

Overlap between moult and autumn migration in passerines in northern taiga zone of Eastern Fennoscandia

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I studied overlap between moult and autumn migration in three passerine species, the Bluethroat *Luscinia svecica*, the Chaffinch *Fringilla coelebs*, and the Reed Bunting *Emberiza schoeniclus*, in the northern taiga zone of Eastern Fennoscandia. For this purpose, recaptures of previously marked birds were analysed. Samples of birds marked at different stages of moult were compared by the estimates of time they stayed at the capture site. Moult stages that coincide with the onset of autumn migratory movements were determined. Sex-related and annual variation in distribution of captures by moult stages is discussed together with age- and species-specific variation in the percentage of moulting individuals among migrants.

Key words: moult, autumn migration, Bluethroat, Chaffinch, Reed Bunting

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1. Introduction

Northern bird populations experience time deficit for the main portions of their annual cycle (breeding, moult, autumn migration) and adapt to such conditions by overlapping nestling and fledgling rearing with moult, and moult with autumn migration (Dolnik & Blyumental 1967, Berthold 1996, Newton 2008, Ryzhanovsky 1988a, b, Artemyev 2008).

Kandalaksha Bay of the White Sea is the northernmost area in Russia (and the northeasternmost in Europe) where mass trapping and ringing of songbirds is performed now, and where moult stages are determined as a part of ringing protocol. Moreover, a number of species are there on the northern edge of their regular breeding, where the northernmost self-sustaining populations breed. Populations that experience the greatest time deficit may be expected to show the greatest degree of moult – migration overlap (Blyumental & Zimin 1966).

When studying bird migration on the basis of ringing data, it is most important to be able to distinguish between local and transit birds. If this is not achieved, the results may be distorted. This is well illustrated by grossly biased estimates of stop-over duration that are obtained if a large proportion of local individuals is included in the sample (Schaub & Jenni 2001, Chernetsov 2010). Without good evidence that birds sampled mainly stem from transit populations, it is difficult to rely on the esti-

mates of passage phenology, physiological and behavioural parameters of migration. Therefore markers that allow exclusion of local individuals from the samples studied are most important.

The aim of this study was to analyse moulting – migration overlap in target species and formalise the identification of transient individuals. I tested the hypothesis of existence of key moulting stages during which a certain proportion of individuals start autumn migration. To achieve this, I compared parameters that reflect migratory activity in individuals of target species ringed at different stages of moulting on the basis of recaptures.

2. Study area, target species, material and methods

2.1. Study area

In this study I analysed the data collected in the Chernaya Reka village (66°31'N, 32°55'E, Fig. 1), Karelia. The village is located in a broader part of the valley of the Chernaya river near the site where it flows into the White Sea. There are ca. 45 homesteads in the village. The area is characterised by a large variety of habitats used by many passerines during postfledging movements and at migratory stopovers. Tall-grass meadows, to a varying degree damp and covered by scrub, are interspersed by steep grazed stony slopes of the river valley, and with vegetable gardens with berry and ornamental bushes and isolated groups of large trees (spruce, birch, rowan tree, alder). The overall area of semi-natural transformed landscapes of the village and its surroundings, including the park-like forests with depressed middle layer, is ca. 1 km².

The main natural habitats in the study area are closed-canopy boreal forest (of the taiga type) and bogs devoid of trees or with sparse depressed trees. Such habitats are generally suboptimal for most songbirds during the postfledging period. Patches of village-inherent semi-natural transformed landscapes are much scattered. Villages closest to Chernaya Reka with similar set of habitats (Poyakonda and Nilma) are located 11 km to the northwest and the east, respectively.

2.2. Target species

The ringing project in the Chernaya Reka village is under way since 2006. Moulting stage is routinely determined in most individuals of most common species. Target species, the Bluethroat *Luscinia svecica*, Chaffinch *Fringilla coelebs*, and Reed Bunting *Emberiza schoeniclus*, are selected because they were common in autumn captures (Table 1) and on the basis of their migration distances and directions, structure and dynamics of their ranges.

Bluethroats practically do not breed in the study area. This is confirmed by the breeding surveys during which just two singing males were recorded over the whole period of study in May and June per ca. 200 km of transect. The bulk of Bluethroats we capture are transit migrants, and our aim was to estimate the proportion of individuals that overlap moulting and migration. The Reed Bunting breeds in the study area

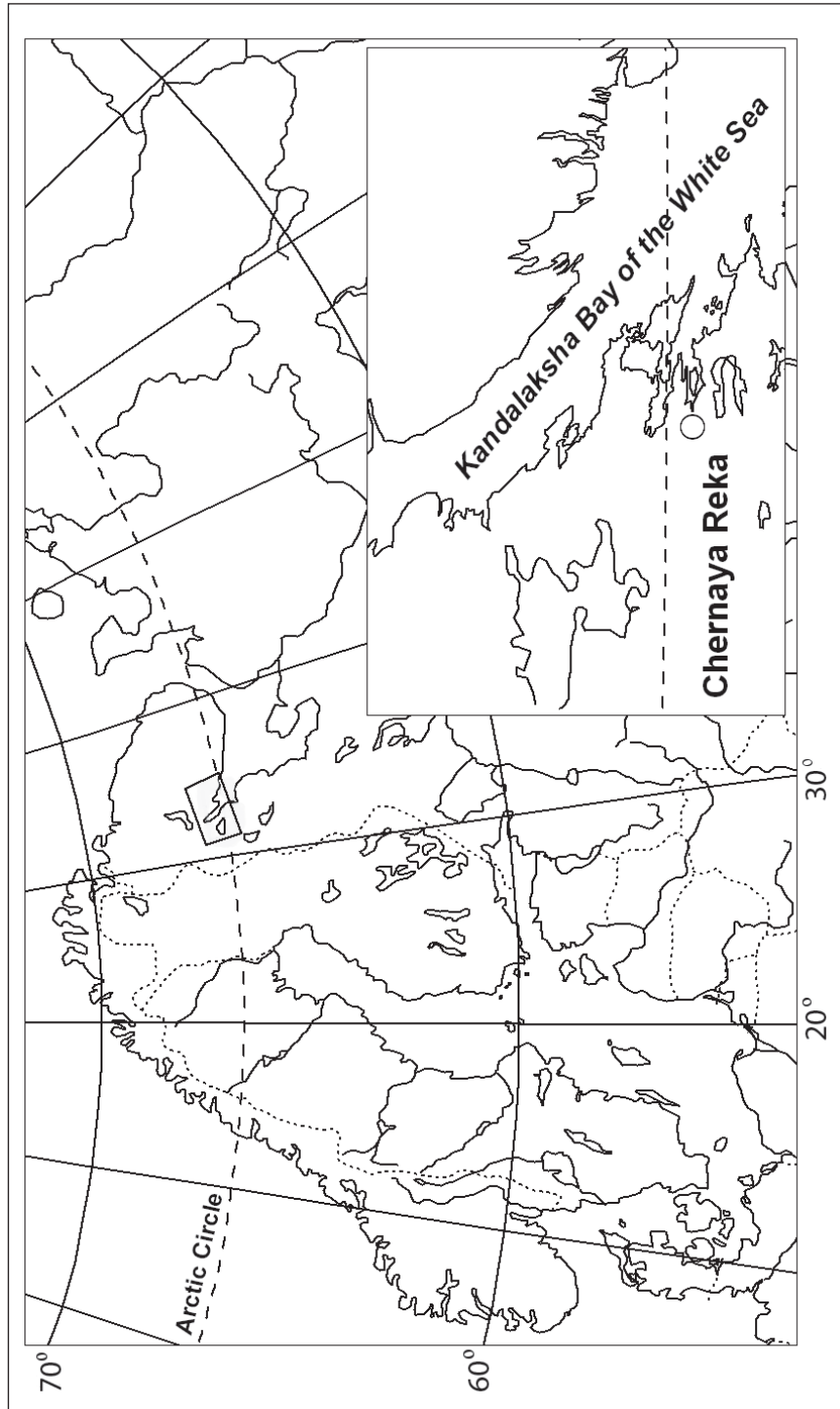


Figure 1. Study area.

Table 1. Trapping figures of the target species with moult stage recorded.

Species	Age	2006	2007	2008	2009	Total
		14.08–13.09	6.08–30.09	11.08–1.10	3.08–2.10	
Bluethroat	1st year	154	352	338	310	1154
	adult	6	57	43	29	135
Chaffinch	1st year	55	31	24	89	199
	adult	29	21	29	44	123
Reed Bunting	1st year	151	157	429	431	1168
	adult	8	17	60	49	134

sporadically, mainly along the river banks and lake shores, and does not occur in the taiga habitats. The Chaffinch has settled the polar areas in the recent 3–4 decades (Ivanter 1969, Bianchi et al. 1993, Sazonov 2004), but has become common here. Its breeding density in typical taiga habitats can locally reach 10 pairs·km² (the highest among the three target species; Panov 2003). Breeding density of the Bluethroat and Reed Bunting reaches its peak in the northernmost part of the northern taiga and in the tundra forest zones (Bianchi et al. 1993), i.e. in Lapland (northern Fennoscandia). Most individuals captured by us apparently originate from these areas.

Northern Reed Bunting and Chaffinch populations are diurnal medium-distance migrants, whereas the Bluethroat is a long-distance nocturnal migrant. The predominant direction of autumn migration in Chaffinches and Reed Buntings is the southwest. However, long-distance recoveries suggest that some Reed Buntings may move towards the south or even south-south-east (unpublished data of Ringing Centre Moscow). The Bluethroats migrate towards their winter quarters in southern Asia. All Bluethroats captured by us were red-breasted ones (the nominotypical subspecies *Luscinia s. svecica*).

2.3. Capture methods

The birds were trapped in mist-nets erected in the main habitats occurring in the village. The overall length of nets was increasing during the period of study: it was ca. 300 m in 2006 and 2007, ca. 490 m in 2008 and ca. 520 m in 2009. The area covered by the nets was also increasing and reached 20 ha in 2009. In this study we disregard the relationship between capture probability of an individual and the number of nets open. Our data shows that increasing the number of nets does not necessarily result in increasing recapture rate. This rate was more dependent on the conditions of the year and response of the birds (proportion of local birds and transients, natural variation of stopover duration etc.) than on our capture effort. In

2006–2009, recapture rate of juvenile Bluethroats after the day of marking was 29, 18, 49 and 35%, and in juvenile Reed Buntings – 18, 45, 30 and 20%, respectively.

Since 2007, song playback has been used. In 2007–2008, during the night we played the record of the Bluethroat song, in 2009 – of other turdids (European Robin *Erithacus rubecula*, Song Thrush *Turdus philomelos*, Redwing *T. iliacus*). During the day, we played the Reed Bunting song in 2008. Tape luring was conducted once per 2–3 days, so that experimental conditions were alternated with the control ones. Frequency distribution of playback days in all cases was not different from the uniform one, and song playback was performed during the whole season of mass passage of the respective species. Bluethroats are attracted by both their conspecifics song and a mix of songs of other turdids (Panov 2010, Panov & Chernetsov 2010b). When playing the Reed Bunting song, on average 16.6 juveniles per day were captured, whereas in the similar season without song playback on average 10.0 birds per day ($N = 12$, $Z = 2.14$, $p < 0.05$, Wilcoxon matched pairs test). Therefore, we analysed moult progress in birds captured under control and experimental conditions.

Ringling protocol followed Blyumental & Dolnik (1962) and Vinogradova et al. (1976).

2.4. Weather conditions, breeding success and phenology of autumn passage in individual years

In most cases we analyse the data for the four years of study pooled (Table 1). This is done to increase sample size and to average the conditions of a particular year that may be considerably different. Weather conditions influence breeding success, percentage of repeat and second clutches both directly and indirectly, through food availability. All these factors contribute to the timing of moult and mass passage. Year conditions were estimated from the weather station data in Chernaya Reka (I.V. Burkovsky, unpubl.), assuming that local weather conditions are correlated with the regional situation. Breeding success was estimated from the abundance of first-year birds captured in August and September and annual variation of the adult : juvenile ratio.

The season of 2006 was characterised by very warm and rather dry weather in the former half of summer and rather cool (close to long-time average) and dry weather in the latter half and in the beginning of autumn. Conditions during the periods of breeding, moult, and onset of migration were most favourable as compared with 2007–2009, and breeding success was the highest one. Therefore, even though we did not cover the whole season by captures in 2006 (Table 1), the results were in most cases included. Moult and migrations occurred in the average season or a little later. The integral parameter representative of autumn migration phenology was the onset of mass passage of Bluethroats that happened on 26–27 August.

June 2007 was very cool and rather wet. In July and August air temperature, conversely, was in most cases higher than average; the same was true of precipitation. Breeding success under such conditions was not high. Many individuals had to make repeat clutches, a significant proportion of which seemed to be successful. Mass passage of Bluethroats started on 24 August.

Spring of 2008 was one of the coldest and most delayed on record. Snow has not completely melted until late May, with occasional snowfalls into early June. The weather was relatively favourable only mid – late June. However, since the end of this month and during the most of July it was rather cool and very wet. In July one-third of the annual normal precipitation fell (ca. 210 mm), and in the former half of the month rain was practically continuous. Under such conditions breeding success was very low. A proportion of breeding pairs seem to have managed to raise repeat broods, resulting in very late autumn passage. The onset of mass Bluethroat passage fell on 29 August.

Weather conditions in spring and summer 2009 were close to the long-term average, with relatively warm and dry May and early June and cool and wet June and July. Breeding success was lower than in 2006 but higher than in 2007 and 2008. Very mild and rather dry September resulted in rather late end of the period of mass passage. Mass passage of the Bluethroat started on 23–24 August. The latest new capture occurred on 25 September which is the latest record of the Bluethroat in the region ever (Bianchi et al. 1993). The last recapture occurred on 30 September.

2.5. Methods of data analysis

2.5.1. Migratory activity at different moult stages

To estimate migratory activity we used capture-recapture data and calculated three parameters: (1) mean minimum duration of stay (MDS, time elapsed between the first and the last capture); (2) proportion of transients (*sensu* Pradel et al. 1997); (3) proportion of conventionally local individuals based on minimum duration of stay.

Usually time elapsed between the first and the last capture is called ‘minimum stopover duration’ (Chernetsov 2010). However, as not all birds included in our study were transit migrants, I prefer to speak of minimum duration of stay, MDS. It included both capture and recapture date, i.e. an individual captured once was assigned the MDS of one day. The word ‘transient’ is traditionally used to denote birds that make a one-day stopover in stopover studies (Pradel et al. 1997, Chernetsov 2010), it is equivalent to ‘flyers’ by Rappole and Warner (1976). For us the proportion of such transients was an additional parameter that characterised the intensity of migratory movements at different stages of moult. We also used the proportion of conventionally local birds as an estimate of participation of birds apparently of local origin in samples of birds at different moult stages. In nocturnal migrants stopover duration usually does not exceed 12–14 days (review: Chernetsov 2010). Passage of diurnal migrants is usually less structured, and their stopover duration is shorter. We considered to be ‘conventionally local’ birds that spent >12 days (for the Bluethroat) and >10 day (for diurnal migrants) in our study area.

Samples of birds marked at different moult stages (stage description see in Appendix) were compared by these three parameters. It is assumed that early (most individuals not yet migrating) and late stages (most are migrating) should not consequently differ by migratory activity parameters. Significant difference should occur at medium stages when certain proportion of birds starts migrating.

Most correct comparisons are for the birds at the same moulting stage, because at different moulting stages capture probability may be unequal, distorting the results. However, it is not infrequent that at recapture the bird is at a subsequent moulting stage. We did not compare groups of birds that have known different capture probabilities, e.g. juveniles with adults. However, this factor cannot be completely eliminated.

2.6.2. Factor that influence the duration of stay

To prove the assumption that in most cases trapping conditions (playback vs. no playback), sex and condition index (body mass corrected for size represented by wing length) had no significant impact on MDS, predictors that may influence the MDS were tested for significance by backward stepwise multiple regression, as implemented in STATISTICA 6.0 (StatSoft 2001). The following factors were tested: sex, trapping conditions, year, Julian date (progress of the season), condition index or fat score and moulting stage. As a result, the rank of significance of moulting stage for migratory activity among other factors was determined.

Table 2 shows the results of calculating backward stepwise regression for factors that significantly influenced the duration of stay, i.e. beta value (except of the year effect where significance is denoted just by the plus sign). The baseline year was 2009. For non-significant factors, just the order of their exclusion by the programme is given.

Song playback, sex and condition index were significant factors only if the whole sample of first-year Bluethroats is pooled. If the assumed local birds at early stages of moulting are excluded (these birds on average stayed for a long time and were mainly captured without playback), only progress of season and moulting stage remain significant factors. These two predictors remain significant in most cases also for other samples. Sex and condition index were excluded. In some cases year was a significant effect.

Therefore, further we treated moulting stage as the main factor that governed assessment of an individual as a local or transient. Additionally, the progress of season was considered. For this purpose, groups of birds at intermediate stages of moulting ringed in different periods were compared.

2.5.3. Frequency distribution of captures by moulting stages

We also analysed the frequency distribution of captures by moulting stages. First, we looked for sex-specific variation within one age group, for annual variation and between captures with and without tape-luring. For the latter comparison, only the data on first-year Bluethroats and Reed Buntings were sufficient.

A fraction of Chaffinches and Reed Buntings display fidelity to their breeding (moulting) locations in subsequent years. Therefore, for adults of these species we could also compare frequency distributions of captures by moulting stages in birds that were recaptured in subsequent years and in those that produced no such recaptures. We assume that most recaptured individuals were local ones, as stopover site fidel-

Table 2. Significance of factors that influenced MSD. Beta values for significant factors are given (except of the year effect where significance is shown by the + sign). For insignificant factors the sequence of their exclusion from the model is given.

Species	Sample	n	Song playback	Year			Sex	Progress of season (Julian date)	Condition index/Fat score*	Moult stage
				2006	2007	2008				
Bluthroat	All first-years	1123	-0.09±0.029	-1	+	+	0.12±0.031	-0.28±0.031	0.1±0.029*	-0.25±0.028
	First-years since moult stage IV	1112	-2	-1	+	+	-4	-0.18±0.030	-3*	-0.11±0.029
	Adults**	127	-4	-5	-1	-9	-3	-7	-8/-2*	-6
Chaffinch	All first-years	183	-	+	-2	-3	-4	-0.47±0.067	-1	-5
	First-years***	194	-	-3	-2	-1	-5	-4	-	-0.44±0.065
	All adults	121	-	+	-3	-1	-2	-4	-5	-0.67±0.07
Reed Bunting	Adults since moult stage VIII	105	-	-5	-3	-2	-7	-4	-1	-6
	All first-years	1120	-	-3	+	+	-1	-0.35±0.033	-2	-0.28±0.033
	First-years since moult stage IV	1020	-	-1	+	+	-2	-0.30±0.031	-3	-4
Bunting	First-years 2008****	391	-4	-	-	-	-2	-5	-1	-3
	Adults	130	-	-6	-5	-3	-4	-0.36±0.083	-2*	-1

Notes: * Condition index is body mass corrected for wing length as size proxy; fat score followed Blyumental & Dolnik (1962) with intermediate scores. Asterisks indicate results for the fat score as a predictor. ** Exclusion of sex and condition index does not result in significant factors. *** Without condition index, sex of some birds at the early moult stages was identified from wing length. **** Since 24 August, when tape luring experiments started. – not tested factor.

ity is extremely rare (Sokolov 1997, Chernetsov 2010). This means that migration generally occurs at later stages of moult when the proportion in birds recaptured in subsequent years significantly lower than in those that produced no such recaptures.

2.5.4. Statistical methods

The means were compared by the non-parametric Mann-Whitney test, proportions were compared by chi-square 2×2 tables (χ^2), and differences in frequency distributions by χ^2 distribution test. STATISTICA 6.0 and PAST 1.5 software packages were used.

3. Results

3.1. Reed Bunting

3.1.1. First-year birds

Our hypothesis of key moult stages was best supported by the data on first-year Reed Buntings. Sample size for this species is the greatest one (Table 3). Pairwise comparison of adjacent values showed significant difference beginning with the pair of II and III stages but more considerable difference is between III and IV stages. On the contrary, no significant difference in the values of these parameters was found between birds at moult stage VI and those with completed moult (Fig. 2, Table 4). Birds at intermediate stages of moult (IV and V) start migration in the course of autumn. Significant variation in all three migratory activity parameters were found between Reed Buntings at moult stage IV marked in August and in September. In August birds duration of stay was longer (4.09 and 1.82 days, respectively; $Z = 4.20$, $p < 0.001$) and the proportion of local individuals higher (14.7% and 2.1%; $\chi^2 = 24.3$, $df = 1$, $p < 0.001$), whereas the proportion of transients was lower (52.9% and 84.2%; $\chi^2 = 10.31$, $df = 1$, $p < 0.002$).

Birds captured at moult stage V showed no such clear-cut difference between different periods of passage. Reed Buntings captured in mid September with moult at stage IV spent even slightly less time at the study site than birds captured at moult stage V (1.46 and 2.0 days, respectively), with a higher proportion of transients (88% vs. 77%). In early September, just six buntings at moult stage III were captured, and just one of them was not a transient. Among Reed Buntings marked at stage V, the mean MDS is most different in the birds captured in mid August (5.7 days, significantly more than in late August [2.43 days]; $Z = 2.17$, $p < 0.05$; in subsequent 10-day periods of September – 2.21, 2.0 and 1.6 days).

Frequency distribution of captures by moult stages did not significantly differ between sexes (males $n = 579$; females $n = 558$; $\chi^2 = 10.6$, $df = 6$, $p = 0.10$). For two sexes in a bulk these distributions were significantly different in all three years (2007–2009) when the whole period of mass passage was covered (pairwise comparisons). In 2007, the proportion of birds captured at stages I and II was greater than

Table 3. Distribution of first-autumn Reed Buntings by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug I	Aug II	Aug III	Sep I	Sep II	Sep III	Total
I	7	5					12
II	21	22	11				54
III	10	25	18	6			59
IV	4	29	103	69	25	1	231
V		10	83	148	71	10	322
VI			37	132	150	21	340
Moult completed			5	46	80	19	150
Total	42	91	257	401	326	51	1168

Table 4. Parameters of migratory activity in first-autumn Reed Buntings at different stages of moult.

Parameter	Moult stage					
	I vs. II	II vs. III	III vs. IV	IV vs. V	V vs. VI	VI vs. moult completed
Mean MDS	Z = 1.50 p = 0.13*	Z = -2.33 p < 0.02	Z = -5.84 p < 0.001	Z = -2.08 p < 0.05	Z = -2.1 p < 0.05	Z = -0.1 p = 0.91
Proportion of transients, df = 1	$\chi^2 = 1.12$ p = 0.29	$\chi^2 = 2.35$ p = 0.13	$\chi^2 = 27.3$ p < 0.001	$\chi^2 = 5.64$ p < 0.02	$\chi^2 = 8.49$ p < 0.01	$\chi^2 = 0.05$ p = 0.83
Proportion of local birds, df = 1	$\chi^2 = 1.55$ p = 0.21	$\chi^2 = 4.89$ p < 0.05	$\chi^2 = 40.11$ p < 0.001	$\chi^2 = 5.14$ p < 0.05	$\chi^2 = 7.58$ p < 0.01*	$\chi^2 = 0.09$ p = 0.76*

Note: * – z-adjusted for small samples, χ^2 is Yates-corrected.

in the other two years. In 2008, the proportion of birds with completed moult was smaller, and in 2009 the proportion of birds at moult stage IV was the greatest.

The dynamics of MDS was similar in different years (Fig. 3): it decreased from the beginning towards the end of moult and is not significantly different between Reed Buntings at stage VI (or V–VI) and those that have completed moult.

Buntings captured in 2008 with and without playback were significantly differently distributed across moult stages ($\chi^2 = 15.14$, df = 4, p < 0.005). Under control conditions more birds at the final stage are captured (Fig. 4). At the same time, migratory activity parameters in birds at the same moult stages captured with and

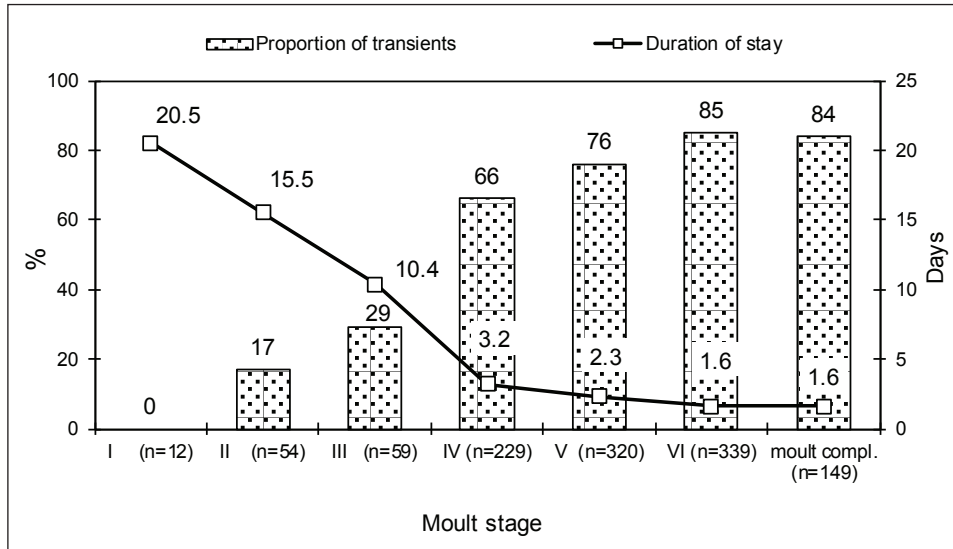


Figure 2. Mean MDS and proportion of transients in first-autumn Reed Buntings at different stages of moult.

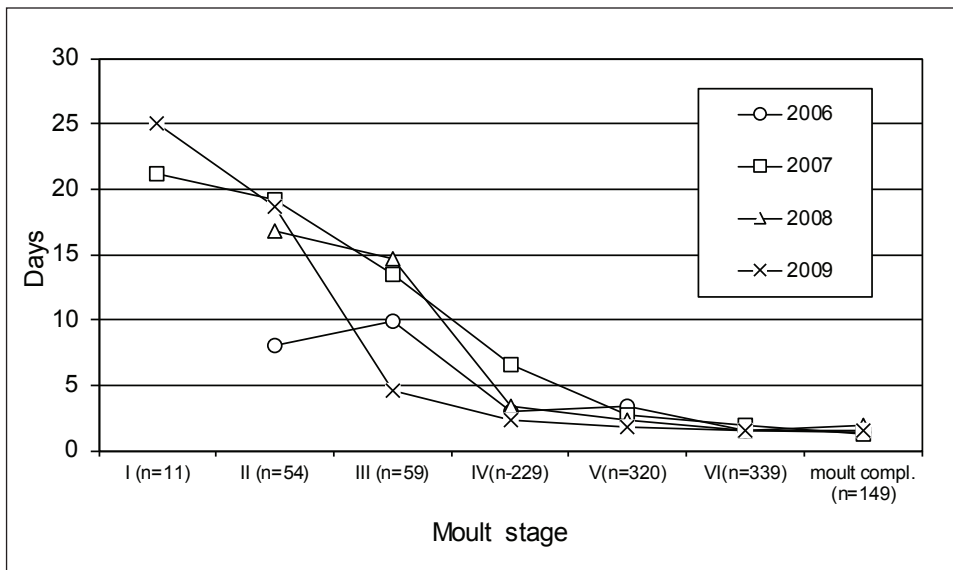


Figure 3. Mean MDS in juvenile Reed Buntings at different stages of moult in each year.

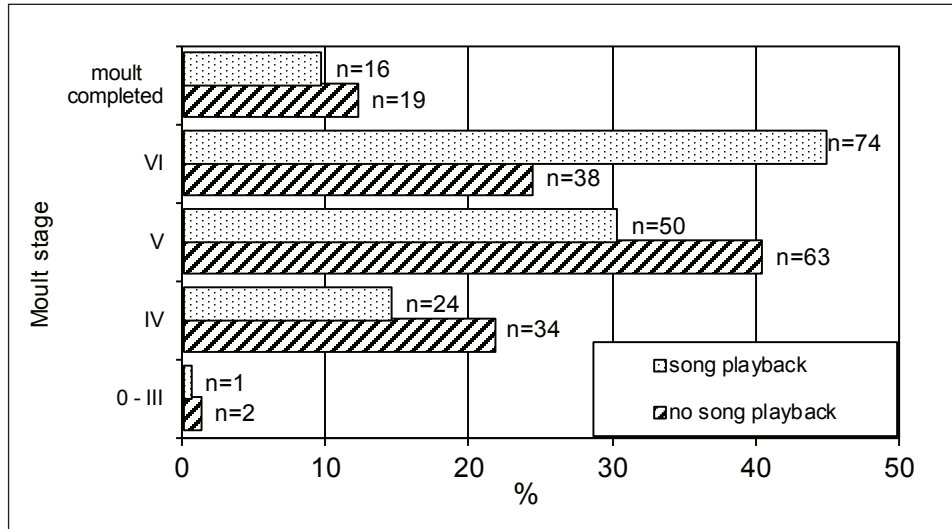


Figure 4. Frequency distribution by moult stages of first-autumn Reed Buntings captured with and without song playback.

without playback were not significantly different. The proportion of transients were similar (the proportion of birds at moult stage IV differed insignificantly, 68 and 79%, respectively; $\chi^2 = 0.93$, $df = 1$, $p = 0.33$), like the mean MDS.

3.1.2. Adults

We never captured adult Reed Buntings in the first half of moult (Table 5). When we look at birds at different stages (Fig. 5), it is apparent that the greatest difference is between stages X and XI: the proportion of transients declines ($\chi^2 = 3.9$, $df = 1$, $p < 0.05$), the difference in MDS is marginally significant ($Z = 1.95$, $p = 0.051$). Migratory activity parameters do not show significant difference between other stages (though, sample sizes are modest). If adult Reed Buntings at moult stages IX and X are pooled, all conventionally local birds at these stages were captured in August ($\chi^2 = 4.02$, $df = 1$, $p < 0.05$). Birds at stage VIII and earlier ones were marked only in August.

Frequency distribution by moult stages did not significantly differ between sexes (males $n = 81$; females $n = 51$; $\chi^2 = 1.39$, $df = 4$, $p = 0.85$). However, annual variation is significant. The year 2008 differed from 2007 ($\chi^2 = 13.23$, $df = 5$, $p < 0.05$) and from 2009 ($\chi^2 = 18.49$, $df = 5$, $p < 0.005$; birds at moult stages before VIII were pooled). In 2007, the proportion of birds with completed moult was significantly higher than in the other two years, in 2008 the same was true for moult stage X, in 2009, for moult stage XI.

Frequency distributions of moult stages in birds captured once and those that produced recaptures in subsequent years (Fig. 6) were generally not much differ-

Table 5. Distribution of adult Reed Buntings by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug I	Aug II	Aug III	Sep I	Sep II	Sep III	Total
0	1						1
VI	1	1					2
VII	1	3	1				5
VIII	3	3					6
IX			6	1	2		9
X			8	8	9		25
XI			6	13	18	7	44
Moult completed				3	26	12	41
Total	6	7	21	25	55	19	133

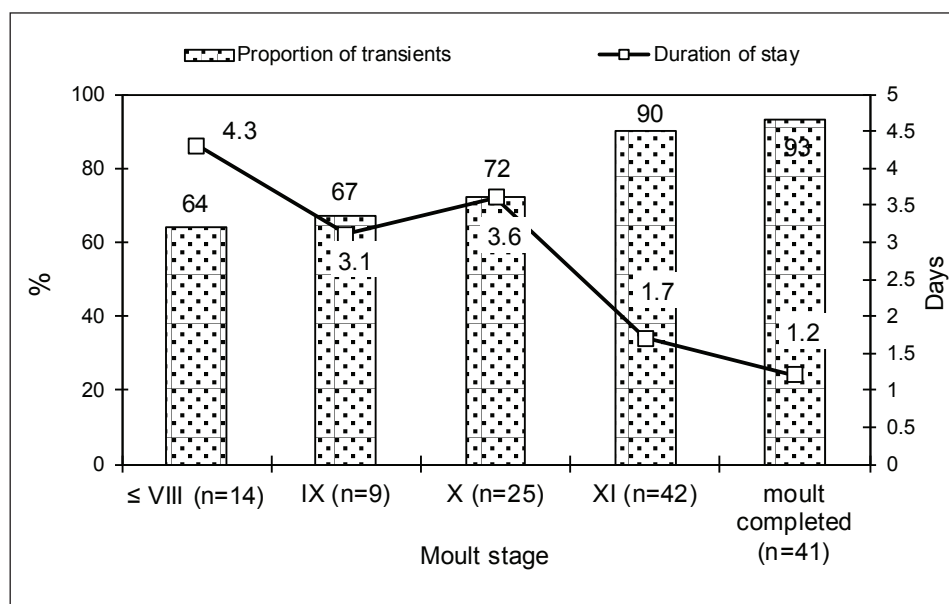


Figure 5. Mean MDS and the proportion of transients in adult Reed Buntings at different stages of moult.

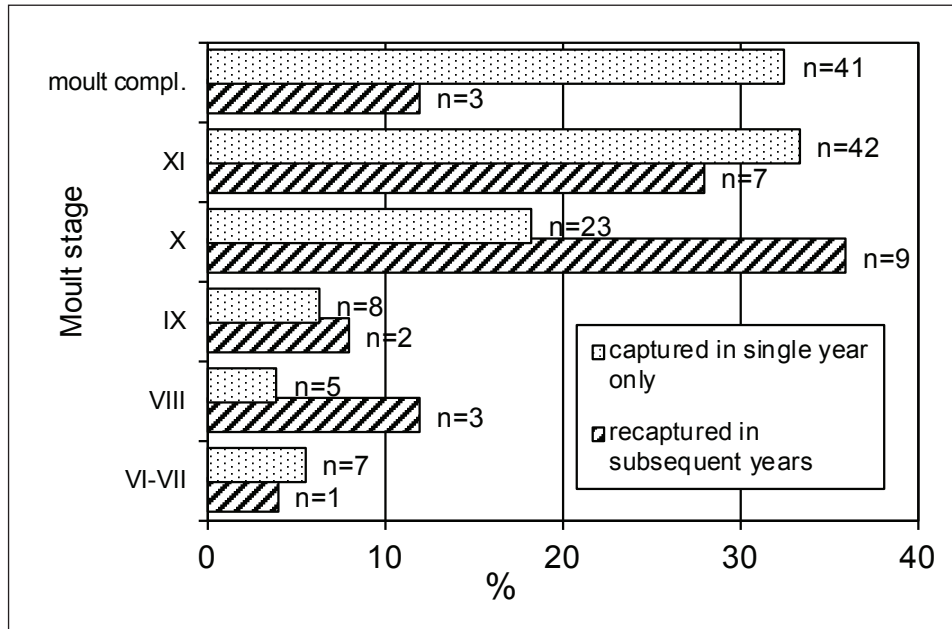


Figure 6. Frequency distribution by moult stages of adult Reed Buntings captured only in one year and those recaptured in subsequent years.

ent ($\chi^2 = 9.57$, $df = 6$, $p = 0.14$). However, among Reed Buntings captured once, the proportion of birds at moult stage XI and of those that had completed moult together was significantly higher ($\chi^2 = 5.9$, $df = 1$, $p < 0.02$). Thus, the proportion of individuals in new plumage and birds at moult stage XI is higher in the former group.

3.2. Chaffinch

3.2.1. First-year birds

Sample size for the Chaffinch was smaller than for the other two species (Table 6), therefore, moult stages had to be pooled (Fig. 7). Parameters are significantly different only between the birds at stages II–III and IV–V: MDS is higher in the former group ($Z = 2.89$, $p < 0.005$), the proportion of conventionally local individuals is also higher ($\chi^2 = 10.72$, $df = 1$, $p < 0.002$), whereas the proportion of transients is lower ($\chi^2 = 8.96$, $df = 1$, $p < 0.005$).

Three facts are noteworthy: (1) most birds were captured at moult stage VI (the onset of mass passage); (2) conventionally local birds are lacking only at later stages (VII and VIII); (3) just one individual with completed juvenile moult has been captured in the course of the study.

Table 6. Distribution of first-autumn Chaffinches by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug I	Aug II	Aug III	Sep I	Sep II	Sep III	Total
0–I	7	4	2				13
II–III	4	9	1	5			19
IV		1	2	6	1		10
V	2	1	5	11	6	1	26
VI		2	14	18	30	2	66
VII			2	18	19	7	46
VIII				2	15	1	18
Moult completed					1		1
Total	13	17	26	60	72	11	199

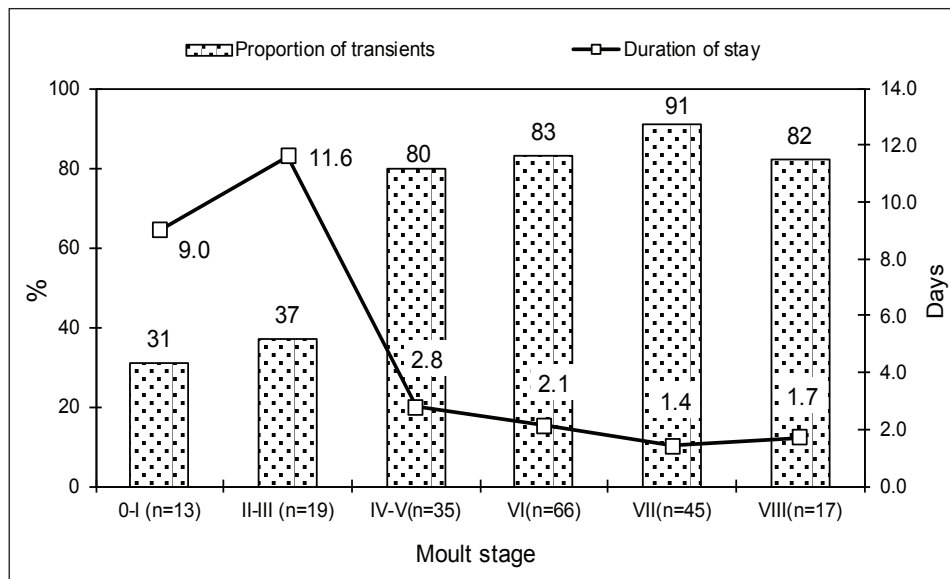


Fig. 7. Mean MDS and the proportion of transients in first-year Chaffinches at different stages of moult.

Frequency distribution of captures by moult stages did not significantly differ between sexes (males $n = 103$; females $n = 82$; $\chi^2 = 6.5$, $df = 5$, $p = 0.25$). Annual variation was significant, with 2007 and 2009 significantly different ($\chi^2 = 12.1$, $df = 5$, $p < 0.05$). In 2007, more Chaffinches at early and medium, and in 2009 more birds at late stages of moult, were captured.

3.2.2. Adults

Among adult Chaffinches, like in adult Reed Buntings, the proportion of birds captured at early stages of moult was also small (Table 7). Regular captures most probably referred to individuals that bred near the study site. They are marked at early stages of moult and remain for a long time (based on recaptures, Fig. 8, and on resightings of colour-ringed birds). Parameters of migratory activity differ at moult stages VII and VIII. At stage VIII, the proportion of transients is greater ($\chi^2 = 4.81$, $df = 1$, $p < 0.05$) and the mean MDS ($Z = 2.22$, $p < 0.05$) and proportion of local birds ($\chi^2 = 4.54$, $df = 1$, $p < 0.05$) are shorter. These parameters do not differ significantly between birds at moult stages VIII–XI. An adult female Chaffinch at moult stage VIII was captured on 23 August 2008 and remained at the study site after that for at least 32 days, as shown by recaptures. Most other birds at moult stage VIII and at more advanced stages were transients (Fig. 8).

No sex-related difference in frequency distribution of adult Chaffinches across moult stages was found ($\chi^2 = 7.18$, $df = 6$, $p = 0.3$). It is worth noting that the number of adult males was much higher than the number of captured adult females (92 and 30, respectively). Female Chaffinches are known to migrate earlier in autumn (Payevsky 2009). However, our data suggests that most females that moulted at the study site remain there nearly as long as the males.

Like in Reed Buntings, in Chaffinches a marked annual variation was observed in the frequency distribution of adults by moult stages. The distribution in 2009 was

Table 7. Distribution of adult Chaffinches by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug I	Aug II	Aug III	Sep I	Sep II	Sep III	Total
0–VI	2	4			1		7
VII	1	6	1	1	1		10
VIII	1	7	8	4	3	1	24
IX		2	1	6	8	1	18
X			1	8	22	9	40
XI			1	4	11	6	22
Moult completed				1	1		2
Total	4	19	12	24	47	17	123

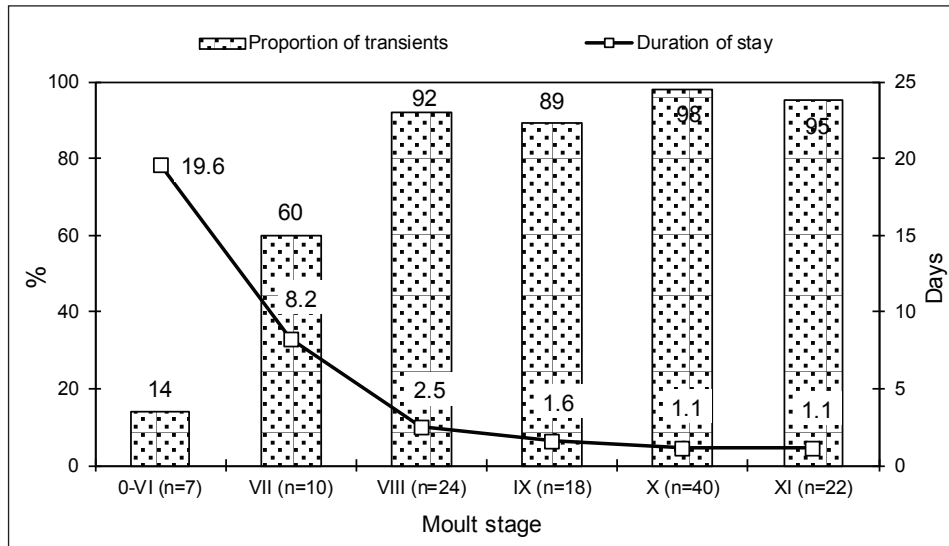


Figure 8. Mean MDS and the proportion of transients in adult Chaffinches at different stages of moult.

significantly different from the one in 2007 and 2008 ($\chi^2 = 11.6$, $df = 2$, $p < 0.005$). After a more favourable summer 2009 the proportion of birds captured at advanced stages of moult was higher.

Frequency distributions of moult stages between Chaffinches captured in one year only and those that produced recaptures in subsequent years were significantly different ($\chi^2 = 15.65$, $df = 8$, $p < 0.05$; Fig. 9). Birds that were not recaptured were more frequently marked at stage IX, since stage X this difference is significant ($\chi^2 = 5.35$, $df = 1$, $p < 0.05$). Therefore, in the former group the proportion of individuals at stages X–XI and molted birds is higher than in the latter one.

3.3. Bluethroat

3.3.1. First-year birds

Sample size for first-autumn Bluethroats is decent (Table 8), and the results are different from the other two species (Fig. 10, Table 9). Very few birds were captured at moult stages I–III. Parameters of migratory activity, starting from moult stage IV, fluctuate weakly, but if all four years of study are pooled, the variation is mostly significant (Table 9). In each individual year, however, most differences are not significant, e.g., the difference in mean MDS between moult stages was only significant in 2006 (Fig. 11) when the end of mass passage was not covered by captures.

Difference in MDS at moult stage IV in birds captured in August and September are not significant despite of a large difference between means 5.22 and 3.11 days,

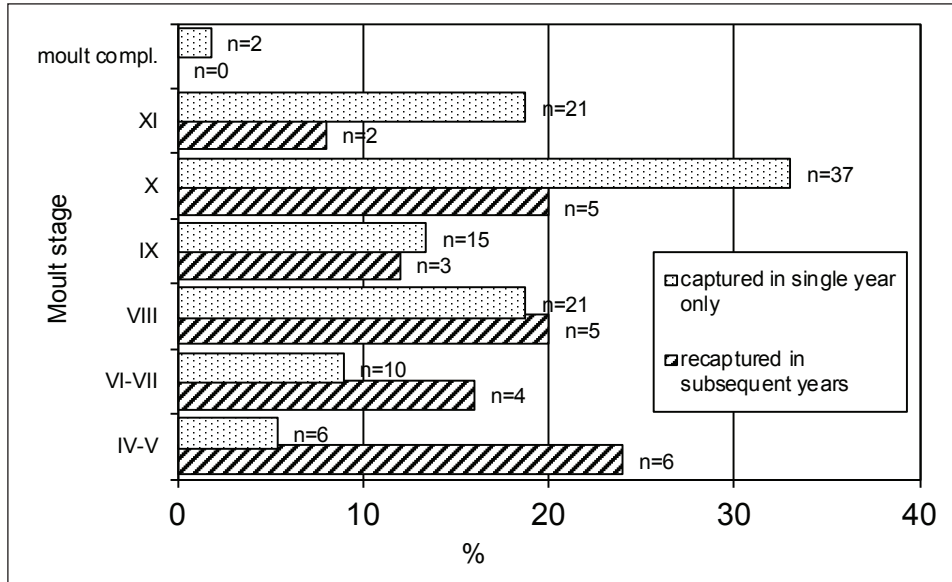


Figure 9. Frequency distribution by moult stages of adult Chaffinches captured only in one year and those recaptured in subsequent years.

Table 8. Distribution of first-autumn Bluethroats by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug I	Aug II	Aug III	Sep I	Sep II	Sep III	Total
I		4					4
II	1	3	2				6
III		6	1				7
IV		5	23	16	11	1	56
V		6	180	336	103	4	629
Moult completed		2	66	309	74	1	452
Total	1	26	272	661	188	6	1154

respectively, $Z = 1.19$, $p = 0.23$). Not a single bird captured in mid August at this stage was a transient.

Our data suggests no sex-specific difference in migratory activity of juvenile Bluethroats at the same moult stages. However, frequency distribution of captured birds across moult stages is sex-specific ($\chi^2 = 14.69$, $df = 3$, $p < 0.005$), mainly due to a larger percentage of males with completed moult (40% vs. 34% among females). First-autumn females migrate significantly earlier than males: the median capture

Table 9. Parameters of migratory activity in first-autumn Bluethroats at different stages of moult.

Parameter	Moult stage		
	I–III vs. IV	IV vs. V	V vs. moult completed
Mean MDS	Z = -2.09 p < 0.05	Z = -2.09 p < 0.05	Z = 3.85 p < 0.001
Proportion of transients, df=1	$\chi^2 = 0.88$ p = 0.35	$\chi^2 = 4.46$ p < 0.05	$\chi^2 = 22.21$ p < 0.001
Proportion of local birds, df=1	$\chi^2 = 12.65$ p < 0.001	$\chi^2 = 5.76$ p < 0.02*	$\chi^2 = 2.65$ p = 0.10*

Note: * Yates-corrected.

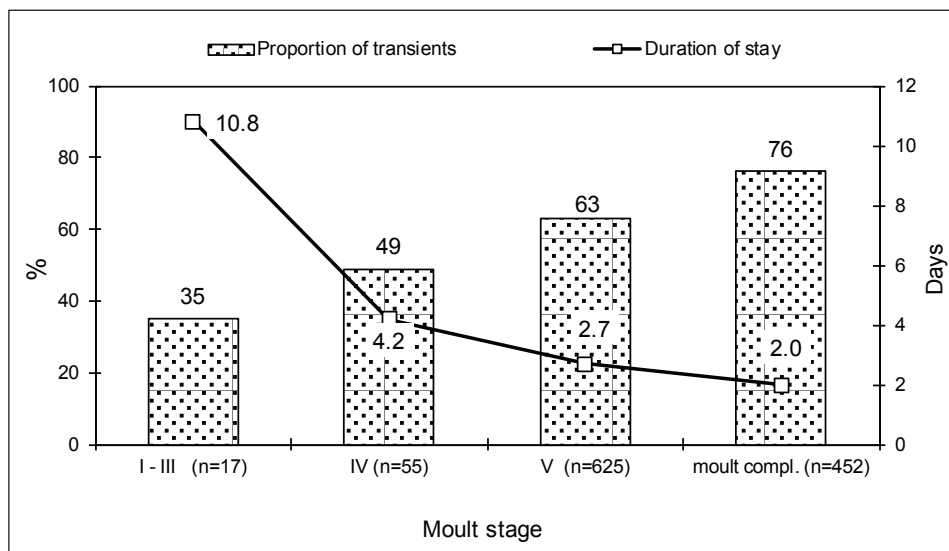


Figure 10. Mean MDS and the proportion of transients in first-year Bluethroats at different stages of moult.

date of birds with moult stage IV or more advanced, was 1 September among females and 5 September among males ($Z = 2.28$, $p < 0.03$; $n_1 = 473$, $n_2 = 653$).

Frequency distributions of moult stages in birds captured with and without song playback were not significantly different when all years are pooled ($\chi^2 = 3.29$, $df = 2$, $p = 0.19$; Fig. 12). However, in some years the difference may be significant, e.g. in 2008 the proportion of Bluethroats at moult stage V was significantly greater (71%) among birds captured with song playback than without it (56%; $\chi^2 = 6.93$,

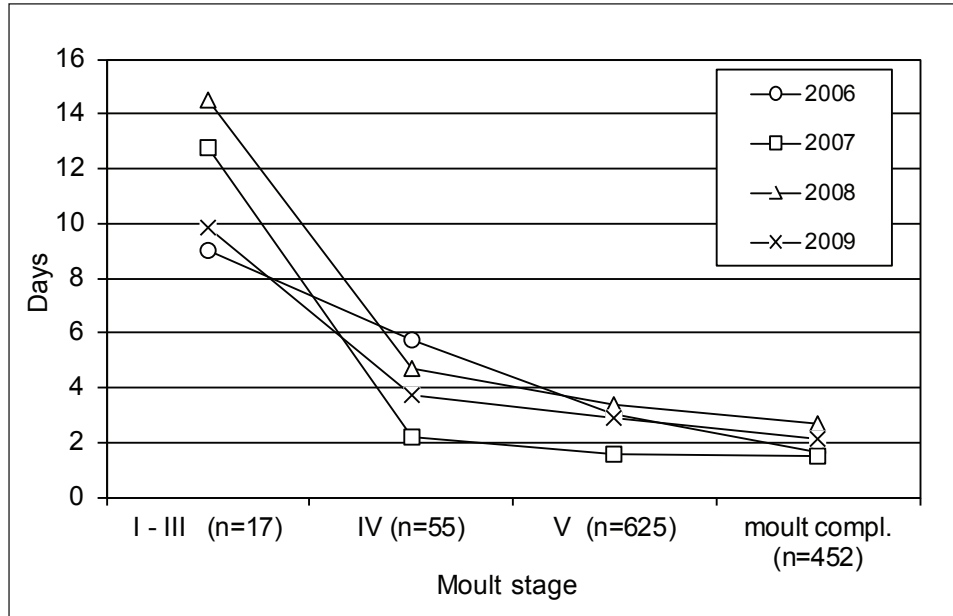


Figure 11. Mean MDS of first-autumn Bluethroats at different stages of moult in different years.

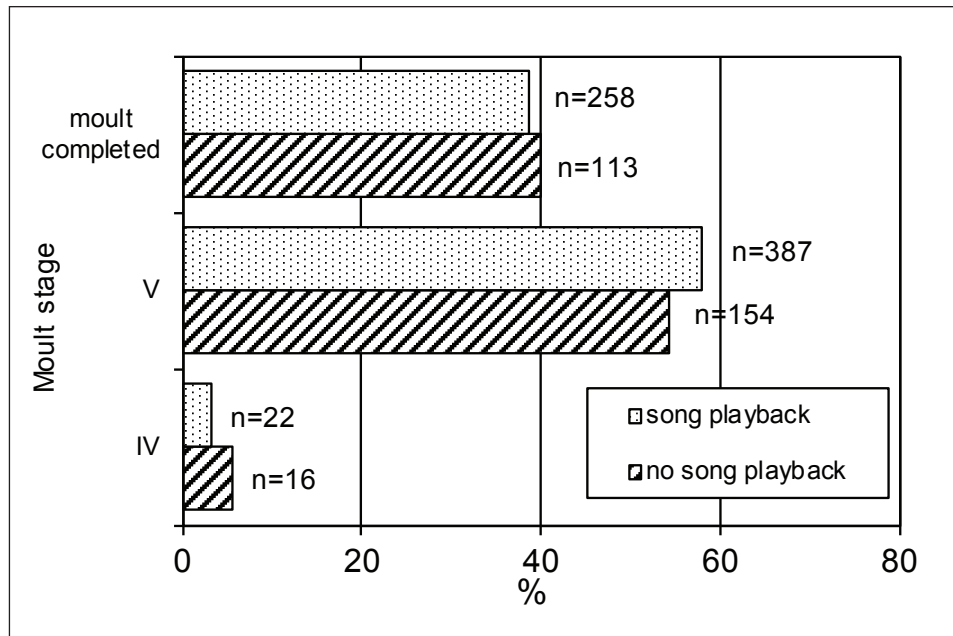


Figure 12. Frequency distribution by moult stages of first-autumn Bluethroats captured with and without song playback.

Table 10. Mean MDS and proportion of transients among Bluethroats at different stages of moult captured with (+) or without (–) song playback.

Moult stage	Play-back	Number of captures	Proportion of transients	MDS, days	Significance of difference in MDS	Significance of difference in % of transients, df=1
IV	–	16	6 (38%)	3.56	Z = 1.47, p = 0.14	$\chi^2 = 3.11$, p = 0.078
	+	21	14 (67%)	2.81		
V	–	150	84 (56%)	3.16	Z = 1.99, p < 0.05	$\chi^2 = 4.06$, p < 0.05
	+	387	253 (65%)	2.42		
Moult completed	–	105	66 (63%)	2.72	Z = 2.56, p < 0.01	$\chi^2 = 10.29$, p < 0.005
	+	258	204 (79%)	1.80		

df = 1, p < 0.01), whereas in 2009 more birds with completed moult (50%) were captured with song playback (without playback 38%; $\chi^2 = 3.65$, df = 1, p = 0.056). Unlike Reed Bunting in which parameters of migratory activity at the same moult stage did not differ between birds captured with or without playback, in Bluethroats this difference is significant. Tape-lured Bluethroats remain for a shorter time, and there are more transients among them. The difference was not significant for 2008 (Panov & Chernetsov 2010b) but was significant when all three years with tape-luring were pooled (Table 10).

3.3.2. Adults

The bulk of adult Bluethroats were captured at moult stages X or XI or after completing moult (Table 11).

Adult Bluethroats showed no significant variation in MDS and proportion of transients in relation to moult stage. Moreover, the mean MDS was even slightly increasing with moult advancement (Fig. 13).

Sex-related difference in frequency distribution of birds at different moult stages in adult Bluethroats was significant, like in juveniles ($\chi^2 = 8.23$, df = 3, p < 0.05): more females were still in moult, and more males had completed feather replacement. This result was mainly due to 2008 data when adult females lagged behind males not only in moult advancement, but also in passage dates (medians 7 and 1 September, respectively, Z = 2.36, p < 0.02). In September 2008 seven females and only two males at moult stage X were captured ($\chi^2 = 5.56$, df = 1, p < 0.02). When the 2008 data is excluded, the sex-related difference is no longer significant.

Table 11. Distribution of adult Bluethroats by season and stage of moult in 2006–2009. Birds that we consider to be migrating are shown by bold italics.

Moult stage	Aug III	Sep I	Sep II	Total
VII & IX	2	1		3
X	1	8	4	13
XI	20	34	3	57
Moult completed	23	35	4	62
Total	46	78	11	135

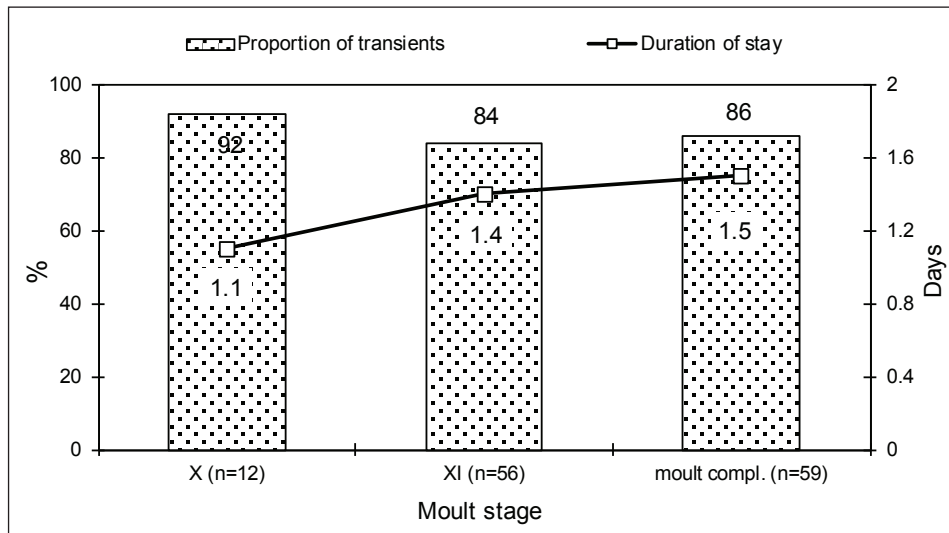


Figure 13. Mean MDS and the proportion of transients in adult Bluethroats at different stages of moult.

4. Discussion

4.1. Factors that influence the parameters of migratory activity.

Impact of song playback. Moulting advancement of birds that were recaptured or not recaptured in subsequent years.

Our results show that moult stage is often a significant factor that governs migratory activity of an individual. However, the relationship between the progress of moult and development of migratory disposition and participation in migratory is not straightforward. Other factors, first of all the progress of season, are also important.

Unlike first-autumn individuals of other species, in juvenile Bluethroats each stage of moult invariably differs from the preceding one by migratory parameters. As a long-distance migrant, the Bluethroat more than the other two species suffers from time deficit. At the early stages of migration first-year birds have to make prolonged stopovers to complete their moult. It might be called a 'soft variant' of moult migration that was reported for this species from Sweden (Ellegren & Staav 1990). It remains open whether adult Bluethroats do the same. In adults, no difference between birds at different moult stages was found, and adults seem to migrate more rapidly than juveniles (Markovets et al. 2008, Panov & Chernetsov 2010a).

Birds in more developed migratory disposition may be stronger attracted by song playback, because migrants are under a great pressure to select stopover habitat quickly and correctly (Hutto 1985, Chernetsov 2006). It might explain the difference in frequency occurrence of birds at different moult stages between individuals trapped with and without song playback in the Bluethroat and Reed Bunting. Development of migratory disposition is apparently correlated with moult advancement. It is not impossible that song playback attracts Bluethroats from the flow of migrants, and that these birds make no prolonged stopover and leave the study site the next night. It could be the reason why Bluethroats with completed moult and at moult stage V captured with tape-luring showed shorter MSD than those captured in control conditions. In the Reed Bunting which is a diurnal migrant bouts of flight and stopovers are less clearly structured and the proportion of birds on migration in captures is smaller. It could be the reason why no significant difference was found between the birds captured under control and experimental conditions.

Mass passage of the three target species seems to occur when most wing feathers have completed replacement, or just 1–2 tracts are finishing moult. In the Reed Bunting at the penultimate stage of moult more wing feathers are moulting than in the other species (Rymkevich 1990a, b; Savinich & Gagainskaja 1990 Noskov 1990). Our data shows that mass passage of adult Reed Buntings does not occur until moult stage XI, and of juveniles until moult stage VI, unlike the Chaffinch and Bluethroat that start mass migration at the penultimate stage or even earlier. Even under the time pressure, moult of wing feathers seems to be an important factor inhibiting migration (Videler 2005).

In two species frequency occurrence of birds at different moult stages differed between individuals that were recaptured in subsequent years and those not recaptured. In spite of some species-specific features, generally both Chaffinches and Reed Buntings that return to the study area in subsequent years are marked at earlier stages of moult. It was an additional argument when we determined moult stages typical of migrants.

4.2. Sex-related and annual variation in distribution across moult stages

Sex-related variation in distribution of captures across moult stages was only found in Bluethroats (both first-year birds and adults). Juvenile females in this species migrate ahead of males, but moult of these groups seems to be better synchro-

nised than migration. Therefore, first-autumn females have to start migration at less advanced stages of moult. Smaller female Bluethroats may survive inclement weather (cold spells with precipitation) less well than males and thus try to avoid them by earlier departure. In adults, sex-related difference may have another reason. Adult males and females depart at similar season, but in years with late breeding (e.g. in 2008) females lag behind males. Female Bluethroats may have more limited possibility to overlap the onset of moult with breeding (as found in northern populations of another long-distance migrant, the Pied Flycatcher *Ficedula hypoleuca*, Artemyev 2008), so that adult males moult and migrate earlier under such conditions.

In the Chaffinch and Reed Bunting sex-related variation in distribution across moult stages were not significant in either age group. This difference from the Bluethroat might be explained, first, by the higher proportion of transients in the former species and second, by the longer route that Bluethroats had travelled before reaching our study site, so that sex-related difference in migratory strategy has become significant.

In all three species distribution across moult stages showed significant annual variation due to individual year conditions that governed timing of breeding and survival of first and repeat broods. For instance, the mean estimated date of onset of moult in the earliest 12 Chaffinches was by more than one month different from the same date in the 12 latest birds (24 July and 1 September, respectively). Annual variation in frequency distribution of captures across moult stages could also be due to varying proportion of transient migrants in captures. They could also suggest that stages of moult that overlap with migration may differ between the years. The latter is another reason not to use moult stage as the sole marker of participation in migration but to account for the progress of season.

4.3. Separation between transit migrants and local birds

Comparison of groups of birds at different moult stages by the parameters of their migratory activity and comparison of frequency distributions of captures across moult stages in Chaffinches and Reed Buntings that did and did not produce between-year recaptures make it possible to identify transient migrants.

4.3.1. First-autumn Reed Buntings

All first-autumn Reed Buntings that had completed moult and at moult stage VI, birds at stage V since late August, and at stage IV since early September were migrating (Table 3, marked bold italic). We based this on the following facts: (1) lack of difference between migratory parameters of birds at the final stage of moult and those with completed moult; (2) long MDS of birds at moult stage V in mid August; (3) significant difference between birds at stage IV captured in August and in September. Thus, the proportion of transient juvenile Reed Buntings in captures reached 77%, 17% of them with completed moult.

4.3.2. Adult Reed Buntings

Among adult Reed Buntings, only birds at moult stage XI and those with completed moult entirely consist of migrating individuals (Table 5). More than one-half of birds (64%) were captured in this plumage conditions, and since the onset of mass passage (beginning of September), the vast majority. This conclusion is supported by the distribution across moult stages of buntings that did not produce recaptures in subsequent years (i.e. many of them were transient migrants). In these birds the proportion of individuals at moult stage XI and with moult completed was significantly higher than in locals. Birds at moult stages IX and X were divided into local and migrating ones by capture season (Table 5) based on (1) the presence of conventionally local birds in August and (2) the progress of season was the only significant predictor of MDS by stepwise multiple regression (Table 2). Therefore, the proportion of transients among adult Reed Buntings was ca. 78%, 39% of them had completed moult.

4.3.3. First-autumn Chaffinches

In first-autumn Chaffinches the progress of season also was a significant factor. Migrating were birds at moult stages VII and VIII that were very infrequent in August and started to occur in perceptible number since mid September. Birds at stages VI and V probably start to migrate in the beginning of mass passage, i.e. in early and mid September. In the end of the season even Chaffinches at moult stage IV are on migration. Local birds constitute ca. one-third of captures (Table 6). The proportion of birds with completed moult in captures is very low.

4.3.4. Adult Chaffinches

Difference in the parameters of migratory activity in adult Chaffinches starts between moult stages VII and VIII. It is not impossible that first birds start to migrate at moult stage VIII. Stages VIII and IX probably occur in the period when some adult Chaffinches begin to migrate. During mass passage in mid and late September most birds captured are at moult stages X and XI. The proportion of individuals at these stages is higher among birds that were captured in one year only than in (local) birds that produced recaptures in subsequent years. Therefore all adult Chaffinches marked at moult stages X and XI are assumed to be migrating (Table 7). The proportion of local birds in captures is close to one-third. We did not capture Chaffinches that had completed moult in any considerable numbers, but cannot rule out the possibility that a fraction of adult Chaffinches can complete their feather replacement in the near-polar areas towards the end of the period of mass passage in October after the end of our trapping sessions. The latest Chaffinches are reported to leave our study area in late October (Bianchi et al. 1993). However, our data suggest that already in early October Chaffinch numbers decline sharply and few individuals remain at the study site.

4.3.5. First-autumn Bluethroats

Unlike Chaffinches, very few juvenile Bluethroats are captured at early stages of moulting (presumably local birds, or those after postfledging dispersal). Significant difference between parameters of migratory activity in birds at moulting stages I–III and IV makes suggest that most birds initially captured at stage IV are on migration. Only Bluethroats trapped before the beginning of mass passage (ca. 20 August) probably do not belong to this category. Therefore, transient migrants (98% of captures) were birds with completed moulting, at moulting stage V and most birds at stage IV (Table 8). The proportion of individuals with completed moulting among migrants was 40% and the other 60% of birds overlapped moulting and migration. The latter figure is higher than one from central Sweden where in 1983 46% of young Bluethroats showed moulting – migration overlap (Lindström et al 1985). The difference in figures may be due to the particular year conditions or the distance from the breeding areas which may be larger in Sweden.

Our data does not make it possible to decide at which stages of feather replacement juvenile Bluethroats start to migrate, because during this time they have not yet reached our study area. We can only guess that it probably happens at moulting stages IV and possibly III. In northern West Siberia, all juvenile Bluethroats overlap the advanced stages of moulting and migration (Ryzhanovsky 1988a, b). We can hypothesize that Bluethroats from northern Fennoscandia captured by us are in a similar situation from the viewpoint of their annual cycle. Milder conditions experienced by Scandinavian Bluethroats in the warm period, as compared with their conspecifics from the lower Ob', are compensated by the longer migratory route in the former population. We can therefore suggest that our Bluethroats also generally start migration at the last stages of moulting. Some of them complete moulting between their natal areas and Chernaya Reka, mainly during the 'prolonged stopovers' described by Ellegren and Staav (1990).

4.3.6. Adult Bluethroats

One can hypothesize that adult Bluethroats captured at moulting stages VII and IX (all three were females) were local birds. All the remaining adults were captured at advanced stages of moulting. Moreover, none of them was trapped before the onset of mass passage in the respective year, suggesting that all of them were transients (Table 11). The proportion of individuals with completed moulting among migrating birds was ca. 47%.

4.3.7. Proportions of migrating birds in different species and age groups

Proportions of transients in captures significantly differ between the three target species. In both adult and juvenile Chaffinches this proportion was lower (e.g. for juveniles $\chi^2 = 10.17$, $df = 1$, $p < 0.002$), and in Bluethroats greater (e.g. for adults: $\chi^2 = 22.6$, $df = 1$, $p < 0.001$) than in Reed Buntings. In no species the age-related difference in the proportion of transients was significant.

These data may be explained by the structure of the species' ranges and seasonal distribution. The bulk of Bluethroats captured by us breed north of our study area, and just a handful are local breeders. A significant proportion of Reed Buntings also originate from the Kola Peninsula, as shown by the control in September 2010 of a bird ringed on the northern coast of Kandalaksha Bay. Breeding density of Chaffinches in the central Kola Peninsula and on the northern coast of Kandalaksha Bay is low (Semenov-Tian-Shansky & Gilyazov 1991, own data). Therefore, the proportion of local birds in the Chaffinch is the highest among the three target species. High proportion of local Chaffinches and Reed Buntings in captures is also related to their re-distribution across habitats that happens at the very beginning of moulting at the latest and is related to dietary shifts. When they start to use mainly plant food, most individuals of these species concentrate in small patches of open natural and anthropogenic habitats with weeds, grass, and sedge (Dolnik 1982). And this process is very prominent in northern taiga.

4.4. Degree and character of moulting – migration overlap in different species and age groups

Proportion of individuals overlapping moulting and migration varies in our study area between species and age groups. More first-autumn than adult Reed Buntings migrate before completing moulting (85 and 61%, respectively; $\chi^2 = 31.6$, $df = 1$, $p < 0.001$). In the Bluethroat this difference is not significant (60 and 53%; $\chi^2 = 2.43$, $df = 1$, $p = 0.12$). Chaffinches of both age groups overlap moulting and migration, 99.2% and 97.6%, respectively.

Among juveniles, the proportion of moulting birds among migrants is higher in Chaffinches than in Reed Buntings (Yates-corrected $\chi^2 = 22.2$, $df = 1$, $p < 0.001$) and in Reed Buntings than in Bluethroats ($\chi^2 = 131.1$, $df = 1$, $p < 0.001$). Among adults, the difference between the Chaffinch and the Reed Bunting is significant (Yates-corrected $\chi^2 = 33.7$, $df = 1$, $p < 0.001$), between the Reed Bunting and the Bluethroat is not significant ($\chi^2 = 1.35$, $df = 1$, $p = 0.25$). If not only migrants but all birds captured are compared, the differences are significant in all cases. In both age groups there are more moulting birds among Chaffinches than among Reed Buntings, and more among Reed Buntings than among Bluethroats.

Among adult migrants there were fewer birds in moulting than among juveniles. In many species at the northern borders of their ranges breeding birds start to replace feathers already when feeding the young (Danilov 1966; Jenni & Winkler 1994; Artemyev 2008). Because of that postbreeding moulting may be completed earlier than postjuvenile moulting of first-year birds, even though the former is much longer. The age-related variation in the proportion of moulting birds among migrants is significant only in the Reed Bunting. This may also be due to the later passage of adults in this species. At our site only in the Reed Bunting migrating adults pass significantly later than juveniles ($Z = 7.57$, $p < 0.001$, median dates 15 and 9 September, respectively). In the Bluethroat proportions of individuals overlapping moulting and migration are different in adults and juveniles, but insignificantly so.

If the two species of medium-distance migrants are compared, it becomes apparent that Chaffinches, especially adult ones, migrate at less advanced stages of moulting than Reed Buntings. This might be explained by the historically recent colonisation of the polar areas by the Chaffinch. Starting migration at early stages of moulting might be the first adaptation of recent settlers that should compensate for the longer migratory route and earlier deterioration of the weather conditions in autumn.

5. Conclusions

Bluethroat, Reed Bunting and Chaffinch in northern part of Eastern Fennoscandia, like many other species that replace many feathers in postjuvenile and postbreeding moulting, overlap the advanced stages of moulting with the beginning of autumn migration. On the Karelian coast of the Kandalaksha Bay most adult Bluethroats at moulting stages X–XI, juveniles at stages IV–V; adult Chaffinches at moulting stages X–XI, juveniles at stages VI–VIII, adult Reed Buntings at moulting stage XI, juveniles at stage VI are migrating. In the latter half of the period of mass passage, i.e. in September, individuals with moulting less advanced by 1–2 stages also have to start migration (Table 12).

The proportion of birds that have completed moulting differs between the three target species and usually between the age groups within one species. Generally, more individuals with completed moulting are among adults. Sex-related difference, if significant, are related to (1) sex-related variation in the timing of migratory departure; (2) apparently with different opportunities to overlap moulting with breeding in males and females, resulting in sex-specific timing of onset of post-breeding moulting.

Moulting – migration overlap is species-specific and may be related to ecological and geographic factors (range structure, foraging patterns, habitat use, historic factors and degree of adaptation of the local populations to northern conditions). In most cases birds start to migrate at the final stages of moulting when plumage replacement in most parts of the wings is finishing.

Table 12. Correspondence of moulting stages and migratory activity and the proportion of birds with completed moulting.

Species	Age	Number of moulting stages	Correspondence of moulting stages and migratory activity			Proportion (%) of birds with completed moulting	
			No mass migration	Beginning of migration	Mass passage	in captures	among migrants
Bluethroat	adult	XI	?	?–IX	X–XI	46	47
	1st year	V	Up to III?	IV?	IV–V	39	40
Chaffinch	adult	XI	Up to VII	VIII–IX	X–XI	1	2
	1st year	VIII	Up to III	IV–V	VI–VIII	1	2
Reed Bunting	adult	XI	Up to VIII	IX–X	XI	31	39
	1st year	VI	Up to III	IV–V	VI	13	17

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Appendix. Moulting advancement in target species

We used moulting description protocols developed by Rymkevich (1990a) on the basis of which working identification guides for moulting stages based on keys were developed for first-autumn and adult individuals of each species. Below the key characteristics of moulting stages from this source are given with our additions based on moulting diagrams.

1. Juvenile moulting

1.1. Bluethroat

Moulting of Bluethroats, like of many other small turdids, follows the pattern given for the European Robin *Erithacus rubecula* (Savinich 1990, Savinich & Gaginskaja 1990). Five stages are distinguished in the juvenile moulting. Stage I is characterised by the beginning of feather replacement in the breast and/or dorsal part. At stage II upper and lower tail coverts start to be replaced; this process is usually completed by the beginning of stage V. At stage III, all body pterilia are in moulting except of the feathers around eye. At stage IV, feathers around eye moulting, the outer part of the wing coverts is replaced. At stage V, shin and usually tail coverts are moulted, feathers are growing in other pterilia.

1.2. Chaffinch

Eight stages are distinguished in the juvenile moulting of Chaffinches (Noskov 1990). At stage I, feather replacement in breast and/or upper propatagium coverts starts. At stage II, thigh and/or shoulder start to moulting. At stage III, upper and lower hand coverts are being replaced, this process is completed by stage V. At stage IV, greater coverts, upper and lower tail coverts start to moulting; intermaxillary and maxillary pterilia are moulting. At stage V, moulting peaks. Nearly all parts of plumage are in moulting, but upper and lower hand coverts are already new. At stage VI, aural part starts to moulting, head in intensive moulting, upper tail coverts are growing. At stage VII, upper and lower tail coverts and greater coverts complete feather replacement. At stage VIII, feathers in head, back, belly complete growth, thigh is new.

1.3. Reed Bunting

Juvenile moulting of Reed Buntings is described following the pattern accepted for most buntings, with six stages (Rymkevich 1990b). At stage I, feather replacement starts in breast and in some birds in other pterilia. During this time, greater and medium coverts are not yet moulting. At stage II, medium coverts start to moulting, after them greater coverts. At stage III, all pterilia are in moulting, greater coverts are finishing their growth. At stage IV, greater coverts are replaced, lower tail coverts are growing. At stage V, lower tail coverts finish their growth, thigh is still in moulting, and many feather tracts have growing feathers. At stage VI, thigh is moulted, and only growing feathers are found in other tracts.

2. Post-breeding moult

Post-breeding moult is longer than juvenile moult and is more complex. In the target species post-breeding moult includes practically the whole plumage, all or most flight feathers including. However, in all species the same number of stages, 11, is distinguished. Stage identification was usually started from the upper parts of the head, where feather replacement starts in the latter half of moult (slightly earlier in the Reed Bunting). When identifying moult stage in adults, we not only used the keys, but also compared the current plumage conditions with the sequence of primary moult which generally (but not exactly) corresponds to moult stages.

2.1. Bluethroat

All adult Bluethroats, except of three individuals, were at least at stage X at first capture. The main characteristic of beginning stage X was the completion of growth of rectrices, upper and lower tail coverts. During this stage, the aural area is in active moult. By the beginning of stage XI, greater coverts finish moult, and two outermost primaries are (nearly) completely grown.

2.2. Chaffinch

In the Chaffinch, moult of the upper part of the head starts at stage VII. This tract is mostly active moulting at stages VIII–IX. Before that, at stages I–II, nearly only primaries and upper primary coverts are moulting; at stage III, the maxillary pterilia and the back, but not the intermaxillary area and rump, are in moult; at stage IV, greater coverts start replacement; at stage V, fresh feathers appear on breast. At stage VI, the anal area start moult, whereas greater coverts finish it. By stage VIII, the tertials are usually fully grown, by stage IX, rectrices, by stage X shin and thigh complete moult. Unlike stage XI, at stage X the proximal parts of the wing are still in moult. After that, flight feathers may be growing, together with feathers in the head, belly, and back.

2.3. Reed Bunting

The post-breeding moult of the Reed Bunting was described following the pattern given for the Rustic Bunting *Emberiza rustica* (Rymkevich 1990b, c). However, as migratory habits of these two species are very different (which may cause the difference in moult patterns), the sequence of replacement of primaries was specially accounted for. The upper head starts active moult at stages IV–V. Before that, at stage I, only primaries and upper primary coverts are moulting; at stages II–III body moult starts. At stage V, upper and lower tail coverts are already in active moult, but not rectrices that usually do not start to be replaced until stage VI. At this stage, greater coverts are actively replaced, but usually not the medium coverts. At stages VII–VIII, secondary replacement starts. We defined the stage IX as the end of upper and lower tail coverts; stage X included the completion of eye area and/or tertials moult; at stage XI, feather growth is completed in all remaining tracts with primaries fully grown.