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Article

Timing of autumn migration of dendrophilous birds in the forest-steppe Trans-Urals

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Abstract. The article presents the results of a study of the dynamics of autumn migration of small birds obtained during their captures with mist nets in the Kurgan Oblast in 2013, 2014 and 2016. Overall, we studied 55 species and report changes in their relative abundance from late July to mid-October as well as the starting, ending and peak dates of the migration for most species. Also, we determined the sequence of their departures from the region, classified the species by the dynamics and the number of main migration waves, defined the dominant species in the captures both for the entire migration period and for its different stages. Moreover, in the article we discuss long-term changes in the timing of autumn bird migration in the forest-steppe Trans-Urals, its direction, duration of stops, timing of migration of individuals from different age and sex groups.

Keywords: small birds, passerines, migration routes, mist nets, captures, ringing, Kurgan Oblast

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Научная статья

Сроки осенней миграции дендрофильных птиц в лесостепном Зауралье

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Аннотация. Представлены результаты исследования динамики осеннего пролета мелких птиц, полученные в ходе их отловов паутинными сетями в Курганской области в 2013, 2014 и 2016 гг. Изучены 55 видов. Показаны изменения их относительного обилия с конца июля до середины октября. Для большинства видов установлены сроки начала, окончания и пика миграционной активности. Определена очередность их отлета из региона, произведена классификация по характеру динамики и количеству основных волн пролета, выявлены доминирующие в отловах виды как за весь период миграции, так и на разных ее этапах. Обсуждаются долговременные изменения сроков осенней миграции птиц в лесостепном Зауралье, ее направление, длительность остановок, сроки пролета особей из разных половозрастных групп.

Ключевые слова: мелкие птицы, воробьеобразные, пути пролета, паутинные сети, отловы, кольцевание, Курганская область

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Introduction

Autumn migration plays an important role in the life cycle of birds (Chernetsov, 2010; Dolnik, 1975; Newton, 2007). Most species move in advance to areas suitable for successful wintering, and the distance of their migratory flights can reach several thousand kilometers. Short-distance migrants take much shorter distances. The timing of departure and the range of migratory movements often depend on the sex and age of the individual (Paevsky, 1985, 2019). The general migration process is combined with post-nesting movements of adults and the dispersal of young birds. In addition, the migratory activity of each species is closely related to the volume and characteristics of its molting (Blumenthal and Zimin, 1966; Panov, 2011). Finally, each species encounters changing environmental conditions in its range and adapts to them, as a result of which the dynamics of autumn migration of birds in each region has its own characteristics. Comparative studies of the timing and nature of autumn migration are important for understanding how such adaptation goes.

Most studies of bird migration are traditionally carried out in areas where migration flows are compressed and follow guide lines. Such lines are sea coasts and the shores of large water bodies, mountain ranges and passes. Over the vast central part of Northern Eurasia, birds fly in a wide front, and here the use of large stationary traps (like the one at Rybachinsky settlement on the Curonian spit in the Kaliningrad Oblast) is unproductive. As a result, there are very few studies of bird migration in the Urals and Western Siberia.

In the Southern Trans-Urals, T.K. Blinova and V.N. Blinov (1997, 1999) studied in 1982–1984 seasonal dynamics of the bird population of the main biotopes of the Kurgan and southern Tyumen regions. The results of the route counts of the bird population, which those authors carried out at two-week intervals from April to mid-October, gave a general idea of the course of migrations. In the subsequent years, no one studied the quantitative characteristics of the autumn migration (timing, duration and intensity) in that area.

In 2013, 2014 and 2016, we carried out mass non-selective trapping of birds with mist nets in the Kurgan Oblast. In addition to determining the migration periods of relatively common and numerous species, we also recorded rare and inconspicuous birds that usually escape visual observation, and as a result, we significantly expanded our understanding of the autumn composition of the regional avifauna (Tarasov and Lyakhov, 2013, 2014, 2016). In addition, in the course of our work, we came to the conclusion that such trappings fairly adequately reflect both the species composition and the intensity of movements of small birds, as well as their relative abundance at different stages of migration. All the species that we observed visually at the trapping sites were also among those caught, and the more often the more numerous they were. This observation is also confirmed by other authors (Ganitsky et al., 2004).

This work is concentrated on the analysis of the timing of migration and the dynamics of abundance of individual species, as well as some general patterns of autumn migration. In addition, we compared the obtained materials with the data of T.K. Blinova and V.N. Blinov (1997) and with the results of similar studies of the dynamics of migration of common species in other regions that made it possible to analyze the changes in the course of bird migration that have occurred over the past 30 years.

Materials and methods

The main method for studying the timing and dynamics of autumn migration of individual species was non-selective capturing of birds with standard mist nets. It allowed us to cover more than two thirds of the representatives of the order Passeriformes of the forest-steppe Trans-Urals, as well as several species of woodpeckers. Only the largest species (corvids) and inhabitants of open spaces (larks, wagtails, stonechats, wheatears, northern species of pipits, Lapland longhorns, snow buntings) mostly did not get into the nets.

Our studies were conducted in the Ketovo, Shadrinsk and Chastoozerye districts of the Kurgan Oblast in the valley of the Tobol River (Tarasov and Lyakhov, 2013), the Iset-Pyshma (Tarasov and Lyakhov, 2014) and Tobol-Ishim (Tarasov and Lyakhov, 2016) interfluves (Fig. 1) in 2013, 2014 and 2016. The terrain in the interfluves is a typical forest-steppe with birch and aspen groves occupying 10–20% of the area, as well as cultivated fields, hayfields and pastures. The Tobol River valley differs from the interfluves by a large pine forest located on a sandy floodplain terrace near the eastern bank of the river. All the sites had various small water bodies (rivers, lakes or swamps) and ravines overgrown with birch-and-willow undergrowth and shrubs along the banks, where we installed nets (Figs. S1–S5) (for more details on the methods of capturing birds and the nature of the habitats, see: Tarasov and Lyakhov, 2013, 2014, 2016). The work was carried out during short trips lasting 4–6 days and taken with

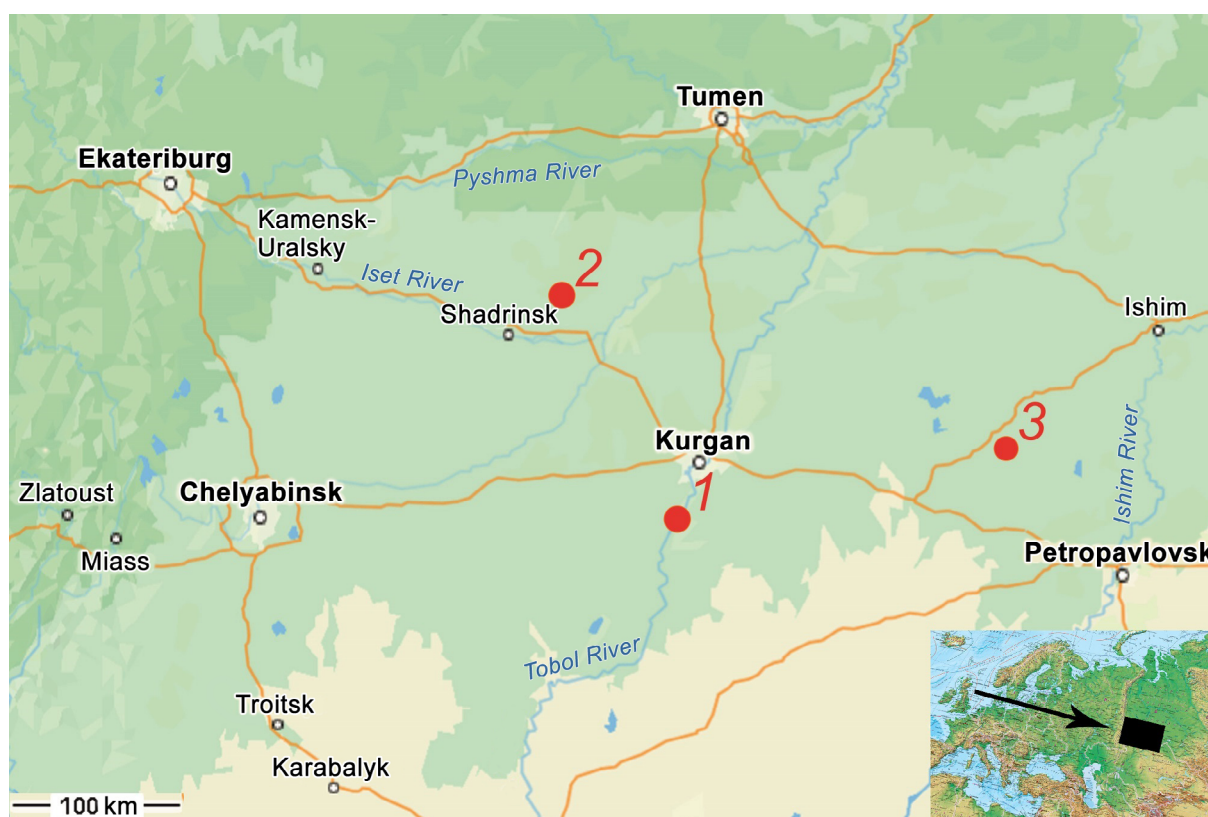


Fig. 1. Sites of bird trapping by mist nets in the Tobol River valley (1), in the Iset-Pyshma (2) and Tobol-Ishim (3) interfluves in 2013, 2014 and 2016.

equal breaks 5–6 times per season. The general study period in different years lasted either from the end of July to the end of September, or from the end of August to mid-October.

The periods of greatest bird activity could be roughly identified by the minimum period of time during which at least half of all individuals were captured, as well as by the median of capture dates. The latter often coincided with the peak of the migration wave, but only for migratory (not nesting in the region) species and only if this wave was single. The degree of mobility of a certain species was more accurately estimated with the dynamics of the average number of individuals caught per one 10 m long net per day (individuals / trap-day). The dates of the beginning, end, and peak of migration activity for each species were calculated by analyzing the trend of this parameter, for which polynomial approximation lines were constructed (Fig. S6), selecting its degree from 2 to 6 in such a way that these lines were most accurately approximated to the experimental data. In addition, a 5-line smoothing filter was used, as well as graphs of the dynamics of the average hit rate of a species over a decade. As a result of such processing of the data array, instead of small migration waves, of which 4 to 10 are traditionally distinguished per season (Dolnik, 1975), we obtained 1–2 large and smoothed ones. It is these large waves that we show in the figures and discuss in the species essays and the text. The relative abundance of species was determined by their share in the catches. For intraspecific comparisons of the migration periods of individuals of different sexes and ages, the Fisher test was used, and for small samples – the Mann–Whitney test. All calculations were performed in Statistica 6.0 (StatSoft Ink., 1984–2001) and Microsoft Excel 2003.

We combined the results of catches from different years into a single sample. From the faunistic point of view, this is entirely justified, since the study sites were located in the same natural region fairly close to one another. At the same time, the species composition of birds in the catches, even the most common ones, and their quantitative ratio in different sites varied significantly. For example, Yellowhammers were caught almost exclusively in the Iset-Pyshma interfluvium, which will be discussed below in the species essays. In addition, the weather conditions, which affected the timing of the start and end of migration, the number of waves and their intensity, were also different in different years. Despite this, we believe that

the data obtained from different sites and in different years complement each other well and allow us to present a general picture of the migration of dendrophilous birds in the considered region.

In the annotated list below, we characterize the relative abundance of 55 species, dividing them into 5 conditional categories: numerous (share in catches of 5% or more), common (from 2% to 5%), few (from 0.5% to 2%), rare (from 0.2% to 0.5%) and very rare (from 0.05% to 0.2%). The first category included 6 species, the second – 9, the third and fourth – 12 each, and the fifth – 16. Species with a share of less than 0.05% were caught 1–2 times over all years, and we do not consider them. We describe the dynamics of migration including, where possible, the dates of its beginning, greatest intensity, and end. The Russian and Latin names of the species, as well as the order in which they are listed, correspond to the “Fauna of Birds...” (Koblik and Arkhipov, 2014); for some birds, subspecies are indicated.

Results

In total, we caught 5.812 individuals of 72 bird species in 3 autumn seasons. Of these, 1354 individuals were caught in the first year, 1911 – in the second, and 2547 – in the third year. Seventeen species can be regarded as accidental in the catches as they were caught in the nets 1–2 times. In addition to small passerines, these included in different years Grey Partridge *Perdix perdix* (L., 1758), Eurasian Woodcock *Scolopax rusticola* L., 1758, Eurasian Nightjar *Caprimulgus europaeus* L., 1758, Eurasian Wryneck *Jynx torquilla* L., 1758, Black Woodpecker *Dryocopus martius* (L., 1758), Common Blackbird *Turdus merula* L., 1758, Great Grey Shrike *Lanius excubitor* L., 1758, Common Magpie *Pica pica* (L., 1758), etc. The highest number of species (59) was recorded in September, fewer – in August (44) and October (34). In the third ten-day period of July, before the start of active migration, 27 species were recorded, and then each ten-day period the number of species caught gradually increased until the beginning of September (when there were 45 of them) and then decreased just as gradually till the second ten-day period of October (16).

The dynamics of the average number of individuals of different species caught per 10 nets each 10 m in length per day (by ten-day period) is presented in Table 1.

Annotated list of species recorded in captures

Woodpeckers – Lesser Spotted *Dendrocopos minor* (L., 1758) (Fig. S7), **White-backed *D. leucotos*** (Bechstein, 1802) and **Great Spotted *D. major*** (L., 1758). They were very rare in the captures (0.05%, 0.09% and 0.2%, respectively). Great Spotted Woodpecker and White-backed Woodpecker were caught in nets only in the Tobol River valley, where there was a large forest area, with Great Spotted Woodpecker caught from September 4 to 24; White-backed Woodpecker – from September 14 to October 4; the period of greatest mobility for these species was from the middle to the end of September. Lesser Spotted Woodpecker was recorded only in the Iset-Pyshma interfluvium, where 3 individuals were caught from August 25 to October 3.

Barn Swallow *Hirundo rustica* (Vieillot, 1808). In the captures, it was recorded only in the Tobol River valley, where 7 individuals were caught on September 6–8. During those days, pre-migratory flocks were forming; a flock of about 300 individuals stayed on a pond near the nets; by September 13, it had disappeared.

Tree Pipit *Anthus trivialis* (L., 1758). A common species (its overall share in the captures was 2%). The majority of the birds flew by until mid-August that means that they were predominantly local individuals. Tree Pipits were most often caught in the nets at the end of July – beginning of August, and the species' share in the captures reached 11–12% at that time. Then its activity dropped sharply, but remained roughly constant until the end of August, and in early September there was even a small surge, probably associated with the influx of northern individuals. The species was recorded in the catches until September 24, in the second ten-day period it was small in number (1%), in the third ten-day period it was rare (0.2%). The median of the catches was August 10. The latest visual record of a single pipit was on October 9 (Tarasov and Boyko, 2013).

Dunnock *Prunella modularis* (L., 1758) (Fig. S8). In the Kurgan Oblast, the species does not nest, it is recorded only during migration. From September 22 to October 3, 7 individuals were caught, all in the Iset-Pyshma interfluvium. In the mathematical model, the peak of activity falls on September 26. The median of the catches was September 24.

Fieldfare *Turdus pilaris* L., 1758. It was quite common in all the capturing sites, but it was rarely caught in the nets (13 individuals in total), apparently due to its rather large size. At the end of September, the share of fieldfares among the caught birds reached 1%, in October – up to 2%. The median of the captures was September 26.

Table 1. Average number of individuals of different bird species caught per 100 m of mist nets per day (by ten-day period) from the end of July to mid-October 2013, 2014 and 2016.

Species	July		August			September			October		Number of individuals caught
	III	I	II	III	I	II	III	I	II		
Lesser Spotted Woodpecker				1	0.2			0.3		3	
White-backed Woodpecker						0.3	0.2	0.4		5	
Great Spotted Woodpecker					0.4	0.8	0.6			11	
Barn Swallow					0.9					7	
Tree Pipit	14	15	3	3	5	1	0.6			145	
Dunnock							0.7	0.2		7	
Fieldfare			0.5				1	0.2	0.6	13	
Redwing					0.1		0.2			3	
Song Thrush				1	1	2	4	5		94	
Common Redstart	0.6	3	2	5	5	11	5	0.6		185	
European Robin				0.4	3	5	8	5	4	163	
Siberian Rubythroat					0.7					3	
Bluethroat	2	3	1	3	4	6	3	0.1		123	
Spotted Flycatcher	2	2		0.2						10	
European Pied Flycatcher	5	2	0.2	0.6	0.6					27	
Cetti's Warbler			0.5							3	
Common Grasshopper Warbler	0.5	3	1	2	0.2	0.1				22	
Lanceolated Warbler			0.4	0.2	0.2					4	
Sedge Warbler	0.2	7	3	1	0.4	0.6				35	
Paddyfield Warbler	7	3	3	2	0.9	0.3	0.2			64	
Blyth's Reed-warbler	14	12	6	6	1	0.4				129	
Great Reed-warbler	1									4	
Booted Warbler	0.5		0.2	0.2						4	
Icterine Warbler	4	5	0.4	0.2						22	
Willow Warbler	15	12	4	9	6	8	13	2		323	
Siberian Chiffchaff	5	17	18	45	45	31	42	5	0.7	1142	
Greenish Warbler	5		0.2	1	0.4	0.1				27	
Yellow-browed Warbler				0.2	0.9	0.4	1	0.2		18	
Garden Warbler	9	15	5	6	5	1	0.6			142	
Common Whitethroat	9	15	3	3	0.1	0.1				72	
Lesser Whitethroat	4	10	6	10	5	0.9	0.5			136	
Goldcrest					0.1	2	0.2	1		22	

Table 1. Average number of individuals of different bird species caught per 100 m of mist nets per day (by ten-day period) from the end of July to mid-October 2013, 2014 and 2016 (end).

Species	July		August			September			October		Number of individuals caught
	III	I	II	III	I	II	III	I	II		
Long-tailed Tit				9	3	10	17	15	9	338	
Willow Tit	2		2	7	5	5	8	4	3	190	
Coal Tit					1	8	0.2	2	0.6	77	
Blue Tit			0.6	2	1	7	7	1	1	103	
Azure Tit	6		1	7	7	7	31	2	15	378	
Great Tit	4	3	5	19	16	23	37	21	3	727	
Eurasian Nuthatch				0.4	0.9	2	0.7	0.9		33	
Eurasian Jay					0.6	0.3	0.3	0.2	0.7	13	
Eurasian Tree Sparrow						0.1	0.4	0.3		6	
Chaffinch	4	5	3	2	5	10	8	4		228	
Brambling					0.2	0.3	3	1	0.6	31	
European Greenfinch					0.1	0.5	0.5	0.4		11	
Eurasian Siskin					2	2	3	0.8		75	
European Goldfinch	0.2					0.1	2	0.7		19	
Common Redpoll									22	36	
Long-tailed Rosefinch		3	1	0.2		1	4	6	18	89	
Common Rosefinch	0.5		0.4		0.5					7	
Common Bullfinch				0.2					7	13	
Yellowhammer			0.2	3	9	10	25	15	2	301	
Pine Bunting	0.3		1	0.8	0.3	0.5	2	0.5		26	
Reed Bunting	0.6	7	0.4	0.3	1	2	7	1		94	
Little Bunting				0.5	2	0.5	0.3	0.2		20	
Rustic Bunting					0.4	0.7				9	

Redwing *T. iliacus* L., 1758. From September 4 to 26, 3 individuals were caught – one at each capturing site.

Song Thrush *T. philomelos* C.L. Brehm, 1831. A species generally not numerous in the captures (its share was less than 2%). A pronounced wave of migration began to form at the end of August (most sharply – from the first ten days of September) and increased until the beginning of October, when Song Thrush became numerous in the catches (its share reached 6%), but in the second ten days of October it was no longer caught in the nets. As expected, we caught most individuals of this species (54%) in the Tobol River valley, where it nests in riverine pine forests, but in the interfluves the autumn dynamics of its abundance in general did not differ. The date of the last registration was October 6. The median of the catches was September 25.

Common Redstart *Phoenicurus phoenicurus* (L., 1758). A relatively common species (its share in the catches was 3%). It was rare in late July and early October (0.2% and 0.4%), common in the first half

of August and the second half of September (3% and 2%), and numerous in the second half of August and the first half of September (6% and 5%). Until mid-August, only local birds were apparently caught in the nets. Active migration occurred from late August to early October, with the most intense migration taking place in mid-September. In the mathematical model, the abundance of the species begins to increase from August 17; by September 13 it reaches its peak, increasing by this time more than threefold, and then decreases to zero by October 5. The date of the last capture was October 6. More than half of the individuals were caught between September 2 and 15. The median of the captures was September 12.

European Robin *Erithacus rubecula* (L., 1758) (Fig. S9). It almost does not nest in the forest-steppe Trans-Urals, but was common in the captures (3% share). It appeared in the nets at the end of August, and from then its abundance steadily increased, reaching a maximum in the last days of September. In comparison with other species, European Robin was common throughout September (at the end of the month, its share reached 4%) and numerous in the first ten days of October (6%). It was recorded in the nets until the end of our work (October 15) and, undoubtedly, it could have been found later (according to our observations, single individuals winter in Yekaterinburg). The curve of the polynomial approximation shows one wave of migration, the peak of which falls on September 29, the beginning – on August 17, the end – on October 20. More than half of the individuals were caught in the period from September 12 to 25. The median of the captures was September 22.

Siberian Rubythroat *Luscinia calliope* (Pallas, 1776) (Fig. S10). Recorded in the Iset-Pyshma interfluvium, where 3 individuals were caught on September 3–4.

Bluethroat *L. svecica* (L., 1758). It was relatively common in the captures from late July to late September (with a share of 2–3%). It was most often caught in the nets in the first and second decades of September. In the mathematical model, the migration activity of Bluethroat began on August 1, by September 12 it had more than doubled and then began to decline, stopping on October 10. The date of the last record in the nets was October 4. More than half of the individuals were caught on September 1–15. The median of the captures was September 8.

Spotted Flycatcher *Muscicapa striata* (Pallas, 1764). Most individuals migrated from the study area as early as July – early August. At that time, the species was small in number (the share in captures was about 1%), in the second and third decades of August it was very rare (0.1%). The date of the last capture was August 24. The median of the captures was July 28.

European Pied Flycatcher *Ficedula hypoleuca* (Pallas, 1764). It was common in the captures in the third ten-day period of July (3% share) and was rare in the first ten-day period of August (1%), then only single individuals were caught in the nets until the end of August, and in the first ten-day period of September the species again became rare (1%). The second wave of migration was weak, lasting from mid-August to mid-September, in the mathematical model at its peak (August 27) the abundance doubles. The last capture was recorded on September 6. The median of the captures was July 28.

Cetti's Warbler *Cettia cetti* (Temminck, 1820) (Fig. S11). Three individuals were caught in the Tobol-Ishim interfluvium on August 13 and 14. They probably arrived there during post-nesting migrations, since this collection point is located 160–170 km to the east and northeast of the nearest known nesting sites of the species (Gashek and Tarasov, 2020).

Common Grasshopper Warbler *Locustella naevia* (Boddaert, 1783). A rare, early disappearing species. Its migration activity increased from late July to mid-August, then began to decrease and ceased in mid-September. The share of the species in the captures in the second and third ten-day periods of August reached 1%. The estimated peak of migration activity falls on August 14. The date of the last capture was September 11. More than half of the individuals were trapped in the period from August 10 to 24. The median of the captures was August 14.

Lanceolated Warbler *L. lanceolata* (Temminck, 1840) (Fig. S12). It was recorded only in the Tobol-Ishim interfluvium, where 4 individuals were caught from August 11 to September 9.

Sedge Warbler *Acrocephalus schoenobaenus* (L., 1758). In the third ten-day period of July, the species was relatively rare in the catches (0.2% share), in the second ten-day period of August it became common (3%) – at that time, apparently, the main migration of individuals from the northern regions took place. In late August and early September, it was small in number (1% and 0.5%). It was recorded in the nets until September 16. The peak of migration activity was August 15. More than half of the individuals were caught on August 10–14. The median of the catches was August 13.

Paddyfield Warbler *A. agricola* (Jerdon, 1845). Probably, only local individuals were caught. At the end of July, the species was numerous (6%); it was common throughout August (2%), and rare in the

first two decades of September (0.2–0.4%). The last record was on September 22. More than half of the individuals were caught between July 29 and August 14. The median of the catches was August 10.

Blyth's Reed-warbler *A. dumetorum* Blyth, 1849. At the end of July, it shared the top position in the abundance list with Willow Warbler (their shares in the catches reached 14% each), and from that time on a pronounced downward trend in the abundance of the species was formed. In the first half of August, the share of Blyth's Reed-warbler was already only 8%, in the second half of August 3%, in the first half of September – 1%. The date of the last catch was September 13. The influx of northern individuals was not pronounced. More than half of the individuals were caught between July 29 and August 14. The median of the captures was August 10.

Great Reed-warbler *A. arundinaceus* (L., 1758). Caught in the nets only in the Tobol-Ishim interfluvium and only in July (4 individuals from the 26th to the 29th).

Booted Warbler *Iduna caligata* (M.H.C. Lichtenstein, 1823) (Fig. S13). A very rare species, recorded only in the Tobol-Ishim interfluvium, where 4 individuals were caught from July 28 to August 24.

Icterine Warbler *Hippolais icterina* (Vieillot, 1817). Relatively common in July (3% of captures), rare in August (0.5%). Date of last capture was August 27. The median of the captures was July 29.

Willow Warbler *Phylloscopus trochilus* (L., 1758). At the end of July, Willow Warbler along with Blyth's Reed-warbler was the leader in the frequency of capture in the nets (14% of the total number of birds each), then until the end of September its share in the captures remained at 5–6%, while in the second half of September we caught Willow Warblers twice as often as in mid-August. The graph of the polynomial approximation shows two waves of migration activity, the first of which was obviously formed by local birds. The second wave lasted from approximately August 21 to October 12, with the peak on September 17. The date of the last record in the nets was October 6. More than half of the individuals were caught in the period from August 26 to September 24. The median of the captures was September 4.

Siberian Chiffchaff *Ph. collybita* (Vieillot, 1817). The most numerous species in the captures, accounting for every fifth bird trapped. It was the leader in abundance throughout August and September (with a share in the captures of 27% and 24%, respectively), and was common at the end of July and the first half of October (4% and 3%). The polynomial approximation curve shows two waves of abundance dynamics, the first of which ends at the end of July (its intensity is apparently low), and the second (main) one begins immediately, reaching a maximum on September 6 and lasting until mid-October. During the period of the greatest activity (in the third ten-day period of August and the first ten-day period of September), the abundance of the species was several times higher than its number at the end of July, indicating an intensive migration of individuals from distant areas of the range. The date of the last capture was October 13. More than half of the individuals were caught in the period from September 7 to 26. The median of the captures was September 8.

Greenish Warbler *Ph. trochiloides* (Sundevall, 1837). The main wave of migration took place in the third ten-day period of July, when the share of the species in the captures reached 4%. The rest of the time, Greenish Warbler was rare (0.2–0.3%). A weak second wave of migration was observed in late August – early September, its peak was on September 1. The date of the last record was September 16. The median of the captures was July 29.

Yellow-browed Warbler *Ph. inornatus* (Blyth, 1842). A rare migratory species. It was recorded in the captures from August 25 to October 13. The graph of the abundance dynamics is a regular bell-shaped curve with a peak in mid-September. More than half of the individuals were caught in the period from September 7 to 21. The median capture date was September 11. Along with the nominative species (Fig. S14), Hume's Leaf-warbler *Ph. (inornatus) humei* (W.E. Brooks, 1878) (Fig. S15) was sometimes caught in the nets; it has recently been designated an independent species (Koblik and Arkhipov, 2014).

Garden Warbler *Sylvia borin* (Boddaert, 1783). Judging by the dynamics of captures of the species, post-nesting migrations immediately turn into flying away, and individuals arriving from northern regions are not numerous enough to compensate for the departure of the local birds. At the end of July, the share of Garden Warbler in catches was 7%, in the first two decades of August it reached 11%, in the third decade of August and the first decade of September it remained at the level of 4%, but by mid-September the species became small in number (0.5%), and by the end of September – very rare (less than 0.2%). The curve of the polynomial approximation of the dynamics of catches shows one wave of migration with a peak on July 29. The date of the last record was September 22. More than half of the individuals were caught in the period from August 10 to September 1. The median of the catches was August 16.

Common Whitethroat *S. communis* Latham, 1787. Quite often got into the nets at the end of July (the share in the catches 8%) and the first half of August (6%). In the second half of August, the share of

the species was already about 1%, and in September only single individuals were caught. The date of the last record in the nets was September 11. The rapid disappearance of Common Whitethroats from the study area indicates the absence of an influx of northern migrants. More than half of the individuals were caught between July 27 and August 10. The median of the captures was July 31.

Lesser Whitethroat *S. curruca* (L., 1758). In August, the species was numerous and it was the second in the share of captures (7%) to Common Chiffchaff, Garden Warbler, and Great Tit. It was common in late July and early September. The polynomial approximation curve shows one wave of migration (indicating that the bulk of the captured birds were non-native individuals), with a peak abundance on August 18. The date of the last capture was September 23. More than half of the individuals were caught between August 10 and 27. The median of the captures was August 25.

Goldcrest *Regulus regulus* (L., 1758) (Fig. S16). Does not nest in the forest-steppe Trans-Urals, occurs in wintering grounds and migrations. Rare in captures (0.4% share). Recorded in the nets in the Tobol River valley from September 8 to October 6 (18 individuals) and in the Iset-Pyshma interfluvium from September 13 to 23 (4 individuals). In the mathematical model, the bird mobility lasts from August 24 to October 22, with a peak on September 29. The median of the captures was September 17.

Long-tailed Tit *Aegithalos caudatus* (L., 1758). Found in the captures from the third ten-day period of August until the end of the work, most often in late September – early October. Common until mid-September, later – numerous; in the first ten days of October, it was the second in catches (15%) to Great Tit and Yellowhammer. The polynomial approximation graph shows one wave of migration, which lasts from August 13 to October 27 and reaches its peak on September 30. More than half of the individuals were caught in the period from September 14 to October 3. The median of the catches was September 23.

Willow Tit *Parus montanus* Conrad von Baldenstein, 1827. It was common in the catches from late July to mid-October (the species share was 1–4%). The dynamics of abundance were weakly expressed. Beginning in early August, the frequency of catches gradually increased, reaching by mid-September (in the mathematical model – by September 14) more than threefold of the initial number, after which it gradually decreased almost to the previous value by the second half of October. More than half of the individuals were caught in the period from September 2 to 24. The median of the catches was September 11.

Coal Tit *P. ater* L., 1758. Not recorded in July and August. On the average, it was common in the catches with a share of 2% in September and the first half of October. Most often caught in the nets in mid-September. The median of the catches was September 11.

Blue Tit *P. caeruleus* L., 1758. Appeared in the catches in mid-August and remained rare until early September (0.7–0.8% of the catches), common from mid-September until the end of our work (1–3%). The dynamics of the Blue Tit abundance was weakly expressed, the species was slightly more often caught in the nets from mid- to late September. In the model, the flight peak occurs on September 15. More than half of the individuals were caught in the period from September 13 to 21. The median of the catches was September 14.

Azure Tit *P. cyanus* Pallas, 1770. One of the most numerous species, the second in abundance to Chiffchaff and Great Tit. It was most often caught in the nets in the third ten-day period of September (the share in the catches reached 14%). It was also numerous in the third ten-day period of August and the second ten-day period of October (7% and 11%), and was either rare or common (1–4%) for the rest of the time. The mathematical model shows two waves of increase in the species' numbers (in July and from mid-August to the third ten-day period of October), with the peak of the second wave occurring on September 27. More than half of the individuals were caught between September 12 and 26. The median of the catches was September 22. Of the 58 individuals caught in the Iset-Pyshma interfluvium, 8 had yellow breast colouration of varying intensity, a sign of hybridization with Blue Tit (Fig. S17) (Lyakhov and Tarasov, 2014; Tarasov and Lyakhov, 2014).

Great Tit *P. major* L., 1758. A numerous species. From the third ten-day period of August and throughout September, Great Tit was the second in the catches to Chiffchaff (the share in the catches 9–16%), and in the first ten-day period of October it was the leader in abundance (21%). The graph of the polynomial approximation demonstrates a uniform intensive flight, which lasts from mid-August (before this time, apparently, only local individuals were caught) to mid-October with maximum values in the middle of the third ten-day period of September. More than half of the individuals were caught in the period from September 8 to 23. The median of the catches was September 14.

Eurasian Nuthatch *Sitta europaea* L., 1758. A small-numbered species, it was recorded from the end of August till the beginning of October. In mid-September and early October, its share in the catches

was 1%, the rest of the time – 0.4–0.5%. The peak of mobility in the mathematical model falls on September 17. More than half of the individuals were caught in the period from September 4 to 17. The median of the captures was September 16. All captured individuals ($n = 33$) belonged to the Siberian subspecies *S. e. asiatica* (Buturlin, 1907) (Fig. S18).

Eurasian Jay *Garrulus glandarius* (L., 1758). A rare species in the captures. It was recorded from September 4 until the end of the study period, slightly more often – in early September (when its share among the captured birds reached 0.8%) and mid-October (0.4%). The dynamics of abundance was not expressed. More than half of the individuals were caught in the period from September 5 to 14. The median of the captures was September 13.

Eurasian Tree Sparrow *Passer montanus* (L., 1758). A very rare species in the captures (share 0.1%). In the Tobol River valley, 4 individuals were caught from September 15 to October 5, and 2 more were caught in the Tobol-Ishim interfluvium on September 23 and 25.

Chaffinch *Fringilla coelebs* L., 1758. It was numerous in the first and second ten-day periods of September (its share in the catches was 5–9%), and was common for the rest of the time from late July to early October (2–4%). In July, only local individuals were probably caught. With the end of their migrations in the first ten-day period of August, the mobility of the species noticeably decreased, and from the middle of August the second wave of migration began, at the maximum of which (approximately September 21), Chaffinches were caught 4 times more often than before its start. That second wave of migration was obviously formed by individuals from more distant northern regions. In the mathematical model, it ends on October 14. The date of the last catch was October 6. More than half of the individuals were caught in the period from September 5 to 23. The median of the catches was September 13.

Brambling *F. montifringilla* L., 1758. It almost does not nest in the forest-steppe Trans-Urals – apparently, that is why it was not caught in the nets until mid-September. In late September – early October, the share in the catches was about 1%. The polynomial approximation shows one wave of migration, which lasts from September 2 to October 16 and reaches its peak on September 27. More than half of the individuals were caught on September 21–24. The median of the catches was September 22.

European Greenfinch *Chloris chloris* (L., 1758). A very rare species. It was recorded in the Tobol River valley (7 individuals) and in the Iset-Pyshma interfluvium (4); in the second half of September, the share of European Greenfinches in the catches reached 0.5%. The date of the last catch was October 6. The median of the catches was September 22.

Eurasian Siskin *Spinus spinus* (L., 1758). Almost never found in interfluvium areas; in the Tobol River valley, it was regularly caught in the nets from early September to early October, most often in the third ten-day period of September. More than half of the individuals, as with the previous species, were caught in the period from September 15 to 24 (almost exclusively young birds). The median of the catches was September 16.

European Goldfinch *Carduelis carduelis* (L., 1758). A rare species in the catches (the share of 0.3%). Caught in the nets mainly in the Iset-Pyshma interfluvium from the second half of September to the beginning of October. More than half of the individuals were caught on September 22–24. The median of the catches was September 23.

Common Redpoll *Acanthis flammea* (L., 1758). A representative of the winter fauna. It was recorded in the catches only in the second ten-day period of October (22% share), when it was the second in abundance only to Long-tailed Rosefinch.

Long-tailed Rosefinch *Uragus sibiricus* (Pallas, 1773) (Fig. S19). It was few in the catches in mid-August (1% share), when probably only local individuals were caught in the nets. Active migrations of Long-tailed Rosefinch began in mid-September, as evidenced by the increasing frequency of their catches in the nets. In the first ten-day period of October, the species' share in the catches was 6% (at that time it was the second in abundance only to Great Tit, Common Bunting and Long-tailed Tit), and in the second ten-day period it was already in the lead with a share of 26%. The median of the catches was October 2.

Common Rosefinch *Carpodacus erythrinus* (Pallas, 1770). A very rare species (the share in the catches 0.1%). It was recorded in the nets in the interfluviums from July to September 8. The median of the catches was August 14.

Common Bullfinch *Pyrrhula pyrrhula* (L., 1758). It was rare in the catches (the share of 0.2%). Active migrations began at the very end of our work, in the second ten days of October, when the share of the species among the caught birds reached 11%. Before the appearance of the migratory flocks, only one juvenile Bullfinch was caught in the Iset-Pyshma interfluvium on August 26. The southern limit of the nesting range of the species is located there (Tarasov, 2000; Tarasov et al., 2005).

Yellowhammer *Emberiza citrinella* L., 1758. It was recorded in the catches only from August 13 (although it is a common nesting species in all study sites), which may indicate its low mobility before that time. Active migrations began in September, reached their maximum in the third ten-day period (in the model – September 24, at that time the birds were caught three times more often than in the first ten-day period) and ended in mid-October. The largest share of the Yellowhammer catches was in late September (8%, when it was the second to Chiffchaff, Great Tit and Yellowhammer) and early October (15%, the second only to Great Tit). The overwhelming majority of individuals (95%) were caught in the Iset-Pyshma interfluve. More than half of the individuals were caught in the period from September 21 to October 2. The median of the catches was September 21.

Pine Bunting *E. leucocephalos* S.G. Gmelin, 1771. Not recorded in the Tobol River valley, it was occasionally caught in the nets in the interfluves almost for the entire period of work (until October 3), a little more often in mid-August and late September, when its share in the catches reached 1% and 0.6%, respectively. More than half of the individuals were caught in the period from September 3 to 22. The median of the catches was September 13. Half of the birds caught in the Iset-Pyshma interfluve had hybrid traits with Yellowhammer: yellow color in different parts of the plumage (Fig. S20) (Tarasov and Lyakhov, 2014).

Reed Bunting *Schoeniclus schoeniclus* (L., 1758). The abundance dynamics show a weak wave of migration in late July – early August (the share of the species in the catches was 0.6–0.8%) and a stronger one in late September (in the second and third ten-day periods, its share reached 2–3%). In the mathematical model, the second wave begins in the third ten-day period of August (at its peak in the last days of September, the abundance of the species increases more than 10 times) and ends in mid-October. The date of the last record in the nets was October 5. More than half of the individuals were caught in the period from September 16 to 26. The median of the catches was September 22. Reed Buntings were visually observed until October 13 (Tarasov and Boyko, 2013).

Little Bunting *Ocyris pusillus* (Pallas, 1776) (Fig. S21). Rare in the captures (0.3% share), caught from late August to early October, slightly more often in the first ten days of September, when its share among the caught birds reached 1%. In the mathematical model, the peak of the species' migratory mobility falls on September 4. The date of the last capture was October 4. More than half of the individuals were caught on September 1–3. The median of the captures was September 2.

Rustic Bunting *O. rusticus* (Pallas, 1776) (Fig. S22). A very rare species (0.2% share in the captures). In the Tobol River valley, 6 individuals were caught from September 5 to 17, in the Tobol-Ishim interfluve, 3 individuals from September 9 to 12. The median of the catches was September 11 (L., 1758).

Leading species in the catches

The leading species in the total number of individuals caught were Siberian Chiffchaff (its share was 20%), Great Tit (13%), Yellowhammer (7%), Long-tailed Tit (6%), Willow Warbler (6%), and Yellowhammer (5%).

In the third ten-day period of July, the most frequently caught species were Willow Warbler and Blyth's Reed-warbler (14% each), while the least frequently caught species were Tree Pipit (12%), Common Whitethroat (8%), Garden Warbler (7%), and Paddyfield Warbler (6%). Throughout August and September, Chiffchaff was the first in catches (its share ranged from 12% in the first ten-day period of August and 19% in the third ten-day period of September to 33% and 31% at the turn of those months). In early August, Tree Pipit, Garden Warbler and Common Whitethroat (11% each), Blyth's Reed-warbler and Willow Warbler (8% each), Lesser Whitethroat (7%), and Sedge Warbler and Reed Bunting (5% each) lagged slightly behind Chiffchaff. In mid-August, it was followed by Garden Warbler (11%), Great Tit and Lesser Whitethroat (7% each), Willow Warbler, Common Redstart, Tree Pipit (6% each) and Blyth's Reed-warbler (5%).

From late August to early October, Great Tit was the second to Chiffchaff in the share of catches (from 9% to 16%). In the third ten-day period of August, those two species were followed by Lesser Whitethroat and Azure Tit (7% each), Willow Warbler (6%) and Blyth's Reed-warbler (5%); in the first ten-day period of September, by Chaffinch, Willow Warbler and Yellowhammer (5% each); in the second ten-day period, by Chaffinch (9%), Common Redstart and Willow Warbler (6% each), Yellowhammer and Long-tailed Tit (5% each); in the third ten-day period, by Azure Tit (14%), Yellowhammer (8%), Long-tailed Tit (7%) and Willow Warbler (5%).

In October, the composition of the dominant species in the catches changed dramatically. In the first ten-day period, Great Tit was the first (21%) followed by Yellowhammer and Long-tailed Tit (15% each),

Long-tailed Rosefinch, Song Thrush, European Robin (6% each), and Chaffinch (5%). In the second ten-day period of October, Long-tailed Rosefinch (26%) and Common Redpoll (22%) were in the lead in the number of captures, followed by Azure Tit and Common Bullfinch (11% each), Long-tailed Tit and Great Tit (6% each).

Dynamics and the sequence of migration of the species

According to the data averaged for 2013–2014 and 2016, two main waves of general migratory activity of birds can be seen (Fig. S6). The peak of the second wave is approximately 50% higher than the peak of the first one. The first wave of migration obviously includes mainly local individuals, most of which migrate from the study area by mid-August; the peak of this wave occurs in late July. The beginning of the second wave connected among other things with the appearance of migrants from northern regions falls on the third ten-day period of August, it reaches its peak (with a 2-fold increase in numbers) approximately by September 18, then the migration activity quickly decreases and ends in the second half of October.

By the end of July, the bulk of Great Reed-warbler, Spotted Flycatcher, Booted Warbler, Icterine Warbler had flown away (although some individuals of those species, with the exception of Great Reed-warbler, continued to be found for almost the entire August), as well as European Pied Flycatcher, Common Whitethroat, Blyth's Reed-warbler, Greenish Warbler (the departure of those species lasted until mid-September), Garden Warbler, Paddyfield Warbler (until the end of September), Tree Pipit and Willow Warbler (until the beginning of October). Throughout August, and for some of the listed species also September, there was a migration of individuals from more distant regions. At the same time, the northern boundaries of their breeding ranges (Ryabitsev, 2014a, b, 2020a, b) run both along the south of the forest zone (Paddyfield Warbler, Great Reed-warbler, Booted Warbler, Icterine Warbler), and along its north (Tree Pipit, Spotted Flycatcher, Pied Flycatcher, Blyth's Reed-warbler, Greenish Warbler, Garden Warbler), and even along the tundra zone (Willow Warbler). However, the number of those migrants was low, and their influx did not cover the departure of the local individuals.

In the first half of August, Tree Pipit, Common Grasshopper Warbler, Lanceolated Warbler, Sedge Warbler, Common Whitethroat, Lesser Whitethroat, Common Rosefinch and also (less actively than at the end of July) Paddyfield Warbler, Blyth's Reed-warbler, Icterine Warbler, and Pied Flycatcher flew away actively. At that time, some species (such as Cetti's Warbler) could fly beyond the nesting area during post-nesting migrations. The first wave of the Chaffinch migration took place at the beginning of August. In mid-August, the activity of almost all birds slightly decreased, and in the third ten-day period, Song Thrush, European Robin, Long-tailed Tit, Eurasian Nuthatch, and the first northern migrants (Yellow-browed Warbler, Little Bunting) began to appear in the catches. At the beginning of September, they were joined by Redwing, Siberian Rubythroat, Goldcrest, Coal Tit, Eurasian Jay, Brambling, European Greenfinch, Eurasian Siskin, and Rustic Bunting. A strong wave of migration was observed in Siberian Chiffchaff at the end of August – beginning of September.

In the first half of September, the bulk of Little Bunting flew by, mainly in the second ten-day period – Common Redstart, Bluethroat, Coal Tit, Eurasian Nuthatch, Chaffinch, and the migration of Eurasian Tree Sparrow began. At the same time, Barn Swallow, Common Grasshopper Warbler, Lanceolated Warbler, Sedge Warbler, Common Rosefinch ceased to be recorded, and by the end of the month – Lesser Whitethroat. In the third ten-day period, European Robin, Long-tailed Tit, Willow Tit, Blue Tit, Azure Tit, Great Tit, Brambling, Eurasian Siskin, European Goldfinch, Yellowhammer, and Pine Bunting flew actively, and Dunnock appeared. After a small decline in the middle of the month, Chiffchaff began to appear in large numbers again. Since the beginning of August, the second wave of the Reed Bunting migration was observed.

In the first ten days of October, the migratory activity of birds sharply decreased. At that time, the migration of Willow Warbler, Yellow-browed Warbler, Common Redstart, Bluethroat, Chaffinch and a number of other species ended. An increase in the number of captures during that period was noted only for Song Thrush and Fieldfare. In the second ten-day period of October, the species composition of birds became entirely that of winter; at that time, mainly Long-tailed Rosefinch, Common Redpoll, Common Bullfinch and tits (more often – Azure Tit) were caught in the nets.

Thus, the bird species recorded in the captures can be conditionally divided into three groups.

The first group consists of species that are the first to disappear from the study area after the end of the nesting season. Their post-nesting migrations are accompanied by a rapid flight to the south; there is no increase in numbers due to the arrival of individuals from the northern parts of their ranges. This

group, as expected, includes species the ranges of which in their northern parts lie in the south of the forest zone, which explains the absence of a large flow of migrants in the captures. These are Common Grasshopper Warbler, Paddyfield Warbler, Great Reed-warbler, Booted Warbler, and Icterine Warbler. This group also includes species distributed much further north from the study area – throughout the entire forest zone or most of it (Barn Swallow, Tree Pipit, Spotted Flycatcher, European Pied Flycatcher, Lanceolated Warbler, Blyth's Reed-warbler, Greenish Warbler, Garden Warbler, Common Whitethroat, Common Rosefinch). The listed species most often form one wave of migration; a weak influx of migrants after the migration of the bulk of local individuals is observed only in Tree Pipit, Pied Flycatcher, Paddyfield Warbler, Greenish Warbler, and Rosefinch, but this influx does not create a second wave of migration comparable to the main one.

The relative abundance of species of the second group gradually decreases during post-nesting migrations, and then increases with the onset of migration from more distant areas. These species form at least two waves of migration, the first of which consists mainly of local individuals, the second, stronger (or there may be several), – more numerous migratory individuals from the northern areas of the nesting range. This group includes Song Thrush, Common Redstart, Bluethroat, Willow Warbler, Siberian Chiffchaff, Eurasian Jay, Chaffinch, European Goldfinch, Yellowhammer, and Reed Bunting. Apparently, Fieldfare should also be included here.

Species of the third group, like species of the first group, form one main wave of migration, but, unlike them, it consists of individuals from the northern parts of the range. Some of them (Sedge Warbler, Lesser Whitethroat, Long-tailed Tit, European Greenfinch, Long-tailed Rosefinch) nest in the forest-steppe zone, but the mobility of local individuals of those species is not noticeable here. The majority (Dunnock, European Robin, Yellow-browed Warbler, Goldcrest, Coal Tit, Brambling, Eurasian Siskin, Common Redpoll, Common Bullfinch, Little Bunting, Rustic Bunting) almost do not nest there or do not nest at all and appear only during migration periods.

These three groups are also well distributed by the timing of migration: the first includes mainly early migrants, the second – middle, the third – late. As exceptions, we can name Sedge Warbler and Lesser Whitethroat, which we attributed to the third group, but the majority of individuals of these species migrated quite early, already in mid-August. For some species (Fieldfare, Eurasian Jay, Pine Bunting), the dynamics of abundance was not expressed, remaining almost at the same level during the entire observation period, maybe due to a lack of data. For all tits, the peak of activity was observed in the middle and second half of September and was obviously associated with the flight of the young. Thus, out of the 597 caught Great Tits, whose age could be determined, 503 were young; out of 312 Azure Tits – 285; out of 93 Blue Tits – 78; out of 61 Coal Tits – 58; out of 15 Willow Tits – 13. At the same time, for some species (Willow Tit, Azure Tit, Great Tit), the dynamics of relative abundance turned out to be similar to the species of the second group, for others (Long-tailed Tit, Blue Tit, Eurasian Nuthatch) – to the species of the third group. In this regard, it is worth emphasizing once again the lack of clear difference between “migratory” and “resident” species. Autumn migrations of the latter often take the form of real migrations (Ryabitsev, 2014a). One of the Great Tits we ringed (an adult male) was found a year later in the extreme south of the Chelyabinsk Oblast which was 440 km from the tagging site.

The sequence of migration of the species also clearly illustrates their distribution by the timing of mass flight – the shortest period of time, which accounted for at least half of the catches per 10 m long net (Fig. 2). It can be seen that the main wave of movements of the species located at the top of the diagram took place in fact even earlier, and those located in the lower part – later, because those waves turned out to be “cut off”: for some – by the start dates of work, for others – by the end dates.

Of course, long-distance migrants were the first to start flying away actively, most of whom were flying away until the end of August or the first decade of September. Those are almost all representatives of the Sylviidae, as well as Tree Pipit, Spotted Flycatcher, European Pied Flycatcher, and Common Rosefinch. The long-distance migrants that flew away later than the others were Dunnock, Common Redstart, European Robin, and Yellow-browed Warbler. They fell into the nets mainly in the middle and second half of September. At the same time, the active movement of nearby migrants and sedentary species began. In general, of the 52 species of small passerine birds shown in the diagram, 7 flew mainly in July, 10 in August, 16 each in the first and second half of September and 3 in October.

Flight dates of birds from different age and gender groups

A number of bird species have differential migration manifested in different flight dates for males and females, adult and young birds, or in different distances covered by each of these groups (Maslovsky

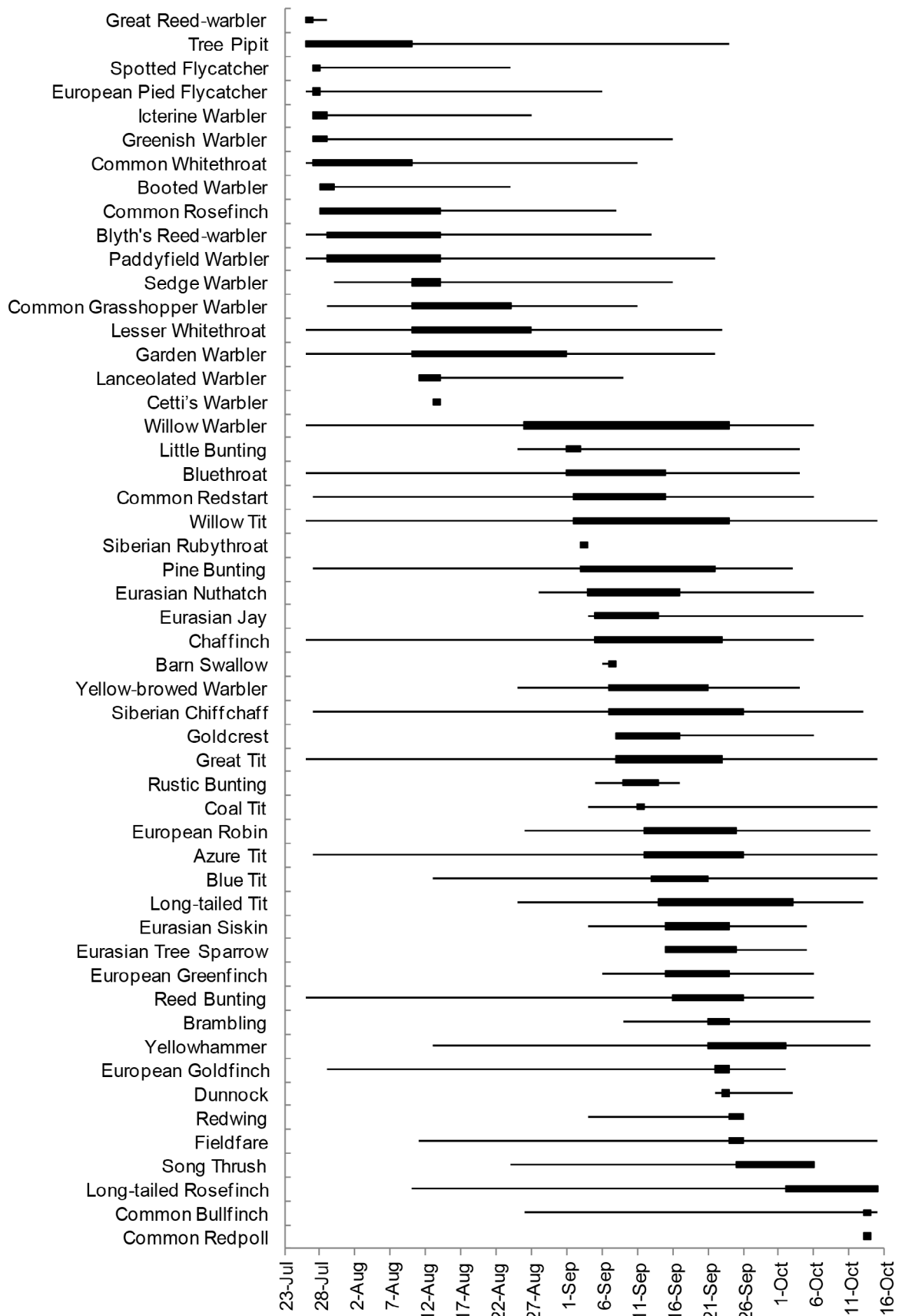


Fig. 2. The dates of records (thin lines) and mass flight (bold lines) of small passerine birds in the Trans-Urals forest-steppe according to the results of catches by mist nets in 2013, 2014 and 2016.

et al., 2018; Paevsky, 1985, 2019). In particular, in Bluethroat, Booted Warbler, Sedge Warbler, Blyth's Reed-warbler, Paddyfield Warbler, Eurasian Reed-warbler, Marsh Warbler, Common Whitethroat, and Common Rosefinch, adults are the first to fly away from the nesting areas, followed by young ones (Chernetsov, 1999, 2008, 2010; Chernyshov, 1977, 2010, 2013; Kovalevsky, 2015; Kovalevsky and Ilyashenko, 2012).

In some years or on the average over the entire observation period, we found statistically significant differences in the timing of migration of males and females and (or) young and adult individuals in 9 species (Table 2). The majority of the young in a number of species (Common Redstart, Great Tit, European Greenfinch, European Goldfinch, Long-tailed Rosefinch) flew earlier than adults. The opposite is true for Blyth's Reed-warbler, Eurasian Siskin, and Reed Bunting. Females flew away before males in Bluethroat and Chaffinch and later in Long-tailed Rosefinch. Our observations are partially consistent with the data of G.L. Nakul and S.L. Volkov (2022), according to which female Bluethroats in the Northern

Table 2. Sex and age differentiation of migration of some bird species in the Trans-Urals forest-steppe.

Species	Gender, age	Median catches (<i>n</i>)			
		For all years	2013	2014	2016
Common Redstart	Young		06.09 (18)	14.09 (97)	
	Adults		15.09 (9)	21.09 (15)	
Bluethroat	Females	06.09 (41)			26.08 (27)
	Males	12.09 (60)			11.09 (21)
Great Tit	Young	14.09 (503)			09.09 (252)
	Adults	22.09 (94)			23.09 (26)
Chaffinch	Females	12.09 (107)		13.09 (26)	
	Males	14.09 (96)		14.09 (29)	
European Greenfinch	Young	16.09 (3)			
	Adults	22.09 (5)			
Eurasian Siskin	Young	14.09 (28)	14.09 (28)		
	Adults	06.09 (5)	05.09 (4)		
European Goldfinch	Young	22.09 (4)			
	Adults	23.09 (9)			
Long-tailed Rosefinch	Young	24.09 (15)			
	Adults	03.10 (49)			
	Females	03.10 (32)			
	Males	26.09 (28)			
Reed Bunting	Young			24.09 (7)	
	Adults			22.09 (4)	

Urals also flew away before males. In addition, those authors found that in European Robin, Bluethroat, and Willow Warbler, young individuals flew away earlier than adults.

Repeated captures and duration of stopovers during migration

When birds are regularly captured with mist nets, some of them are recaptured the following day or several days later. These may be local individuals that have not yet begun their migration, or migrants that have stopped to replenish their energy reserves or cannot continue their migration for some reason (usually weather-related). They are usually called "non-transit" – in contrast to "transit" ones, which make migratory stopovers for only one day (Pradel et al., 1996). The duration of bird stopovers on the migration route varies, but usually does not exceed 10–20 days. In practice, it is not possible to estimate it for each individual, since the dates of arrival and departure are unknown. Therefore, the concept of the minimum duration of a stopover is used, meaning the time between the first and last capture (Chernetsov, 2010).

Cases in which a bird is caught in the net twice in a day are not taken into account. We recorded repeated captures ($n = 231$) of ringed individuals in 33 species. Table 3 lists 19 such species in which at least two individuals were recaptured. As expected, the resident species and short-distance migrants were recaptured more often than others: Eurasian Jay, Long-tailed Rosefinch, Common Redpoll, Willow Tit, and Long-tailed Tit. These species (except for Redpoll) are also characterized by the longest average minimum duration of a stopover (11–15 days). In addition to them, the same duration of stopovers is found in Azure Tit, Great Tit, and Yellowhammer, although only 4–6% of individuals were recaptured.

Table 3. The proportion of recaptures (P) of individuals of different species, the average minimum duration of a stopover ($T \pm SE$, days), the minimum and maximum interval between the first capture and recapture (lim, days) and the number of recaptured individuals (n).

Species	P	T	lim	n
Eurasian Jay	15%	15 ± 5	11–18	2
Long-tailed Rosefinch	15%	11 ± 3	1–34	12
Common Redpoll	14%	1 ± 0	1–1	5
Willow Tit	13%	13 ± 2	1–29	23
Long-tailed Tit	11%	12 ± 1	1–19	35
Common Grasshopper Warbler	9%	2 ± 1	1–2	2
Common Whitethroat	7%	7 ± 4	1–18	5
Eurasian Nuthatch	6%	4 ± 4	1–6	2
Azure Tit	6%	12 ± 3	1–30	22
Blyth's Reed-warbler	5%	3 ± 2	1–10	6
Bluethroat	4%	5 ± 3	1–16	5
Yellowhammer	4%	11 ± 2	1–19	12
Coal Tit	4%	7 ± 7	1–19	3
Great Tit	4%	12 ± 3	1–44	28
Siberian Chiffchaff	3%	6 ± 1	1–20	36
Willow Warbler	3%	4 ± 2	1–13	10
European Robin	3%	9 ± 6	1–30	5
Reed Bunting	2%	7 ± 4	4–9	2
Common Redstart	1%	1 ± 0	1–1	2

For long-distance migrants, this duration did not exceed a week, and a relatively high proportion of repeat captures (4–9%) was recorded only in Common Grasshopper Warbler, Common Whitethroat, Blyth's Reed-warbler, and Bluethroat. At the same time, for the listed species, with the exception of Bluethroat, the influx of individuals from more distant northern areas of the range is not expressed (see Fig. S6), and this gives reason to believe that repeated captures occurred mainly among local birds, and not among migratory birds on a stopover. The remaining long-distance migrants either did not provide repeated captures at all (except for single individuals), or their proportion did not exceed 1–3% (Siberian Chiffchaff, Willow Warbler, Reed Bunting, and Common Redstart).

Considering the species that do not nest or almost never nest in the study area, but are found only during migration periods (and therefore local individuals were not captured), only European Robin made relatively long stops during migration. They were recaptured in 9 days on the average (up to 30) after ringing, although the proportion of such individuals was small (3%). According to our observations, in the Middle Urals (unpublished data), some individuals of this species stay until the snow cover sets in, and some even overwinter. Apart from Robin, among the species that do not nest in the study area, the only recapture was recorded for Dunnock, and it happened the next day after tagging. Thus, we can say that the overwhelming majority of long-distance migrants apparently stop in the study area for no more than one day, i.e., they are “transit”.

Discussion

Long-term changes in the timing of autumn migration

A comparison of the timing of bird departure from the forest-steppe Trans-Urals in the 1980s (Blinova and Blinov, 1997) and 2010s shows, in general, no differences. Almost all species now fly away in autumn at approximately the same time as 30 years ago. Only a few species can be named as exceptions. Thus, T.K. Blinova and V.N. Blinov almost did not record Garden Warbler in August, while we observed it throughout almost all of September. European Robin, which, according to our observations, was quite common throughout September and half of October, was not found by those authors at all. Willow Warbler migrated mainly in August in the 1980s, and in September in the 2010s. In the past, the migration of Lesser Whitethroat almost ended by the end of August, Common Redstart – by mid-September, and in our captures they were still common in the first and second halves of September, respectively. It is possible that Paddyfield Warbler, which previous researchers observed only occasionally in September, but we still saw it quite regularly, began to stay longer. On the other hand, Sedge Warbler flew mainly in the first half of September in the 1980s, and in mid-August in the 2010s. We recorded Common Grasshopper Warbler and Rustic Bunting in our captures until mid-September, while T.K. Blinova and V.N. Blinov also found them in the second half of this month, and the second species – in October.

Apparently, the global warming, which, as noted by many authors (Jonzen et al., 2006; Møller et al., 2010; Palm et al., 2009; Sokolov, 2006, 2010; Zalakevicius et al., 2006, etc.), leads to an earlier arrival of birds in spring, has not yet affected the timing of their departure from the considered region in autumn. At the same time, according to data from the Sverdlovsk Centre for Hydrometeorology and Environmental Monitoring, a steady reduction in the duration of the snow period has been observed in the Kurgan Oblast since the mid-1970s (Tarasov, 2011). Perhaps, in the future due to an extension of the frost-free period, if it continues, more species will begin to fly away from the forest-steppe Trans-Urals at later dates.

Bird migration periods in some regions and migration direction

Small passerines of the Subarctic have two main wintering areas. These are, on the one hand, South and Southeast Asia and, on the other hand, Africa, the Middle East, and Southern Europe. The area of our work in the forest-steppe Trans-Urals is almost equidistant from the centers of these areas and is a kind of crossroads of migration routes. Some species here move in the southwest and west direction, and others – in the southeast and south.

To analyze the timing and direction of migration of individual species and some general patterns, we used relatively recent data on bird trapping with mist nets in Chuvashia (south of the forest zone of the Russian Plain) (Ganitsky et al., 2004), at the biological station of the Kemerovo University (southeast of Western Siberia) (Kovalevsky, 2015; Kovalevsky and Ilyashenko, 2010; Kovalevsky et al., 2014) and in the upper reaches of the Pechora River (the Northern Cis-Urals) (Nakul and Volkov, 2022). These study sites are located in 1.1 thousand km to the west, 1.4 thousand km to the east, and 0.9 thousand km to

the northwest respectively from Kurgan. The wintering areas of the species were determined according to the reference books of V.K. Ryabitsev (2014a, b, 2020a, b).

A comparison of the terms of autumn bird migration in the Southern Trans-Urals and Northern Cis-Urals suggests a generally predictable picture: northern populations begin it earlier. The difference in the timing of mass migration is most often 1–2 weeks (Dunnock, European Robin, Common Redstart, Willow Warbler, Chaffinch, Common Rosefinch, Yellowhammer, Pine Bunting, Reed Bunting) or more (Song Thrush). Resident species also begin migrations earlier in the Northern Cis-Urals: some – 1–2 weeks earlier (Willow Tit, Eurasian Nuthatch), others – almost a month earlier (European Goldfinch). For some species (Bluethroat, Spotted Flycatcher, Lesser Whitethroat, Little Bunting, Rustic Bunting) there were practically no differences, and one species (Sedge Warbler) was recorded in the upper reaches of the Pechora River even later in the year than in the Trans-Urals. The absence of differences in the timing of the departure of these species may be explained by the fact that they fly from the Northern Cis-Urals and Southern Trans-Urals to their Southeast Asian wintering grounds via different routes.

Analyzing the timing of autumn bird migration in the Kurgan and Kemerovo regions and Chuvashia, located at approximately the same latitude, we assumed that species flying from Central Siberia to European and African wintering grounds would be recorded longer in autumn in the Trans-Urals and especially in the Russian Plain. Conversely, birds from Eastern and Northeastern Europe flying to Southeast Asia would be observed longer in the east of Western Siberia. Data on bird catches in the Kurgan and Kemerovo regions show that this pattern is indeed observed in many species. Thus, Common Redstart, European Pied Flycatcher, Icterine Warbler, and Garden Warbler flying to wintering grounds in the western and southwestern directions were caught en masse 1–2 weeks earlier in the Kemerovo Oblast than in the Kurgan Oblast, and Willow Warbler – almost a month earlier. Song Thrush and Tree Pipit, which can fly both to Africa and to Southern Asia, also migrated almost a month earlier in the Kemerovo Oblast. At the same time, the expectation of seeing earlier migration in the Kurgan Oblast for Blyth's Reed-warbler, Chaffinch, Brambling, Common Rosefinch, and some species of buntings (Pine, Little, Rustic), wintering in South or Southeast Asia, was not justified. There are also no differences in the timing of migration for Bluethroat, Spotted Flycatcher, Great Reed-warbler, Lesser Whitethroat, and Chiffchaff, but the wintering areas of these species are located both in Africa and in Southern Asia, and individuals from the western and eastern regions of Western Siberia can fly in different directions. There are no differences in the timing of autumn migrations for resident species (tits, Eurasian Nuthatch, Goldcrest, Eurasian Jay) and short-distance migrants (Yellowhammer).

Not much more difference in the timing of autumn migration of birds is found between the forest-steppe Trans-Urals and the south of the forest zone of the Russian Plain. The approximate 1–2 week shift in the Russian Plain was observed in European Robin, Bluethroat, Spotted Flycatcher, Sedge Warbler, and Icterine Warbler, which may serve as a confirmation of the predominantly western or southwestern direction from the Trans-Urals in these species. On the other hand, Common Redstart, which also winters in Africa and presumably should be recorded later, flew in Chuvashia approximately 2–3 weeks earlier. Perhaps, this is explained by the fact that Chuvashia is located not southwest from the Kurgan Oblast, but lies to the west and northwest of it (or by the presence of wintering grounds in Southern Asia). A mass migration of Brambling (a short-distance migrant whose wintering grounds are scattered across Southern Europe and most of Southern Asia) and some resident species (Long-tailed Tit, Blue Tit) took place on the Russian Plain approximately 1–2 weeks later than in the Trans-Urals.

Thus, an analysis of the available materials on the timing of autumn bird migration in the above-mentioned regions suggests that most species from the forest-steppe Trans-Urals fly to winter mainly in the southern direction, fewer – in the southwestern direction, and even fewer – in the southeastern direction. And those few that migrate in the latitudinal direction within Western Siberia fly only to the west. Consecutive movements from its eastern regions through the Trans-Urals to European Russia are traced only in one species – Icterine Warbler.

Conclusion

Thus, the obtained data allow us to presume the presence of two strong waves of autumn migratory activity of birds in the forest-steppe Trans-Urals. The first one covers mainly local individuals, most of which migrate from the study area by mid-August (the peak of this wave falls on the last days of July). The second wave is formed mostly by migrants from northern regions, it begins in the 3rd ten-day period of August and reaches its peak (with a 2-fold increase in the number of birds) by the end of the second ten-day period of September.

By the dynamics of migration and the number of waves, the species recorded in the catches are divided into three groups. The first one is the species that disappear from the study area soon after the end of the nesting season (flycatchers, grass warblers, many reed warblers, sylviid warblers, Booted Warbler, Icterine Warbler, Greenish Warbler, Barn Swallow, Tree Pipit, Common Rosefinch). In this group, the departure is often initiated by adult individuals molting in wintering areas or in intermediate areas, while first-year migrants fly later – after the completion of post-juvenile molting. The species of the second group form two (or more) waves of migration, the first of which consists mainly of local individuals, the second (more powerful) – of numerous migratory individuals from the northern parts of the nesting areas. The species of the third group, like the species of the first group, form one main wave of migration, but it consists of individuals from the northern parts of the areas. These are mainly transit species that do not nest in the forest-steppe Trans-Urals and appear in significant numbers only during migration periods. The small number of repeated captures of long-distance migrants indicates that the overwhelming majority of them do not stay in the study area for more than one day.

The studied bird species fly from the forest-steppe Trans-Urals to winter mainly in the south, less often in the southwest and even less often in the southeast direction. An analysis of their departure dates in the 1980s and 2010s reveals no differences for most species, although several of them have begun to stay longer in the region in autumn.

We believe that studies of the migration process by trapping birds with mist nets are important not only for identifying its quantitative characteristics in specific regions, but also for comparative analysis in both neighbouring and distant areas, and such studies should be fully welcomed.

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APPENDIX



Fig. S1. A mist net set in willow thickets in the Tobol River valley near Kurgan, September 17, 2013.



Fig. S2. Bottomland forest in the Tobol River valley near Kurgan, September 23, 2013.



Fig. S3. Flooding of a small river in the Tobol River valley near Kurgan, September 25, 2013.



Fig. S4. Shrub thickets among hay meadows in the vicinity of Shadrinsk, September 22, 2014.



Fig. S5. Lakeside willow thickets in the vicinity of Chastoozerye village, Kurgan region, September 24, 2016.



Fig. S7. Lesser Spotted Woodpecker, October 3, 2014, the vicinity of Shadrinsk. in the Trans-Urals forest-steppe (by day).

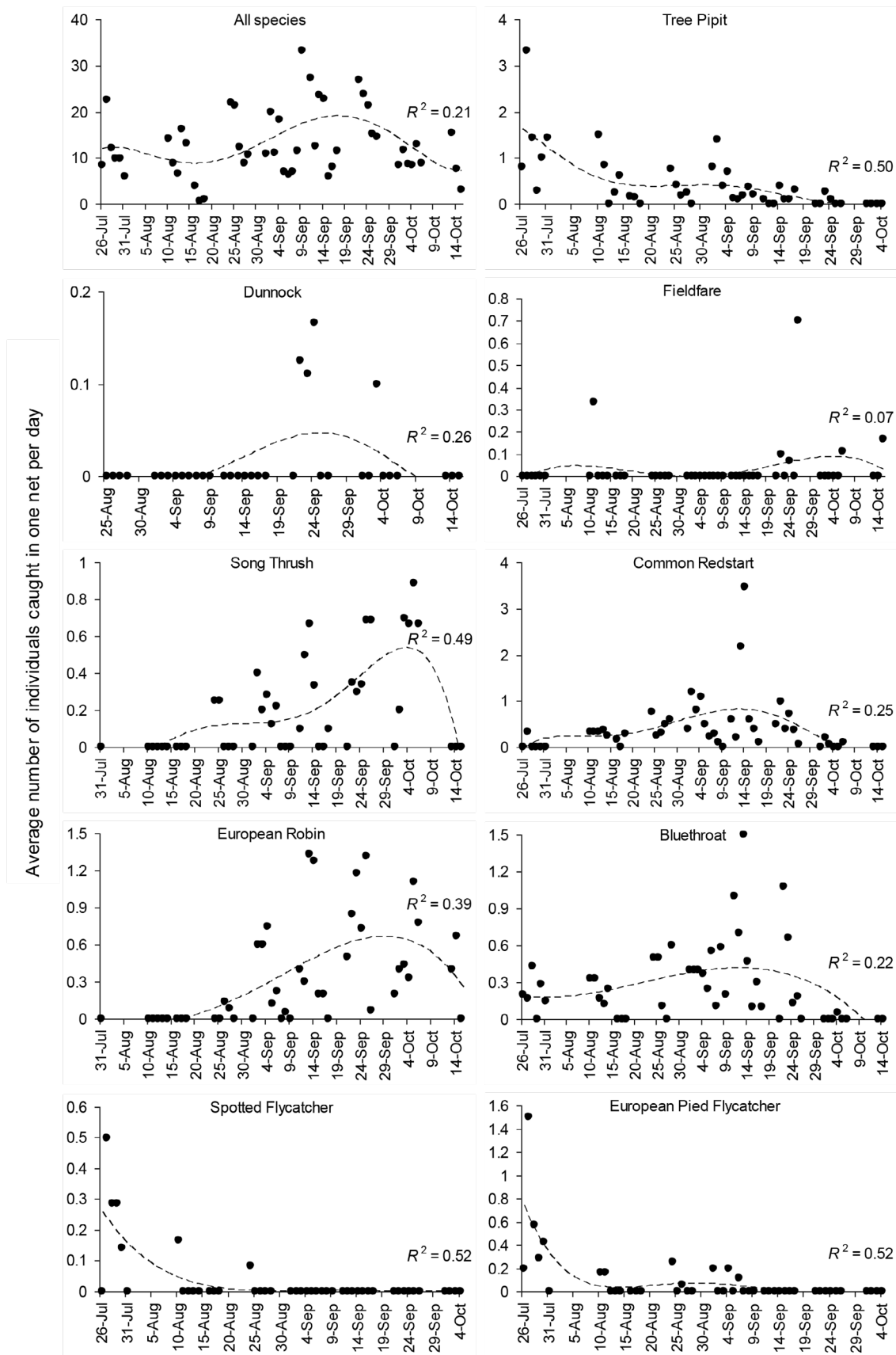


Fig. S6. Dynamics of the frequency of getting into mist nets of different bird species in the Trans-Urals forest-steppe (by day).

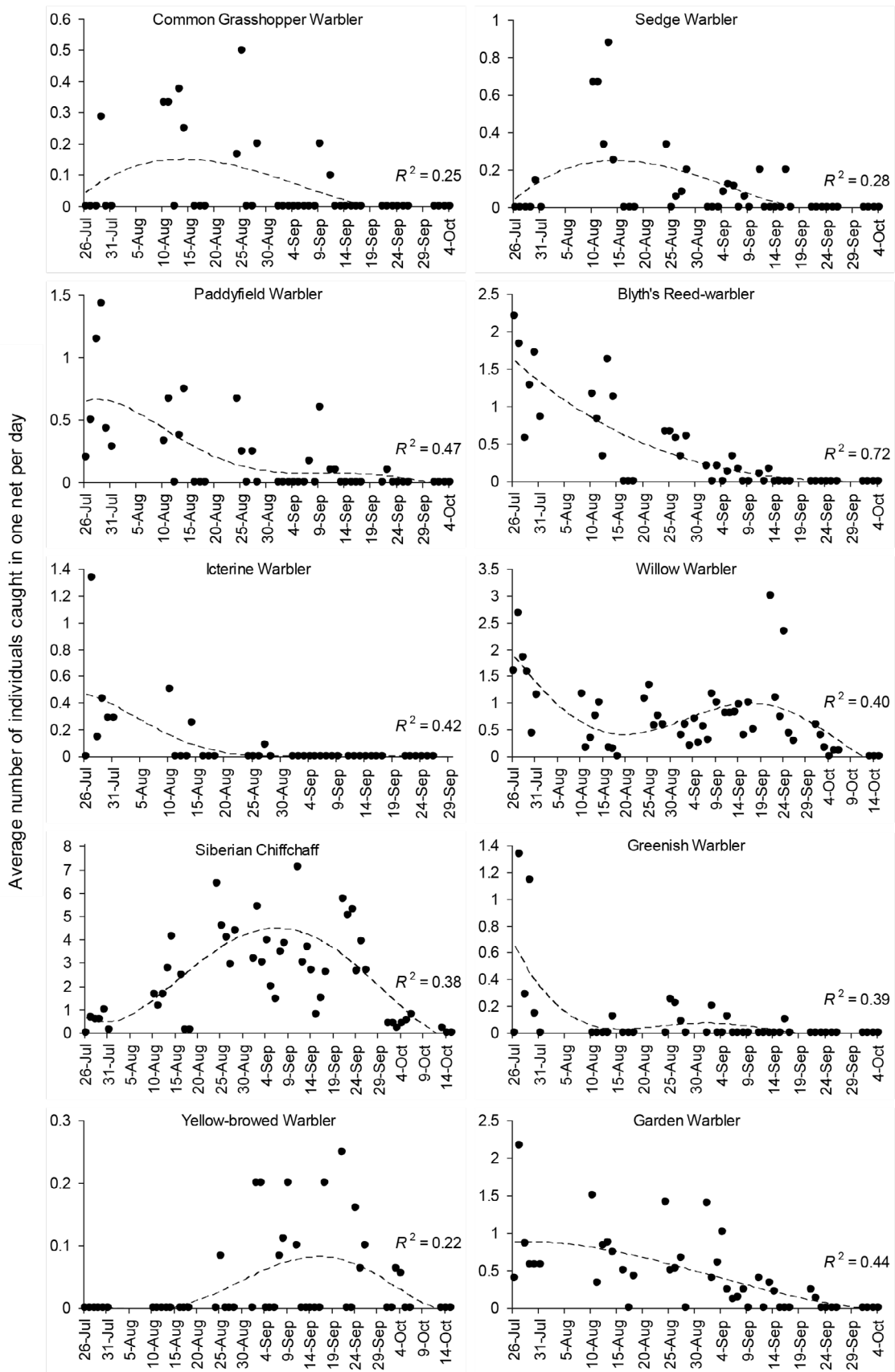


Fig. S6. Dynamics of the frequency of getting into mist nets of different bird species in the Trans-Urals forest-steppe (by day) (continuation).

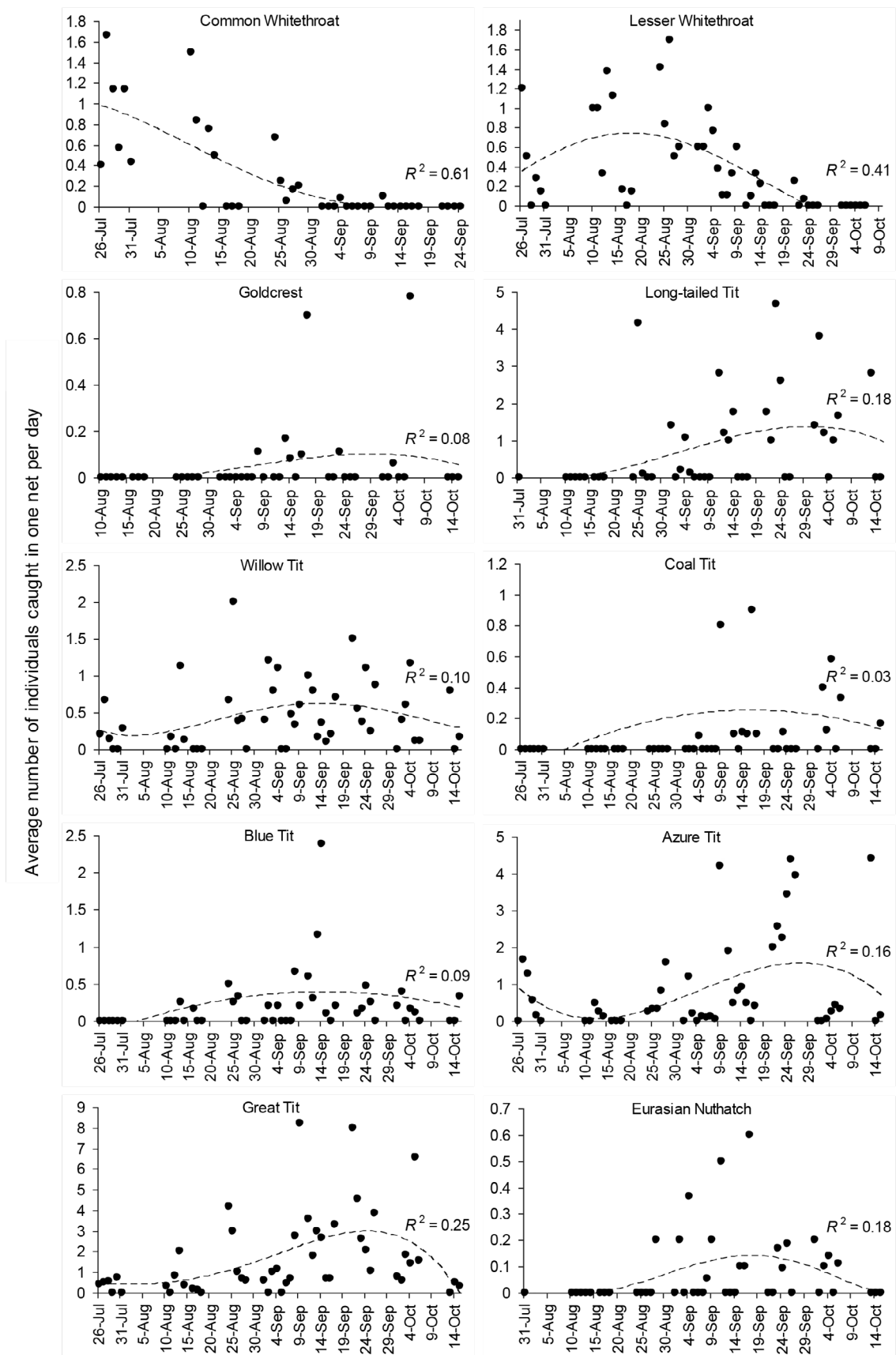


Fig. S6. Dynamics of the frequency of getting into mist nets of different bird species in the Trans-Urals forest-steppe (by day) (continuation).

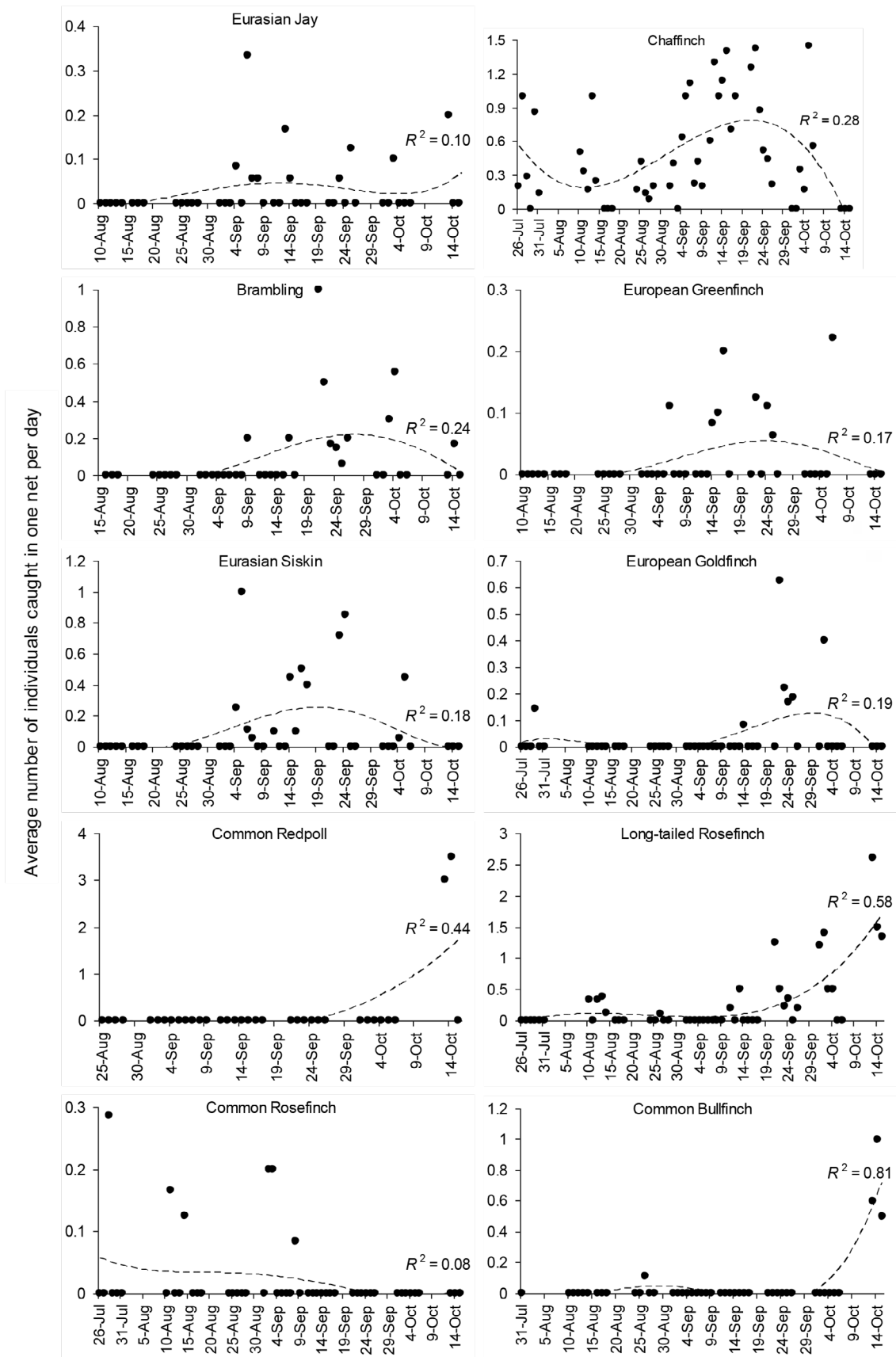


Fig. S6. Dynamics of the frequency of getting into mist nets of different bird species in the Trans-Urals forest-steppe (by day) (continuation).

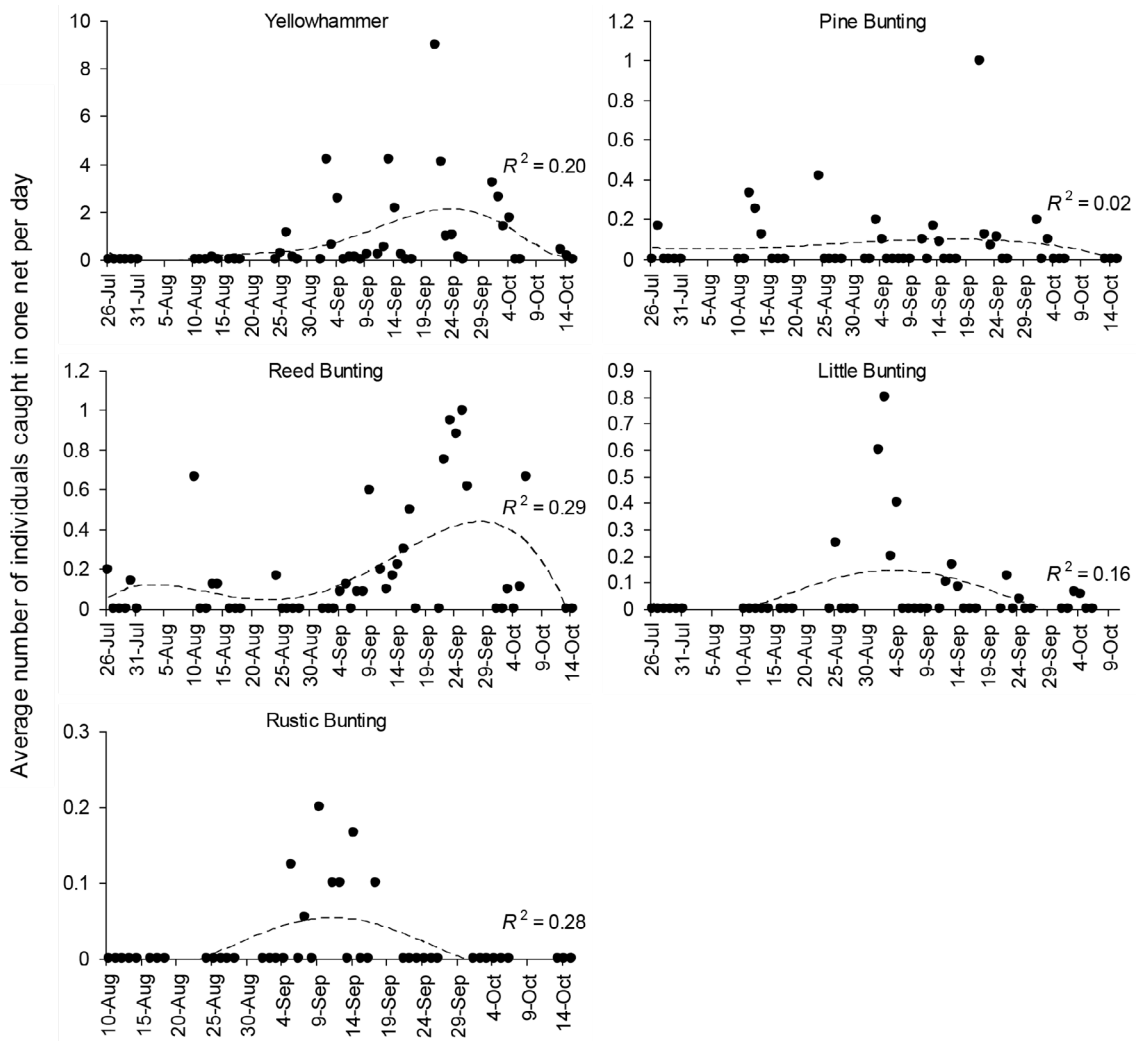


Fig. S6. Dynamics of the frequency of getting into mist nets of different bird species in the Trans-Urals forest-steppe (by day) (end).



Fig. S8. Dunnock, September 22, 2014, the vicinity of Shadrinsk.



Fig. S9. European Robin, September 15, 2013, the vicinity of Kurgan.



Fig. S10. Siberian Rubythroat, September 3, 2014, the vicinity of Shadrinsk.



Fig. S11. Cetti's Warbler, August 14, 2016, the vicinity of Chastoozerye village.



Fig. S12. Lanceolated Warbler, September 9, 2016, the vicinity of Chastoozerye village.



Fig. S13. Booted Warbler, August 24, 2016, the vicinity of Chastoozerye village.



Fig. S14. Yellow-browed Warbler (nominative subspecies), August 25, 2016, the vicinity of Chastoozerye village.



Fig. S15. Hume's Leaf-warbler, October 3, 2013, the vicinity of Kurgan.



Fig. S16. Goldcrest, September 17, 2013, the vicinity of Kurgan.



Fig. S17. "Yellow-breasted Tit" (hybrid of Azure Tit and Blue Tit), September 14, 2014, the vicinity of Shadrinsk.



Fig. S18. Eurasian Nuthatch (the Siberian subspecies), September 17, 2013, the vicinity of Kurgan.



Fig. S19. Long-tailed Rosefinch, September 26, 2016, the vicinity of Chastoozerye village.



Fig. S20. Hybrid of Pine Bunting and Yellowhammer, September 21, 2014, the vicinity of Shadrinsk.



Fig. S21. Little Bunting, October 3, 2013, the vicinity of Kurgan.



Fig. S22. Rustic Bunting, September 9, 2016, the vicinity of Chastoozerye village.