

Population dynamics in 20 sedentary and migratory passerine species of the Courish Spit on the Baltic Sea

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I analysed trends of population dynamics in breeding populations of 20 sedentary and migratory passerines of the Courish Spit on the Baltic Sea. In the bulk of species in the 1960s and 1980s an increase was recorded, in the 1970s and 1990s a decline was evident. Breeding numbers and numbers of juveniles during post-fledging period were estimated by trapping in Rybachy-type traps during 3 months each year. In all species except Lesser Whitethroat *Sylvia curruca* and Barred Warbler *S. nisoria* a positive association between the numbers of juveniles during post-fledging period and the mean temperatures of April and May was revealed. The numbers of local juveniles trapped during the post-fledging period were significantly correlated with the numbers of breeding birds trapped in the subsequent year. The number of second-year birds in a population is significantly higher following a year with high numbers of juveniles. Our analysis suggests the population dynamics in these passerines is shaped mainly by external factors such as temperature and human activity that influence the survival of adults, especially in winter and in spring, and their breeding success. Other factors, including density-dependent ones, that may have an impact on population numbers are probably of secondary importance.

Key words: population dynamics, passerines, density-dependent factor, climatic factor, air temperature.

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1. Introduction

Many concepts were suggested to explain the dynamics of animal numbers. The discussion started in the 1920s, to a great extent initiated by Eiton (1924) who suggested that population booms are connected with activity of the Sun. Three models were suggested: (1) that no cycles occur in the fluctuation of animal numbers; (2) that cycles occur, but they are not caused by the Sun activity; (3) that cycles occur and are caused by the Sun (Maximov 1984).

Factors that shape the population dynamics were classified in several ways. Very often they distinguish between density-dependent and density-independent factors (Lack 1954, Ricklefs 1976). Density-dependent factors are predators, parasites, disease, food shortage, infra-specific competition, etc. Ricklefs (1976) emphasised that density-dependent factors are not necessarily the biotic ones, and density-independent factors are not always of physical nature. Climate and other physical factors, as suggested by Ricklefs (1976), are also acting density-dependently, as they determine the availability of food.

Advocates of the "climatic" concept (Thompson 1956, Andrewartha 1963, Maximov 1984) explain population dynamics of animals, including birds, mainly by long-term climate change (over decades and centuries). Climate is influenced by a number of physical factors, astronomical, geophysical, meteorological, and, the last but not the least, human-induced (Borisenkov 1988). Influence of the Sun activity is much debated. A number of climatologists believe that there are reasons to accept the correlation between climate and 11-year and 22-year cycles in the Sun activity (in: Borisenkov 1988, Kondratiev 1992). This relationship is not straightforward due to large number of factors acting simultaneously. According to Kliashtorin & Sidorenko (1996), dynamics of many fish species in the Pacific in the 20th century was to a great extent shaped by two climatic and production cycles with maxima in late 1930s and in the 1980s. The latter cycle is not yet completed but has already entered the last phase which corresponds to the 1940s - 1950s and influences both marine and terrestrial ecosystems.

Many authors suggest that models of animal, including avian, population dynamics based on climatic factors are not appropriate when evidence from cycles is considered (for review see Payevsky 1983). These authors believe that population cycles cannot be explained by a weak correlation with physical factors as sun activity, ozone level, etc., because the explanation of the cyclical nature of the external

factor is lacking (Watson & Moss 1980). Thus, the concept of density-dependent regulation of bird numbers re-emerged. Advocates of this concept suggest that during the period of high numbers a population over-exploits food stores, fills all habitats suitable for breeding, attracts predators and encourages diseases. The ultimate consequence is a decline in population. To avoid these proximal consequences, a population needs adaptations that would stabilize its density at the level that is allowed by the resources.

Long-term trends in bird numbers in the Baltic area were considered in detail by Dolnik & Payevsky (1976a, 1979) and Payevsky (1983, 1985, 1990a,b, 1999). These authors analyzed numbers of migratory passerines of 41 species caught in Rybachy-type traps on the Courish Spit of the Baltic Sea over 2-3 decades. They concluded that along with a decline recorded in a number of species many other species showed fluctuations that largely correspond to cycles with the period of 5-10 years and more. The authors suggested that trends in numbers of some species were caused by several factors with climate change and environment pollution by pesticides being probably most important. However, analysis of species of different trophic level and with differential winter quarters failed to prove the hypothesis that pesticides were the main cause of the decline. Other hypotheses were not tested in detail by the authors.

The aim of the present study was to test the impact of physical (= climatic) and biotic (= density-dependent) factors on dynamics of breeding populations in passerines. I used the results of nearly 40-year monitoring of breeding populations on the Courish Spit of the Baltic Sea, which is done by the Biological Station Rybachy.

2. Material and methods

Birds were trapped and ringed from 1957 by staff of the Biological Station Rybachy at the permanent field station "Fringilla", 12 km south of Rybachy on the Courish Spit of the Baltic Sea. Birds were caught in Rybachy-type traps (detailed description in: Dolnik & Payevsky 1976b).

I analysed long-term pattern of numbers of adults (12 species) and juveniles (20 species) caught before early or mid-August in two Rybachy-type traps open to the NE and SW. At this time the bulk of local birds have already left the natal area, as shown by re-traps (Sokolov 1991a). This allows us to trap both adults breeding in the area and juveniles during post-fledging movements, in a standardised fashion over a long period.

Long-term dynamics of breeding population was estimated in each of 12 species on the basis of the number of adult birds trapped mainly between June 1 and July 31. To reveal long-term trends, three partly overlapping periods were considered: between 1959 and 1978 (20 years); between 1978 and 1991 (14 years); and between 1985 and 1998 (14 years). I took into consideration that from autumn 1977 a new trap was put up which is still in operation. The requirement for long enough time intervals resulted in constructing overlapping time periods in the analysis. Long-term dynamics of numbers of juveniles was estimated for each of 20 species over the same periods.

Statistical significance of trends was tested by Spearman rank correlation (Lloyd & Ledermann 1984). When analysing the impact of air temperature on avian populations I used the data on mean monthly temperatures in the study area in spring and in summer over 32 years (1959-1990). Correlation was statistically tested by Spearman rank correlation. Regression analysis was used to test the relationship between the number of second-year birds in a population, philopatry, numbers of adult breeding birds, and numbers of juveniles. I used logio transformation of actual numbers, as it better reveals relative fluctuation of numbers and makes distributions symmetrical (Williamson 1972).

3. Results

3.1. Long-term trends in numbers of adults

In five species out of 12 analysed numbers of adults in the local population significantly decreased in the 1970s compared with the 1960s (Fig. 1, Tab. 1). In three other species a tendency for a decline was revealed. However, in the Willow Warbler *Phylloscopus trochilus*. Lesser Whitethroat *Sylvia curruca*,

and Scarlet Rosefinch *Carpodacus erythrinus* a positive trend was recorded. In the 1980s a significant or barely significant positive trend compared with the 1970s was recorded in the majority of studied species. Only in the Barred Warbler *Sylvia nisoria* a highly significant decline in numbers of adults was revealed. In the 1990s a significant decline was again recorded in nearly all studied species. This was valid for both long-distance migrants and species that spend their winter within Europe.

In five species. Chaffinch *Fringilla coelebs*. Tree Pipit *Anthus trivialis*, Wood Warbler *Phylloscopus sibilatrix*. Garden Warbler *Sylvia borin*, and Icterine Warbler *Hippolais icterina*, fluctuations of the number of adults in the local population were synchronous over the whole period 1959-1998. Over shorter periods both positive and negative trends coincided in the vast majority of species (Tab. 1).

Table 1. Long-term trends of the numbers of adult birds in the breeding population on the Courish Spit (Spearman's rank correlation coefficient; +p<0.10, *p<0.05, **p<0.01, ***p<0.001).

Species	Years 1959-1978	Years 1978-1991	Years 1985-1998
<i>Fringilla coelebs</i>	-0.45*	0.47+	-0.74**
<i>Anthus trivialis</i>	-0.46*	0.70***	-0.59*
<i>Phylloscopus trochilus</i>	0.21	0.20	-0.64*
<i>Phylloscopus sibilatrix</i>	-0.53 *	0.76**	-0.59*
<i>Ficedula hypoleuca</i>	-0.16	0.65*	-0.60*
<i>Sylvia atricapilla</i>	-0.23	0.69**	-0.38
<i>Sylvia curruca</i>	0.29	0.37	-0.68**
<i>Sylvia communis</i>	-0.24	0.02	-0.43
<i>Sylvia borin</i>	-0.56-	0.62*	-0.82***
<i>Sylvia nisoria</i>	-0.03	-0.81***	-0.79**
<i>Hippolais icterina</i>	-0.60* *	0.65*	-0.91***
<i>Carpodacus erythrinus</i>	0.32	-0.11	-0.75**

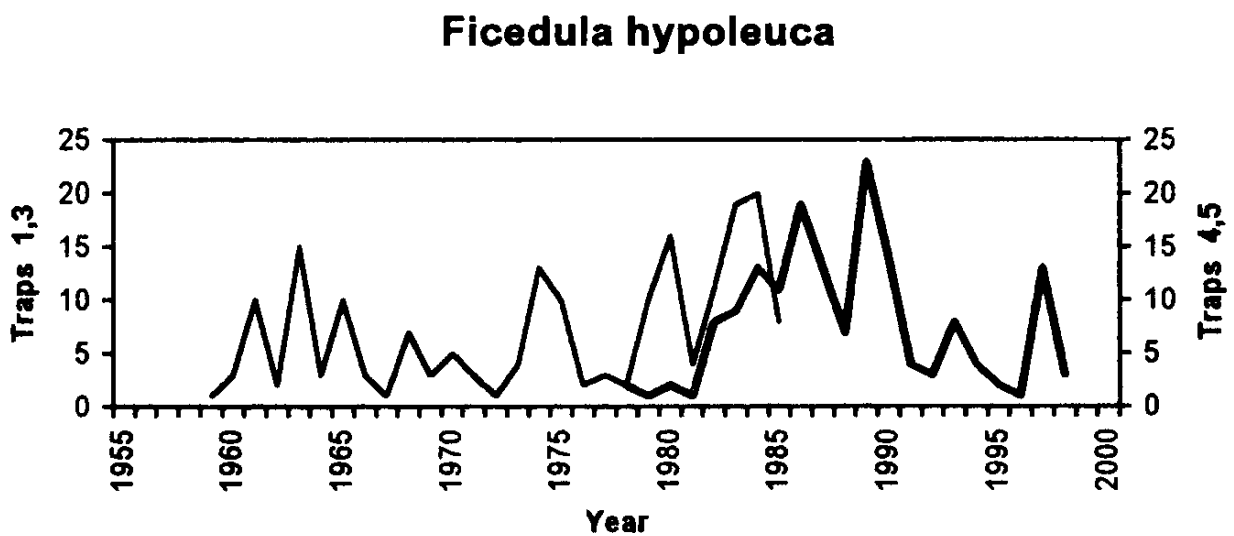
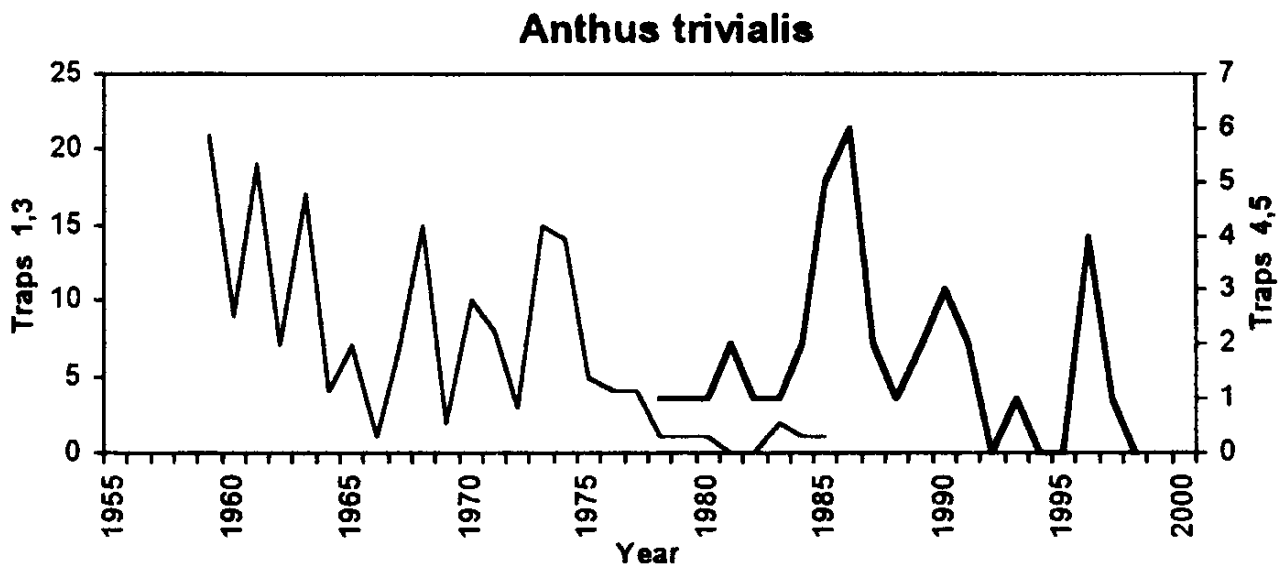
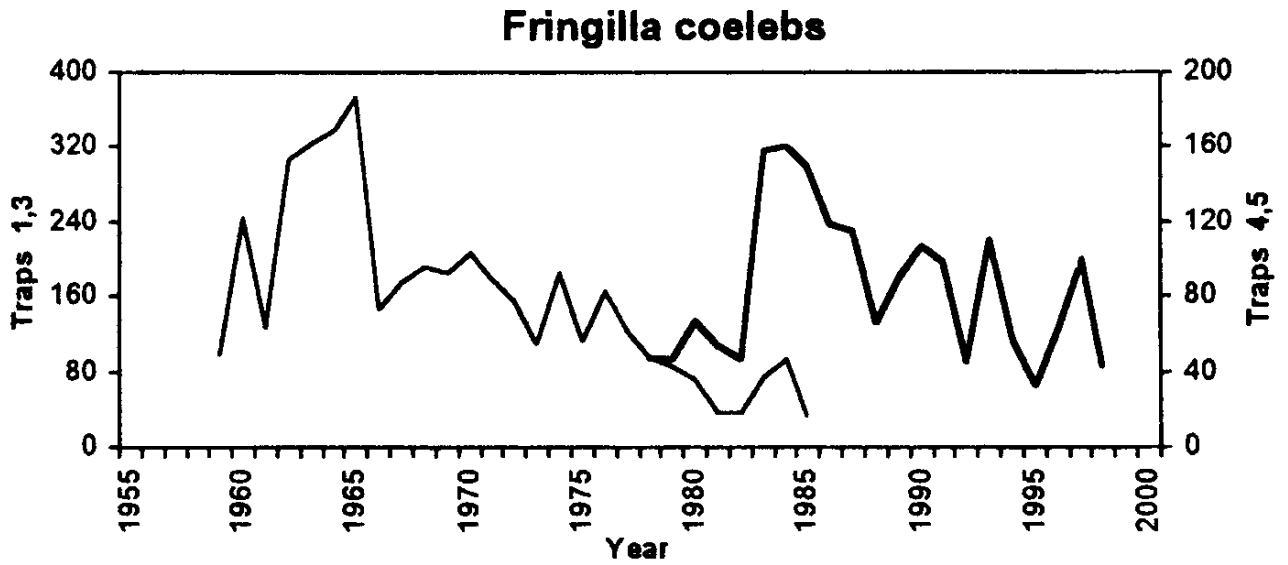
3.2. Long-term trends in numbers of juveniles

In the majority of species the number of juveniles trapped during post-fledging period was higher in the 1960s and 1980s compared with the 1970s and 1990s (Fig. 2). A pronounced trend towards higher numbers in the 1970s compared with the 1960s was recorded only in the Lesser Whitethroat, Blackcap *Sylvia atricapilla*, and Willow Warbler (Tab. 2). In the 1980s a significant decline was observed only in the Barred Warbler and Lesser Whitethroat. In the 1990s in not a single species were higher numbers recorded.

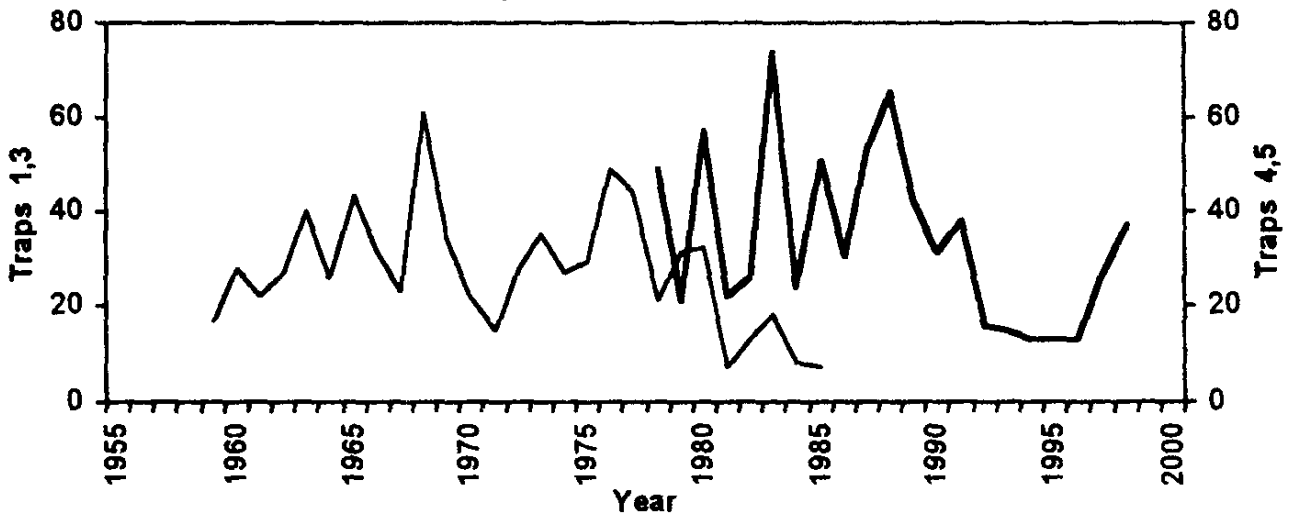
3.3. Association between numbers of juveniles and air temperature in spring and in summer

I analysed the relationship between number of juveniles trapped during post-fledging period, and air temperature in the study area in spring and in summer over 32 years (1959-1990). In all species except for Lesser Whitethroat and Barred Warbler, the number of juveniles was significantly related to the mean temperatures of April and/or May when local adults arrive to their breeding area (Tab. 3). A positive relationship with the mean temperature of March was revealed only in the Blue Tit *Parus caeruleus* and Blackcap that spend their winter within Europe. A strong correlation between numbers of juveniles and May temperature was found mainly in species arriving late. In not a single species was a significant correlation with summer temperatures revealed (Tab. 3)

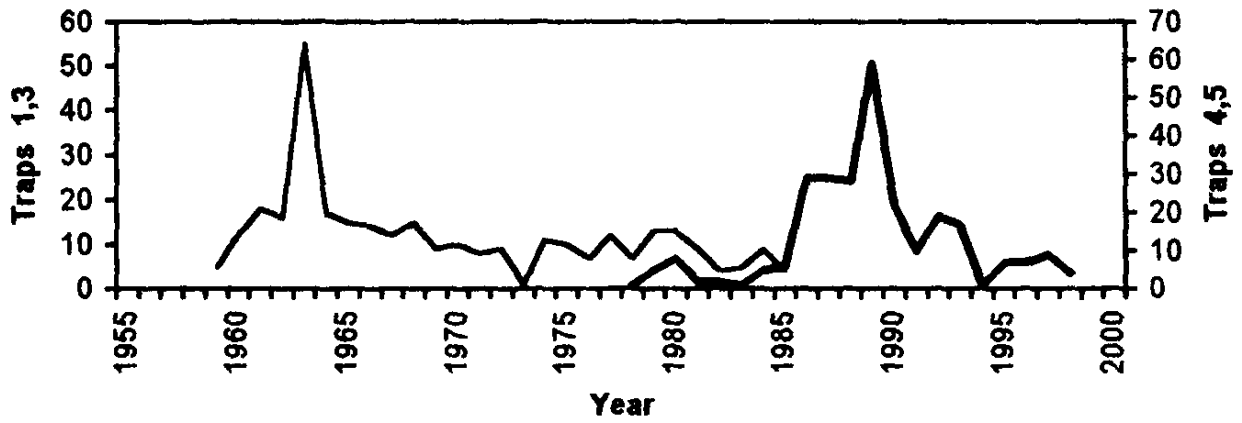
Figure 1. Dynamic of the number of local adult birds in the breeding period on the Courish Spit.



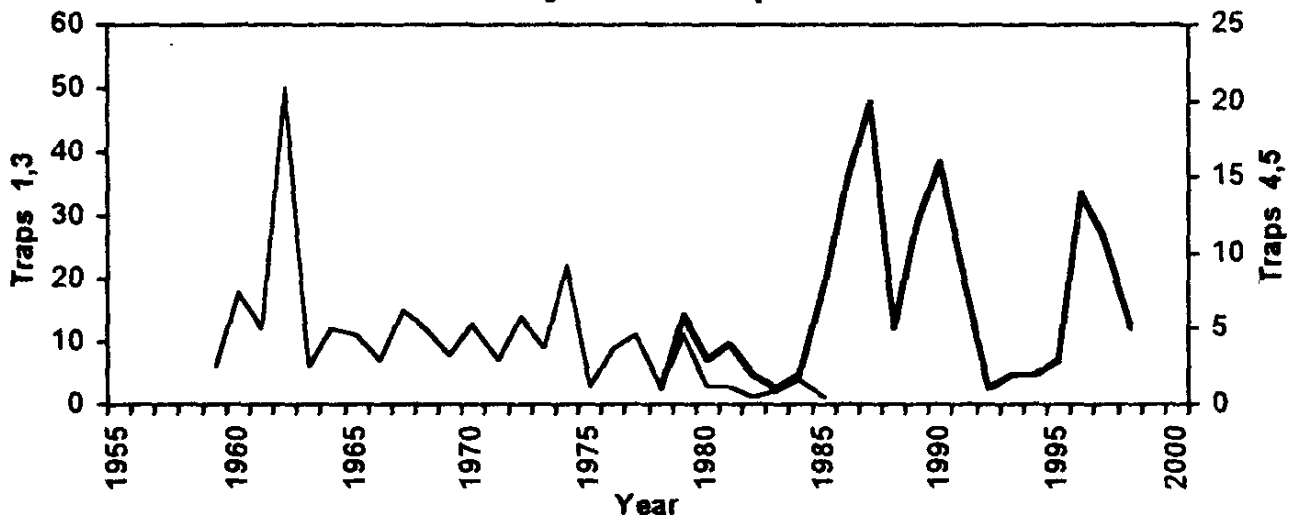
Phylloscopus trochilus



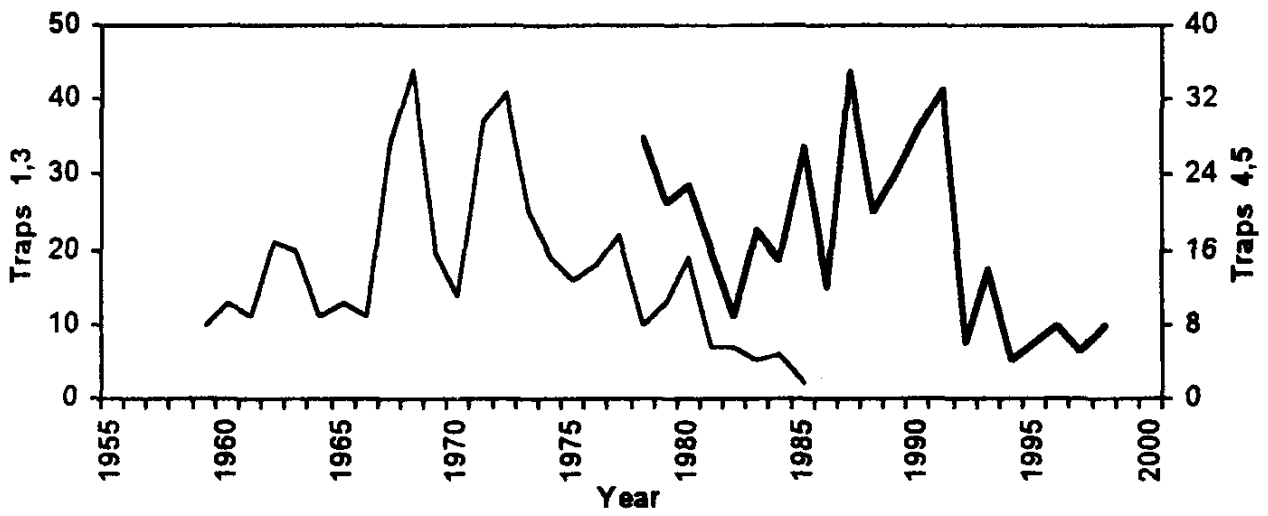
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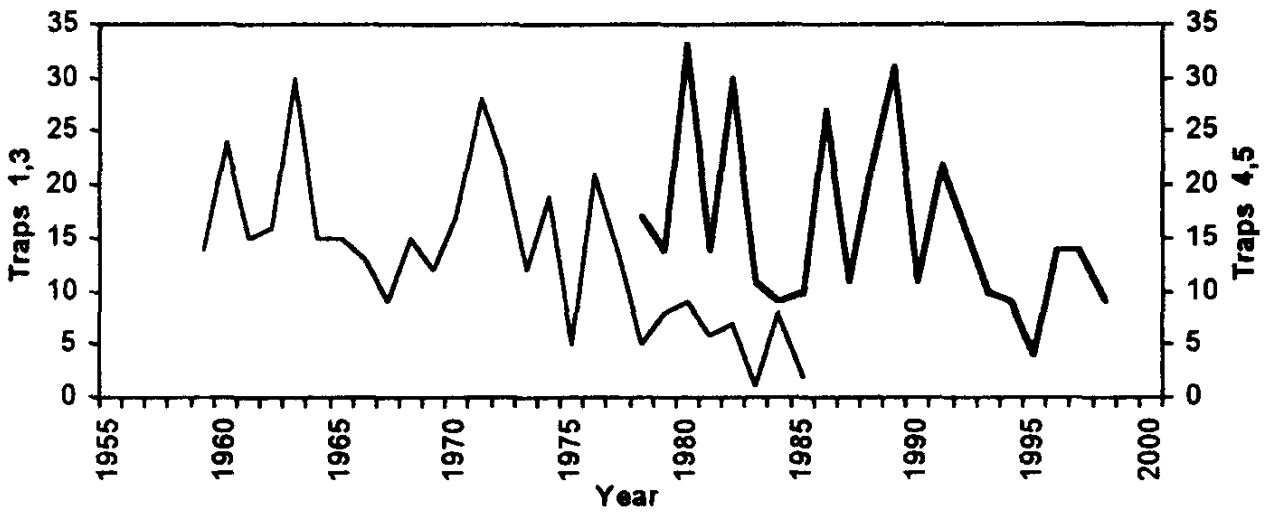
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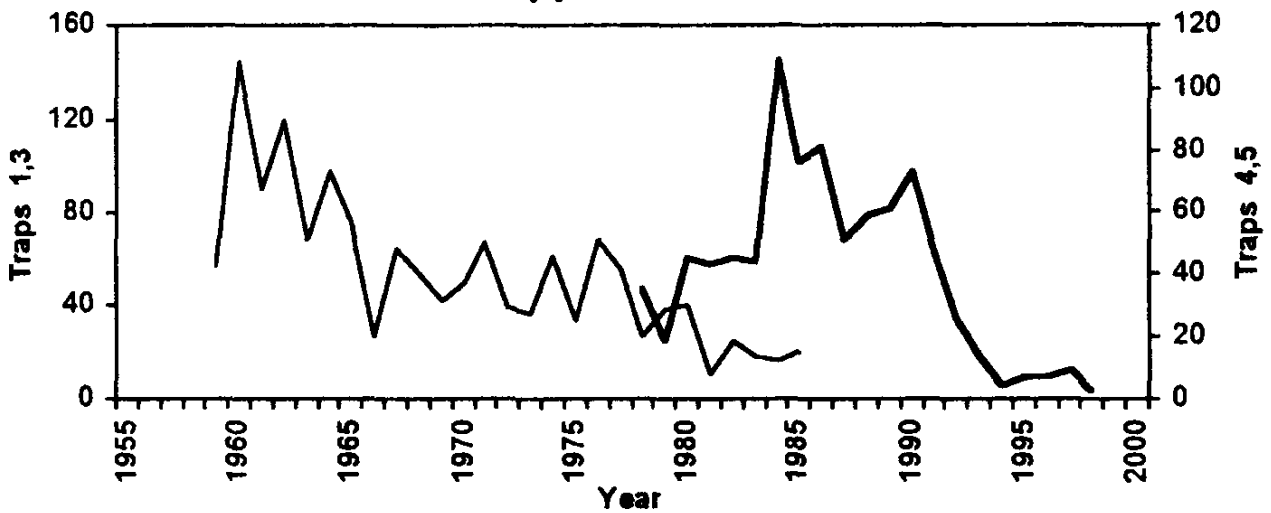
Sylvia curruca



Sylvia communis



Hippolais icterina



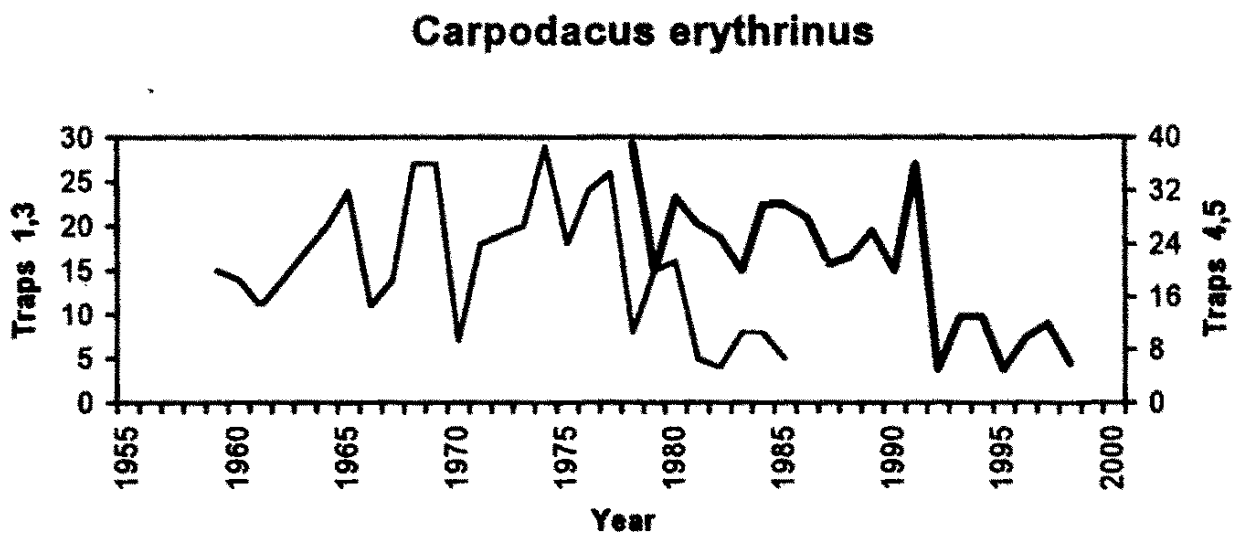
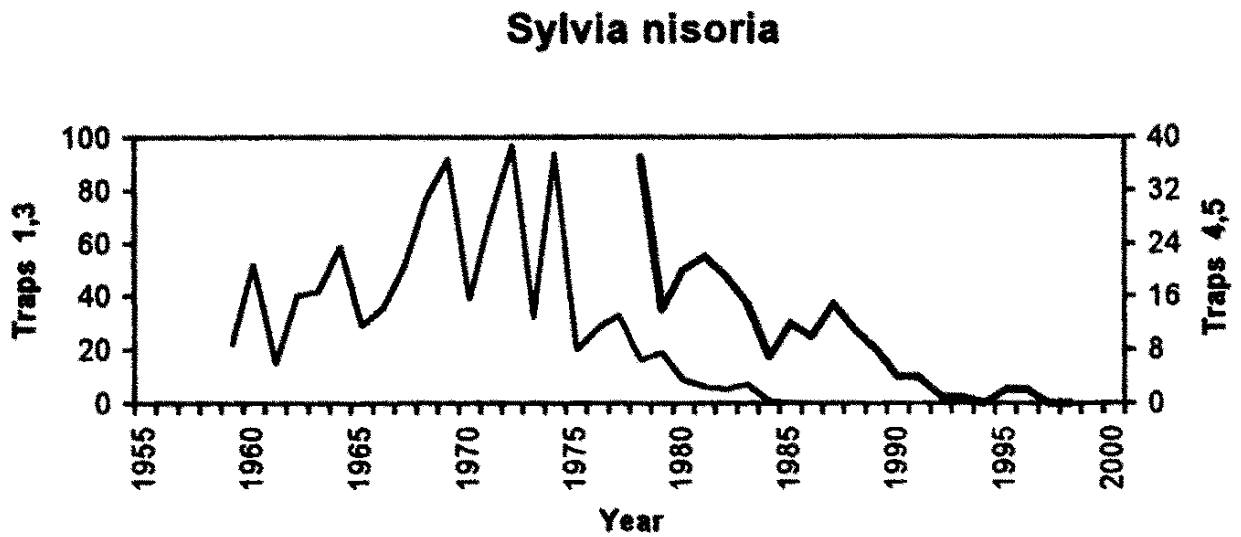
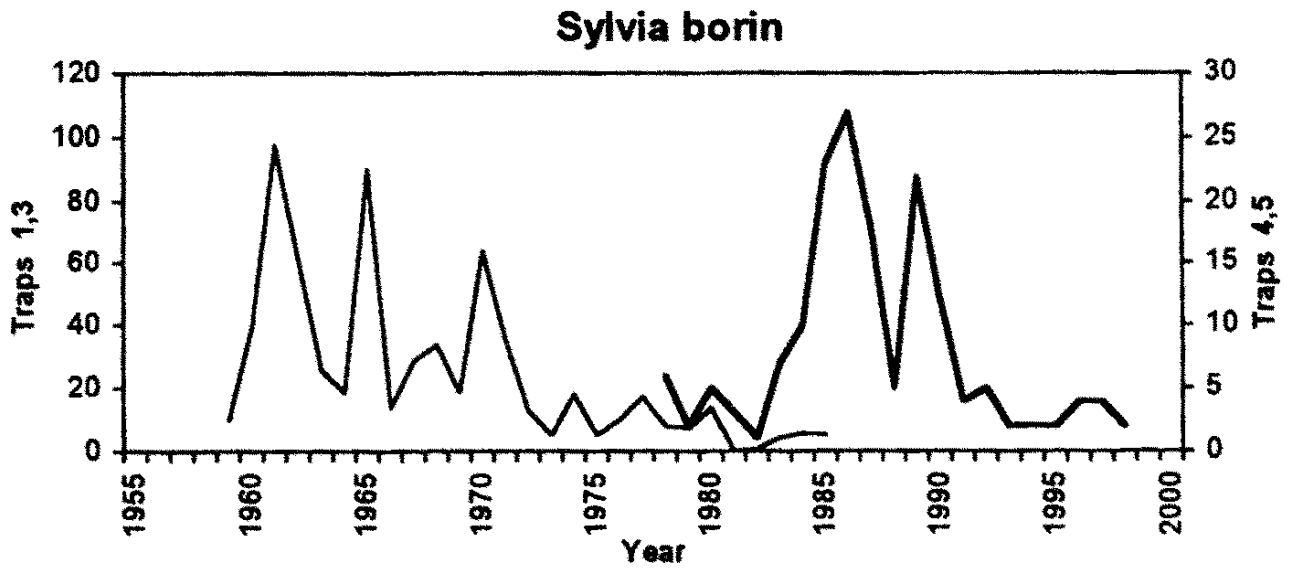


Table 2. Long-term trends of the numbers of local young birds in post-Hedging period on the Courish Spit (Spearman's rank correlation coefficient: +p<0.10, * p<0.05, **p<0.01, *** p<0.001).

Species	Years	Years	Years
	1959-1978	1978-1991	1985 - 1998
<i>Parus cristatus</i>	0.17	0.86***	-0.50+
<i>Parus palustris</i>	-0.02	0.78**	-0.58*
<i>Parus major</i>	-0.06	0.73**	-0.07
<i>Parus caeruleus</i>	-0.46*	0.48+	0.01
<i>Fringilla coelebs</i>	-0.79***	0.54*	-0.61*
<i>Phoenicurus ochruros</i>	-0.46*	0.32+	-0.25
<i>Emberiza dtrineJa</i>	-0.46*	0.64*	-0.19
<i>Phylloscopus collyhita</i>	-0.384	0.68**	-0.61*
<i>Phylloscopus trochilus</i>	0.26	0.65*	-0.72**
<i>Phylloscopus sibilatrix</i>	-0.40+	0.64*	-0.57*
<i>Anthus trivialis</i>	-0.56*	0.52+	-0.23
<i>Ficedula hypoleuca</i>	-0.21	0.72**	-0.79**
<i>Sylvia atricapilla</i>	0.37+	0.68**	-0.71**
<i>Sylvia curruca</i>	0.61**	-0.43	-0.74**
<i>Sylvia communis</i>	-0.45*	0.70**	-0.54*
<i>Sylvia borin</i>	-0.54*	0.69**	-0.69**
<i>Sylvia nisoria</i>	0.07	-0.92***	-
<i>Hippolais icterina</i>	-0.45*	0.13	-0.57*
<i>Carpodacus erythrinus</i>	-0.39+	0.20	-0.81***

3.4. Association between numbers of juveniles and the timing of juvenile dispersal

I compared numbers of juveniles during the post-fledging period with their average trapping date that reflects the timing of breeding (Sokolov & Payevsky 1998). In 14 out of 19 analysed species a significant negative correlation was found: early breeding and juvenile dispersal were associated with high numbers of juveniles during post-fledging period (Tab. 4).

3.5. Significance of local juveniles in the population during the following spring

In several species a significant positive correlation between the number of juveniles during post-fledging period, and trapping numbers during the following breeding season was found (Fig. 3). The number of second-year birds is significantly higher in years following seasons with high numbers of juveniles (Fig. 4).

Figure 2. Dynamic of the number of young birds in the post-fledging period on the Courish Spit.

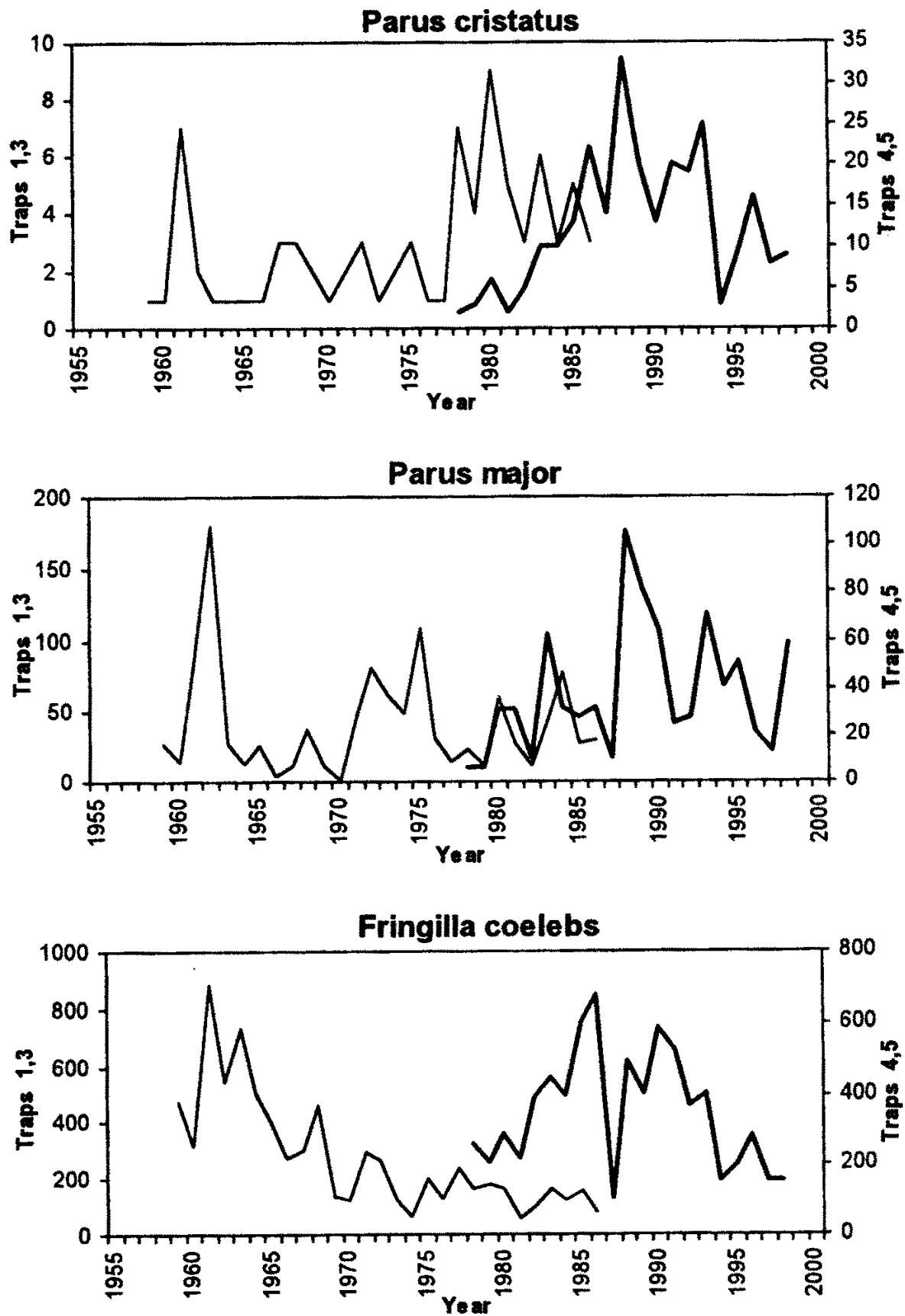
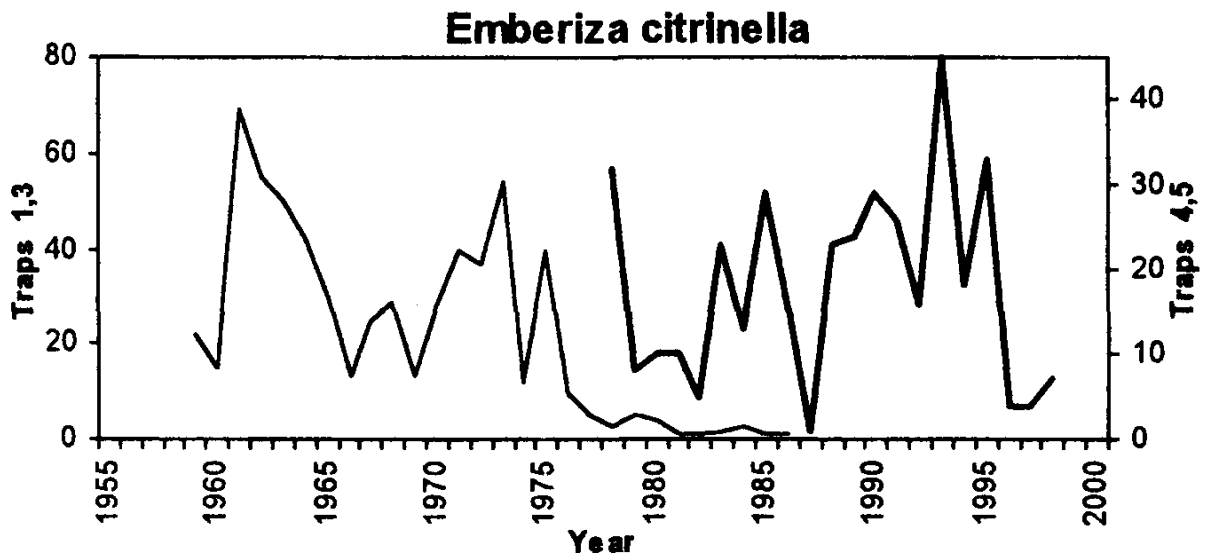
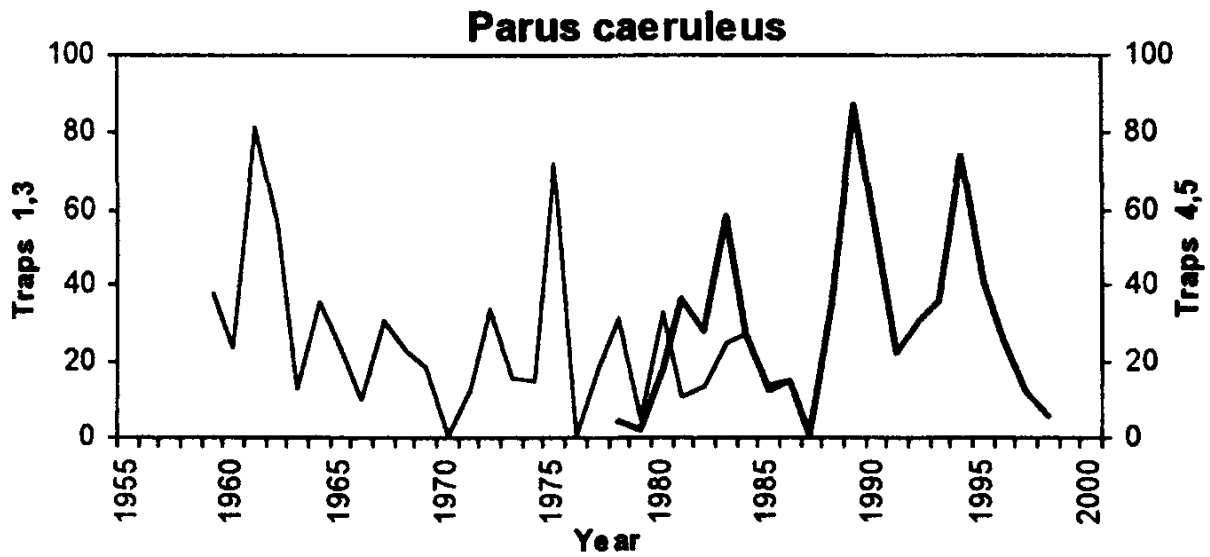
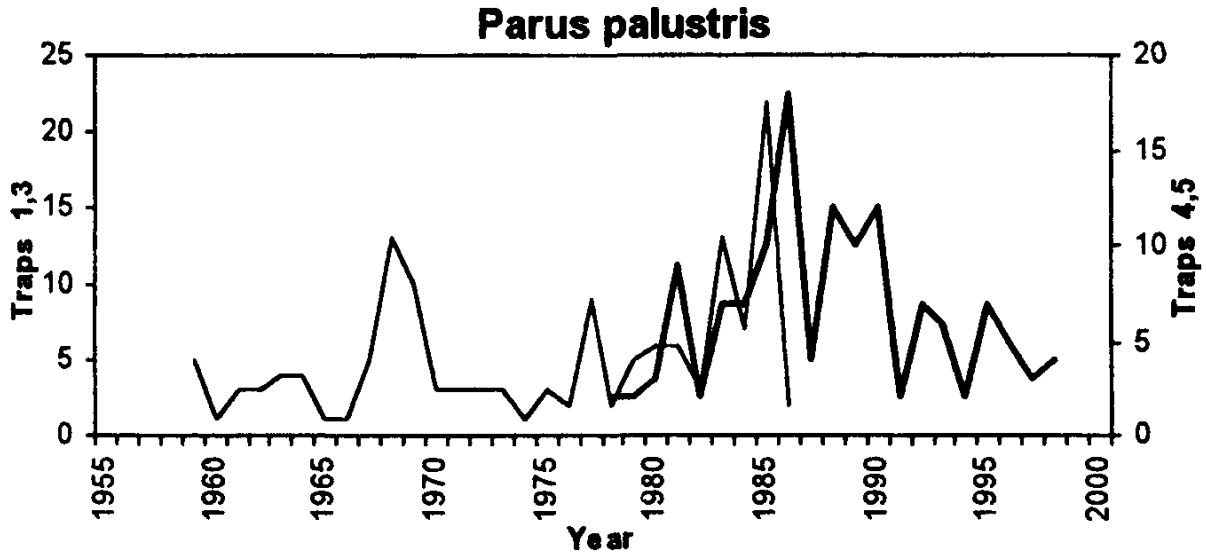
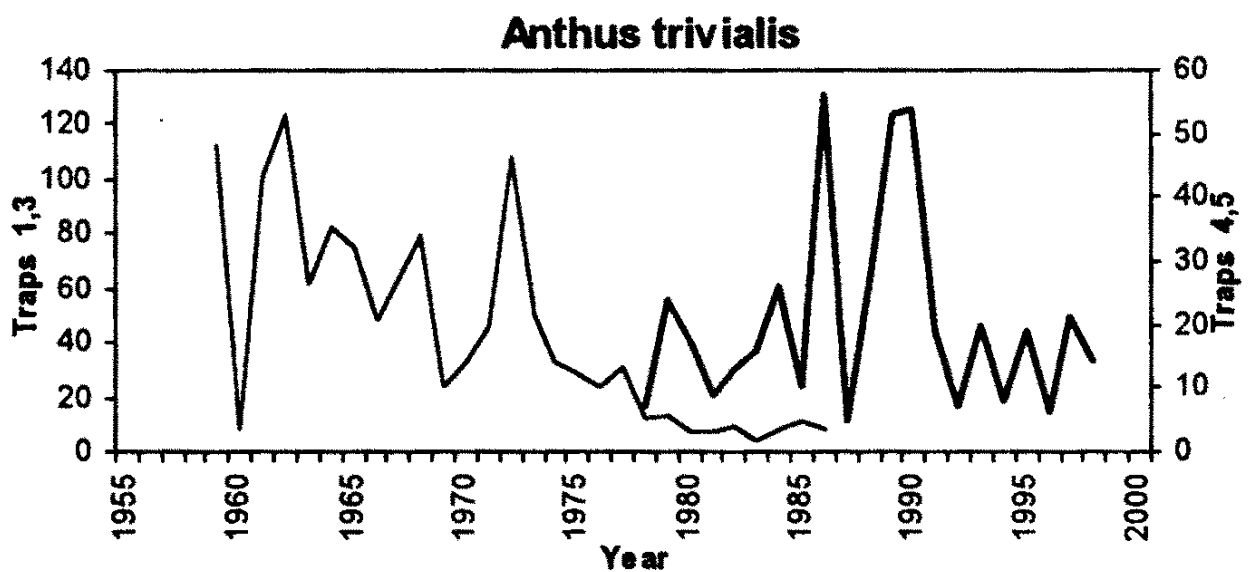
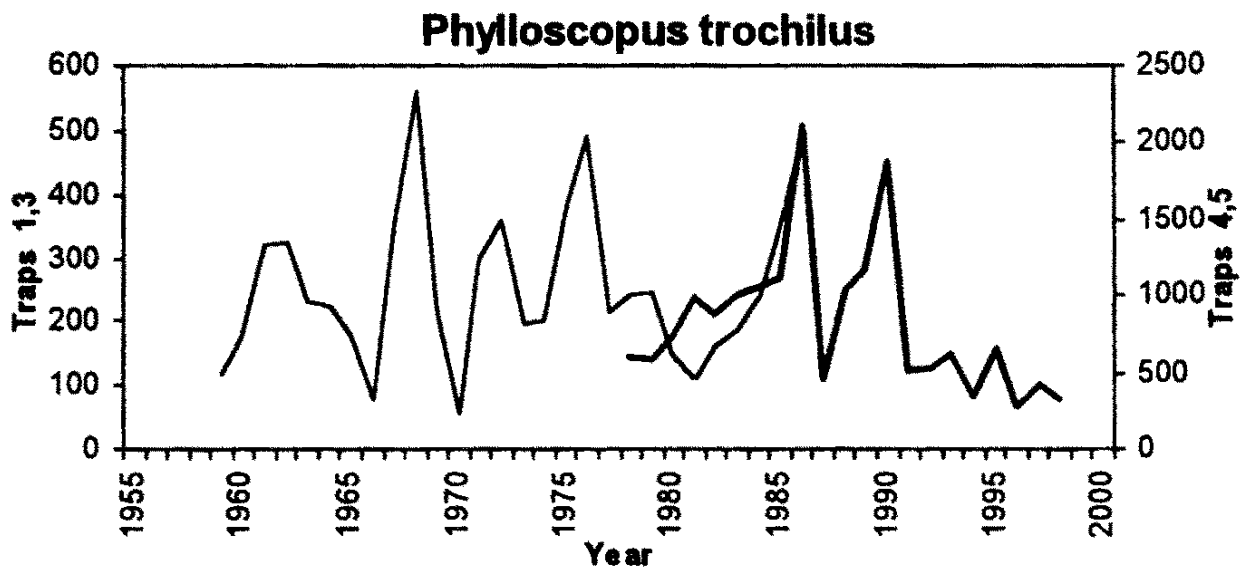
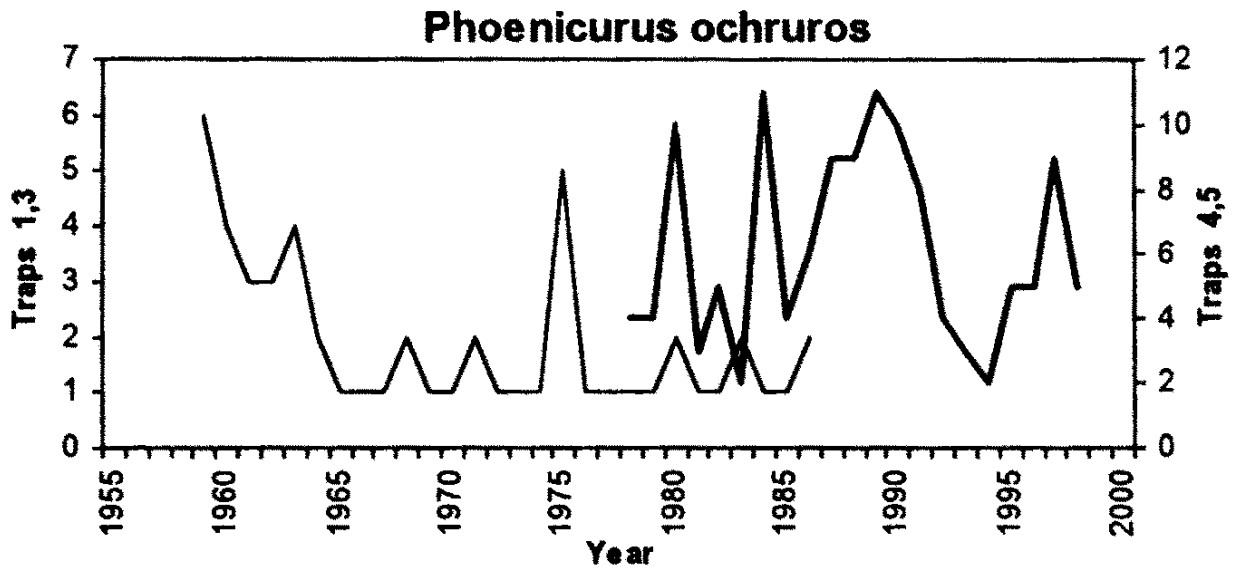
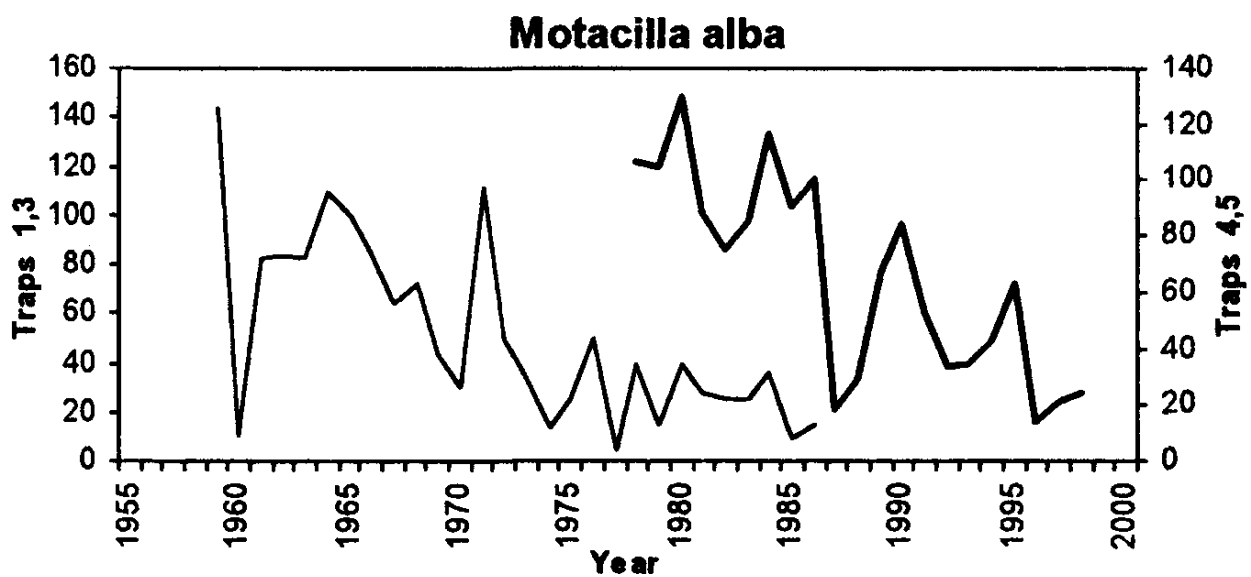
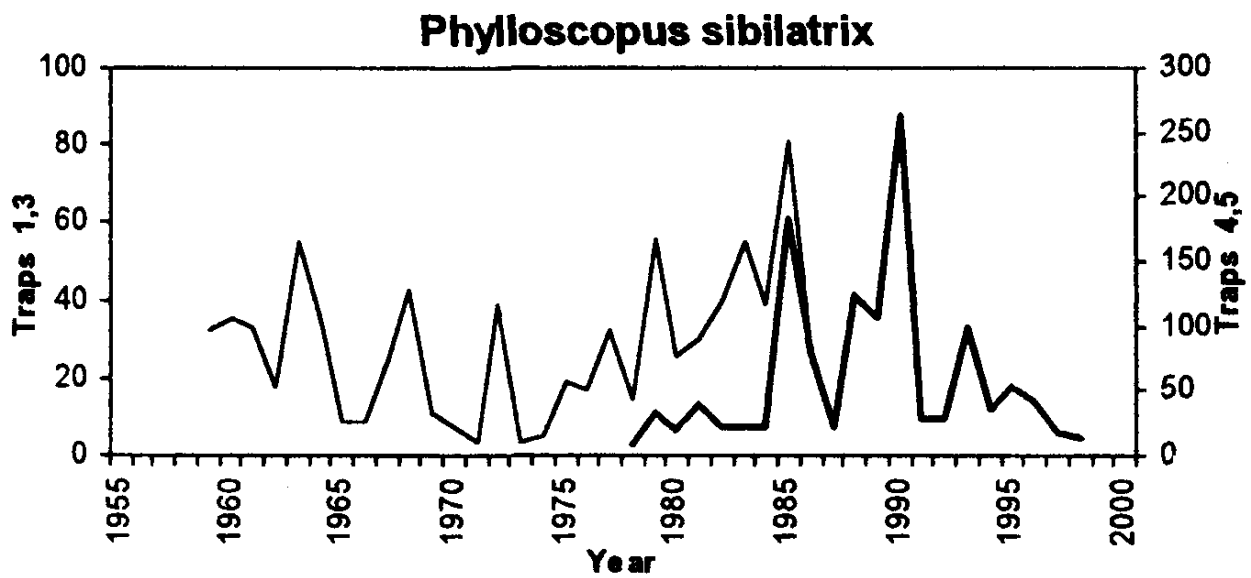
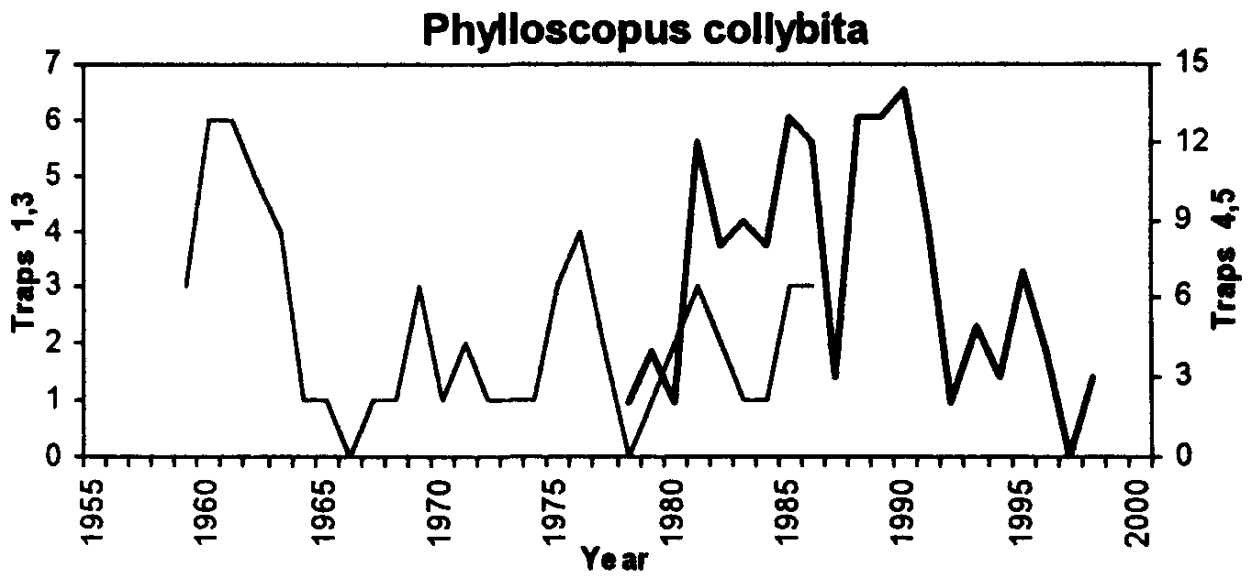
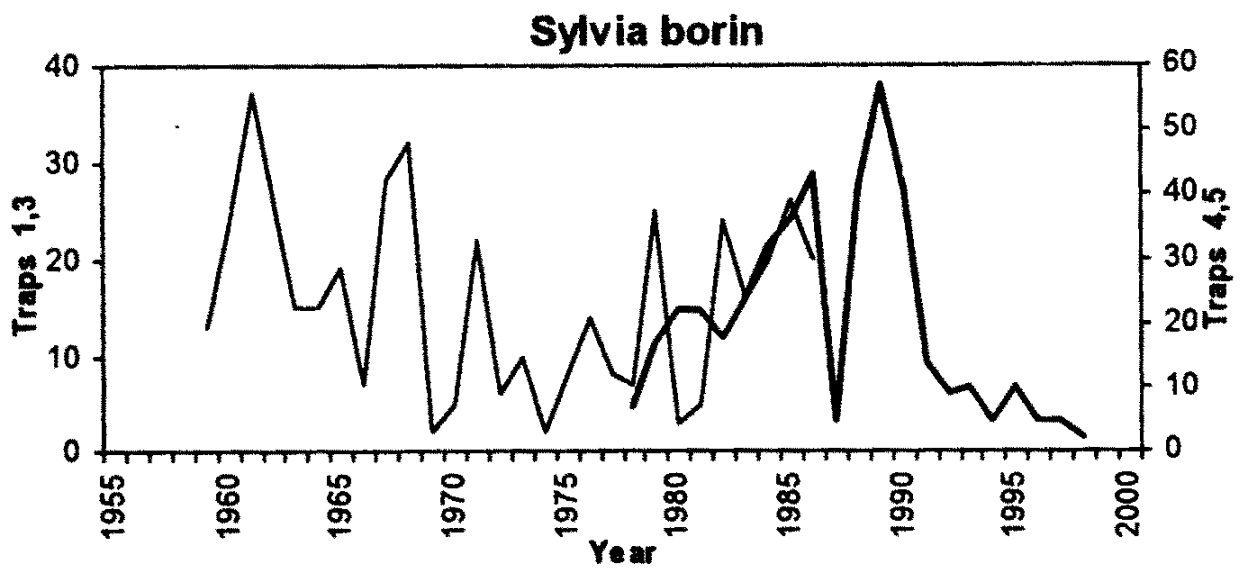
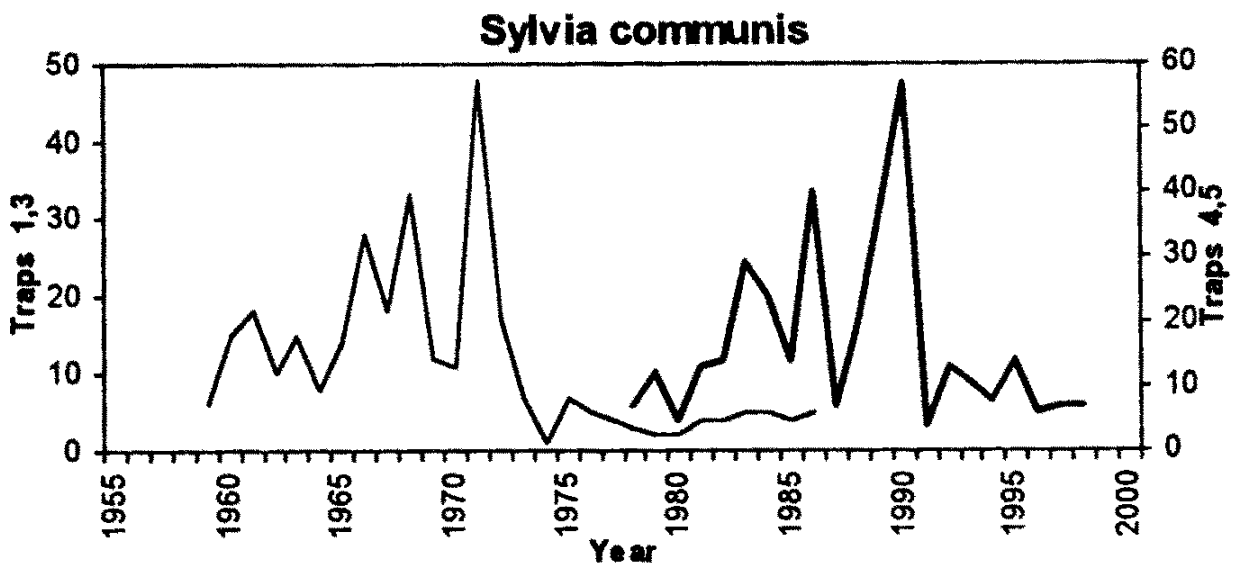
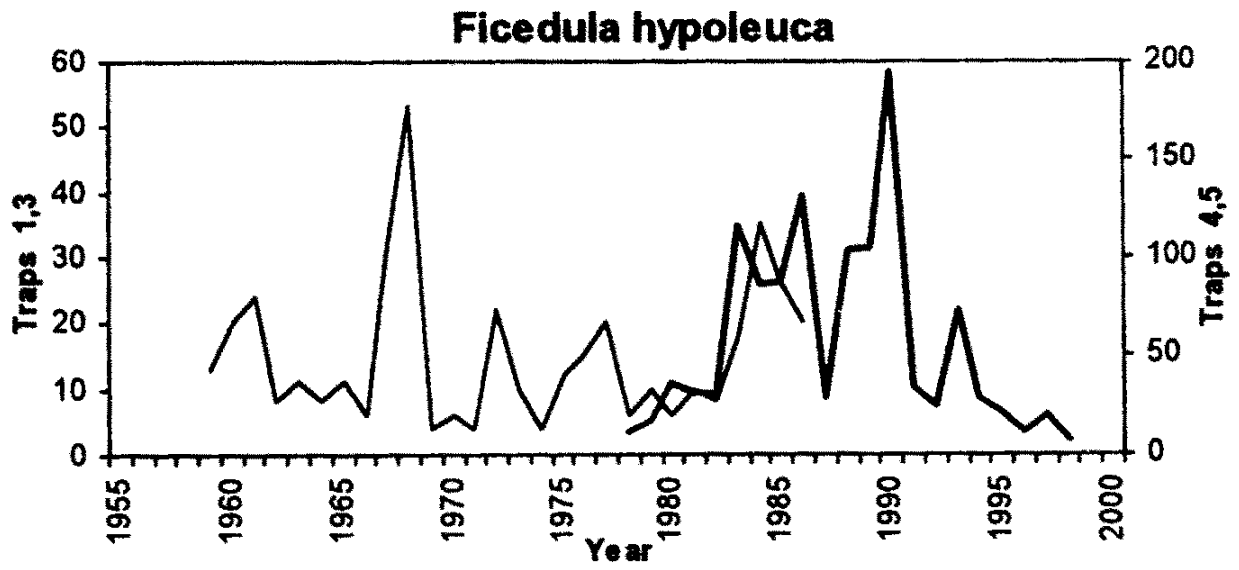


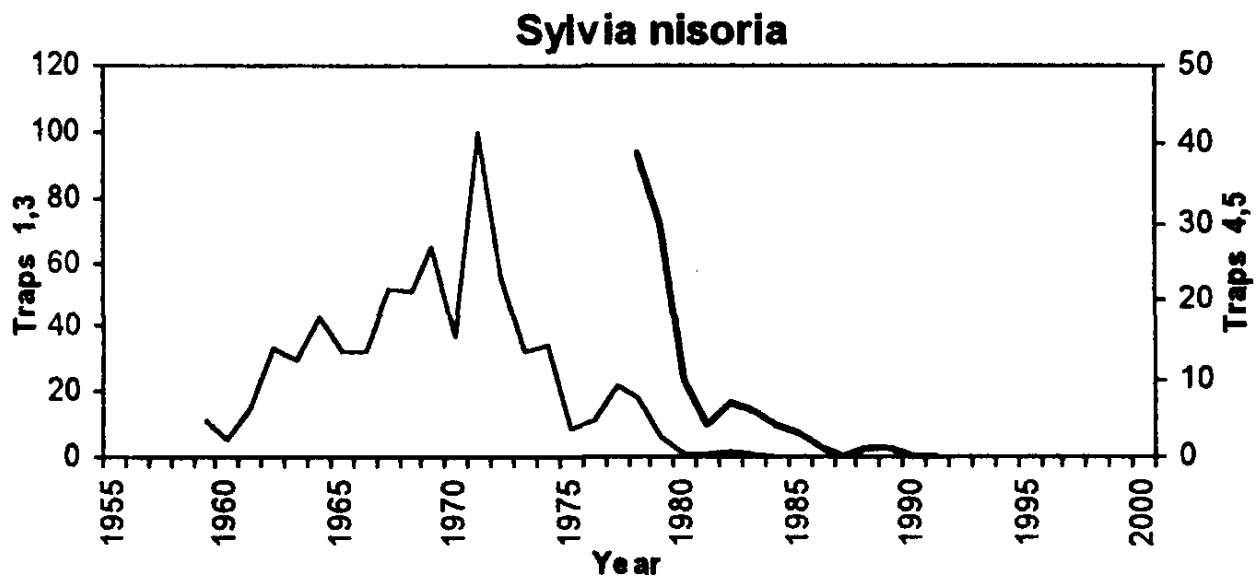
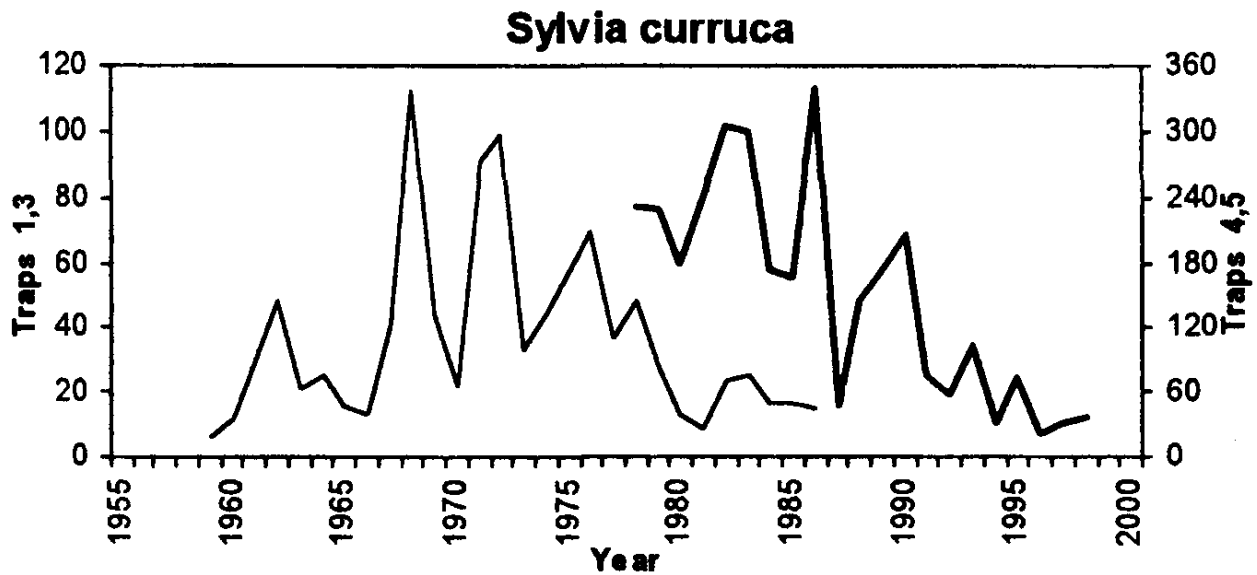
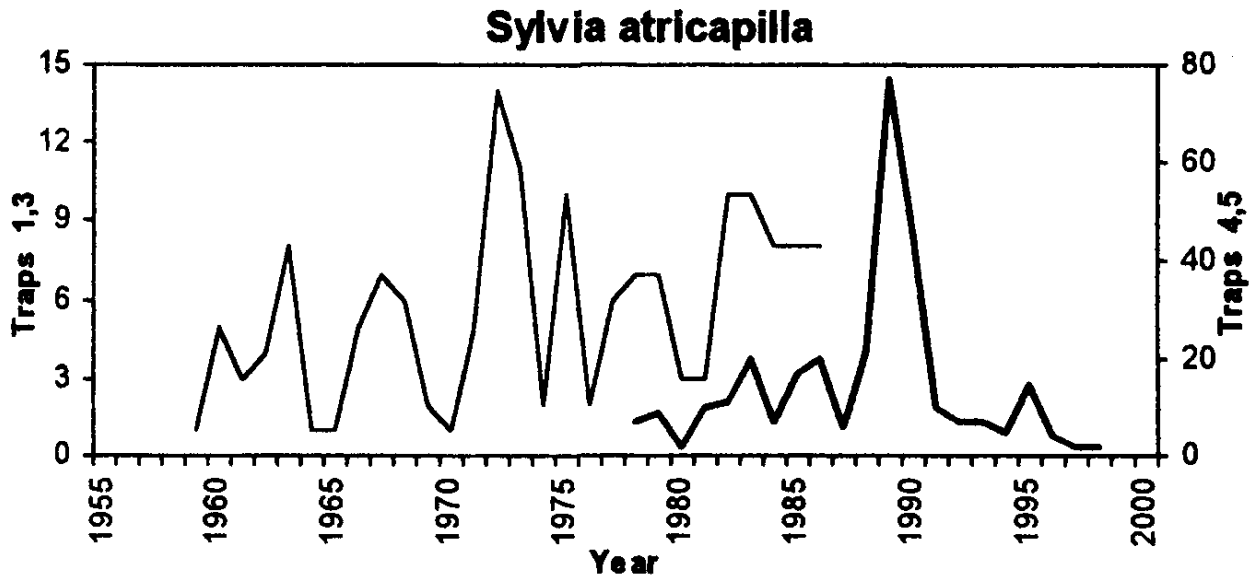
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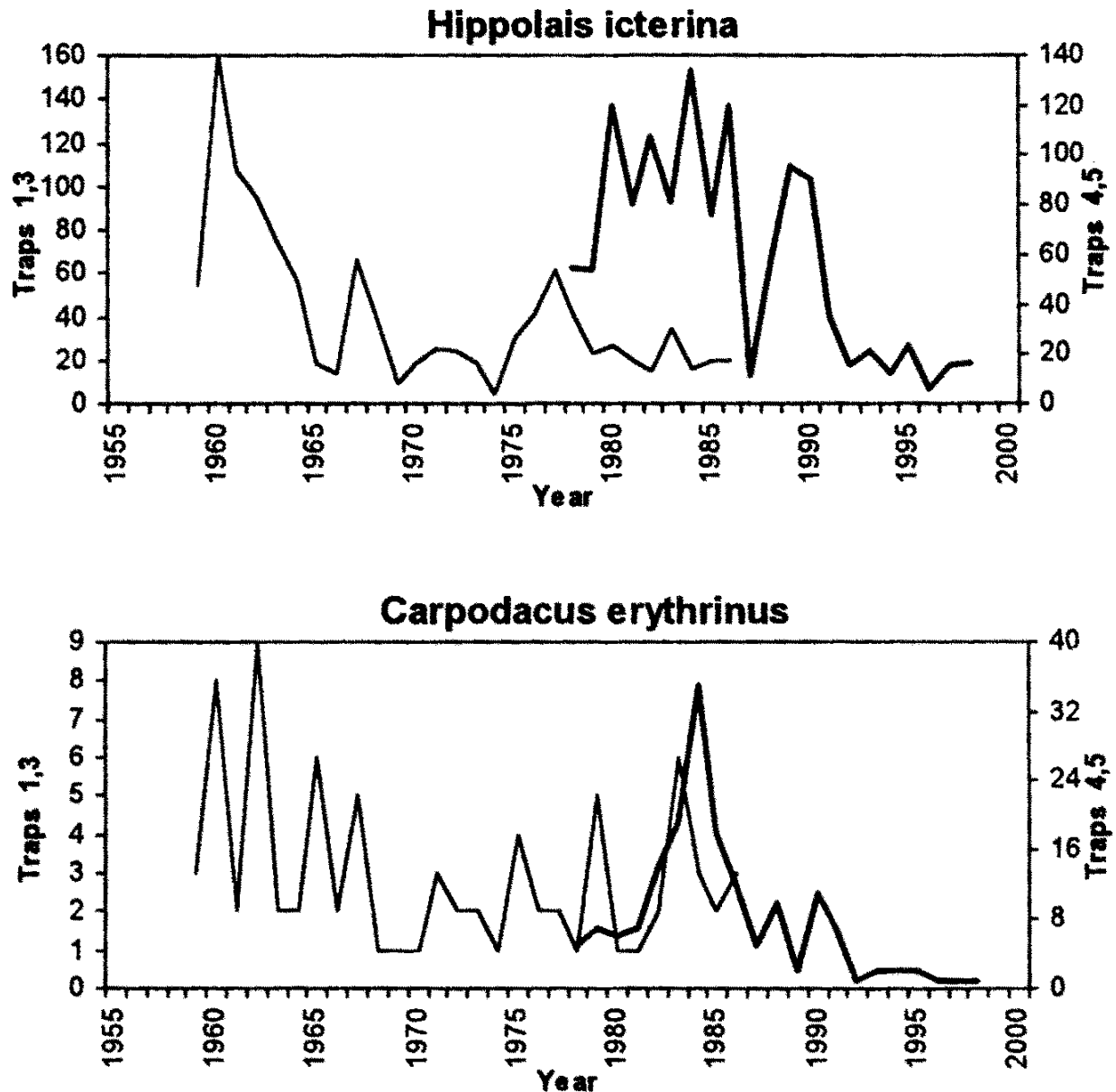












3.6. Impact of numbers of juveniles during post-fledging period on philopatry

I analysed the relationship between philopatry (proportion of birds ringed as pulli and fledglings and retrapped in the subsequent year at the same place), and number of juveniles trapped during post-fledging period. In the Chaffinch I found a significant positive correlation between return rate of birds ringed as pulli and number of juveniles trapped during the previous post-fledging period (Fig. 5). In the Willow Warbler and Icterine Warbler this relationship was barely significant. If we consider the philopatry of birds ringed as juveniles during post-fledging period, we do not find any difference in return rate between individuals born in "good" and in "bad" years (Fig. 5).

Table 3. Correlation between the number of juvenile birds and mean spring and summer air temperatures in some passerines on the Courish Spit, 1959-1990 (Spearman's rank correlation coefficient: + p<0.10, * p<0.05, ** p<0.01, *** p<0.001).

Species	t °C March	t °C April	t °C May	t °C June
<i>Parus cristatus</i>	0.27	0.33+	0.36*	-0.16
<i>Pans palustris</i>	0.14	0.34+	0.33+	0.11
<i>Parus major</i>	0.27	0.59***	0.16	-0.04
<i>Parus caernleus</i>	0.41*	0.43*	0.09	0.08
<i>Fringilla coelebs</i>	0.04	0.61***	0.32+	0.13
<i>Phoenicurus ochwras</i>	-0.08	0.35+	0.20	-0.10
<i>Embema citrinella</i>	0.12	0.44*	0.13	0.11
<i>Phylloscopus collybita</i>	0.08	0.33+	0.56**	-0.16
<i>Phylloscopus trochilus</i>	0.24	0.41*	0.27	-0.14
<i>Phylloscopus sibilatrix</i>	0.18	0.42*	0.47**	0.19
<i>Motacilla alba</i>	-0.18	0.32+	0.15	0.02
<i>Anthus trivialis</i>	0.13	0.39*	0.20	0.21
<i>Ficedula hypoleuca</i>	0.25	0.37*	0.27	0.08
<i>Sylvia atricapilla</i>	0.46*	0.38*	0.58***	-0.07
<i>Sylvia curruca</i>	0.15	0.17	0.23	-0.26
<i>Sylvia communis</i>	0.21	0.52**	0.50**	0.15
<i>Sylvia borin</i>	0.16	0.63***	0.43*	0.05
<i>Hippolais icterina</i>	0.05	0.42*	0.34+	-0.09
<i>Carpodacus erythrinus</i>	-0.05	0.21	0.43*	-0.26

4. Discussion

4.1. The "climatic" hypothesis of control of avian numbers

During the 20th century two relatively long periods of warm weather were recorded, with maxima in the 1930s - 1940s and then in the 1980s, a weaker wanning was recorded in early 1960s (Borisenkov 1988; Kondratiev 1992, 1993). Elsewhere (Sokolov et al. 1998) we analysed annual fluctuations of spring monthly temperatures at 10 sites in European Russia, from the Smolensk Region up to the Kola Peninsula, and showed that spring temperatures vary synchronously over vast territories. During the recent four decades two significant long periods of increased April temperature were recorded, in 1960s and 1980s compared with 1970s (Sokolov et al. 1998). During these warm periods spring migration of birds occurred earlier in the Baltic area (Zaiakevicius 1997, Sokolov et al. 1998), in Ukraine (Fesenko et al. 1996), in Germany (Moritz 1993), and in England (Mason 1995, Loxton et al. 1998, Crick 1999). Moss (1998) stated that changes in temperatures and rainfall during spring and summer are already allowing many species of Britain's birds to begin breeding earlier, lay larger clutches and raise more young. Studies by the BTO have shown that 20 common species are nesting significantly earlier now than they were 25 years ago, with laying dates on average nine days earlier (Crick et al. 1997, Crick & Sparks 1999). In our study area in passerines a significant shift towards earlier breeding was also recorded (Sokolov & Payevsky 1998).

Table 4. Correlation between the number of juvenile birds and mean dispersal date in the post-fledging period in some passerines on the Courish Spit, 1959-1990 (Spearman's rank correlation coefficient, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Species	r_s
<i>Parus cristatus</i>	-0.26
<i>Parus palustris</i>	-0.20
<i>Parus major</i>	-0.37*
<i>Parus caeruleus</i>	-0.48**
<i>Fringilla coelebs</i>	-0.68***
<i>Phoenicurus ochiurus</i>	-0.40*
<i>Emberiza citrinella</i>	-0.40*
<i>Phylloscopus collybita</i>	-0.47**
<i>Phylloscopus trochilus</i>	-0.45*
<i>Phylloscopus sibilatrix</i>	-0.50**
<i>Motacilla alba</i>	-0.20
<i>Anthus trivialis</i>	-0.13
<i>Ficedula hypoleuca</i>	-0.52**
<i>Sylvia atricapilla</i>	-0.55**
<i>Sylvia curruca</i>	-0.16
<i>Sylvia communis</i>	-0.53**
<i>Sylvia borin</i>	-0.63***
<i>Hippolais icterina</i>	-0.62***
<i>Carpodacus erythrinus</i>	-0.58***

Our study showed that bird numbers, both adults and juveniles, were higher in the 1960s and 1980s compared with the 1970s and 1990s. Most probably it should be explained by the climatic influence. Warm and early springs that were frequent during these periods, influenced the timing of arrival and breeding, and enhanced breeding success. In contrast, cold and late springs that dominated in the 1970s and 1990s delayed arrival and breeding, and reduced breeding success. Unexpectedly, in not a single species was a correlation between numbers of juveniles and summer temperatures found (Tab. 4). I expected that temperature should strongly influence survival of nestlings (mainly in June) and fledglings (mainly in July) but this did not happen. Thus, breeding success of a population is determined mainly by spring temperatures, not by summer ones. However, in some years (e.g. in 1974, 1987, and 1998) when in summer very cold and rainy weather prevailed, nestling and fledgling mortality may be very high, influencing numbers of juveniles trapped during the post-fledging period (Payevsky 1982, 1985, Sokolov 1991a, and unpubl). Digby & Milwright (1998) found a positive correlation between production of the Golden Oriole *Oriolus oriolus* in the eastern Britain and June temperature, and there is also a significant negative relationship with June rainfall. Production was lower in years with a cool wet June (1987, seven fledged from 12 nests, and 1991, nine from 11 nests), and higher in the warm dry Junes (1992, 15 from nine nests, and 1993, 17 from six nests).

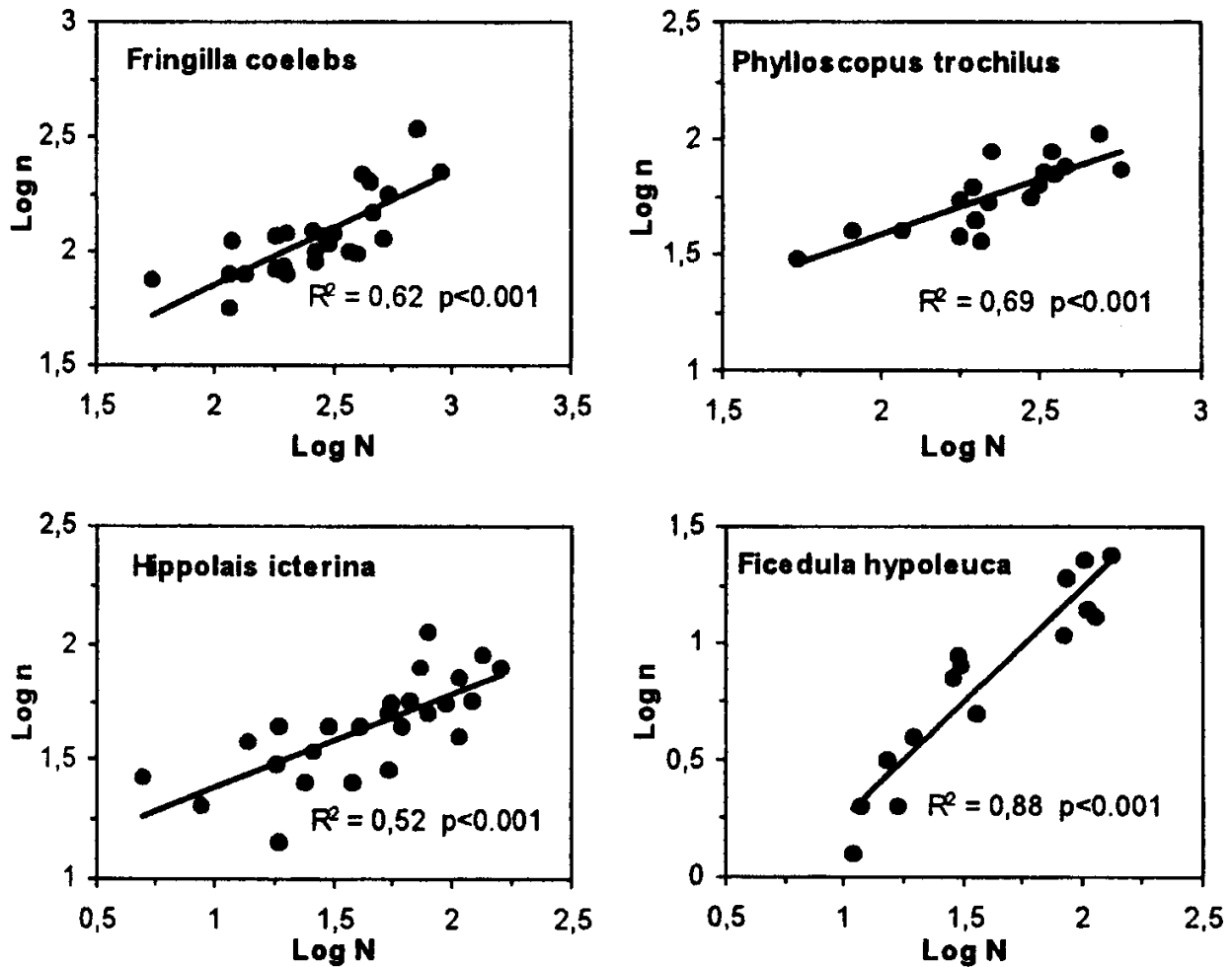


Figure 3. Relationships between the number of juvenile birds of some migratory species in the post-fledging period (N) and the number of breeding birds captured in the study area in the next year (n) on the Courish Spit.

Payevsky (1985) believes that breeding numbers of many passerine species are controlled by spring mortality that may be considerable, especially during cold springs. Slagsvold (1975) found a high positive correlation between numbers of sedentary populations of Great Tits *Parus major* and Blue Tits and temperature, especially between February 24 and April 5. This author believes that many birds may die *in* early spring when the weather is adverse, and second-year birds have not attained territories yet. He suggests that air temperature before breeding is an important factor in density regulation. Senar & Copete (1995) report that in the House Sparrow *Passer domesticus* survival of adults between October and March is considerably reduced in winters when January temperature drops below 0 °C for 10 and more days (in normal winters survival is ca. 40-50%, in cold winters it is ca. 17%). Smith (1995) followed survival of 155 marked Black-capped Chickadees *Parus atricapillus* in Massachusetts and found that mortality of second-year females with an inexperienced mate was much higher in years with cold spring. It was caused by the fact that such males supply their females with food during laying and incubation less efficiently than experienced ones. This effect is more pronounced when the weather is adverse. Peach et al. (1998) reasoned that the many of the pronounced fluctuations in the abundance of passerines in Britain and Ireland can be ascribed to unfavourable weather conditions either in Britain or in the African winter quarters of migratory species. The severe winter weather of February 1991 probably accounts for the reduced catches of many resident species in 1991 (Wren *Troglodytes troglodytes*, Robin *Erithacus rubecula*, Blackbird *Turdus merula* and Song Thrush *T. philomelos*). Catches of Blackcaps and Chiffchaffs *Phylloscopus collybita* which are thought to winter primarily in the Mediterranean basin, also declined dramatically in 1991. Stormy weather over the Mediterranean in April 1991 may have affected these species. Unfavourable spring weather conditions

in Britain can have profound effects on the breeding success of songbirds and this might explain the large reductions in juvenile catches Great Tit, Blackcap, Dunnock (Peach et al. 1998). All these data suggest that in both sedentary and migratory species, in warm and early springs, more individuals start breeding than in cold and late springs. It may be considered the initial step after wintering towards higher numbers in favourable years.

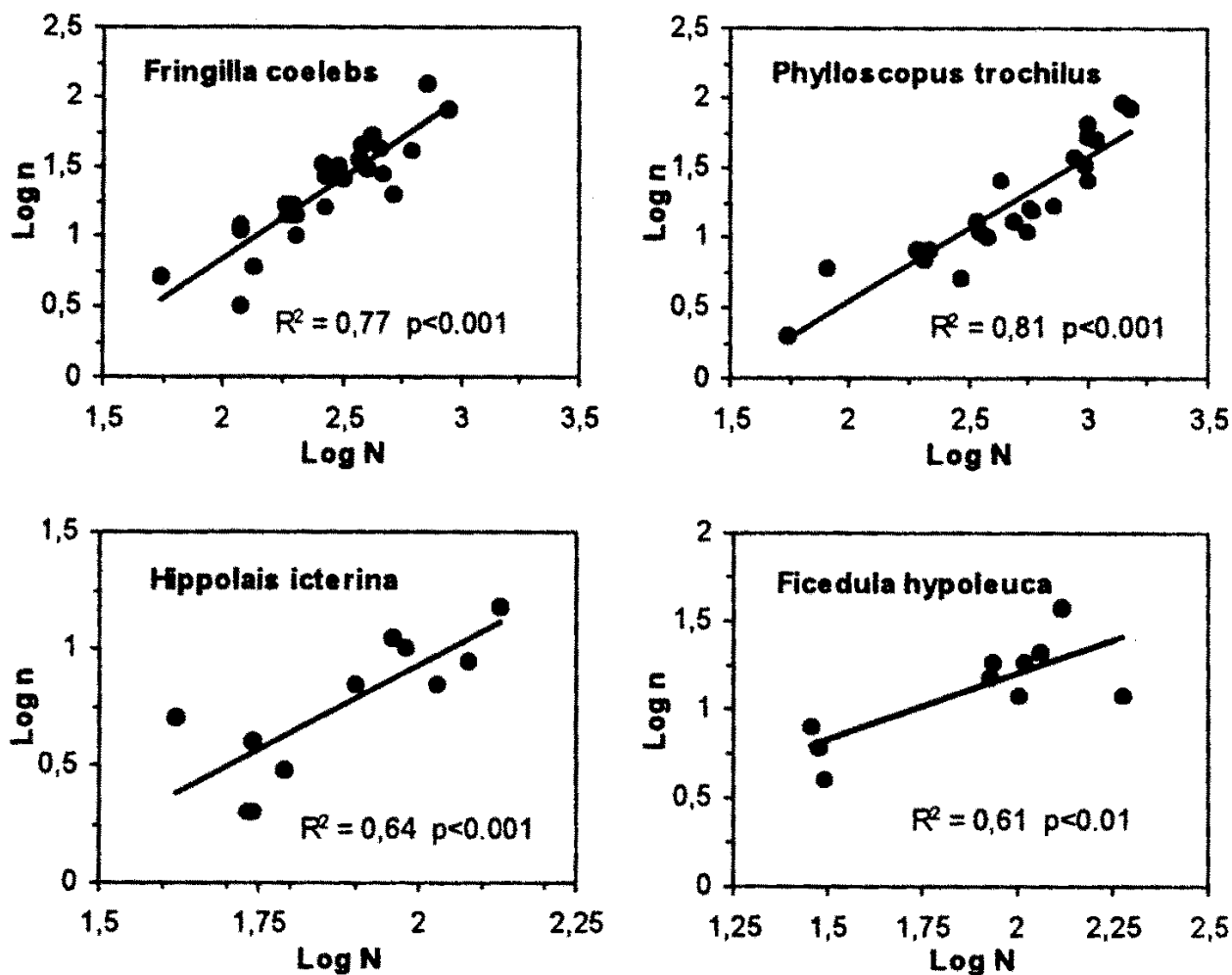


Figure 4. Dependence of the number of second-year birds (n) ringed when young on the number of juvenile birds captured in the post-fledging period in the previous year (N) on the Courish Spit.

Further, for a number of passerines it was demonstrated (also on the Courish Spit) that clutch size is not infrequently higher in early breeders (Payevsky 1985, Zimin 1988). Thus, clutch size in some warbler species (Lesser Whitethroat, Barred Warbler) on the Courish Spit was higher in the "early" 1960s than in the "late" 1970s (Payevsky 1999). Polenets et al. (1995) studied inter-annual variation in fecundity and breeding success in passerines in the tundra of Yamal Peninsula (Russia). They found that variation in the mean clutch size correlates well with variation in laying dates that is dependent on the timing of spring. In years with early breeding fecundity was higher, and when breeding occurred late it was lower. The authors believe that the impact of factors other than temperature were very limited. Even in large passerines spring influenced clutch size and breeding success. Rytkonen et al. (1993) found considerable inter-annual variation in the mean clutch size and number of fledglings in the Rook *Corvus frugilegus*. Rooks that started breeding early had larger clutch and thus brought up more offspring than those that bred late. Timing of breeding and breeding success in this species may be predicted on the basis of the pattern of temperature in May and the period of ground frost. Thus, it is not improbable that in the years with early breeding the total number of laid eggs in a local population may be much higher than in "late" years. This is the second possible step towards higher numbers in years with favourable spring temperatures.

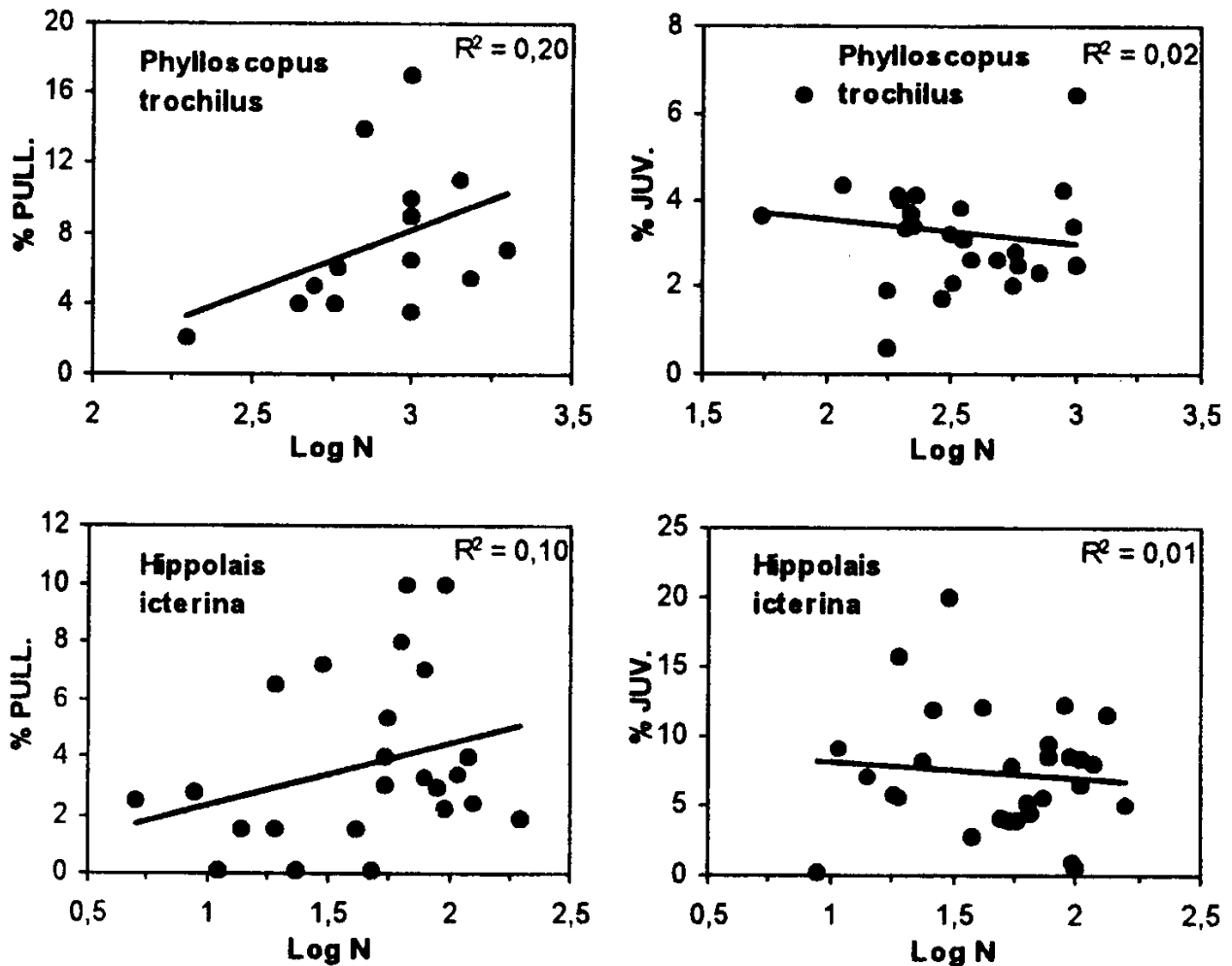


Fig. 5. Dependence of the return rate (%) of second-year birds ringed as nestlings (PULL.) and juveniles (JUV.) on the number of young birds captured in the post-fledging period in the previous year (N) on the Courish Spit.

The next important step which influences the number of juveniles in a population is hatching success and survival of nestlings and fledglings. Much information is available that in years with cold and rainy summer embryonic and nestling mortality is considerably higher than in "good" years. Payevsky (1999) showed that breeding success in the Blackcap that arrives to the Courish Spit relatively early, was significantly higher in the 1980s (71%) than in the 1970s (52%) and in the 1990s (41%). In the Garden Warbler that arrives late, breeding success was significantly higher in the 1960s (78%) than in the 1970s (60%). Markovets (unpubl.) found a significant relationship between breeding success of the Marsh Tit *Parus palustris* and the mean temperature of April. Pen-ins (1996) showed on large material that hatching success in a sedentary English population of the Great Tit increases with increasing egg weight, and the egg weight depends not only on laying date, but on air temperature as well: egg are smaller when the temperature is lower during the period when they are being formed. Nestling survival also rises with increasing egg mass. Potti & Merino (1996) found that in the Pied Flycatcher *Ficedula hypoleuca* hatching success is related to egg weight: it was considerably lower in small eggs. Clutches containing large eggs yielded more individuals recruited into the population. Jarvinen (1996) studied the relationship between egg weight and clutch size in Finnish Lapland. He found that that if air temperature prior to and during laying is low, egg weight and clutch size are negatively correlated. In a "warm" breeding season a large clutch containing large eggs is the optimal combination which provides high breeding success. Thingstand (1997) found that weather conditions in the early breeding season in Central Norway were important and explained most of the variation, particularly the mean number of eggs laid and hatched in the Pied Flycatcher. The mean air temperature between 17 and 31

May, together with the mean temperatures between 6 and 10 June and 21 and 25 June, seem to have been the critical factor for production of young birds. This author found a negative long-term trend in the breeding success during the study period (1986-1995). Morton (1992) studied breeding biology of the White-crowned Sparrow *Zonotrichia leucophrys oriantha* in the mountains of California and found that numbers of juveniles during post-fledging period were strongly related to the timing of snow melting. In years with late and cold spring duration of breeding period is much reduced which leads to reduced productivity of the population. Glue (1992) reported that early and warm spring of 1992 in Britain was favourable for breeding in many passerines and non-passerines. The birds arrived to breeding grounds and started breeding earlier which facilitated successful breeding. Our data confirms that early breeding in the majority of studied passerines enhances productivity, which causes higher numbers of juveniles during post-fledging period (Tab. 3). Population monitoring of passerines in Finland showed that in four species, Skylark *Alauda arvensis*, Starling *Sturnus vulgaris*, Robin, and Wren cold winters were followed by population declines (Vaisanen et al. 1989). These authors report that numbers of long distance migrants declined after 1987 when breeding success was low due to cold and rainy summer. In our study area both summer and spring were cold in 1987, causing considerable decline in numbers of juveniles in many species (Fig. 2) and second-year birds the following year (Fig. 4). Higher mortality in nestlings and fledglings, and also in adult passerines during cold weather was also reported by other authors (Cawthorn & Marchant 1980, Marchant et al. 1990, Greenwood & Baillie 1991, Peach et al. 1995).

Thus, the presented data suggest that dynamics in the numbers of birds is to a large extent governed by the temperature which has great impact on the survival of adults (especially in winter and in spring) and their breeding success. Similar patterns of the dynamics in numbers of species differing in migratory habits (sedentary and long-distance migrants), in breeding biology (hole breeders and open breeders, with nests on the ground, in bushes and trees), and in diet (insectivorous and seed-eaters) could be caused by a fundamental external factor, as e.g. the climate.

4.2. Human influence

The dramatic decline in the numbers of the Barred Warbler in our study area is most probably caused by humans (Vinogradova 1988, Sokolov 1991b). Cuts of the stands of Mountain Pine *Pinus montanns*, Common Juniper *Juniperus communis*, and Common Barberry *Berberis vulgaris* that were done by forest wardens in 1975 and 1984 had a very pronounced negative impact on breeding conditions for the Barred Warbler and Red-backed Shrike *Lanius collurio*. I analysed the proportion of Barred Warblers trapped in spring and staying for breeding in the study area and found that during the period of high numbers it varied between 20-70%, whereas during the period of decline it was as low as 1-20% (Sokolov 1991b). Vinogradova (1988) reported that six male Barred Warblers claimed territory in 1984, and five of them did not find a mate and left the area. Wassmann (1986) reports that the main cause of Barred Warbler's decline in Germany is the habitat change, in particular scrub cutting.

4.3. Population cycles and the concept of density-dependent feedback

It should be noted that in spite of wide distribution of concept of density-dependent regulation of avian population, convincing data confirming this theory is not very numerous. One of classical examples is predator-prey interactions (for reviews see Galushin 1980, Payevsky 1983, 1985). Nonetheless, Payevsky (1983) noted that populations of prey species may fluctuate independently from the predator, and only fluctuations of the predator species may be caused by prey numbers.

Lack (1966) demonstrated density-dependent associations concerning clutch size and fledging success in the Great Tit. Kluyver (1966) showed in the experiment with the same species that if in an isolated island the number of fledglings is reduced in 40% from the annual mean, survival of both adults and first-years doubles. Some researchers suggest as the feedback mechanism direct competition for resources, leading to death of low-ranking individuals during high density (Lack 1954). Others believed

that territorial conflicts play a role, causing reduced birth rate in losers in the struggle for territory (Wynne-Edwards 1962). In many recent papers territorial behaviour is treated as a density-dependent factor, regulating population numbers.

Newton et al. (1998) point to two problems in the study of density-dependent feedback: (1) many bird population studies occur over too few years; and (2) many bird population in recent decades undergo marked upward or downward trends, which complicates the detection of density-dependence. The authors analysed the results of annual counts of five bird species in an oak wood in SE England (Blackbird, Robin, Wren, Great Tit, Blue Tit) over the 22-year period 1958-1979. No significant linear trend was recorded in any population. The breeding population was estimated on the basis of repeated counts of singing males in the 16-ha survey area. In each species years with lowest breeding density were followed by the most marked increase, and peak years were followed by the most drastic decline. The authors concluded that in all studied species density-dependent regulation may explain 20-60% of year-to-year variation of numbers. Nonetheless, in the Wren and Robin nearly 60% of the variation is explained by the weather conditions in winter, in particular by the snowlie. In a similar study of population dynamics of British songbirds over a 27-year period in none of 39 studied species was a density-dependent feedback detected (Greenwood & Baillie 1991). In The Netherlands a negative relationship between population density and the fraction of pairs with second clutches was found in the Great Tit (Kluyver 1951). However, studies in Karelia where breeding density is low, failed to detect density-dependent regulation of numbers in this species (Zimin 1988, Artemyev 1993). In an unstable environment other factors, in particular external ones (weather, food) have larger impact on the breeding success. Some authors suggest a feedback mechanism which eliminates a proportion of juveniles after a successful breeding season, and after an unsuccessful one the survival of juveniles increases (Michelson et al. 1986, Payevsky 1983, 1985). Elsewhere I showed that this model is not valid for passerines, at least in our study area on the Courish Spit (Sokolov 1991a, 1997, this study). When many juveniles are hatched, more individuals are recruited into the breeding population the following year (Fig. 3). It happens mainly due to increased number of second-year birds in the population (Fig. 4). An increased proportion of second-year birds in a breeding population the year following successful breeding was also found in Pied Flycatchers breeding in nest boxes (Sokolov et al. 1989). Certainly situations may occur when after a successful breeding the number of second-year birds is low due to high mortality in winter quarters or during migration (Sokolov 1991a). Nonetheless, the described pattern in general hold valid since several decades in passerine populations of the Courish Spit.

Stenning et al. (1988) analysed density-dependent variation in clutch size, mortality, and immigration in a Pied Flycatcher population during 1948-1964 and concluded that seasons with high breeding density followed seasons with many fledglings, but increases in the number of breeding pairs were due to immigration. Nestling mortality was not related to breeding density. To the contrary, our study of Pied Flycatcher population ecology showed that after successful breeding seasons the fraction of breeders of local origin increased (Sokolov et al. 1989, Sokolov 1991a). In The Netherlands the number of second-year Great Tits of local origin is positively related to the number of fledglings trapped in the previous year, and to beach crop (Balen 1980). In Germany a significant positive relationship was found in the Coal Tit *Parus ater* between the reproductive success and the retrap rate in the following year (Winkel & Winkel 1994). In the White-crowned Sparrow the number of second-year birds in a Californian population was strongly dependent on the breeding success in the previous year which was related to the timing of snow melting in spring (Morton 1994).

Our study does not support the existence of a mechanism that the surplus of juveniles would eliminate after a successful breeding. After years with large numbers of juveniles return rate remains high (Fig. 5). The increase of return rate in birds ringed as pulli after years with high numbers of juveniles during post-fledging period is not necessarily related to higher philopatry after successful breeding seasons. In "good" seasons juveniles suffer less mortality during first two weeks after fledging (before being caught in Rybachy-type traps) and thus show higher return rate in subsequent years. This is evident from captures in the post-fledging periods of birds ringed as pulli (Sokolov 1991a). The proportion of such birds captured in traps during post-fledging period is significantly lower in years with late breeding. It is noteworthy that no decrease in philopatry is recorded after seasons with high recruitment,

which speaks in favour of no density-dependent feedback as described above. Thus, if density-dependent feedback mechanisms do act in passerines, their role in cyclic fluctuations of numbers is not decisive. Our data do not confirm the hypothesis of self-regulation of passerine population suggesting that mortality during post-fledging period is density-dependent.

References

- Andrewartha, H.G. 1963. The Introduction to the Study of Animal Populations. Univ. of Chicago Press, Chicago-London.
- Artemyev, A.V. 1993. Breeding biology of the great tit *Parus major* on southeast coast of the Ladoga Lake. Russ.J. Ornithol. 2(2): 201-207 (in Russian with English summary).
- Balen J. H. 1980. Population fluctuations of the Great Tit and feeding conditions in winter. Ardea 68: 143-164.
- Borisenkov, E.P. 1988. Climate Fluctuations on Last Thousand Yeas. Gidrometeoizdat Press, Leningrad (in Russian).
- Cawthorn, R.A. & Marchant, J.H. 1980. The effects of the 1978/79 winter on British bird populations. Bird Study 27: 163-172.
- Crick, H.Q.P. 1999. The impacts of climate change on bird populations. The Ring 21: 1.
- Crick, H.Q.P. & Sparks, T.H. 1999. Climate change related to egg-laying trends. Nature 399: 423-424.
- Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. 1997. UK birds are laying eggs earlier. Nature 388: 526.
- Elton, C.S. 1924. Periodic fluctuations in the numbers of animals: their causes and effects. Brit. J. Exp. Biol. 11: 119-163.
- Digby, R. & Milwright, P. 1998. Breeding biology of the Golden Oriole *Oriolus oriolus* in the fenland basin of eastern Britain. Bird Study 45: 320-330.
- Dolnik, V.R. & Payevsky, V.A. 1976a. Long-term dynamics of birds in the North-West USSR during last fifteen years. In: Proceedings of the IX Baltic Ornitholog. Conf., Vilnius: 86-88 (in Russian).
- Dolnik, V.R. & Payevsky, V.A. 1976b. Rybachy-type trap. In: Ilychev, V.D. (ed.) Ringing in the Study of Bird Migrations in the USSR: 73-81. Nauka Press, Moscow (in Russian).
- Dolnik, V.R. & Payevsky, V.A. 1979. Dynamics of the numbers of Baltic bird populations during 1960-1976.4:59-69 (in Russian)
- Fecenko, H.V., Mikhalevich, O.A. & Knysh, N.P. 1996. Are there conformities of spring bird arrival dates to the seasonal evolution of ecosystems? Communication 1. Structure of significant correlations between the spring arrival dates of birds and the dates of first flowering of plants in the forest-steppe zone of the Sumy Region. Vestnik Zool. 4-5: 36-45 (in Russian with English summary).
- Galushin, V.M. 1960. The modern state of the numbers of birds of prey in European part of the USSR. In: Ecology, Geography and Protection of Birds, Leningrad: 156-167 (in Russian).
- Glue, D.E. 1992. Favourable weather conditions enhance the breeding performance of many of Britain's birds in 1992. j. Meteorol. 172: 253-255.
- Greenwood, j.D.D. & Baillie, S.R. 1991. Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm. Ibis 133: 121-133.
- Jarvinen, A. 1996. Correlation between egg size and clutch size in the Pied Flycatcher *Ficedula hypoleuca* in cold and warm summers. Ibis 138: 620-623.
- Myashtorin, L.B. & Sidorenkov, N.S. 1996. The long-term climatic changes and pelagic fish stock fluctuations in the Pacific. Izvest. TINRO 119: 33-54 (in Russian with English summary).
- Kluyver, H.N. 1951. The population ecology of the Great Tit, *Parus m. major* L. Ardea 39: 1-135.
- Kluyver, H.N. 1966. Regulation of a bird population. Ostrich. Suppl. 6: 389-396.
- Kondratiev, KJ. 1992. The Global Climate. Nauka Press, St. Petetsburg (in Russian).
- Kondratiev, KJ. 1993. The recent in estimates of the global climate fluctuations. Izvest.of the Russian Geographic Society 4: 1-11 (in Russian).
- Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford Univ. Press.
- Lack, D. 1966. Population Studies of Birds. Oxford: Clarendon Press.
- Lloyd, E. & Ledermann, W. 1984. Handbook of Applicable Mathematics. Vol. 6: Statistics. Part B, A Wiley-interscience Publication John Wiley & Sons Ltd.
- Loxton, R.G. Sparks, T.H. & Newnham,j.A. 1998. Spring arrival dates of migrants in Sussex and

- Leicestershire (1966-1996). The Sussex Bird Report 50: 182-196.
- Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P. 1990. Population trends in British breeding birds. Tring: British Trust for Ornithol. Nature Conserv. Council.
 - Mason, C.F. 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study* 42: 182-189.
 - Maximov, A.A. 1984. Long-term Fluctuations of the Animal Numbers. Nauka Press, Novosibirsk (in Russian).
 - Mihelson, H., Mednis, A. & Blums, P. 1986. Population Ecology of Migratory Ducks in Latvia. Zinatne Press, Riga (in Russian with English summary).
 - Moritz, D. 1993. Long-term monitoring of Palaearctic-African migrants at Helgoland (German Bight, North Sea). *Ann. Sci. Zool.* 268: 579-586.
 - Morton, M.L. 1992. Effects of sex and birth date on premigration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. *Condor* 94: 117-133.
 - Morton, M.L. 1994. Endocrine and behavioral responses in White-crowned Sparrows to high altitude conditions. *J. Ornithol.* 135: 376.
 - Moss, S. 1998. Predictions of the effects of global climate change on Britain's birds. *British Birds* 91: 307-325.
 - Newton I., Rothery, P. & Dale, L.C. 1998. Density-dependence in the bird populations of an oak wood over 22 years. *Ibis* 140: 131-136.
 - Payevsky, V.A. 1982. Reproduction and demography of the Chaffinches at the Kurische Nehrung according to twenty-years data. In: Dolnik, V.R. (ed.). Population Ecology of the Chaffinch (*Fringilla coelebs*): 165-190 Nauka Press, Leningrad (in Russian with English summary).
 - Payevsky, V.A. 1983. Population dynamics of birds. The central problems. *Usp. sovr. biol.* 96: 296-307 (in Russian).
 - Payevsky, V.A. 1985. Demography of Birds. Nauka Press, Leningrad (in Russian).
 - Payevsky, V.A. 1989. Long-term dynamics of some land bird populations based on trappings at the Courish Spit. Baltic Sea. In: XI Internal. Conf. on Bird Census and Atlas Work. Abstracts: 55, Prague.
 - Payevsky, V.A. 1990a. Population dynamics of birds during 1960-1986 according to trapping data on the Courish Spit of the Baltic Sea. In: Proceed. 5 Conf. on the Study and Conservation of Migratory Birds of the Baltic Basin (Baltic Birds 5). Vol. 2: 69-73. Zinatne Press, Riga.
 - Payevsky, V.A. 1990b. Population dynamics of birds according to trapping data on the Courish Spit of the Baltic Sea during twenty seven years. *Zool. zhurn.* 69: 80-93 (in Russian with English summary).
 - Payevsky, V.A. 1999. Breeding biology, morphometrics, and population dynamics of *Sylvia* warblers in the Eastern Baltic. *Avian Ecol. Behav.* 2: 19-50.
 - Peach, W., C. du Feu & McMeeking J. 1995. Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis* 137: 497-507.
 - Peach, W.J., Baillie, S.R. & Balmer, D.E. 1998. Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study* 45: 257-275.
 - Penins, C.M. 1996. Eggs, egg formation and the timing of breeding. *Ibis* 138: 2-15.
 - Polenets, E.A., Ryabitsev, V.C., Alekseeva, N.S. & Tyulkin, Yu.A. 1995. Inter-season differences of the production and breeding success of birds in tundra. In: Questions of the Ornithology: 59-60. Barnaul (in Russian).
 - Potti J. & Merino, S. 1996. Causes of hatching failure in the Pied Flycatcher. *Condor* 98: 328-336.
 - Ricklefs, R.E. 1976. The Economy of Nature. Chiron Press. Inc. Portland, Oregon.
 - Rytkonen, S., Koivula, K. & Lindgren, E. 1993. The population size and northern Finland. *Ornis Fenn.* 70: 202-212.
 - Senar, J.C. & Copete, J.L. 1995. Mediterranean house sparrows (*Passer domesticus*) are not used to freezing temperatures: an analysis of survival rates. *J. of Applied Statistics* 22: 1069-1074.
 - Slagsvold, T. 1975. Critical period for regulation of Great Tit (*Parus major* L.) and Blue Tit (*P. caeruleus* L.) populations. *Norw.J. Zool.* 23: 67-88.
 - Smith, S.M. 1995. Age-specific survival in breeding black-capped chickadees (*Parus atricapillus*). *Auk* 112: 840 - 846.
 - Sokolov, L.V. 1991a. Philopatry and Dispersal of Birds. Proceed. of the Zool. Inst. Vol. 230, Leningrad (in Russian).
 - Sokolov, L.V. 1991b. Long-term study of population dynamics and philopatry of nine migrating species at the Courish Spit. In: Ecological and Population Research of Birds. Vol. 231: 174-194, Leningrad (in Russian).

Russian with English summary).

- Sokolov, L.V. 1997. Philopatry of Migratory Birds. In: Phys. Gen. Biol. Reviews. Vol. 11: 1-58. Harwood Acad. Publ., The Netherlands.
- Sokolov, L.V. & Payevsky, V.A. 1998. Spring temperatures effects on year-to-year variations in breeding phenology of passerines on the Courish Spit. Avian Ecol. Behav. 1: 22-36.
- Sokolov, L.V., Markovets, M.Yu., Shapoval, A.P. & Morozov, Yu.G. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. Avian Ecol. Behav. 1: 1-21.
- Sokolov, L.V., Vysotsky, V.G. & Baidin, A.V. 1989. Breeding area fidelity and dispersal of the Pied Flycatcher (*Ficedula hypoleuca*) at the Courish Spit. In: Proceed. Zool. Inst. Vol. 197: 121-134, Leningrad (in Russian with English summary).
- Stenning, M.J., Harvey, P.H. & Campbell, B. 1988. Searching for density-dependent regulation in a population of Pied Flycatchers *Ficedula hypoleuca* Pallas. J. Anim. Ecol. 57: 307-317.
- Thingstad, G. 1997. Annual and local reproductive variations of a Pied Flycatcher *Ficedula hypoleuca* population near a subalpine lake in Central Norway. Ornis Fenn. 74: 39-49.
- Thompson, W.R. 1956. The fundamental theory of natural and biological control. Annual. Rev. Entom. 1: 379-402.
- Vaisanen, R.A., Hilden, O. & Pulliainen, E. 1989. Suomen pesiva maalinnusto 1979-88 piste- ja linjalaskentojen valossa. Lintumies 24: 60-67.
- Vinogradova, N.V. 1988. On the population of the Barred Warbler on the Courish Spit in 1974-1986 in connection with a slump in numbers. In: Study of Birds in USSR, Their Protection and Rational Utilization, 42-44, Vilnius (in Russian).
- Wassmann, R. 1986. Zur Biologie der Sperbeigrasmuecke (*Sylvia nisoria*). Voliere 9: 270-272.
- Watson, A. & Moss, R. 1980. Advances in our understanding of the population dynamics of Red Grouse from a recent fluctuation in numbers. Ardea 68: 103-111.
- Williamson, M. 1972. The Analysis of Biological Populations. London. Winkel, W. & Winkel, D. 1994. Cost and benefits of a second brood in coal tits *Parus ater*. J. Ornithol. 135:22.
- Wynne-Edwards, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Edinburgh-London.
- Zaiakevicius, M. 1997. Bird migration and climate change. Acta Zool. Lithuanica 6: 20-30.
- Zimin, V.B. 1988. Ecology of Passerine Birds of the North-West USSR. Nauka Press, Leningrad (in Russian).