

Age structure of passerine migrants at the eastern Baltic coast: the analysis of the “coastal effect”

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Abstract

The trapping data of 12 migrant passerine species comprising more than 1,025,000 birds were used to determine age structure of migrants. The data were collected at the Courish Spit of the Baltic Sea during 1972–1995. Six species which are predominantly nocturnal migrants showed the “coastal effect”, that is a disproportionately high percentage of immature birds, as opposed to diurnal migrants. The comparison of these results with the data

from other studies in the Baltic region incline us to think that the coastal effect is caused by differential behaviour of adults and immatures during landfall after a nocturnal flight over large bodies of water.

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Introduction

Various studies of autumn passerine migration in North America have shown that the proportion of young birds captured at coastal sites is significantly higher (85–95 %) than at inland sites (65–75 %) in all species of nocturnal migrants (Drury & Keith 1962, Murray 1966, 1976, Ralph 1971, 1978, 1981, Stewart et al. 1974, Dunn & Nol 1980). This phenomenon has been termed the “coastal effect” by Ralph (1978). Several hypotheses have been proposed by these authors to explain the cause of the effect. The hypotheses are primarily based on different behaviour of adult and young birds during the migratory flight and landfall.

In Europe, however, in spite of many studies of bird migration (Alerstam 1990), and very intensive bird trapping, data on the coastal effect are available only in a few papers (e.g. Evans 1968, Jenni 1984). I have also myself already touched on the coastal effect at the eastern Baltic coast (Payevsky 1982, 1985). The continued massive bird trapping at the Courish Spit at the southeastern corner of the Baltic Sea now provides much more data on the age and sex ratio of migratory birds. This enables a more detailed analysis of the coastal effect in the Baltic region. The ringing recoveries show that the migra-

tory birds belong to populations from Finland, parts of Sweden, north-western Russia and the eastern Baltic States (Payevsky 1973).

The aims of this paper are as follows: (1) to present the data on age structure of passerines during autumn and spring migrations, (2) to show the differences of age ratios between diurnal and nocturnal migrants, (3) to consider the demographic parameters of the populations in question, and (4) to discuss the fitness of our data to the proposed hypotheses.

Material and methods

Birds have been trapped and ringed from 1957 by the staff of the Biological Station Rybachy of the Zoological Institute at a permanent field station “Fringilla” located 12 km south of Rybachy at the Courish (or Curonian) Spit (formerly German Kurische Nehrung now in Russian Kaliningrad region). The spit is a strip of land, separating the Courish Bay from the Baltic Sea; the width of the spit varies between 0.4 and 3.7 km. The spit stretches from northeast to southwest which coincides with the main directions of bird migration in the region.

The birds were caught in the “Rybachy-type traps”.

Table 1. Average percentages (\pm SE) of adult birds among passerines caught at the Courish Spit during 1972–1995. Figures in parentheses are annual range. Seasons with less than 20 specimens of every sex are excluded from the calculations.

Genomsnittlig procent (\pm SE) adulta fåglar fångade vid Kurskaja Kosa under åren 1972–1995. Siffror inom parentes visar spridningsintervallet. Säsonger med färre än 20 fåglar av varje kön har uteslutits från beräkningarna.

Species <i>Art</i>	Totals caught <i>Summa fångade</i>	Autumn <i>Höst</i>			Spring <i>Vår</i>		
		Males <i>Hanar</i>	Females <i>Honor</i>	Unsexed <i>Obest.</i>	Males <i>Hanar</i>	Females <i>Honor</i>	Unsexed <i>Obest.</i>
Mainly nocturnal migrants							
<i>Huvudsakligen nattflyttare</i>							
Willow Warbler <i>lövsångare</i> <i>Phylloscopus trochilus</i>	85990* (632–8649)	–	–	3.0 \pm 0.2 (1.8–5.5)	–	–	–
Goldcrest <i>kungsfågel</i> <i>Regulus regulus</i>	232240 (524–37324)	3.4 \pm 0.4 (1.2–8.4)	4.3 \pm 0.5 (1.7–8.6)	–	6.9 \pm 0.8 (1.0–15.8)	7.6 \pm 0.7 (4.6–16.9)	–
Redstart <i>rödstart</i> <i>Phoenicurus phoenicurus</i>	1907*, ** (21–161)	6.1 \pm 2.1 (3.0–10.6)	–	–	–	–	–
Robin <i>rödhake</i> <i>Erithacus rubecula</i>	40021 (600–4115)	–	–	8.2 \pm 0.7 (2.4–13.7)	–	–	18.1 \pm 0.8 (12.0–25.8)
Blackbird <i>koltrast</i> <i>Turdus merula</i>	2955 (34–245)	11.9 \pm 1.0 (3.7–22.7)	14.2 \pm 1.4 (3.9–23.2)	–	31.8 \pm 6.4 (4.3–52.0)	35.0 \pm 3.7 (14.8–47.6)	–
Song Thrush <i>taltrast</i> <i>Turdus philomelos</i>	11544 (92–1496)	–	–	6.5 \pm 0.7 (0.0–17.5)	–	–	19.2 \pm 1.9 (0.0–33.8)
Mainly diurnal migrants							
<i>Huvudsakligen dagflyttare</i>							
Blue Tit <i>blåmes</i> <i>Parus caeruleus</i>	41478* (109–5229)	8.9 \pm 1.1 (1.6–22.0)	14.4 \pm 1.2 (2.6–30.8)	–	–	–	–
Great Tit <i>talgoxe</i> <i>Parus major</i>	116867 (1049–10455)	12.9 \pm 1.6 (5.6–38.5)	13.3 \pm 1.3 (6.5–33.5)	–	21.5 \pm 2.2 (5.9–44.7)	16.3 \pm 1.8 (6.5–36.2)	–
Chaffinch <i>böfink</i> <i>Fringilla coelebs</i>	385585 (3066–45641)	40.5 \pm 1.9 (26.0–63.3)	42.9 \pm 1.9 (28.3–63.2)	–	42.6 \pm 1.9 (28.5–65.6)	43.4 \pm 1.8 (28.4–64.9)	–
Brambling <i>bergfink</i> <i>Fringilla montifringilla</i>	17893** (38–1880)	35.2 \pm 2.1 (18.7–58.5)	–	–	42.1 \pm 2.6 (27.3–70.2)	–	–
Siskin <i>grönsiska</i> <i>Carduelis spinus</i>	87596 (722–10116)	22.4 \pm 1.5 (8.9–37.7)	18.9 \pm 1.2 (7.3–31.5)	–	32.2 \pm 2.0 (15.1–59.6)	26.0 \pm 1.9 (9.8–52.3)	–
Bullfinch <i>domherre</i> <i>Pyrrhula pyrrhula</i>	3751* (57–571)	33.8 \pm 4.3 (13.5–77.8)	21.0 \pm 3.0 (9.9–50.8)	–	–	–	–

* Autumn only *endast höst*, ** Males only *endast hanar*

These traps, resembling the Heligoland traps in their outward appearance, differ in having nonrigid frame, absence of a place to attract the birds and very great size: entrance width 20–30 m, height 12–15 m (detailed description in Dolnik & Payevsky 1976). The birds were trapped every year from 1 April to 1 November.

In 1957–1995 a total of nearly two million birds of 181 species were caught and ringed. The data presented below concern the migration during 1972–1995 of twelve species. Their names and trapping totals are listed in Table 1. These species have been chosen for analysis because of their abundance during both autumn and spring migration, and because they represent two types of migration, namely diurnal and nocturnal ones. The nocturnal migrants are caught mainly during their diurnal movements through the vegetation after the landing and the diurnal ones when flying into the trap on active migration. It is well known, however, that such classification is inexact, because some species can fly during day as well as during night. But by convention I have divided the species into two groups: predominantly nocturnal and predominantly diurnal migrants.

All birds captured were aged and sexed using mainly plumage colour, and specific details of wear and molt according to the methods of Svensson (1970), which subsequently were tested and somewhat supplemented by us (Vinogradova et al. 1976).

Particular attention was given to the question of how to calculate the age ratios. The problem lies in the fact that European passerines of different age and sex tend to migrate in different terms of the season (Weigold 1926, Drost 1935, Payevsky 1985). However, the numbers of birds trapped in different days and periods are different, and the periods with great numbers give the main contribution to the average ratio. To avoid temporal bias I have tried to uniform the distribution of the data for the whole time of migration. For this purpose I have calculated the age and sex structure within separate seasons by the average proportions of values obtained in each five-day period. If the numbers caught in five days were less than 20 birds, the adjacent five days periods were pooled. It must be emphasized that the range of the difference between percentage value for the total number in the whole season and an average obtained from a number of values representing five days periods varied between years. For example, the difference of these averages was insignificant for the Robin in autumn 1990 (6.5% and 6.3%), but significant for this species in autumn 1981 (11.5% and 13.5%).

Statistical analysis was carried out by standard methods (Sokal & Rohlf 1981, Hollander & Wolfe 1973). Significant difference refers to probability level of 5% or higher.

Results

The average age and sex ratios are given in Table 1, and the detailed data for both autumn and spring during each year are shown in Figure 1. The distribution-free Friedman's test for randomized blocks was used to check homogeneity of the age-ratio distribution between species and between years as class variables. With average proportions of adult birds for each species during each year I found that the age-ratios did not differ between years ($\chi^2 = 9.75$, $df=23$, n.s.), but differed significantly between species ($\chi^2 = 233.46$, $df=11$, $p < 0.001$).

I have also calculated the total averages for all diurnal migrants and for all nocturnal ones, that is pooled data for both sexes of every species from all five days values of all the years, including the sum from the seasons when the numbers caught were less than 20 birds of every sex. These total averages give a good indication of the differences in age composition (Table 2).

The proportions of adults in diurnal migrants are significantly higher than in nocturnal ones (F ϕ -test of Fisher) both during autumn (F $\phi = 54366.4$, $df 1$, $p < 0.001$) and during spring (F $\phi = 2047.9$, $df 1$, $p < 0.001$). Hence, it is safe to assume that this very high proportion of immature birds in all species of nocturnal migrants can be considered as a distinctive characteristic of them as opposed to that of diurnal migrants.

Now it needs to be ascertained if these age ratios are consistent with potential productivity of the populations in question. On the basis of published data I have attempted to estimate the average number of fledglings per pair and breeding season for nine species (Table 3). It is known that the mortality of fledglings after leaving the nest is high, whereas the mortality of adults during this period is low. Let us assume that the mortality of adults during the period between the completion of breeding and the beginning of autumn migration can be neglected. In such a situation the age ratio of 50% of adults during the autumn implies that from the young fledged per pair two birds only survive up to the start of autumn movements, and in the same manner, 40% of adults implies that three young survive per pair, 33% – four young, 25% – six young, 20% – eight young, 14% – twelve young. Table 3 shows that only the Chaffinch

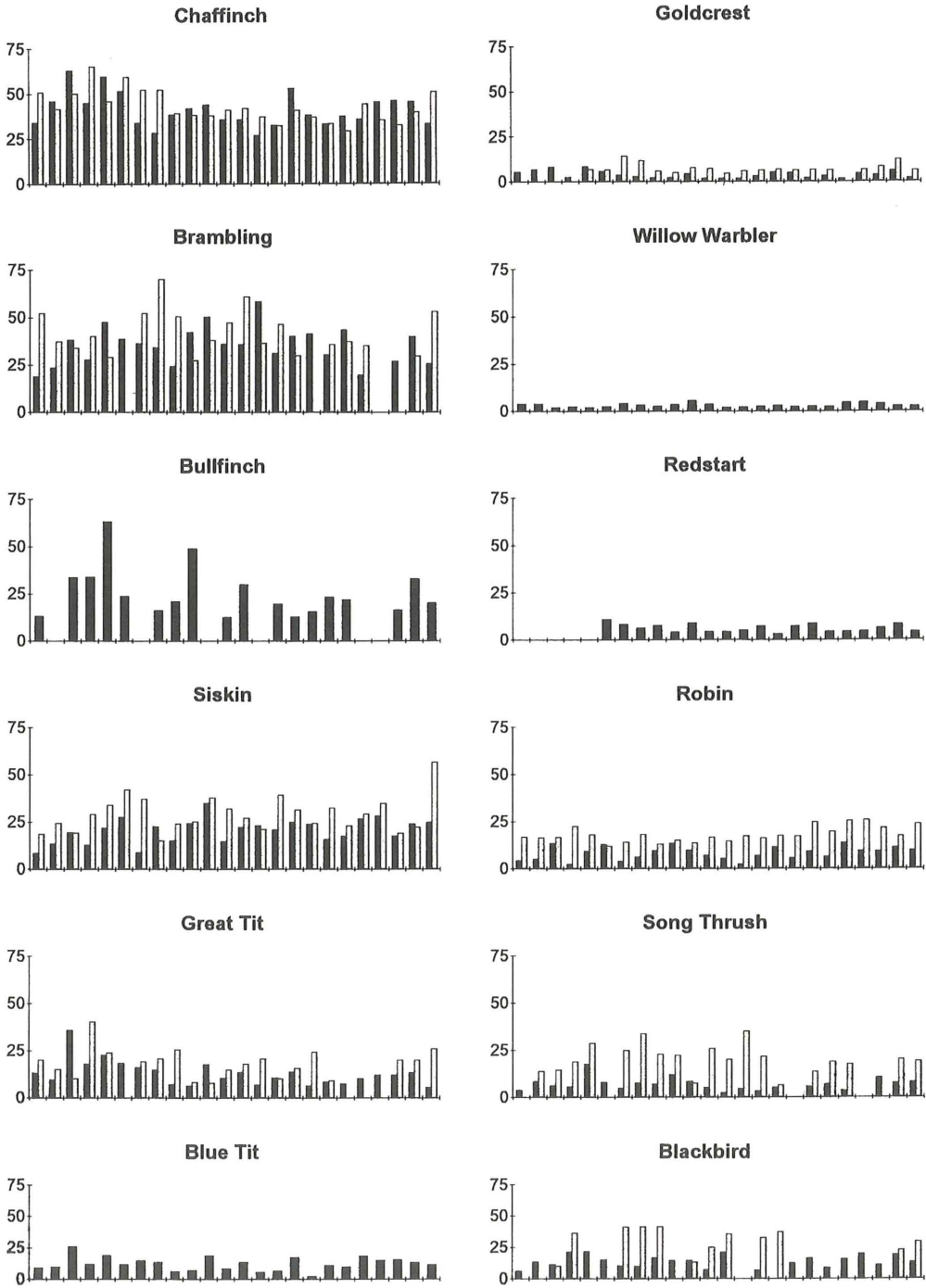


Figure 1. The percentages of adult birds trapped in 1972–1995, separately for the autumn (black) and spring (grey). For the purpose of the comparison of diurnal (on the left) and nocturnal (on the right) migrants the data are presented in equal scale. *Procenten adulta fåglar fångade åren 1972–1995, separat för hösten (svart) och våren (grått). För jämförelsen mellan dagflyttare (till vänster) och nattflyttare (till höger) visas värdena i samma skala.*

has an age ratio which is in rough agreement with the potential productivity of the population. Other species, especially the nocturnal migrants, have impossibly high percentage of immatures. The age ratios of 3–8 per cent of adults during autumn, as in the Willow Warbler, Goldcrest, Redstart, Robin, and Song Thrush, are disproportionate ratios which indicate either that the populations of these species produced from 25 to 50 young per pair (which is impossible), or that this is the result of differential behaviour of adult and immature birds.

Discussion

Thus I found that the “coastal effect”, that is, the abnormally high percentages of immature birds in the traps, is typical for species of nocturnal migrants, as opposed to the species of diurnal migrants, which have significantly lesser percentage of immatures.

First of all, consideration must be given to the supposition that the data obtained by the traps show the true pattern of age ratios in migratory birds at the Courish spit. The possibility of differential escaping from the Rybachy-type trap by adult and immature birds has been discussed elsewhere (Payevsky 1985). There is no evidence to suggest such an age bias in trapping.

Another problem is the differential timing of migration. It is common knowledge that sex and age groups of birds differ with respect to timing of migration. Males and adult birds of most migrant species precede females and first-year birds in arriving at the breeding grounds. Various differential patterns are also recorded with respect to timing of autumn migration. However, it is apparent that in order to have reliable demographic parameters from the migration data, one must take care to sample the birds throughout the entire migratory period

(Payevsky 1985, Ramos 1988). As pointed out above, our data were collected by the standard traps over a long period, the whole time of migration, and the age and sex structure within separate seasons are the average proportions from the values obtained in each five-day period.

It is well known that certain species are neither completely resident nor completely migratory. Some populations show age and sex differences in migration: some birds migrate in the autumn, while the rest of the population remains resident for the winter. In the Goldcrest in Finland, as an example, the proportions of residents and migrants are about equal, and young birds clearly predominate among the migrants (Hildén 1982). The populations of Great Tit and Blue Tit also show age and sex differences of migratory behaviour with significant correlation between the number of migrating immatures and males, on the one hand, and on the other, the total population number (Frelin 1971, Hildén 1978, Heldbjerg & Karlsson 1997). Among the nocturnal migrants it is only in the Goldcrest, and maybe to some extent in the Blackbird, that one would expect increased proportion of young for the reason of greater residence of adult birds than because of the coastal effect. For the diurnal migrants the predominance of young birds for that reason is most probable for the Great Tit and Blue Tit.

The hypotheses which have been advanced to explain the coastal effect can be summarized as follows. Drury & Keith (1962) suggested the following alternatives: (1) the adults have a tendency to move on courses which keep them over the mainland, (2) the concentration of immatures upon the coast results from their indecision while adults unhesitatingly strike out across the water. Murray (1976) believes that at the end of a nocturnal flight over the ocean young birds land at the first available

Table 2. Comparison of mean proportions (%) of adult birds in diurnal and nocturnal migrants of all species studied. *Jämförelse mellan medelproportionen (%) adulta fåglar hos dag- och nattflyttare för alla studerade arter.*

Type of migrants <i>Typ av flyttare</i>	Per cent of adult birds* <i>Autumn Höst</i>	<i>Procent adulta fåglar*</i> <i>Spring Vår</i>
diurnal <i>dagflyttare</i>	27.70±0.06	33.13±0.02
nocturnal <i>nattflyttare</i>	6.93±0.04	18.87±0.26

* Calculated from all the values of all the years 1972–1995, representing pooled data for all the birds trapped. *Beräknade på alla värden från alla åren 1972–1995, representerande sammanslagna data för alla fångade fåglar.*

Table 3. The average productivity of migratory populations in the region of their breeding.
Genomsnittlig produktion av ungar för flyttande populationer i sina häckningsområden.

Species and area	Per cent of pairs with second breeding	Size of first clutch	Ratio of fledglings to eggs laid	Source of the data	Number of fledglings per pair per season*
<i>Art och område</i>	<i>Procent par med två kullar</i>	<i>Storlek av första kull</i>	<i>Andel flygga av lagda ägg</i>	<i>Källa</i>	<i>Antal flygga ungar per par och säsong*</i>
Willow Warbler, Karelia, NW Russia	0	6.13	0.89	Lapshin 1993	4.64
Goldcrest, Fennoscandia	~70	9.80	~0.64	Haftorn 1978a,1978b	8.39
Redstart, Kilpisjärvi, Northern Finland	0	6.42	0.77	Hildén et al. 1982	4.20
Robin, South Karelia, NW Russia	61	6.43	0.78	Zimin 1988	6.39
Blackbird, South Karelia, NW Russia	~20	4.31	0.53	Khokhlova 1988	2.26
Song Thrush, Leningrad region, Russia	~22	4.76	0.47	Malchevsky & Pukinsky 1983	2.24
Blue Tit, Finland	12	10.00	0.92	Haartman 1969, and Hilden et al. 1982	8.62
Great Tit, Askainen, SW Finland	20	9.90	0.81	Haartman 1969	7.93
Great Tit, near St. Petersburg, Russia	28	11.00	0.71	Smirnov & Tiurin 1981	8.16
Chaffinch, South Karelia, NW Russia	0	4.86	0.65	Zimin 1988	2.69

* The calculations were performed with regard to the following approaches (Payevsky 1985): a) on the average for Passerines, the size of normal second clutch consists of 0.82 from the size of first clutch, b) on the average for twenty common species of Passerines, the breeding success estimated by the most plausible Mayfield' method (Mayfield 1975) consists of 0.85 from the values calculated by the traditional method (that is, the ratio of fledglings number at successful nests from all eggs laid).

Beräkningarna utfördes på följande sätt (Payevsky 1985): a) andrakull för tättingar är i genomsnitt 0,82 av förstakull, b) i genomsnitt för tjugo vanliga tättingar är häckningsframgången uppskattad med Mayfields metod (Mayfield 1975) till 0,85 av värdet som beräknats med den traditionella metoden (d.v.s. andelen flygga av lagda ägg i framgångsrika bon).

landfall, whereas adults fly farther inland. Ralph (1978,1981) has suggested that the coastal effect reflects concentrations of young with lack of some navigational capabilities because the coast is the edge of the regular overland route of most species; many young birds probably perish in the ocean. Dunn & Nol (1980) suggest that immatures are more likely than adults to turn back to the nearest land when finding themselves over water at the end of a

migratory flight, and/or are more likely to hesitate at starting off over the water.

Ideally, to study the coastal effect, one should compare the trapping data from the coast with similar data from inland, as with birds in North America (Dunn & Nol 1980, Ralph 1981). Unfortunately, for us it is impossible, because all ringing stations in the eastern Baltic are located on the Baltic coasts. It is my opinion that our data about the coastal effect best

support the hypothesis of different behaviour of adults and immatures at the end of a nocturnal flight: the immatures drop into the first available land, whereas the adults fly farther inland. Theoretically, of course, there is the possibility of different behaviour after a simultaneous landfall: the immatures move, whereas the adults don't. However, I have no evidence in support of such an hypothesis. In either case, the Courish spit is a small piece of land, and if the young birds, as distinct from the adults, at once finished their nocturnal flight as soon as they see the land in the sea, one might expect increased concentration of young birds on this land, and correspondingly, in the traps.

If the above logic is valid, it is reasonable to suppose that there are bound to be rare days (nights) when the landfall of the adults and immatures is simultaneous because of some peculiar atmospheric events. Actually, the analysis of results of trapping for every day shows the following. During the autumn there are some days with unusually normal percentage of the adult birds in nocturnal migrants: 13.8% (n=52) in the Willow Warbler, 23.2% (n=86) in the Robin, 21.6% (n=47) in the Song Thrush, and 22.4% (n=134) in the Goldcrest.

It should be particularly emphasized that during the high nocturnal overwater flight in the Baltic the birds have normal age ratios. Such is the case for the extensive findings of dead birds smashed against the lighthouses in Denmark: 26% of adult birds in the Willow Warbler, 24% in the Robin, 24% in the Redstart, and 35–40% in the thrushes (Hansen 1954). The comparison of these data with our results provides reason enough to consider that the hypothesis about the different behaviour of the adults and immatures during landfall is correct.

In conclusion, I would suggest that the coastal effect may have peculiar features in each species or population of nocturnal migrants, and it is not to be supposed that all birds are identical in this respect.

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Sammanfattning

Åldersstrukturen hos flyttande tättingar vid Östersjöns ostkust: analys av "kusteffekten"

Studier av flyttande tättingar i Nordamerika har visat att proportionen ungfåglar är signifikant högre

på kustlokaler än på inlandslokaler bland alla nattflyttare. Detta fenomen har benämnts "kusteffekten" av Ralph (1978). I Europa saknas däremot en beskrivning och analys av fenomenet trots att det är välkänt bland ornitologer på kustbelägna fågelstationer.

Fångstdata från åren 1972–1995 för tolv flyttande tättingar, omfattande över 1.025.000 fåglar, användes för att bestämma åldersstrukturen. Uppgifterna insamlades av personalen på den biologiska stationen Rybachy vid en permanent märkstation "Frin-gilla" belägen 12 km söder om Rybachy (tidigare Rossitten) på Kurskaja Kosa (tidigare Kurische Nehrung) i sydöstra delen av Östersjön.

De genomsnittliga ålders- och könskvoterna ges i Tabell 1, och detaljerade data för både höst och vår visas i Figur 1. Åldersstrukturen skilde sig inte mellan åren, men skilde sig signifikant mellan arterna. Beräkningen av de totala medelvärdena för varje grupp av flyttare (d.v.s. för alla fåglar av sex arter dagflyttare och alla fåglar av sex arter nattflyttare) ger en god bild av skillnaderna i ålderssammansättning (Tabell 2). Proportionen adulta fåglar bland dagflyttarna är signifikant högre än bland nattflyttarna både höst och vår.

Med hjälp av publicerade uppgifter har det genomsnittliga antalet flygga ungar per par och häckningssäsong uppskattats för nio arter (Tabell 3). En jämförelse visar att det bara är bofinken som i fångstmaterialet visar en ålderssammansättning som är ungefär lika med den man kan vänta sig utifrån den potentiella ungfågelproduktionen. Övriga arter, särskilt nattflyttarna, har en ungfågelandel som är omöjligt hög. Ungfågelandelarna för lövsångare, kungsfågel, rödstjärt, rödhake och taltrast är så höga att de indikerar antingen en ungpåproduktion på 25 till 50 ungar per par (vilket är omöjligt) eller att de är ett resultat av olika beteende hos gamla och unga.

Kusteffekten, d.v.s. den abnormt höga andelen ungfåglar i fallorna, är alltså typisk för nattflyttare till skillnad från dagflyttare. De hypoteser som förts fram för att förklara kusteffekten sammanfattas i uppsatsen. En jämförelse mellan resultaten från Rybachy och andra studier i Östersjöområdet gör det troligt att kusteffekten orsakas av olika beteende hos gamla och unga fåglar när de upptäcker land efter en nattlig flygning över en stor vattenyta: ungfågarna faller på första bästa landområde medan de gamla fåglarna fortsätter längre inåt landet.