animals, it is difficult for find evidence of density-dependent population regulation. The critics raise the point that controlling factors of both types, density-dependent and independent, affect avian numbers. In any dataset, be it breeding results or annual surveys of numbers, it is difficult to separate the density-dependent results from the results of extrinsic factors. However, in the birds it appeared possible, on one hand, to demonstrate the impossibility of an exact identification of the mechanism discussed (Greenwood & Baillie, 1991), on the other hand, to show considerable evidence of this mechanism's effect in various species.

The dependence of breeding parameters, in particular of clutch size, on population density was found in many, but not all, species studied. In one review

(Sinclair, 1989, after Both, 1998) it was shown that just 26% of studies demonstrated an effect of population density on clutch size, and 32% of studies on nestling growth rate and their survival. Another review (Both, 2000) showed that among 57 studies on 10 avian species, the relationship between clutch size and density was shown in 22 (39%), whereas in the Great Tit the effect was found in roughly one-half of the studies, and in the Pied Flycatcher – in none. The hypothesis has been proposed that migrants fail to fit their clutch size to population density because of their protracted period of arrival and start of breeding (Alatalo & Lundberg, 1984).

Clutch size of passerines in Karelia (in particular, the Great Tit, the Pied Flycatcher, the Willow Warbler and other species) varied between the years irrespectively of the breeding density (Zimin, 1988; Artemyev, 1993, 2005). The same was true of the *Acrocephalus* warblers on the southeastern coast of Lake Ladoga (Popelnyukh, 2002). In the Oka nature reserve the relationship between clutch size and breeding density of Pied Flycatchers was different even within the same study area: under low density, no relationship was recorded, under medium density the relationship was positive and under high density it was negative (Numerov, 1995). In a Common Redpoll population on the Yamal Peninsula in the years of high density the fecundity was also high (Alekseeva, 1986).

Other results were obtained by simulation modelling. Modelling of the dynamics of population density of titmice on the basis of a bioenergetics and matrix model of age structure and density resulted in a conclusion of the leading role of density-dependent mortality in the regulation of numbers (Karelin & Gilmanov, 1992). An analysis of factors that limit population numbers of North American Black-throated Blue Warbler (*Dendroica caerulescens*) demonstrated that the number of fledglings and annual recruitment of yearlings were inversely related to breeding density. A matrix population model showed that the numbers of this population are limited by negative feedback with density-dependent annual fecundity (Sillett & Holmes, 2005).

More than 100 field experiments have been performed in the past 40 years to test the roles of food, predation, parasites, and competition, in the limitation of breeding bird density. Usually the number of breeding birds in a study plot was recorded over some years, then some factor was artificially altered, e.g. new nest boxes were added, predators were removed, additional food was provided etc., and the numbers were recorded again. All these experiments revealed the following (Newton, 2003b): (1) The main potentially limiting factors, especially food and natural enemies, indeed limit the breeding bird density; (2) Populations of different species may be limited by different factors in different areas or in different years; (3) Most experiments resulted in at least doubling of the breeding density as compared with the control (much greater increase in hole breeders).

5.1.3. The importance of territorial behaviour in birds for the regulation of breeding density

The role of territorial behaviour as a mechanism of regulation of breeding density in birds has been discussed over many years (Lack, 1954; Wynne-Edwards, 1962; Krebs, 1971, etc.). From this viewpoint territorial behaviour is studied by removal experiments. After spring settling in the territories, a proportion of birds is captured and removed, and if vacant territories are occupied by other individuals, especially from the pool of non-territorial birds ('surplus') of the same population, it is concluded that territorial behaviour limits breeding density. Over 60 experiments with 48 species of passerines, gallinaceae, birds of prey, ducks, waders, and alcids were performed (for reviews see Ryabitsev, 1993; Newton, 2003b). In ca. 80% of the experiments the removed birds were quickly replaced. This means that some population reserve exists, and limiting of the breeding density by territorial behaviour is common among birds. The behavioural mechanism may be based on varying food availability in different territories. An example of this is the inverse relationship between territory size and density of food objects in an American passerine, the Ovenbird (*Seiurus aurocapillus*; Smith & Shugart, 1987). Studies of foraging ecology of waders and experiments in two species, the Pectoral Sandpiper (*Calidris melanotos*) and the Ruff (*Philomachus pugnax*) in Yakutian tundra showed that their spring breeding density is limited by territorial behaviour, but territory size is limited not by food availability in this season, but the projected food availability for the nestlings (Khlebosolov, 1999).

Under the conditions of low population density, e.g. in peripheral parts of the range, especially in the Subarctic, density-dependent regulation mechanisms may fail to act, or act not in all birds. This has been shown by V. Ryabitsev (1993) in the Yamal Peninsula and in Subarctic Urals. Experimental removal of territorial males in these regions forced the author to conclude that overpopulation and population reserve are uncommon in the Subarctic. At these latitudes many species show weak if any territorial aggression, or it is transformed in such a way that does not serve as a mechanism of population density regulation.

In most cases territorial behaviour, like any other kind of dominant behaviour, acts as a strong regulatory mechanism that fits the population density of the birds to the local resource abundance.

5.1.4. The interaction and delayed action of limiting factors

Limiting factors often act in a combination, and their role is sharply increased by interaction. For instance, food shortage may increase predation, because hungry birds compromise their safety. Availability of specific nesting places is a *conditio sine qua non* for breeding for a number of species, and if shortage of such places is combined with food shortage, breeding becomes impossible. I. Newton (2003b) believes that the importance of breeding place availability for limiting breeding density is strongly underestimated in the books by D. Lack (1954, 1966). This limiting is obvious not only for hole breeders, but also for many other species that need special places for their nests: reedbeds, islets in lakes, cliffs, niches in the rocks etc.

In a number of cases, food availability and temperature conditions in one season influenced breeding numbers in the subsequent breeding season. In a Finnish Pied Flycatcher population an increase in the number of breeding birds followed a 'good' year, when production of juveniles per breeding pair was high, and declined after a 'poor' year (Virolainen, 1984). The same has been shown for the Willow Warbler and the Icterine Warbler on the Courish Spit in the Baltic (Sokolov, 1999b). These examples demonstrate the absence in the populations studied of a mechanism of numbers self-regulation that would eliminate the surplus of individuals after a successful breeding season, and enhance the survival rate of the young after a poor year. However, it is not possible to be sure that such a surplus indeed existed. It cannot be ruled out that the observed fluctuations in numbers did not reach the threshold of carrying capacity of the environment.

5.1.5. Demographic processes and range expansion in birds

Significant changes in the population numbers are often accompanied by range expansion. As indicated in the reviews of range expansions in European birds (Nowak, 1971; Murray, 1979, Payevsky, 2004), 49 species, i.e. 15% of the avifauna, underwent considerable range changes in the past 200 years. Most frequently breeding ranges shifted towards the north and west across Northern Europe, from north-western Russia and Finland to the British Isles (see e.g. section 4.9 on the Common Rosefinch).

All the factors that were implicated to explain the causes of the observed range expansions of different bird species (Nowak, 1971; Golovatin et al., 2002; Krivenko, 2002; Payevsky, 2004), can be reduced to several groups: a) climate change, i.e. warming; b) landscape change, including the anthropogenic effects; c) population processes causing the growth of numbers or gene drift. It has also been assumed that many cases of expansion may be treated as filling the faunistic gaps (Belik, 2003), as the ecosystems of Northern Eurasia are believed to contain many vacant ecological niches.

It is possible that any natural demographical range expansion is based on the stable excess of birth rate over mortality rate and excess of the normal population density. Therefore, the factors above may cause primarily population growth, and as a consequence, range expansion to the novel areas. In birds, population growth may be achieved in three ways: 1) increase in success rate of each breeding attempt; 2) increase of number of clutches laid per breeding season; 3) decrease of mortality rate of the young after gaining independence from parents. In all three cases, favourable weather conditions may be instrumental. However, sometimes in the study of range expansions it is possible to follow E. Mayr (1951) and to assume an exclusive role of the genetic factor, i.e. the advent of mutant individuals that have a special urge to disperse, causing avalanche-like gain in new areas. This was probably the case during the expansion of the Eurasian Collared Dove (*Streptopelia decaocto*) which is one of the most graphic and best documented cases in zoogeography. A similar mechanism cannot be ruled out in the Serin case. During 170 years, the Serin occupied ca. 2.5 million km^2, i.e. nearly one-half of its current range (Nowak, 1971).

Quite significant for this topic is also the pattern of territory dispersal. Any population contains a proportion of immigrants of unknown origin, so that the processes of emigration and immigration may significantly shape the dynamics of population numbers even without clearly documented range expansion.

5.1.6. Long-term trends in avian numbers

Long-term trends in avian numbers based on long-term survey data at a given site deserve special attention and analysis. The mechanisms of their formation, in spite of the long history of research, still remain a topical problem in ecology. The populations with long-term upward or downward trends are not regulated around a constant equilibrium. It is very difficult to detect a density-dependent regulation mechanism in such populations. Therefore it is most important to distinguish long-term trends from annual fluctuations around these trends. However, in such cases the study of density-dependent regulation faces a double problem: short data series may be inadequate to detect the regulation, but longer series may contain long-term trends that also hamper the detection of regulation mechanisms (Newton et al., 1998).

When analysing the contribution of different factors, i.e. the weather and climate, anthropogenic, and intrinsic ones, it is most important to estimate the input of each factor and their interaction. Besides, when working in the former Soviet Union and when analysing the results obtained there it is necessary to take into account the consequences of the recent sharp economic crisis which caused a decline in industry and agriculture. These processes are known to have significantly improved the habitats and food availability for the birds (Galushin et al., 2001).

Since the early 1970s, a large number of papers on the population dynamics of birds have been published (Berthold, 1973; Järvinen & Väisänen, 1978b; Dolnik & Payevsky, 1976a, 1980; Österlöf & Stolt, 1982; Svensson et al., 1986; Berthold et al., 1986; Payevsky, 1985a, 1990a,b; Baumanis, 1990; Marchant, 1992; Busse, 1994; Sokolov, 1999a,b; Sokolov et al., 2000; 2001a,b; Sæther et al., 2000; Newton, 2004; Berthold & Fiedler, 2005; Sanderson et al., 2006; etc.). This interest towards population dynamics was initially caused by a sharp decline of many species in Europe, especially insectivorous and carnivorous species, which was then mainly explained by the use of pesticides and herbicides in agriculture and forestry.

In the following years, on the one hand, a greater diversity in the trends of populations, especially of songbirds, was revealed; on the other hand, publications of different authors devoted to the same species appeared to be controversial. Some authors reported very significant, often dramatic, declines in many passerine species (Berthold et al., 1986, 1998, 1999; Busse, 1994; Busse et al. 1995; Berthold & Fiedler, 2005; Hüppop & Hüppop, 2007), whereas others claimed that species vary in this respect, and that populations of a number of species, long-distance migrants included, not only did not decline but even grew (Payevsky, 1990a,b; Marchant, 1992; Sokolov, 1999b; Payevsky, 2000c; Štastný et al., 2004).

During the past 30 years numbers of a few North American passerines wintering in the tropics also have declined, so that some species appeared on the brink of local extinction (Askins et al., 1990; Holmes & Sherry, 2001). Some authors claim that the causes of declining numbers of these species are the increased habitat fragmentation and degradation on the breeding grounds, whereas other draw attention to the increased numbers of brood parasites. It has been also suggested that the possible reasons behind the population trends may differ between the species, and the existing alternative hypotheses are equally likely. However, these species spend their winter between Mexico and northern South America that in the recent years has suffered large-scale forest destruction, which may be the main reason of population decline in migrants (Bibby, 2003).

Migratory birds are very different from the sedentary species in respect to the limiting impacts on their populations, because conditions in more than one part of the world may affect different parts of their annual demographic cycle. Factors acting in the regions of migratory stopovers and wintering may through carry-over effects limit bird numbers on the breeding grounds, and vice versa. I. Newton (2004, 2008) called winter-limited the breeding populations whose numbers are regulated by the factors acting in the non-breeding season, and summer-limited the breeding populations whose numbers are limited by whatever factors operate in the breeding season. Assuming that significant negative change of avian habitats are equivalent to the decline in food availability, the answer to the question where the roots of declines in migratory populations lie, depends on the relative force of limiting factors in the breeding and wintering areas (Sutherland, 1996; Holmes & Sherry, 2001; Sillett & Holmes, 2002). In winter quarters the density-dependence acts through mortality rate, and in the breeding area through the declining productivity.

Most generally, any avian population dynamics may depend on the five main components (Fig. 29): 1) Rate of mortality due to extrinsic factors (astronomic, weather and climate, anthropogenic, and natural disasters [fires, floods, etc.]). 2) Rate of mortality due to population density-dependent factors (food, predation, diseases, nest site availability, and competition related to these factors driven though behaviour, territorial behaviour included). 3) Population-level survival rate: fecundity as clutch size and number of clutches per season, productivity as the number of surviving young, annual survival rate of adults. 4) Overall species-level survival rate (longevity of mature individuals, age of the first breeding). 5)Immigration and emigration rates.

Annual variation of all these components apparently governs the observed dynamics of numbers. However, it does not seem possible to simultaneously estimate and analyse all of them. If long-term survey data are available, it currently seems most promising to study the impacts of extrinsic factors on population changes by the comparative method. A deeper understanding of avian population dynamics may be facilitated by the study of demographic parameters, initially annual survival rate.

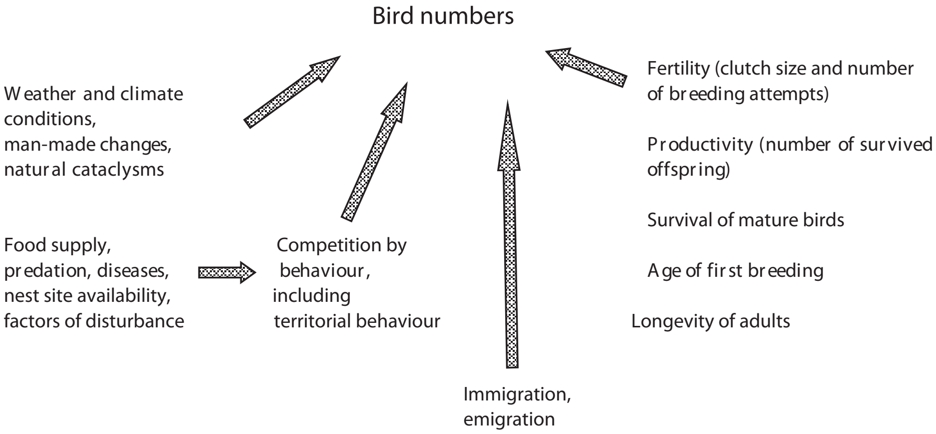

Fig. 29. Factors that govern the dynamics of avian population numbers.

5.1.7. Vulnerable periods in the annual cycles of numbers

The above topics are directly related to the problem of adaptive significance of seasonal migration. Movements of the whole population or a part of the population from the breeding area to winter quarters and back allow the species to maintain its numbers in a much larger area than it would have been possible without migration. The question of the benefits to migrants can hardly be called an unsolved one. Annual movements exist just in order to keep the mortality rate of migrants below the mortality of the remaining individuals. However, the literature is filled with indications that the migratory period is especially dangerous for the birds. In one review a special section entitled 'Dangers expecting the birds during migration' reports huge losses suffered by avian populations during the whole migratory period (Curry-Lindahl, 1975). Another review (Creutz, 1987) gives examples of catastrophic mortality of thousands of birds, from swallows to storks, under the especially adverse weather during migratory season. Disastrous impacts of severe weather conditions on migrating birds are mentioned in many articles and books, popular literature included. Species whose annual cycle includes migration are claimed to be especially vulnerable (Cloudsley-Thompson, 1978). A very detailed discussion of dangers of migration was recently given by I. Newton (2004, 2006, 2007, 2008), who wrote that the conditions experienced by migrating birds may considerably limit population numbers.

Thus, on one hand, migration is a regular stage in an avian life cycle; on the other hand, it is a dangerous period with a constant risk of mass mortality. Are migrations indeed so dangerous for the birds? To answer this question, anecdotal reports of mortality, even very impressive mass mortality, are insufficient.

An analysis of seasonal distribution of the overall annual mortality is required, looking for differences between migratory periods and other parts of the annual cycle. Such an analysis was performed on the basis on long-term ringing efforts of 10 avian species that breed and winter mainly within Europe (Payevsky, 1999b).

The difficulty estimating season-related variation in avian mortality rates is mainly due to the lack of basic comparative data. The analysis of monthly variations in survival rate is based on calculations from the mean annual mortality rate (Caughley, 1977; Bardin, 1986). Therefore the simplest materials for such analysis are the primary ringing results, i.e. dead recoveries. In a number of the species analysed the autumn and winter distribution had already been tested for between-year homogeneity and no significant variation was found (Payevsky, 1994c; Payevsky, 1995), therefore the data for all study years (1957-1992) were pooled for analysis. Of the 10 species included in this analysis, four were passerines: the Great Tit, Chaffinch, Eurasian Siskin, and European Starling. The remaining ones were the Mallard (*Anas platyrhynchos*), Osprey (*Pandion haliaetus*), Sparrowhawk, Common Coot (*Fulica atra*), Northern Lapwing (*Vanellus vanellus*), and Common Black-headed Gull (*Larus ridibundus*).

The monthly distributions of the numbers of dead recoveries in the four songbird species are given in Fig. 30). I found (Payevsky, 1999b) that for each of the ten species that the species was a highly significant predictor of the monthly distribution of dead recoveries ($\chi^2 = 37.77$, df 9, $p < 0.001$), whereas the season was not a significant predictor ($\chi^2 = 3.38$, df 11, n.s.). For a more detailed analysis of mortality rates in different seasons I tested for the significance of the difference between the numbers of dead recoveries within each species, sex and age group in three main periods: summer, migratory periods (spring and autumn) and wintering period. The null hypothesis was that the proportion of dead birds is equal in the time periods compared. The results for the passerines are presented in Table 31.

In most cases the number of dead recoveries significantly differed between the seasons. However, the seasons of peak and minimum mortality did not coincide in different species. For example, in the Chaffinch and the European Starling

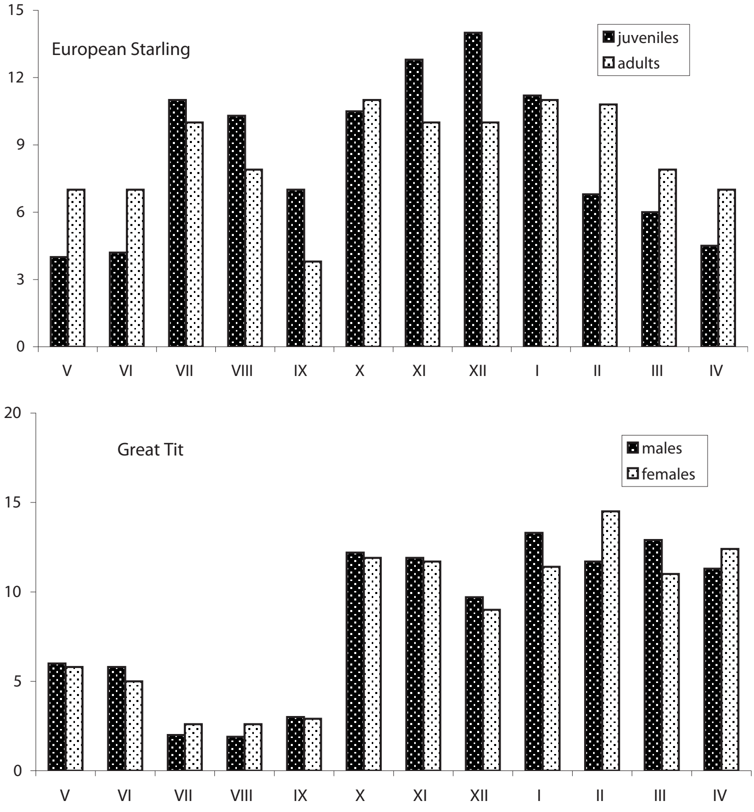

Fig. 30. Monthly distribution of dead recoveries. X axis – months, Y axis – proportion.

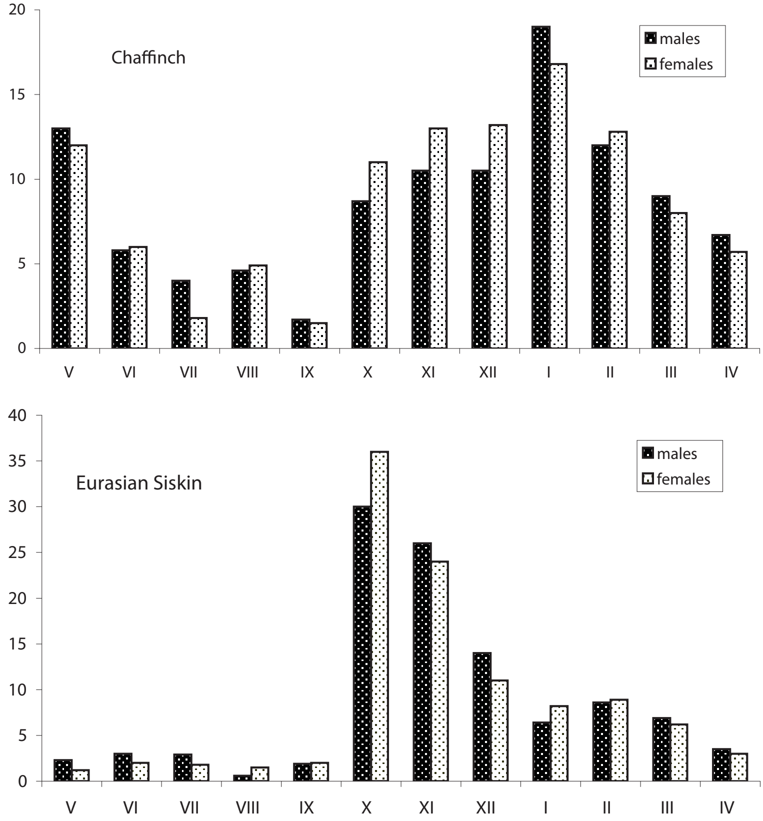

Fig. 30. Continued.

mortality rates during the winter period were found to significantly exceed mortality rates in other seasons. In the Great Tit and the Eurasian Siskin the occurrence of dead recoveries during migration and wintering were roughly the same. In the Chaffinch mortality rates during migration and during breeding showed no significant difference. Mortality rates during spring and autumn passage vary significantly, but the direction of difference was species-specific. Age and sex-related variation was tested by χ^2 criterion in a 2 × 2 table. The Great Tit, Chaffinch and Eurasian Siskin showed no sex-related variation in the seasonal distribution of mortality events (χ^2 values varied between 0.09 and 2.1, df 1, n.s.).

In general, in all species a significantly higher occurrence of dead recoveries was found during the winter period when compared with migratory period in 10 cases, and the reverse was true in 3 cases out of 18. Mortality was higher during migration than during breeding in 12 cases out of 18. Finally, mortality rate during wintering exceeded the mortality rate during breeding in 16 cases out of 18. The

Table 31. Significance of difference between numbers of dead recoveries in different seasons in four species

Species	**Age, sex**	**n**	**Seasons, proportions and significance of difference**							
			M/W	χ^2	M/S	χ^2	S/W	χ^2	SM/AM	χ^2
European Starling	Juveniles	414	38/62	16.1***	48/5249/52	0.2 n.s.	40/60	13.2***	38/62	6,5*
	Adults	400	40/60	10.8***		0.3 n.s.	42/58	7.3**	49/51	0.04 n.s.
Great Tit	Males	522	46/54	3.1 n.s.	73/27	57.4***	24/76	84.6***	62/38	11.3***
	Females	530	45/55	5.1*	71/29	49.4***	25/75	83.5***	63/37	13.5***
Chaffinch	Males	753	33/67	62.9***	49/51	0.04 n.s.	34/66	59.8***	63/37	11.8***
	Females	619	32/68	60.1***	51/49	0.3 n.s.	31/69	68.0***	54/46	1.1 n.s.
Eurasian Siskin	Males	593	45/55	6.5*	86/14	151.3***	11/89	207.5***	26/74	57.3***
	Females	420	49/51	0.4 n.s.	91/9	141.5***	9/91	153.1***	21/79	64.7***

Notes. W – winter period (November – February), S – summer period (May – August), SM – spring migration (March, April), AM – autumn migration (September, October), M – migratory period (SM+AM).

Significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$, n.s. – non-significant.

values averaged across the 10 species studied are given in Fig. 31. This averaging makes it possible to conclude that mortality rate during migration comprises on average 36% of the total mean annual mortality, whereas mortality rate during wintering makes up 45%, consequently significantly higher than during passage.

These results allow us to conclude that seasonal migrations are equally dangerous for the birds as other periods of their annual cycle. The main burden of mortality risk indeed falls to the non-breeding period, but the risk is more or less evenly distributed across time. I. Newton (2006, 2007, 2008) believes that the conditions on the migratory routes and at stopovers may negatively affect population numbers. However, stopover behaviour of migrants is apparently equally adaptive as their behaviour during winter. For instance, spatial behaviour of long- and short-distance nocturnal migrants at stopovers is governed by a complex interaction between their species-specific foraging behaviour, weather conditions and habitat (Chernetsov, 2005). Moreover, the study of the question which period, breeding or non-breeding, is most critical for the subsequent change of population numbers showed that different groups of birds may react differently to weather and climatic conditions (Sæther et al., 2006; see also the next section).

The cases of mass catastrophic mortality during migration, caused by adverse weather or e.g. by oil pollution of the water, remain accidental, i.e. rare irregular events that are variable in their negative impact on avian populations. The analysis of the impact of synoptic weather processes on bird migration showed

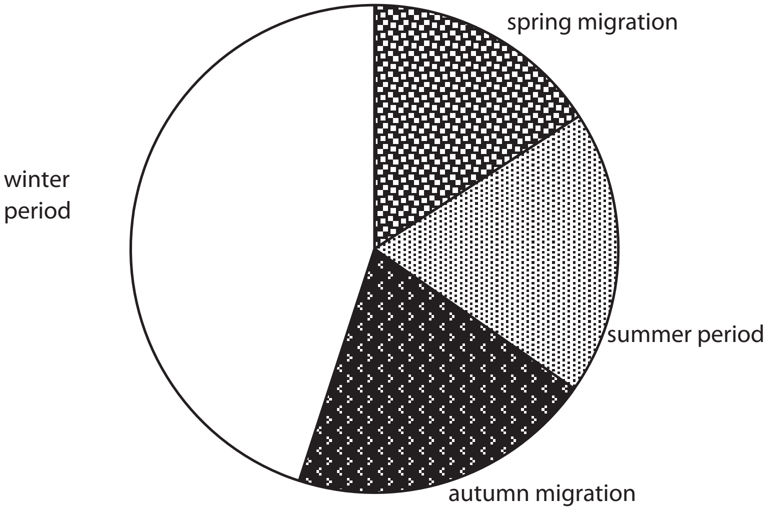

Fig. 31. Averaged death rates of birds of 10 species from different Orders in different periods of the year.

that migrants avoid the areas of low pressure and atmospheric fronts and try not to fly into thunderstorms, gale-strength winds, fog, rain, snowfall and icing (Richardson, 1978; Nazarenko & Amonsky, 1986; Alerstam, 1990). Otherwise the energetic cost of migratory flight is increased sharply (Bulyuk & Chernetsov, 2000), which leads to failed migration. Birds that migrate in arid and mountainous areas of Asia make a detour to avoid the most inhospitable parts of the migratory route (Bolshakov, 2002).

Do the cases of mass mortality of birds have a selective importance? Under disastrous climatic and weather influences survival of individuals is random and does not depend on special adaptations, therefore selection does not act in such situations. Movements between breeding and wintering areas are adaptive for the populations, and random disastrous mortality events, in my opinion, have no adaptive significance.

5.1.8. The impact of global climate change on the timing of migration and breeding and on songbird numbers

In the past decade, more and more publications appear that report the shifts in the timing of seasonal events in the life of the birds that the authors relate to the process of global warming (Bairlein & Winkel, 2001; Møller et al., 2006). During the recent 15-20 years, the timing of spring migration and arrival of European birds has considerably shifted towards earlier dates (Mason, 1995; Sokolov et al., 1998; Sokolov & Payevsky, 1998; Crick & Sparks, 1999; Bairlein & Winkel, 2001; Żalakevicius & Żalakeviciute, 2001; Forchhammer et al., 2002; Cotton, 2003). The timing of autumn migration has also changed, but this change is less universally pronounced. Some species started to depart earlier, others later. This may also influence the tactics of migratory stopovers and generally prolong the summer part of the annual cycle (Lehikoinen et al., 2006).

Decreasing precipitation in Africa in January – March, and increasing winter air temperatures in sub-Saharan Africa in the recent decades seem to force migrants to depart from the winter quarters much earlier than before. This is supported by the correlation between February precipitation in Africa at 2.5-7.5°N and arrival dates to the Eastern Baltic (Sokolov & Kosarev, 2003). Apart from this paper, a series of publications by L. Sokolov and co-authors is devoted to the analysis of impact of climate and weather change on the timing of seasonal events and on songbird numbers in Europe (Sokolov & Payevsky, 1998; Sokolov, 1999a,b, 2006; Sokolov et al., 2000, 2001a,b; Sinelschikova & Sokolov, 2004; Sokolov & Gordienko, 2008). Comparison of mean air temperatures in spring and summer with the mean hatching dates on the Courish Spit in 1959-1998 showed a significant inverse relationship in 10 passerine species (Table 32). Higher spring temperatures cause early breeding. March temperatures were related to the timing of breeding of the Great Tit and the Chaffinch that arrive early; April temperatures influence these species and also the Wood Warbler, Pied Flycatcher, Blackcap and Lesser Whitethroat. May temperatures were clearly related to the timing of breeding in eight species. As the correlation between the mean hatching dates and the mean capture dates of juveniles was significant and positive, the latter parameter was also used as a proxy for the timing of breeding. A comparison of the timing of breeding in 36 songbird species with air temperature confirmed that in early arriving species the timing of breeding is inversely related with March and April temperatures, and in late arriving birds a similar relationship with April and May temperatures exist (Sokolov & Payevsky, 1998). Further research resulted in unequivocal conclusions on the effect of weather and climatic conditions on the timing of breeding and on breeding performance. In different regions of Europe in the 1960s and 1980s population numbers of many species were significantly increasing, whereas in the 1970s and partly 1990s they significantly dropped. The causes of such long-term trends in numbers were the fluctuations of the weather and climatic factors. Evidence of this was the significant correlation between trapping figures and April air temperature (Fig. 32), and between bird numbers and the timing of their breeding and breeding performance. High air temperatures in spring cause early arrival and early breeding, increase breeding success rate and result in population growth.

Table 32. Relationship between the mean hatching date in a number of songbird species and the mean air temperature in spring and summer months from 1959 to 1998 (Spearman's rank correlation coefficient under different levels of significance: + $p<0.10$, *$p<0.05$, **$p<0.01$, ***$p<0.001$).

Species	Number of years	Under mean monthly air temperature			
		March	April	May	June
Icterine Warbler	16	-0.10	-0.24	-0.34	-0.28
Barred Warbler	18	-0.08	-0.32	-0.65**	0.05
Blackcap	18	-0.18	-0.40*	-0.26	-0.02
Garden Warbler	20	-0.03	-0.16	-0.51*	-0.26
Whitethroat	16	0.11	-0.07	-0.38	-0.62*
Lesser Whitethroat	20	-0.21	-0.45*	-0.33	-0.37
Willow Warbler	20	-0.30	-0.28	-0.61**	-0.03
Wood Warbler	18	-0.38	-0.61*	-0.49^{+}	0.12
Pied Flycatcher	20	-0.21	-0.45*	-0.59**	-0.23
Great Tit	20	-0.39^{+}	-0.42^{+}	-0.58*	-0.53*
Chaffinch	29	-0.38*	-0.40*	-0.66***	-0.22
Common Rosefinch	18	-0.13	-0.22	-0.75**	0.09

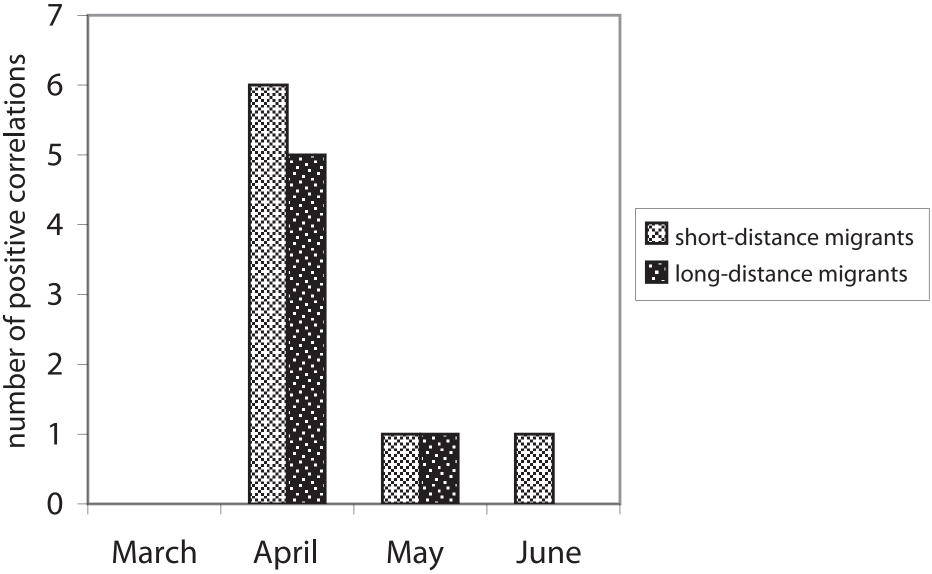

Fig. 32. Correlations between numbers of juveniles (9 long-distance and 12 short-distance migrants) and air temperatures in different months in their breeding grounds (from Sokolov et al., 2000).

Similar relationships of all breeding and population productivity parameters with the temperature regimen of spring were obtained by A. Artemyev (2002) for the Pied Flycatcher in Karelia. Overall numbers were also related to spring temperatures in the duck populations of northern Kulunda (western Siberia; Mikhantiev & Selivanova, 2002) and for the bird populations in Barguzinsky nature reserve (eastern Siberia; Ananin, 2001). It may however be noted that many such papers report just a coincidence of bird number variation with the weather and climate fluctuations, but evidence of the causal relationship is lacking (Fiedler, 2003). Of special interest are therefore the studies on the European White Stork (*Ciconia ciconia*) and the Black-browed Albatross (*Thalassarche melanophrys*) when a relationship between breeding performance, survival rate and population recruitment and local and global climatic variation was shown (Nevoux & Barbraud, 2006).

It should be stressed that the great importance of spring air temperatures for the normal process and success rate of breeding in birds, and therefore for their numbers, was shown long ago (Svärdson & Durango, 1950; Slagsvold, 1975, Payevsky, 1985a). Spring cold spells and snowfalls that increase the mortality rate of potential breeders, or early and warm spring (that increase productivity) have a stronger effect on short-distance migrants that arrive early. However, recent studies showed that late arriving long-distance migrants may also be under the strong influence of spring temperature fluctuations. The ongoing large-scale climate change is believed to affect avian population dynamics in the future to a much greater extent than is recorded at present (Sæther, 2006). Testing the two hypotheses of the impact of climate on bird numbers (breeding vs. non-breeding regulation) shows the following. In altricial birds in the northern part of the temperate area population numbers vary in a close agreement with climate variation in the non-breeding season. Conversely, in praecocial and semi-praecocial birds it is only during breeding that the foundations of the numbers during the subsequent breeding seasons are laid, as the numbers of future recruits are defined by the breeding success resulting from impacts of climate change (Sæther et al., 2006). For discussion of the impact of the global climate change on long-distance migrants that spend their winter in Africa see also in section 5.2.2.

Climate warming, including in Europe, and shift of the phenological events towards earlier dates may also have a negative effect on birds. Population numbers of the Pied Flycatcher in the Netherlands declined dramatically in the recent years. The reason was assumed to be inadequate food provision of the birds that arrived and started breeding in the usual season typical of this population. Earlier development of vegetation and insects did not match the timing of breeding of the birds, so that the nestlings were not fed adequately (Coppack & Both, 2002; Both et al., 2006; Visser et al., 2006). It however remains unclear why Dutch Pied Flycatchers become an exception when compared with many other long-distance migrants in many regions of Western Europe that benefited from this shift (increased duration of breeding and moult).

Studies aimed at testing the hypothesis that global warming may have a negative effect on avian communities composition resulted in encouraging conclusions. Bird specific compositions in 21 European regions were compared in 1970-1977 and 1987-1995. In particular, the proportions of long- and short-distance migrants were expected to respond to climate change differently. In the areas where spring got warmer, numbers of both long- and short-distance migrants increased, and the numbers of sedentary species did not change (Lemoine et al., 2007). Therefore, climate warming already affects abundance and specific structure of avian communities, but this effect cannot be called negative.

In many parts of Russia long-term trends in the timing of spring arrival had different impact on different bird species. For example, in Il'men nature reserve (eastern foothills of the South Urals) the timing of spring arrival, as shown by the annual monitoring data, hardly changed across 34 years. The reason is the lack of a significant trend in the mean monthly air temperatures, even though a significant dependence of arrival time on temperature was found in both short- and long-distance migrants (Sokolov & Gordienko, 2008).

5.2. THE MECHANISMS OF THE POPULATION DYNAMICS OF EUROPEAN BIRDS THAT SPEND THEIR WINTER IN AFRICA

Annual seasonal movements of birds between breeding and wintering areas are generally well known. A very important migratory system in the Old World is the Palaearctic – African migration system with crossing of the Sahara. Every year many millions of birds migrate to Africa. In spite of the long history of research into these movements (Moreau, 1972; Morel, 1973), only in the two recent decades have well planned studies commenced on the role of arid and mountainous areas as ecological barriers for migrants, on one hand (Dolnik, 1985a,b; 1987, 1990; Bairlein, 1992; Bolshakov, 2002), and of population mechanisms that govern the dynamics of numbers of these migrants, on the other hand (Marchant, 1992; Baillie & Peach, 1992; Newton, 2008). Important impetus for the development of research of migration ecology was given by the 1991 meeting in the UK "The ecology and conservation of Palaearctic-African migrants" (Crick, 1992), 3rd meeting of the European Ornithologists' Union in the Netherlands "The avian calendar: Exploring biological hurdles in the annual cycle", international research programme "European-African Songbird Migration Network" (Bairlein et al., 1995), and the regular Pan-African Ornithological Congresses.

5.2.1. The distribution of migrants and the environmental factors along migratory routes and in wintering areas

When the fundamental work of R.E. Moreau (1972) on the Palaearctic – African bird migration system was published, systematic bird surveys had just begun, and population dynamics of birds that participated in these seasonal movements was not known. Many environmental features of the migratory route were also poorly known. It was assumed that the whole Sahara across its 1600 km expanse along the north-south axis is completely unsuitable for the normal existence of birds, except of the few oases.

After crossing the Mediterranean at any place, Moreau wrote, the birds must start again "without delay on their crossing of the Sahara, a tremendous all-or-nothing hazard with practically no food, no water, no shade… they disperse indiscriminately over the area of some 8 million km^2 afflicted with great heat and high saturation deficit." (Moreau, 1972, p. 32). It was assumed that migrants heading for tropical Africa crossed the Sahara by single non-stop flight that last for at least 40 hours. This view was supported by the well-known fact that in autumn and spring migrants accumulate large subcutaneous fat stores that are used up during (non-stop) flight.

The next monograph on bird migration in Africa (Curry-Lindahl, 1981) assumed a larger role for the oases, but its author believed that local African bird species utilised them to a greater extent than Palaearctic migrants. These and other studies gradually formed that now universally accepted hypothesis of migratory strategy of birds in different parts of the world. It is based on the fact that migrants make regular stops in suitable areas for rest and refuelling (Dolnik, 1975; Alerstam, 1990; Houston, 1998; Berthold, 1990; Chernetsov, 2003; Moore et al., 2005), i.e. in so-called stopover sites. The most pronounced rhythm of migratory flights and stopovers is typical of nocturnal migrants that fly at night and make stopovers and forage within limited areas during daytime (Bairlein, 1992). These areas are species- and possibly population-specific (Fransson et al., 2005). Spatial distribution of suitable stopover sites, i.e. the landscape aspect of migration, is a most important but underestimated part of bird migration research (Jenni & Schaub, 2003; Ktitorov et al., 2008).

Across the whole of Africa, especially north of the equator, vegetation condition governs foraging conditions for transient, stopping-over, or wintering birds, both insectivores and plant matter consumers. A most important area where migrants from Eurasia migrate, stop over, or winter, is the Sahel which lies south of the Sahara. Even though the limits of the Sahel vary somewhat depending on annual precipitation, generally it stretches from Senegal and southern Mauritania in the west to Chad and western Sudan in the east. This is a transition zone between semi-deserts and savannas, where 80% of precipitation is lost to evaporation. The rainy season lasts 2 – 3.5 months and starts in June or July. The annual sum of precipitation varies between 250 and 500 mm which is much more than in the Sahara where it averages 127 mm. This means that when Palaearctic migrants reach the Sahel in autumn in normal years without droughts, they encounter green vegetation and sufficient food stores (Curry-Lindahl, 1981). Some birds remain in the Sahel for 4-10 weeks and do not resume their southward movement until then. The duration of their further migration mainly depends on the precipitation (Morel, 1973; Pettersson & Hedenström, 1986).

Many Eurasian migrants spend their winter in the Sahel and do not proceed further south. It was found that in the end of the 8-9 month long dry season when the environmental conditions seem to be at its least supportive, the birds prior to spring migration do not lose mass, but, conversely, quickly gain fat. This situation typical not only of the western Sahel where many European migrants winter, but also of the eastern part of the Sahel and of the whole Sudan where migrants from the whole Eurasia stop over (Curry-Lindahl, 1981), is known as the Moreau paradox. It appeared that different habitats in the Sahel even in the dry season are not as poor as they look. Trees and bushes in the dry season are at different stages of development and fruitage, some plants are evergreen and provide substrate for the insects. In western Africa the basins of the Senegal and the Niger rivers greatly improve the environmental situation (Curry-Lindahl, 1981; Lövei, 1989; Morel & Morel, 1992; Pearson & Lack, 1992).

However the Sahel is the subject to catastrophic droughts. Dry periods are most severe along the northern edge of the Sahel where the lack of water was especially deadly in 1968, 1972, 1973, 1982, 1983, 1984 and 1990 (Jurry, 1997; Newton, 2004, 2008). The Palmer index which reflects the severity of droughts in Africa shows that in the recent decades, the most severe period were December 1982 – January 1983 (Dai et al., 1998). The droughts caused the reduction of water surfaces, vegetation degradation and decline in insect numbers, i.e. habitat degradation that increased the mortality rate of wintering birds. It should be noted that droughts in southern Africa may be less disastrous for migrants than in the Sahel. Bird surveys in different plant communities around the Kalahari desert showed that the proportions of migrants in areas subject to regular droughts did not differ between the years with the least precipitation and the years with normal precipitation (Herremans, 1993).

The overall numbers of avian species and subspecies that breed in Eurasia and reach Africa during their autumn migration is 479, but passerines form the bulk of Palaearctic migrants. Of the local African birds 532 species and subspecies also perform within-African movements (Curry-Lindahl, 1981). Therefore, in the whole of Africa movements of a large number of birds, primarily passerines occur constantly. The studies of population numbers and the factors that influence their dynamics were initiated in passerines.

Palaearctic migrants are very unevenly distributed across Africa. Generally the largest number of species occurs in the savannas belt south of the Sahara, and their number gradually decreases towards the south. Besides, at all latitudes more wintering species and individuals occur in the eastern regions than in the western ones. The highest concentration of wintering birds occurs in Kenya, Uganda and the Democratic Republic of Congo, with Kenya and Uganda being the zone of maximum species richness, breeding species including: 985 and 1060 species, respectively (Lövei, 1989). In 57 terrestrial species wintering areas are less than two-thirds of their breeding areas. This means that carrying capacity of the environment in the wintering areas is larger than in the breeding areas (Newton, 1995).

Most passerines spend their time in Africa in semi-arid areas and in northern savannas, and in forest savannas and wet meadows. Pooling the data on winter ranges of 66 Eurasian passerine species reported in the main monographs (Moreau, 1972; Curry-Lindahl, 1981) shows that not more than 11% of them winter south of the equator. Most species spend their winter only north of the equator, and the remaining ones in both Northern and Southern hemispheres. In West Africa, i.e. between the Atlantic and Lake Chad, and between 21°N and

5°N, 64 songbird species from 9 families winter. Of them, 11 species are nomadic and are not confined to certain areas (Morel & Morel, 1992). Winter range of some species extends much further north than assumed earlier, mainly due to woody areas in the highlands and gardens in towns. In East Africa, i.e. in Sudan, Ethiopia, Eritrea, Somali, Kenya, Democratic Republic of Congo, Uganda, Rwanda, Tanzania, 74 – 125 species of Palaearctic migrants from 9 families winter (Pearson & Lack, 1992; Newton, 1995). They inhabit loose forests, often in the mountains, scrubland and open meadows, and vast wetlands around the Nile, Lake Victoria and other large lakes. In the wet seasons the arthropod biomass increases 5-6-fold as compared with the dry season (Lövei, 1989). Along with very large winter ranges of some species, e.g. the Willow Warbler, others have rather small wintering areas.

When Palaearctic migrants arrive to their winter quarters, they encounter a large community of resident African birds. They have to compete for food, water, and territory with the residents and between themselves. The results of some studies indicated that the main strategy of Palaearctic migrants is the utilisation of locally abundant sporadically occurring resources that are usually not used by the residents (Lack, 1986; Lövei, 1989). Unlike resident African species, Palaearctic visitors prefer more open habitats and show greater plasticity in their food selection and foraging methods (Leisler, 1992; Herremans, 1997). In general, they use structurally more diverse habitats than ecologically close African species (Leisler, 1993). Winter behavioural strategies of different passerine species show important variation. For example, the Pied Flycatcher is very territorial and shows a large variety of foraging techniques, whereas the Willow Warbler occupies similar African habitats but is quite specialised and has to move constantly looking for locally abundant food (Salewski et al., 2002). However, a recent review of the ecology of Palaearctic migrants in Africa showed numerous contradictions between these conclusions and the results of more recent studies (Salewski & Jones, 2006). The main conclusion drawn by the authors of the review was that the results of studies into competitive interactions between Palaearctic visitors and African residents still remain inconclusive.

In this context a question arises whether the so-called migratory connectivity is pronounced in Palaearctic passerines. This trendy term means the degree of fidelity of individuals and populations to the same geographic areas during two or several periods of their annual cycle (Boulet & Norris, 2006). Strong migratory connectivity means that all or the majority of birds from a certain area migrate to the single wintering locality and back. Ringing results from the Courish Spit suggest that migratory connectivity at the specific or population level is not typical of them, even though some examples of fidelity to the individual wintering site in different years are available.

5.2.2. The population dynamics of trans-Saharan migrants

The first reports of population decline in a number of songbirds wintering in Africa appeared in the early 1970s (Ash, 1970; Berthold, 1972, 1973). The dramatic decline of Western European Whitethroat populations in 1969 was discussed in much detail, and a paper by a British author was characteristically entitled 'Where have all the whitethroats gone?' (Winstanley et al., 1974). One hypothesis on the causes of population decline blamed the use of insecticides in the countries on migratory routes and in wintering areas (Berthold, 1973), another one suggested the role of mortality due to lack of food, water and shelter during the severe drought in the Sahel in 1968 (Winstanley et al., 1974).

In subsequent years many publications on the change in numbers of European avian populations appeared, and many of them discussed long-distance migrants (for references see section 5.1.6). The main reasons for the discussed population trends were related either to the change in population productivity, or to the change in survival rates, or both. The suggested reasons could be lumped into three main groups of factors: (1) anthropogenic factors, i.e. structural changes of forests, and pollution of the environment in the breeding area and in migration and wintering areas, mainly by using pesticides and herbicides in agriculture and forestry; (2) climatic and weather factors, from the dynamics of mild and severe winters and springs to droughts in African winter quarters and to the global climate warming; (3) intrinsic population factors, when due to competition and the buffer effect a part of the population breeds in suboptimal habitats and produce fewer young. The stronger the buffer effect is, the smaller is the average population productivity.

In some publications that discussed the change in numbers in the 1960s – 1980s, examples of similar population trends in different survey areas were given (Fig. 33). It was therefore assumed that a factor responsible for the change in numbers acted across large areas. However later, when longer time series and more regions were included in the analysis, fewer trends remained similar across different regions. Some publications reported dramatic population declines in many European species, whereas other authors reported stable or even increasing population numbers of the same species. A good example was the contradictory trends in the Whitethroat populations that were the starting point of the close attention to the trends in numbers of European birds (Fig. 34). This controversy could be either due to the fact that in reality different populations of this species were subject to very different environmental effects on the local scale, or indicate that the used methods of analysis were inadequate. It should be noted that the adequate methods, i.e. detailed population studies, including long-term studies of productivity and survival rates, are quite labour-intensive, and for most species no such data are available.

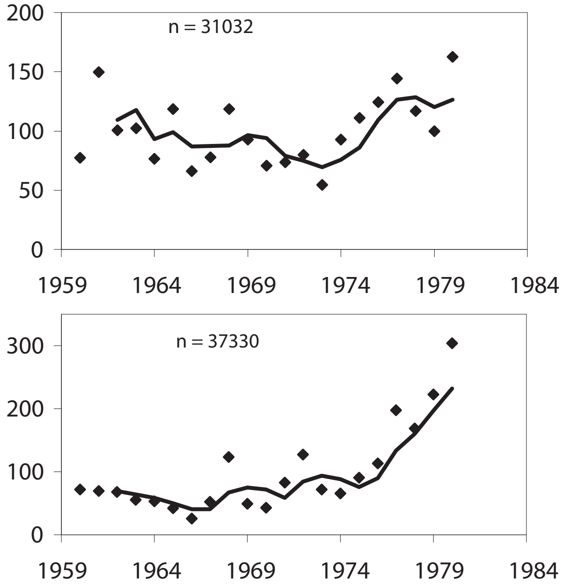

Fig. 33. Fluctuations in trapping numbers of Willow Warblers at two Baltic sites from 1960 to 1980. At each site capture methods were standardised. Above – Ottenby bird observatory in Öland (Sweden; Hjort et al., 1981). Below – Biological Station Rybachy on the Courish Spit. Y axis represents the proportion of the annual mean. The trend line is the linear filtration by three values.

Capture data from Poland and Germany (Busse, 1994; Busse et al., 1995; Berthold et al. 1998, 1999) allowed the authors to conclude that numbers of many passerine species, especially long-distance migrants, were constantly and dramatically declining during the whole second half of the 20th century. Publications based on the data collected on the Courish Spit (Sokolov, 1999a,b; Sokolov et al., 2000, 2001a,b) claimed that these conclusions were questionable, because such trends could be due to local habitat change at the trapping sites, causing decreasing capture efficiency. In the Czech Republic some species, long-distance African migrants including (e.g. the Spotted Flycatcher, Common Redstart, and Whinchat) significantly increased their numbers in 1982-2001 (Štastný et al., 2004). What causes nearly universal population decline of the Red-backed Shrike (except the Czech population) and the Barred Warbler (Olsson, 1995; Shirihai et al., 2001; Payevsky et al., 2003), in these papers (Sokolov et al. 2001a,b) the reason was found in the anthropogenic degradation of the breeding conditions rather than in the negative effect of African droughts on winter survival. It may be theorised that in some populations the combined action of both these factors could indeed result in dramatic decline of the breeding numbers. For example, the population decline

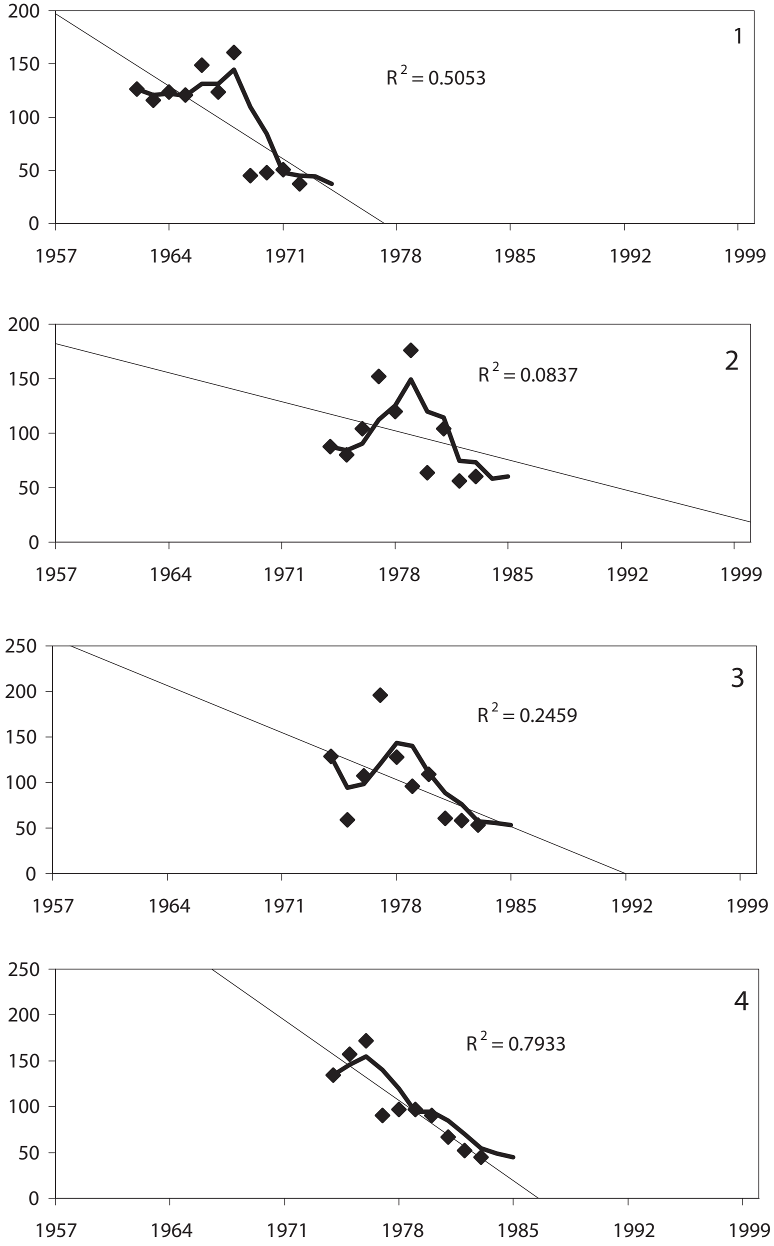

Fig. 34. Dynamics of the Whitethroat numbers at different European sites from different survey and trapping methods.
1 – UK (Winstanley et al., 1974); *2, 3* and *4* – southern and northern Germany and Austria, respectively (Berthold et al., 1986)

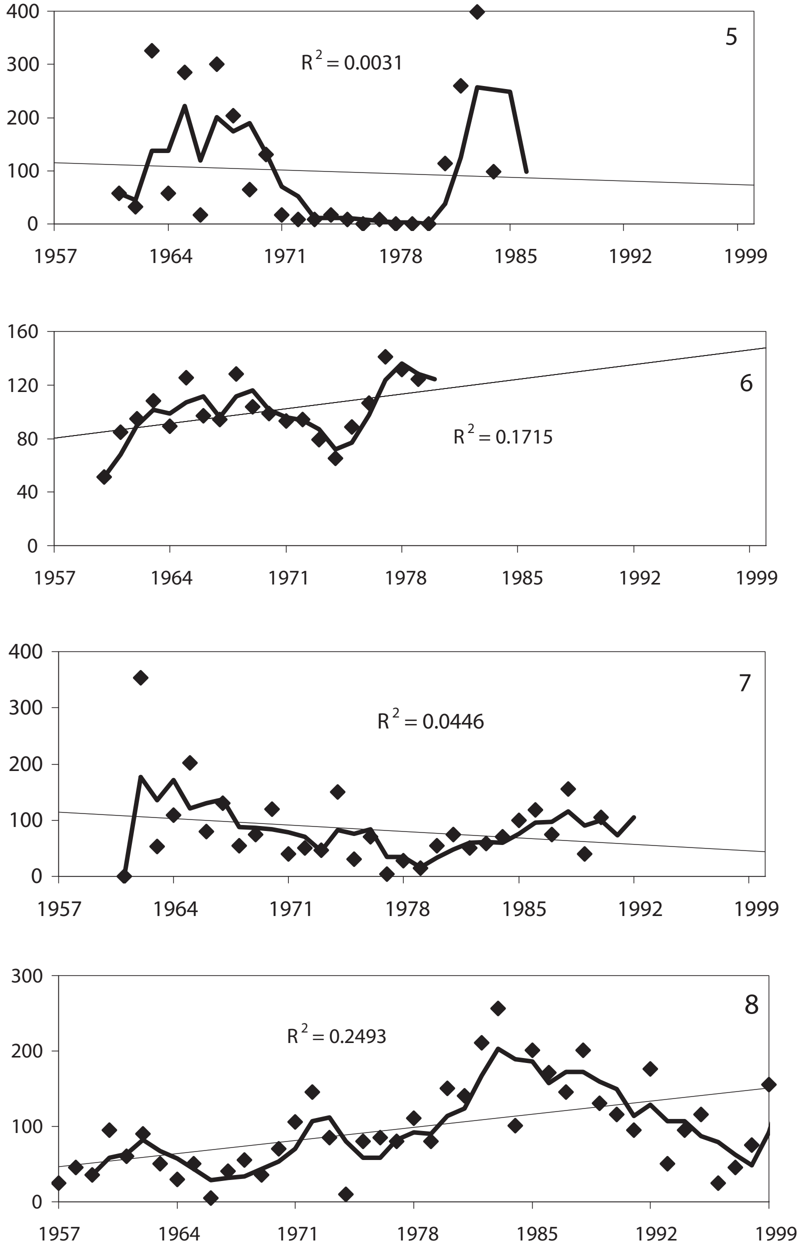

Fig. 34. Continued.
5 – Sweden (Österlöf & Stolt, 1982), *6* – northern Poland (Busse, 1994), *7* – Belgium (Nef et al., 1988), *8* – Courish Spit, eastern Baltic (Sokolov et al., 2001). Y axis represents the proportion of the annual mean.

in the Red-backed Shrike is usually explained not by the events in the winter range alone, but also by the changes in agricultural practice in the breeding area that increased density and height of the grass and negatively affected the abundance of insects that are most often taken by these birds (Koop & Klose, 2006).

To study the most general characteristics of change in population numbers of long-distance migrants in the second half of the 20th century (Payevsky 2006a) I pooled the results of a study of population trends at 10 European bird observatories in 18 avian species, 16 passerines and two non-passerines (Table 33, Fig. 35, some

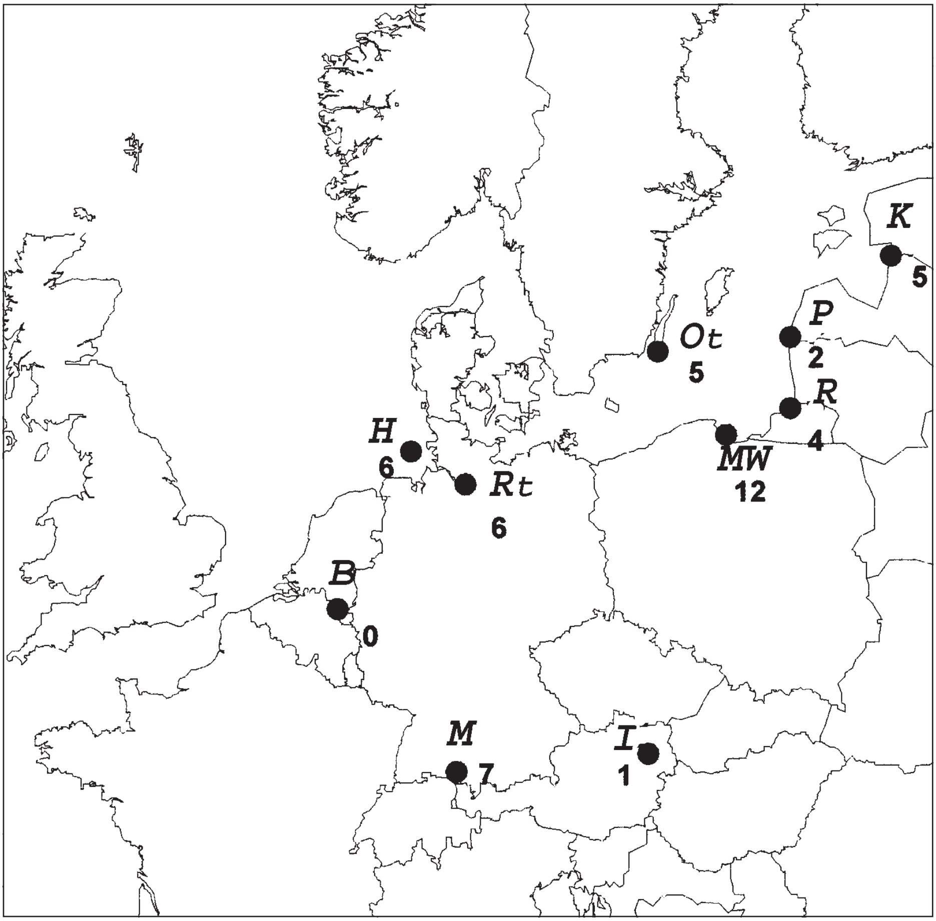

Fig. 35. Locations of European ornithological stations where trapping data discussed in section 5.2.2 originate from. *B* – Bokrijk, Belgium; *H* – Heligoland, Germany; *I* – Illmitz, Austria; *K* – Kabli, Estonia; *M* – Mettnau, Germany; *MW* – Merzeja Wiślana, Poland; *Ot* – Ottenby, Sweden; *P* – Pape, Latvia; *R* – Fringilla (Rybachy), Russia; *Rt* – Reit, Germany. The figures refer to the number of species showing negative trends in numbers of birds trapped.

Table 33. Population trends in 18 migrants to Africa from trapping data (mainly in autumn or spring and autumn pooled) at 10 European bird observatories. Shown are the trends, negative (neg) or positive (pos) with significance level from p<0.05 to p<0.001, non-significance of trend (ns, p > 0.05) and the mean annual trapping figure.

Species	**European ornithological stations (see fig. 35) and years of bird trapping**									
	Bokrijk, Belgium 1961-1984 (Nef et al., 1988)	Heligoland, Germany 1960-1991 (Moritz, 1993)	Mettnau, Germany 1974-1993	Reit, Germany 1974-1993	Illmitz, Austria 1974-1993	B-H-MW***, Poland 1961-1990 (Busse, 1994)	Ottenby, Sweden 1955-1996 (Pettersson, 1997)	Fringilla (Rybachy), Russia 1957-2000 (Payevsky, 1990a; Sokolov et al., 2000, 2001b)	Pape, Latvia 1967-1999	K-H**, Estonia 1971-2000
			(Berthold et al., 1999)						(Sokolov et al., 2001b)	
White Wagtail	-	-	-	-	-	-	ns 229	ns 100	-	ns 14
Tree Pipit	-	-	-	-	-	ns 28	pos 52	neg 19	ns 3	neg 5
Red-backed Shrike	-	-	neg 8	ns 3	neg 36	neg 20	neg 190	ns 23	neg 3	ns 4
Common Redstart	ns 6	neg 316	neg 42	neg 19	ns 14	neg 421	ns 257	ns 106	ns 73	ns 19
Eurasian Reed Warbler	pos 56	ns 20	ns 1908	ns 856	ns 2706	-	pos 8	-	-	ns 49
Icterine Warbler	ns 5	neg 14	ns 27	ns 34	ns 4	ns 7	pos 43	ns 114	ns 1	neg 5
Barred Warbler	-	-	-	-	-	neg 5	neg 10	neg 29	-	neg 2
Garden Warbler	pos 51	ns 540	ns 451	ns 61	ns 24	neg 175	ns 109	ns 61	ns 85	ns 42
Blackcap*	pos 48	-	pos 677	ns 97	ns 37	neg 264	ns 54	ns 36	ns 32	ns 41

Species	**European ornithological stations (see fig. 35) and years of bird trapping**									
	Bokrijk, Belgium 1961-1984 (Nef et al., 1988)	Heligoland, Germany 1960-1991 (Moritz, 1993)	Mettnau, Germany 1974-1993	Reit, Germany 1974-1993	Illmitz, Austria 1974-1993	B-H-MW***, Poland 1961-1990 (Busse, 1994)	Ottenby, Sweden 1955-1996 (Pettersson, 1997)	Fringilla (Rybachy), Russia 1957-2000 (Payevsky, 1990a; Sokolov et al., 2000, 2001b)	Pape, Latvia 1967-1999	K-H**, Estonia 1971-2000
			(Berthold et al., 1999)						(Sokolov et al., 2001b)	
Whitethroat	ns 12	ns 60	ns 23	neg 71	ns 14	neg 22	neg 124	ns 37	ns 3	ns 26
Lesser Whitethroat	pos 4	-	neg 117	neg 107	ns 15	neg 62	- 172	ns 134	ns 12	ns 22
Willow Warbler	ns 79	pos 275	neg 360	neg 374	ns 61	neg 712	pos 749	ns 2430	ns 228	ns 263
Common Chiffchaff*	pos 126	-	ns 864	ns 201	ns 133	neg 102	ns 41	ns 59	ns 80	pos 320
Wood Warbler	-	-	neg 3	ns 1	pos 23	neg 11	pos 46	ns 54	ns 9	neg 13
Spotted Flycatcher	ns 6	neg 34	neg 35	neg 13	pos 6	neg 114	ns 115	ns 85	neg 18	neg 23
Pied Flycatcher	ns 2	neg 234	ns 29	neg 10	pos 49	neg 174	ns 133	ns 74	ns 54	ns 11
Common Cuckoo	-	neg 1	-	-	-	-	neg 4	neg 13	-	ns 1
Eurasian Wryneck	-	neg 7	neg 7	ns 2	ns 2	ns 6	neg 6	neg 14	-	- 1

Notes. * Some populations remain to winter in Europe; ** K-H means two nearby sites: Kabli и Häädemeeste; *** B-H-MW means three nearby sites: Bukowo, Hel and Mierzeja Wiślana.

parameters were calculated anew from the original datasets). Apparently, during the very long periods, from 20 to 40 years and more, some periods with significant positive and negative trends always occurred. Generally, across the whole periods the tendency could be statistically insignificant, i.e. population numbers varied randomly or quasi-cyclically.

Of the 142 long-term trends in numbers, 48 were negative, 16 were positive, and 78, i.e. 55%, were not statistically significant. In only five species, three passerines and two non-passerines, negative trends occurred significantly more often than the positive ones. The proportion of negative trends was 0.63 in the Red-backed Shrike, 1.00 in the Barred Warbler, 0.60 in the Spotted Flycatcher, 0.75 in the Cuckoo and 0.57 in the Eurasian Wryneck (*Jynx torquilla*).

The analysis of the data presented in Table 33 also showed that the proportion of negative trends in each species was inversely related to the trapping figures (Spearman's correlation coefficient $r_s = -0.672$, $p < 0.05$). If trapping figures are assumed to be a proxy for population numbers, this means that the more common a species is, the less likely is a long-term decline of its numbers. Most vulnerable are the uncommon species. On the other hand, if some species showed a broad variety of population trends across Europe, then even if some population suffers a dramatic decline and even becomes extinct, the possibility of recovery due to dispersal from other populations remains.

Significant habitat change in both breeding and wintering areas may cause serious change in population numbers. All migrants are subject to greater and sometimes critical influence in just one area, but whether it is the non-breeding or breeding area depends on the impact of extrinsic factors.

What events in the environment and in the life of populations are most critical for maintaining the more or less stable numbers? To answer this question, it is necessary to analyse the results of studies based on the exact surveys of breeding numbers, survival rates and key factors during the breeding, migratory, and wintering periods. Such analyses were performed in the following 11 European bird species: Collared Sand Martin (Cowley, 1979, Szep, 1995), Barn Swallow (Møller, 1989; Robinson et al., 2003), Common Redstart (Järvinen, 1987; Marchant, 1992), Pied Flycatcher (Virolainen, 1984; Järvinen, 1987; Stenning et al., 1988), Sedge Warbler (Peach et al., 1991; Foppen et al., 1999), Willow Warbler (Baillie & Peach, 1992; Peach et al., 1995), Blackcap and Whitethroat (Baillie & Peach, 1992), Barred Warbler (section 4.1.3., Payevsky et al., 2003), and in two non-passerines, the Purple Heron (*Ardea purpurea*; Den Held, 1981; Cavé, 1983) and the European White Stork (Kanyamibwa et al. 1990).

The results of these studies show, first, that in population fluctuations all cases were caused by loss of adults or full-grown juveniles, and were not related to breeding success rate (even though the mortality rate of fledglings is quite important for maintaining stable numbers). Second, in eight species, i.e. in the majority, population decline that sometimes resulted in local extinction was caused by the increasing mortality in African winter quarters, mainly due to strong droughts in the Sahel. The same reasons (Payevsky, 2005) could enhance the negative trends in the local Red-backed Shrike populations caused by anthropogenic landscape transformation in the European breeding areas. This relationship was initially not found in the Pied Flycatcher, Willow Warbler, and Blackcap populations. It was believed on the basis of the analysis of the key factors and removal experiments with territory owners that the numbers of these three species could be regulated through territorial behaviour with spring recruitment into the breeding population (Baillie & Peach, 1992). However, subsequently, evidence for the Willow Warbler of the critical impact of African droughts on declining population numbers was eventually found (Foppe & Reijnen, 1996; Balmer & Peach, 1998; see section 4.4).

Thus, the population dynamics patterns of Palaearctic migrants wintering in Africa are quite variable. They may be governed to a large extent by the environmental conditions in the winter quarters. Long-distance migrants, unlike the short-distance ones, are more vulnerable to any fluctuations of the environment, because they are more dependent on the endogenous basis of annual cycles. Species- and population-specific variation of population dynamics patterns may probably be influenced by the uneven distribution of the migrants within Africa. In the Sahel zone which is favourable for migrants in the years with normal precipitation, the situation changes dramatically in the dry periods. In the years of droughts habitat quality deteriorates, and competition for food causes an increase in the mortality rates of wintering migrants. Even though local residents do not directly compete with Palaearctic visitors, variable wintering strategies of the latter cause species-specific variation in the survival rates under extreme weather conditions. The more common a species is, the lower is the probability of its long-term population decline.

SUMMARY

The whole array of theoretical issues related to conservation of the qualitative and quantitative diversity of the fauna as a component of the global biosphere is currently based on the study of limiting impacts on populations. To estimate the condition of natural populations, it is first of all necessary to obtain information of their numbers and its long-term dynamics. As numbers result from other demographic parameters, the basis for population dynamics studies is formed by the data on the variation of birth and death rates, and characteristics of dispersal, emigration and immigration rates in the population studied. Studies of population fluctuation and age structure of animal populations have become especially topical due to the recent trends of global warming and the increasing degree of urbanisation.

In this monograph, the results of investigations of breeding and migrating populations of songbirds of various species, primarily the European ones, are summarised. These studies were pursued in the framework of the fundamental problem of animal population biology, concerning the mechanisms of maintaining the optimal numbers in natural populations. Age and sex structure of populations and survival rates of different age and sex cohorts were studied in order to investigate the array of extrinsic and intrinsic factors limiting population numbers (during breeding, migratory, and wintering seasons). The search for and the use of adequate methods to compare annual demographic parameters in the populations under study with the effects of limiting factors across the whole summer and winter ranges made it possible to pinpoint the presumed causes of the observed population dynamics in a number of species.

The main points of the chapters, referring to both methodology and results, are briefly summarised below.

1. The study of the efficiency of bird ringing in relation to the species, sex, age, season and region of ringing showed no direct positive relationship in any species between the numbers ringed and the number of recoveries. This means that the results of ringing depend on the particular conditions of each year and season and emphasises the need to estimate demographic parameters from stochastic capture-mark-recapture calendar time-dependent models. This however does not preclude the use of annual means for any demographic comparisons.

2. The results of trapping projects can be used as a representative method of studying the population dynamics for long-term population monitoring purposes only if a number of conditions are rigorously met. The same capture method must be used at the same site in an unchanging landscape. As age structures of local breeding and transient migrating populations of different species are very similar, estimates based on captures of diurnal migrants are as reliable as the ones based on captures in the breeding areas. However, age ratio of nocturnal migrants is of very limited use for the aims of demographic analysis due to the coastal effect, i.e. the very low proportion of post-hatching year birds among nocturnal migrants in coastal areas.

3. For populations of 21 songbird species whose age structure was estimated from 35-year mark-recapture studies, an averaged age structure was calculated. Yearlings and two-year-old birds formed the bulk of breeding populations in all the species studied, varying between 70 and 90%. Age structures of different species were very similar, as shown by coefficient of variation of proportions of birds in each age group. The lowest variation was in the age group of 2 years, the highest one in 8-year-old birds. The proportion of yearlings was not significantly different from the mean mortality rate in 19 cases out of 27. This means that in spite of the observed annual fluctuations of numbers, most of the populations studied on average maintained their numbers across the 35 years.

4. From the analysis of long-term trapping data in breeding birds, autumn and spring passerine migrants showed a clearly male-biased sex ratio. The analysis of sex-specific survival rates confirmed a sustained tendency for higher annual survival rates in males as compared with females. The widely accepted concept of higher mortality of males in all animals is not supported by the data on birds. Higher survival rates of males are reflected in the numerical prevalence of this sex in the populations. This male-biased sex ratio may result in acute competition during breeding, enhancing behavioural and physiological population variability.

5. Annual variation of age structure and its difference in autumn and in spring was studied in the six most common bird species. The proportion of adults varied in respect to year, season, and sex. Age structure significantly varied among the species within both diurnal and nocturnal migrants. No correlation between age structure in each autumn and the subsequent spring was found. Annual variation of age structure was mainly related to different population productivity. Season-related difference between age composition of migrating populations (in spring, in most species the proportion of adults was higher than in autumn) suggests age- and sex-biased winter survival rates. Adults survived better than first-winter birds, and males better than females.

6. Sex- and age-related bias in migratory distance in relation to survival rate was studied in three common finch species. No significant sex or age-related variation in migratory direction was found in any species. Sex- and age-related bias was

significant in the two species studied. Both adult and juvenile females spend their winter further south than males do. Adult males winter further south than juvenile males. Unlike males, females showed no age-related variation. Adult males occupy the optimal wintering areas which are not too far from the breeding grounds and experience less severe weather. Juvenile males seem to benefit from wintering in poorer conditions but with less acute competition with adult males.

7. Empirical relationships between annual survival rate and maximum recorded lifespan were tested in two datasets: ringing results of passerines on the Courish Spit and literature data on 130 species from 13 avian orders. The results showed that the mean annual survival rate is significantly related to the maximum lifespan recorded in the same populations. Significant correlations were obtained in all five variants of the initial dataset. Even though the species-specific maximum lifespan is unclear, mean adult annual survival rate and their potential lifespan are significantly positively related.

8. Different demographic parameters were analysed in passerines and non-passerines in relation to their body size, taking into account ecological and evolutionary interpretations. In the most evolutionary advanced birds with altricial development and smaller body size (songbirds included) these parameters show on average higher values than in larger birds with praecocial young.

9. Analysis of population trends of European-African migrants at European trapping stations showed that during the long-term monitoring studies, periods of significant growth or declines of numbers always occur. However, of all long-term trends just one-third were negative, and more than one-half were non-significant. The proportion of negative trends in a species is negatively related to overall trapping figures: the commoner a species is the lower is the probability of its long-term population decline. To understand the mechanisms of the effect of environmental variables on population dynamics, an analysis of census or trapping data is insufficient: more detailed studies including the analysis of the key factors and survival rates are required. A review of recent studies of European species showed that the most striking declines in a number of cases resulted not from breeding disturbance, but from dramatically increasing mortality rates in African winter quarters due to catastrophic droughts.

10. The observed population dynamics of birds are governed by annual variation of mortality rates due to extrinsic and density-dependent factors, and by immigration and emigration rates. However, models that would account for all these factors are hardly possible. Given the availability of long-term census data, the most promising way to study the impact of environmental factors on populations is the comparative method. For a deeper insight into the population dynamics of birds, the study of demographic parameters, primarily of annual survival, is of great importance.

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INDEX OF BIRD NAMES

SUBJECT INDEX

Colour Plates

Plate 1. The Courish Spit is a sandy strip of land between the Baltic Sea and the Courish Lagoon, 98 km long and 0,36 to 3,9 km wide. A considerable part of the shoreline from the lagoon side is created by the huge sand dunes, devoid of vegetation and with tops up to 68 m. Photo by the author.

Plates 2 & 3. Between the eastern and western coasts of the Courish Spit the landscape changes through a sequence of bare sandy dunes, through fixed dunes and young pine plantations to the plots of deciduous and mixed forest. Photo by the author.

↑ **Plate 4.** One of the forest habitats on the Courish Spit. Both southern (Russian) and northern (Lithuanian) parts of the Spit are national parks which together form a UNESCO World Heritage site as a cultural landscape. Photo by the author.

↗ **Plate 5.** The sea coast of the Courish spit. Photo by the author.

→ **Plate 6.** The vegetation of the Courish Spit; near the seashore after a storm. Photo by the author.

Plate 7. The general appearance of the Rybachy-type traps on the Courish Spit. Photo by the author.

Plates 8 & 9. The entrance to a Rybachy-type trap reaches to 12 metres in height. Photo by the author.

Plate 10. The birds enter into the trap un-aided. Photo by D. Konstantinov.

Plates 11 & 12. The birds can also be flushed into the trap. Photo by the author.

Plate 13. End compartment of a Rybachy-type trap with captured migrating Chaffinches. Photo by the author.

Plate 14. A collection of the captured birds (Barn Swallows) in the end compartments of a Rybachy-type trap. Photo by the author.

Plate 15. Before ringing each bird was examined and measured. Photo by the author.

Plate 16. Sand Martins and Barn Swallows in the end compartment of the trap. Photo by the author.

Plates 17 & 18. Apart from the birds, bats and large insects, especially dragonflies, may enter the traps. Photo by the author.

Plate 19. Rybachy-type traps are open 24 hours, and in twilight or in darkness nocturnal migrants are captured at take-off and landing. Photo by A. Shapoval.

Plate 20. European Robins are the first birds in the trap in the morning. Among captured Robins, adults comprise in autumn just 8 % and in spring 18 % due to the coastal effect (a dis-proportionate number of adults at sea coasts during nocturnal migration). In reality, the proportion of adults in breeding populations is much higher, as their annual survival rate is on average 42 %. Few birds reach 6 years old. Photo by the author.

Plate 21. The maximum age of Great Tits in different populations varies between 6 and 10 years. Young birds that managed to survive until the next breeding season face on average, one more year of life. However, the mean life expectancy at fledging is just 5 to 7 months. Photo by "Klassik" and the author.

↑ **Plate 22.** Annual survival rates of adult Baltic Lesser Whitethroats (are about 48 %) similar to their conspecifics from Lincolnshire (UK, about 44 %). With the mean number of fledglings equal to 4, to be able to maintain more or less stable population numbers the mortality rate of juveniles until the next breeding seasons should be roughly 70 %. Photo by the author.

↗ **Plate 23.** The Barred Warblers of the Baltic have suffered a drastic population decline becoming locally extinct. None of the productivity parameters have changed, but survival rate of adults has dropped to zero. A severe drought in their wintering location in Africa from December 1982 to January 1983 coincided with the extinction of the population studied. Photo by N. Zelenova and the author.

→ **Plate 24.** The Chaffinch was one of the most studied subject species in all research projects at the Biological Station Rybachy and the most common species trapped (683,000 ringed individuals). At 7 to12 days old nestlings the sex ratio is 1:1, and starting from the age of one month, the males are consistently in preponderance (about 55 %). It is assumed that females suffer greater mortality than males, soon after fledging. Photo by A. Shapoval.

↑ **Plate 25.** The Willow Warbler is one the most common species in Eastern Europe along with the Chaffinch. Population trends shown by Willow Warblers fluctuate widely in different parts of Europe. Captures on the Courish Spit over 40 years, despite annual fluctuations, showed no significant trend. Photo by the author.

↗ **Plate 26.** Numbers of all European Starling populations have recently sharply declined. The analysis of survival parameters of Starlings in the Eastern Baltic shows little change, conversely the demographic analysis of British populations has concluded that decreasing numbers are probably due to the declining survival of juveniles. Photo by A. Shapoval and the author.

→ **Plate 27.** The Song Thrush is the most common Baltic thrush wintering in Western Europe where they are subject to strong hunting pressure, especially in France, Italy and the Iberian Peninsula. The survival rate of Song Thrushes in the British Isles where they are year-round residents and are not hunted does not differ from the survival rate of Baltic populations. Mortality due to hunting seems to be compensated for by higher productivity. Photo by L. Sokolov and the author.

↑ **Plate 28.** The Common Rosefinch has three features that make it an interesting subject for demographic study: Intensive range expansion occurs towards the northwest; there is population and sex-related variation in the proportion of yearlings that breed and a very low rate of natal philopatry. On the Courish Spit 26 breeding pairs included old red males and 19 pairs had yearling grey males. No significant difference in breeding performance was found between these groups of nests. Photo by V. Moseikin and the author.

↗ **Plate 29.** The mass summer irruptions of adults and juveniles are well known for Red Crossbills. On the Courish Spit males outnumbered females in numerous migrating flocks: their proportion is 53% amongst adults and 56% amongst juveniles. Photo by the author.

→ **Plate 30.** In some years, mass summer movements of Eurasian Siskins are recorded on the Courish Spit, most often moving towards the north. As with Red Crossbills, adult birds, with signs of completed breeding fly together with the juveniles. Nearly all transient females have incubation patches. It is suggested that Siskins may breed twice a year in different regions of Europe. Photo by L.Topulia and the author.

↑ **Plate 31.** Bramblings that migrate through the Courish Spit breed in Finland and northwestern Russia, and winter in Western Europe. Both adult and juvenile females spend their winter, on average, further south than the males; adult males winter further south than the juveniles. Photo by A. Shapoval and the author.

↗ **Plate 32.** The numbers of Goldcrests captured in spring on the Courish Spit and at other migration survey sites along the coasts of the Baltic and the North Sea, are just 3 to 20% of their annual trapping totals. The reason for this is not only winter mortality, but also their very early return movements towards breeding quarters which are before the onset of the trapping season. Photo by Alexander G.T. and the author.

→ **Plate 33.** For Eurasian Blackbirds migrating and breeding on the Courish Spit the proportion of adults in spring (32 % of males and 35 % of females) is significantly higher than in autumn (12 and 14 %, respectively). This is apparently due to the higher mortality rate of first-winter birds when compared with the adults. Photo by L. Sokolov and the author.

Plate 34. The numbers of Eastern Baltic populations of the Red-backed Shrike, as well as across the whole Europe, have considerably decreased during the recent decades. The presumed reason has been the combined effect of the African drought on their winter survival and the anthropogenic deterioration of breeding conditions. Photo by the author.

Plate 35. The numbers of the Golden Oriole on the Courish Spit are small but stable. The only ringing recovery available suggests they migrate towards their African ~~breeding~~ quarters through Lebanon. Climate change seems not to have had any effect yet on this population. Photo by the author.

Plate 36. The number of migrant Jays trapped on the Courish Spit varies considerably between the years: from nil to 814 birds. Photo by A. Shapoval and the author.

↑ **Plate 37.** The Pied Flycatcher along with the Great Tit is the most popular study subject for European ornithologists. Unlike other songbird species, Pied Flycatchers show no relationship between clutch size and population density, either in Western or in Eastern Europe. Photo by the author.

↗ **Plate 38.** Of all thrush species that migrate through the Courish Spit, Fieldfares winter closest to the ringing site, although adults migrate somewhat further than juveniles. Like other thrushes, Fieldfares suffer significant hunting pressure, especially in France and Italy. Photo by the author.

→ **Plate 39.** The numbers of the Western European Whitethroat population fell drastically in 1969 due to droughts in their African winter quarters. However, the analysis of long-term dynamics shows conflicting trends in different populations of this species. Photo by the author.

↑ **Plate 40.** The data from 10 European bird observatories did not show a single significant positive trend in populations for the Common Redstart, while four showed trends that were declining significantly. Photo by L. Sokolov and the author.

↗ **Plate 41.** For irregular migrants such as Long-tailed Tit and Coal Tit, a highly significant relationship was found between autumn numbers of juveniles and trapping figures during the subsequent spring. This suggests that after an irruption, some juveniles survive the winter and return in the spring. Photo by L. Sokolov.

↔ **Plate 42.** Eurasian Treecreepers on the Courish Spit show a significant positive population increase trend over the years 1957 to 2000. Photo by the author.

Plate 43. Annual mortality rate of adult Icterine Warblers is 65 %. Only 15 birds older than 5 years occur in every thousand; the maximum recorded lifespan is 10 years. Photo by the author.

Plate 44. During recent decades, the timing of spring arrival of Barn Swallows, as with some other species, has shifted towards earlier dates. This was related to higher mean May temperatures. Photo by A. Shapoval and the author.

Plate 45. The age structure of the White Wagtail population is similar to the pattern known in many other songbirds. Yearlings (1 year old) together with two-year old birds make up the bulk of the population; up to 80%. Photo by A. Shapoval and the author.

Plate 46. In the Blue Tit the young birds are more common throughout the autumn migration. The proportion of adults is significantly higher among females than among males, possibly due to the more frequent occurrence of sedentary behaviour in adult males. Photo by A. Shapoval and the author.

Plate 47. The trapping figures suggest that the numbers of Wood Warblers on the Courish Spit have markedly increased. This has happened mainly due to immigration because philopatry rate in this species is very low. Photo by the author.

Plate 48. The vagrant birds captured on the Courish Spit include such unexpected North American species as the Indigo Bunting. Photo by A.B.C.