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Age and sex structure, mortality and spatial winter distribution of Siskins (*Carduelis spinus*) migrating through eastern Baltic area

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Abstract: PAYEVSKY, V. A. (1994): Age and sex structure, mortality and spatial winter distribution of Siskins (*Carduelis spinus*) migrating through eastern Baltic area. – Vogelwarte 37: 190–198.

The trapping and ringing data of the Siskins migrating through the Courish Spit of Baltic Sea during 1957–1987 were used to determine the winter distribution of sex and age groups. Up to 1991 a total of 149,378 ringed Siskins resulted in 1156 recoveries (0.77%). In spite of some examples of differences in migration distances between some groups in question, there were no significant differences between the sexes and ages, neither in the distance between ringing and recovery locations nor in the direction of migration. The males outnumbered females in adults (59.7%) and in immatures as well (52.2%). No differences were found in the annual survival rates between males and females and between adults and immatures, the survival rates being various in the range 42–47%. These results are discussed under three hypotheses developed to explain the causes of differential migration. The results are not consistent with these hypotheses, probably because of the pronounced gregariousness of this species.

Key words: Age structure, sex structure, mortality, differential migration, winter distribution, Siskin (*Carduelis spinus*).

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1. Introduction

Differential migration is a phenomenon which is common to many bird species. The birds in the Northern Hemisphere often show geographical and temporal segregation of the age and sex cohorts during nonbreeding season, both in Europe (WEIGOLD 1926, DROST 1935, DORST 1962, SCHIFFERLI 1963, PAYEVSKY 1985) and in North America (KING et al. 1965, KETTERSON & NOLAN 1979, NICHOLS & HARAMIS 1980, GAUTHREAUX 1982, RISING 1988, PRESCOTT & MIDDLETON 1990). The general pattern of differential migration among the sex classes is that females migrate farther than males, but among the age classes the pattern varies between species (PAYEVSKY 1985, PRESCOTT & MIDDLETON 1990). Differential migration has a direct relation to general problems of avian biology such as population dynamics, population structure and age- and sex-specific mortality.

The Siskin is a wandering and migratory flocking bird in all parts of its range throughout Europe and Asia. This paper is concerned with populations which migrate through the Courish, or Curonian Spit (Kurische Nehrung) of the Baltic Sea. Earlier results of bird ringing in this place by the Biological Station Rybachy were published twenty years ago (PAYEVSKY 1973).

The aim of this paper is as follows: (1) to determine age and sex structure of migrating Siskins and to examine changes of the structure from decade to decade during the migratory seasons, (2) to compare distances between ringing and recovery locations in birds of the respective sex and age cohorts and thus to find whether or not a geographical segregation of these cohorts exists, (3) to calculate survival estimates of the Siskins using ringing recovery data, (4) to discuss the question of relations between differential migration and sex/age specific survival.

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2. Material and methods

2.1. Material

The Siskins were trapped and ringed from 1957 by staff of the Biological Station Rybachy at a permanent field station „Fringilla“ located 12 km south of Rybachy at the Courish Spit. A detailed description of the site was given by DOLNIK & PAYEVSKY (1982). The birds were caught in „Rybachy traps“, which resemble Heligoland traps but are larger in size and differ in the method of construction (DOLNIK & PAYEVSKY 1976).

In 1957–1987 we trapped and ringed a total of 149,378 Siskins. Up to 1991 these birds resulted in 1156 recoveries (0.77%). Ageing criteria for Siskins became available from 1972 and therefore all data for 1957–1971 were categorized by sex only, and data for population structure were used only from 1972 through 1987.

2.2. Methods

From 1972 we sexed and aged Siskins by the method of SVENSSON (1970), which subsequently was tested and supplemented (PAYEVSKY 1976, VINOGRADOVA et al. 1976). For ageing we place strong emphasis on the completeness of moult of the great coverts: immatures show a contrast between inner moulted and outer retained juvenile coverts. Rarely are all great coverts moulted in immatures too, but such birds should be aged as adults only if all tail-feathers are quite fresh with tips rounded. An additional point to emphasize is that the yellow colour differs between adults and immatures (to the experienced eye). In spring we use the same characters as in autumn though more attention is required because of feather abrasion. Sexing juveniles before post-juvinal moult is possible by measuring the length of black (dark) marking along the shaft on the fifth tail-feather (numbered ascendently): the length ranges from 10 to 21 (on average 16.1) mm in juvenile males and from 17 to 28 (on average 21.7) mm in juvenile females (Payevsky 1976). To analyse age and sex structure within different seasons I calculated average proportions from values obtained in each decade of the study period.

I used FRIEDMAN's test for randomized blocks (HOLLANDER & WOLFE 1973) to check homogeneity of bird distributions between years. Based on data for years with greatest numbers of recoveries (1960, 1965–1968, 1971 and 1973) I found no annual differences in the proportions of recoveries when these were grouped into 4 latitudinal ranges: 36–42°, 43–44°, 45–48° and 49–53° ($\chi^2 = 1.07$, df 6, $p > 0.05$). I therefore pooled all years for analysis of geographical distribution of age and sex classes during winter.

The distance between ringing and recovery locations and the direction of migration were calculated using the method introduced by BEKLOVA (1978). The hypothesis on differential winter distribution of sex and age classes was tested by comparison of the distances between ringing and recovery locations using one-way ANOVA test (ZAYTSEV 1984). The direction of migratory movements of each age and sex group were analysed by calculation of the average azimuth and their comparison by WATSON-WHEELER test (BATSCHLET 1965).

Unfortunately I could not use the estimators of survival rates which are based on real biological assumptions (BROWNIE et al. 1985), because the recovery rates of Siskins are very low. Therefore I used three variations of life table analysis for survival estimations. The method of HALDANE (1955) in its variation by MARTIN-LÖF (1961) which is based on the principle of maximum likelihood was used for the data of 1972–1983 (311 recoveries from 67240 birds ringed). For a comparison of the results I also used for the same years the method developed by BALHAM and MIERS (CAUGHLEY 1977). Moreover for the years from 1957 to 1987 I used the method of LACK, described in detail by PAYEVSKY (1985).

3. Results

3.1. Sex and age structure

The average data on sex and age ratios are shown in Table 1, and the change in the proportions of adult and immature Siskins in migrating flocks are shown in Fig. 1. In adults, ♂ significantly outnumbered ♀ both in spring ($\chi^2 = 565.4$; $p > 0.001$) and in autumn ($\chi^2 = 2168.8$; $p < 0.001$), and ♂ were also more numerous in juveniles during summer ($\chi^2 = 10.9$; $p < 0.001$), in immatures during autumn ($\chi^2 = 111.6$; $p < 0.001$), and in yearlings during spring ($\chi^2 = 35.4$; $p < 0.001$). Average

Table 1: Age and sex structure during 1972–1987. – Altersstruktur und Geschlechterverteilung von 1972–1987.

Parameters	April–May	June–August	September–October
Numbers trapped			
All years	18 250	2717	57 614
Annual variation	165–3569	4–824	201–9167
Percentage of adults			
In males Average	30.9 ± 0.5	–	21.3 ± 0.2
Annual variation	15.5 – 42.9	–	8.9 – 37.7
In females Average	26.1 ± 0.5	–	18.1 ± 0.2
Annual variation	14.6 – 44.2	–	7.3 – 31.5
Pooled data Average	28.7 ± 0.3	–	19.6 ± 0.2
Annual variation	15.8 – 42.2	–	8.2 – 34.9
Percentage of males			
In adults Average	58.8 ± 0.7	–	59.7 ± 0.5
Annual variation	44.3 – 65.9	–	51.3 – 68.8
In immatures (yearlings in spring) Average	52.2 ± 0.4	–	52.2 ± 0.2
Annual variation	45.7 – 58.4	–	47.6 – 54.3
In juveniles Average	–	53.2 ± 0.9	–
Annual variation	–	48.5 ± 55.7	–
Pooled data Average	55.5 ± 0.4	–	53.2 ± 0.2
Annual variation	45.1 – 59.4	–	49.9 – 56.6

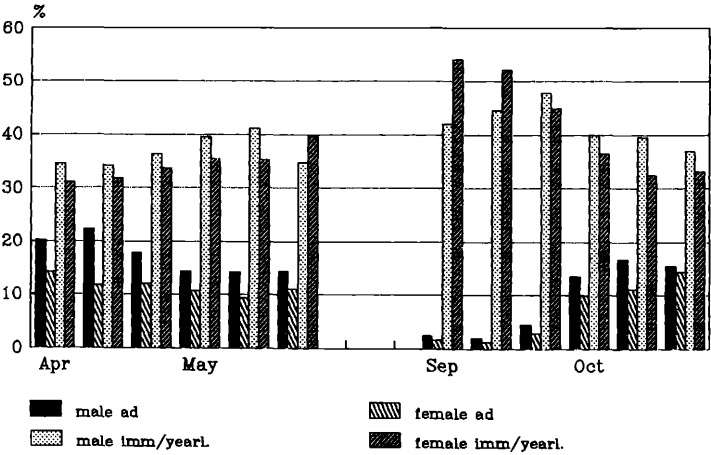


Fig. 1: Changes in age and sex structure during spring and autumnal migrations (pooled data for 1972–1987). Abscissa: decades from 1 April in spring and from 29 August in autumn; Ordinate: percentage of birds of each sex/age class.

Abb. 1: Unterschiede in der Altersstruktur und im Geschlechterverhältnis zwischen Frühjahrs- und Herbstzug (Daten der Jahre 1972–1987).

proportions of adults are significantly higher in ♂ than in ♀ both during spring ($\chi^2 = 50,6$; $p < 0,001$) and during autumn ($\chi^2 = 92,7$; $p < 0,001$). Proportions of adults in spring are significantly higher than in autumn both in ♂ ($\chi^2 = 932,1$; $p < 0,001$) and in ♀ ($\chi^2 = 258,2$; $p < 0,001$).

The proportions of adult birds during the period of spring migration (Fig. 1) significantly decrease both in ♂ ($r = -0,88$; $df\ 4$, $p < 0,05$) and in ♀ ($r = 0,79$; $df\ 4$, $p = 0,05$). The increase in the proportions of yearling birds in spring is significant only for ♀ ($r = 0,95$; $df\ 4$, $p < 0,001$).

The opposite trend takes place during the period of autumn migration (Fig. 1). The proportions of adult birds gradually and significantly increase from beginning to the end of autumn migration both in ♂ ($r = 0,93$; $df\ 4$, $p < 0,01$) and in ♀ ($r = 0,95$; $df\ 4$, $p < 0,001$), whereas the proportions of immature birds in this period decrease significantly only in ♀ ($r = -0,96$, $df\ 4$, $p < 0,001$).

In some years the spring migration of Siskins has developed into summer migration. During such migrations in May, June and July the Siskins often fly in northern directions and are caught in the traps for spring migrants. The flocks often consist of adult and juvenile birds, moreover, many adult and yearling ♀ have brood patches in the stage of postbreeding development. The first ♀ with brood patches usually appear at the end of April. In the years 1984–1987 the proportions of ♀ with brood patches during summer varied annually from 22.6% to 90.7% in adult birds (308 ♀ trapped) and from 34.7% to 85.9% in yearling birds (1230 ♀ trapped).

3.2. Winter distribution of age/sex classes

The distances migrated by the Siskins between the ringing site at the Courish Spit and recovery sites are shown in Fig. 2. It has been found that average distances in different months for all birds from October to March are: 1240, 1414, 1538, 1540, 1467 and 1240 km. The distances in adjacent months (i. e. between October and November, November and December and so on) were compared using F-test of FISHER testing the hypothesis that the lack of significant difference between the distances implies a cessation of migrational movements in these months. It has been found that an insignificant difference only occurs between distances in December and January ($F = 0,6$; $df\ 130$ and 76 , $p > 0,05$), therefore it must be assumed that the grounds of the recoveries in these months are the winter quarters of the population in question (average distance 1539 km from the Courish Spit).

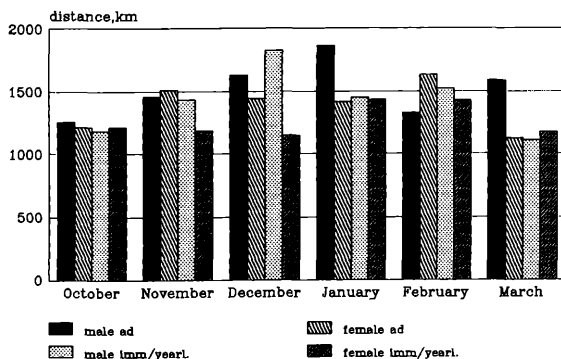


Fig. 2: Average distance between ringing and recovery locations from October to March in 1957–1989 (years pooled; direct and indirect recoveries pooled).

Abb. 2: Durchschnittliche Entfernung zwischen Beringungs- und Wiederfundort von Oktober bis März (Daten der Jahre 1957–1989).

One-way ANOVA test was used to determine differences in the distances moved by the respective sex and age classes and in the average azimuths of these classes. In spite of examples of some longer migration of the ♂ as compared to ♀, there is no significant difference between the distances of the sex and age classes, both in all autumn and winter months ($F = 1,3$; df 5 and 30, $p > 0,05$) and in December and January only ($F = 2,3$; df 5 and 6, $p > 0,05$). The average azimuth (calculated by the method of BATSCHELET 1965) for all birds in each month slightly changed from

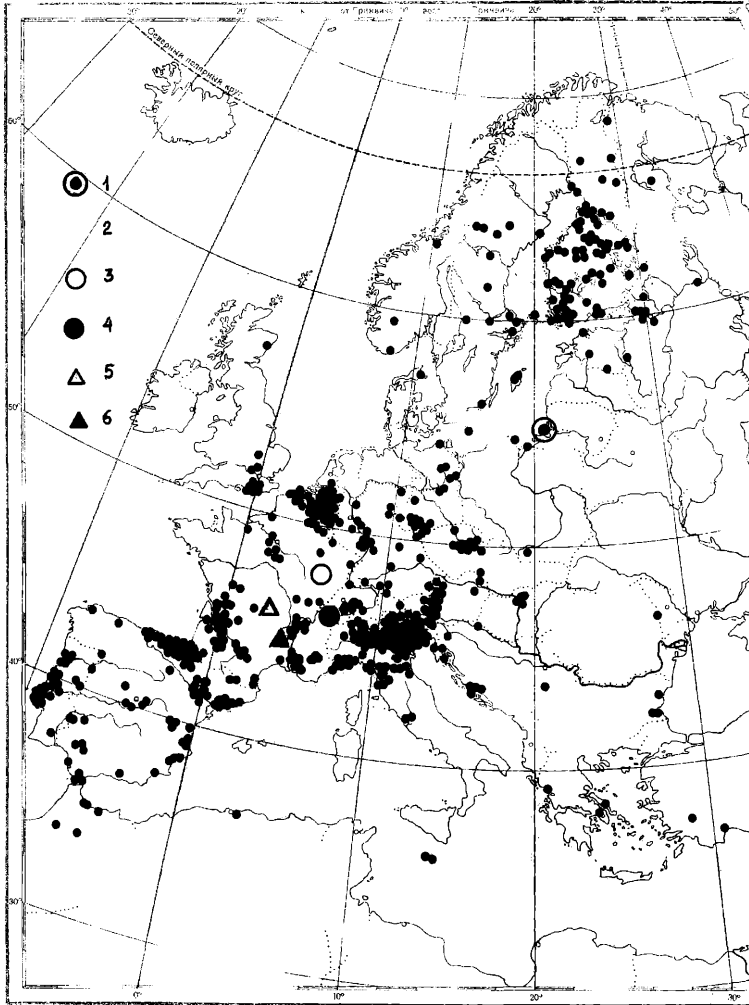


Fig. 3:

General pattern of recovery distribution of the Siskins migrating through the Courish Spit, and the average points of wintering grounds in December and January for the different age and sex classes, obtained by calculation of average distance and average azimuth. 1 – place of ringing, 2 – point of recovery, 3 – average wintering point for ♀ imm, 4 – same for ♀ ad, 5 – same for ♂ imm., 6 – same for ♂ ad.

Abb. 3:

Wiederfundkarte von auf der Kurischen Nehrung beringten Erlenzeisigen mit Kennzeichnung des jeweils mittleren Wiederfundortes im Dezember und Januar getrennt nach Geschlecht und Alter.

218° in October to 231° in March. No significant differences were found in average azimuths of migration in any age and sex group ($F = 2,0$; df 5 and 30, $p > 0,05$). The comparison of average azimuths of ♂ and ♀ (pooled data) by WATSON-WHEELER test (BATSCHELET 1965) also yielded no difference ($F = 1,4$; df 1 and 10, $p > 0,05$). Nevertheless the average distances and average azimuths for each age and sex group of the Siskins in mid-winter, namely December and January, are the basis for the outlined geographical pattern of winter age and sex distribution in the species against a background of general pattern of the recoveries (Fig. 3).

3.3. The survival of the Siskins

The survival estimation produced by each of the methods used is given in Table 2. The difference between survival rates obtained by three methods is insignificant (chi-square test with the correction for continuity, from ZAYTSEV 1984), the values of χ^2 varies from 1,6 to 3,7 at df 1, $p > 0,05$). Nevertheless, the values of annual survival rates from 42 to 48% agree more with other annual survival estimations for this species which are in the range 38–44% (PAYEVSKY 1974, ASENSIO & CARRASCAL 1990), except 30% obtained by ERIKSSON (1970). No significant differences are found in the annual survival between ♂ and ♀ (χ^2 varies from 0,1 to 0,8) and between adult and immature birds (χ^2 varies from 0,2 to 0,6), although the survival rate of adult birds is slightly higher than of immatures.

Table 2: Survival rates as calculated by different methods. – Überlebensrate, kalkuliert mit Hilfe verschiedener Methoden.

Methods	Annual survival rate (in %)			
	adult males	immature males	adult females	immature females
BALHAM and MIERS (in: CAUGHLEY 1977)	59.1 ± 7.0	53.0 ± 4.0	64.4 ± 7.9	56.3 ± 4.9
MARTIN-LÖF 1961	47.6 ± 7.4	44.9 ± 4.2	44.6 ± 8.5	42.4 ± 5.1
LACK (in: PAYEVSKY 1985)	43.2 ± 2.8	–	42.1 ± 3.3	–

4. Discussion

The results show that the age structure of the migrating populations varies with time during periods of trapping: the proportions of adult birds decrease gradually during spring and increase during autumn, suggesting that on average the adults fly earlier in spring and later in autumn as compared with immatures (yearlings). The proportions of adults in spring are higher than in autumn and the ♂ outnumbered ♀ both among adults and immatures and both in spring and in autumn, but no differences were found in the survival between age and sex classes.

The available data are not sufficient to support the assumption that the pattern of winter distribution of the Siskins results from the distances travelled from the breeding grounds, but I consider that this is the case. The Siskins are highly flocking birds and any geographical differences in winter distribution by sex and age may exist only with permanent changes of membership in flocks; however such behaviour is too costly to this species (SENAR et al. 1990a). In spite of some examples of significant differences in migration distances between age/sex groups, as a whole there were no differences between the sexes and ages, neither in distance between ringing and recovery locations nor in the direction of migration.

Table 3: Wing lengths and body mass from 15 September to 15 October 1983* – Flügellänge und Körpermasse vom 15. September bis 15. Oktober 1983.

	Wing length (mm)			Body mass (g)		
	range	$\bar{x} \pm \text{SE}$	t**	range	$\bar{x} \pm \text{SE}$	t**
All males, n = 1002	67–77	72.83 \pm 0.05	25,61	10.0–16.6	12.58 \pm 0.04	7.42
All females, n = 813	67–76	70.83 \pm 0.06		10.0–15.4	12.16 \pm 0.04	
Adult males, n = 194	69–77	73.44 \pm 0.11	6.46	10.4–15.5	12.42 \pm 0.07	2.60
Immature males, n = 808	67–77	72.66 \pm 0.05		10.0–16.6	12.63 \pm 0.04	
Adult females, n = 124	68–76	71.31 \pm 0.13	3,98	10.5–14.3	12.15 \pm 0.07	0.12
Immature females, n = 689	67–76	70.74 \pm 0.06		10.0–15.4	12.16 \pm 0.04	

* Wing length is the distance between the carpal joint and the tip of the longest primary, measured with an accuracy of 1 mm, with the wing flattened and straightened. The weighings are made to 0.1 g.

** Student's t-test between sexes and between age groups.

Many studies of birds, and finches in particular, show that ♂ winter north of ♀ (KING et al. 1965, KETTERSON & NOLAN 1976, PAYEVSKY 1985, PRESCOTT & MIDDLETON 1990). There are several hypotheses which have been proposed to explain age and sex differences in winter distribution: (1) the social dominance hypothesis suggests that more dominant birds (♂ and adults) can cause subordinate birds (♀ and immatures) to migrate beyond the distribution of the dominant birds to sub-optimal territories to avoid competition (KETTERSON & NOLAN 1979, GAUTHREAUX 1982); (2) the arrival time hypothesis suggests that intrasexual selection favors ♂ that arrive earlier on the breeding grounds to defend them and thus selects for wintering closer to nesting places; (3) the body size hypothesis suggests that body size can influence survival in both juvenile and adult birds because the greater cold tolerance leads the larger sex to winter in colder and more unpredictable conditions. These hypotheses are not mutually exclusive and the pattern of winter distribution of each species obviously results from interaction among all proposed mechanisms (KETTERSON & NOLAN 1979, 1983; MYERS 1981, RAMOS 1988).

As in many other birds the Siskin ♂ are socially dominant over ♀ (SENAR et al. 1990b) and adults dominate over immatures. On evidence derived from measurements of the Siskins at our ringing station, the wing lengths and body mass of ♂ are larger than of ♀, and adults are longer-winged than immatures but not heavier (Table 3). These data are consistent with the hypotheses but the absence of significant difference in the winter quarters of age/sex groups is inconsistent with the hypotheses.

The immatures should, in general, suffer higher mortality than adults, and ♀ should suffer higher mortality than ♂ (PAYEVSKY 1985, BREITWISCH 1989). KETTERSON & NOLAN (1983) proposed that higher ♀ mortality due to longer migration is offset by higher ♂ mortality due to harsher conditions of wintering and the result is a sex ratio of unity. Our results show a higher proportion of adults in ♂ than in ♀ both during spring and autumn. This is probably a result of higher mortality in ♀ but the difference in annual survival rates between ♂ and ♀ is insignificant.

In conclusion it may be said that the lack of distinct sex and age differences in all aspects of winter biology of the Siskins is probably attributable to the pronounced gregariousness of this species, and that the flock of Siskins is exposed to environmental factors as a unit.

Zusammenfassung

Altersstruktur, Geschlechterverteilung, Mortalität und räumliche Verbreitung im Winter bei Erlenzeisigen (*Carduelis spinus*) mit Zugweg durch das östliche Baltikum.

Aus Fang- und Beringungsdaten von Erlenzeisigen, die zwischen 1957 und 1987 über die Kurische Nehrung in der Ostsee zogen, wurde die Winterverbreitung der Geschlechter und Altersgruppen ermittelt. Bis 1991 ergaben insgesamt 149 378 beringte Zeisige 1156 Wiederfunde (0,77%). Trotz einiger Fälle von unterschiedlich langen Zugstrecken bei einigen der untersuchten Gruppen gab es weder hinsichtlich der Entfernung noch hinsichtlich der Zugrichtung signifikante Unterschiede zwischen Geschlechtern oder Altersklassen. Die Zahl der ♂ überwiegt gegenüber den Zahlen adulter (59,7%) und immaturer (52,2%) ♀. Bei der jährlichen Überlebensrate, die im Bereich zwischen 42 und 47% variiert, wurden keine Unterschiede zwischen ♂ und ♀ oder zwischen adulten und immaturren Vögeln gefunden. Diese Ergebnisse werden unter 3 Hypothesen diskutiert, die zur Erklärung der Ursachen für unterschiedliches Zugverhalten entwickelt wurden. Die Ergebnisse stützen diese Hypothesen nicht, was möglicherweise durch die Bildung großer Schwärme beim Erlenzeisig erklärt werden kann.

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