

Relations between the Yellowhammer (*Emberiza citrinella*) and the Pine Bunting (*Emberiza leucocephalos*) in the Forested Steppe of the Trans-Urals

A. S. Rubtsov^{a, *} and V. V. Tarasov^{b, **}

^aState Darwin Museum, Moscow, 117292 Russia

^bInstitute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia

*e-mail: alexrub@darwinmuseum.ru

**e-mail: grouse@bk.ru

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Abstract—We studied the phenotypic composition of the populations and variability of songs in two bunting species in three localities on the western border of the sympatry zone: in the southern part of Tyumen' oblast and in the center and southern of Kurgan oblast. Over the last several decades, the zone of contact of the studied species has expanded significantly. The pine bunting started breeding regularly in the area at the end of the 20th century, and at present it is considered a common species comparable in abundance to the yellowhammer. The share of phenotypic hybrids varies from 25 to 50% reaching its maximum at the boundary of the pine bunting's nesting range. East of this boundary, the hybridization level is reduced, this being seen in a sharp decrease in the share of "leucocephala hybrids." An analysis of the phenotypic variability of the hybrids shows that they can be divided into two groups similar in coloration to the parental species. The study results let us presume that the hybridization is limited and hybrids return mostly to backcrossing with the parental species. This presumption also finds support in an analysis of the song structure: the yellowhammer and the pine bunting have songs of different, easily distinguishable dialects.

Keywords: birds, natural hybridization, isolating mechanism, song variability

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INTRODUCTION

Understanding the ways and mechanisms of speciation remains one of the most urgent problems in evolutionary biology. The key moment of speciation is the rejection of individuals of closely related species to form heterospecific couples. Therefore, one of the most used and productive approaches in studying the processes of speciation is detailed investigation of natural hybridization: analysis of the causes and consequences of the destruction of the system of reproductive isolation enables us to understand better the ways of its genesis and the mechanisms of functioning.

Among the numerous examples of natural hybridization in birds (Panov, 1989; McCarthy, 2006; Price, 2008), two extreme variants are the most common: (1) random hybridization between substantially diverging species in the wider zone of sympatry, which has no significant effect on the gene pools of the parent species and (2) mass hybridization between sister forms in the narrow zone of secondary contact. The intermediate type—more or less regular hybridization in a wide zone of contact—is much less common. According to Price (2008), the rarity of this type of

hybridization is explained by the fact that all these cases are examples of young hybrid zones, the situation in which is unstable and dynamically developing.

The case of natural hybridization of the yellowhammer (*Emberiza citrinella*) and pine bunting (*E. leucocephalos*) belongs to the rare third type of hybridization. The sympatry zone of these two species extends for 2500 km from the Ural Mountains to Lake Baikal. Throughout the entire contact zone, these species form mixed populations the phenotypic composition of which is susceptible to significant spatial and temporal dynamics. In particular, the proportion of phenotypic hybrids varies in different populations from 15 to 45%, but even in those populations where the proportion of hybrids reaches the maximum values, hybridization is limited: a significant share of the population consists of individuals of parental species that have no signs of hybrid origin (Panov et al., 2003, 2007; Rubtsov, 2007). The partial biotopic segregation contributes to the restriction of hybridization: in mountainous and hilly terrain, the pine bunting more often occupies the larch forests of the mountain slopes and the tops of hills, whereas the yellowhammer occupies floodplain forests of river valleys (ibid.).

In the course of previous research, we (Panov et al., 2003, 2007) described in detail the phenotypic composition of populations and the nature of interspecies relations of the yellowhammer and pine bunting in the eastern and central parts of the contact zone, but the situation in its western part, in the interfluvium of Tobol and Irtysh, remained unexplored. According to published data, both species are common here (Solov'ev, 2005) and form mixed colonies, the songs of males belonging to different species are easily distinguishable to the ear and phenotypic hybrids are absent (Kolpakova, 2005). These data contradict the results of our research, as in all the regions examined by us, the phenotypic hybrids accounted for a significant proportion of the population, while the songs of the two species under study were similar in structure, and the differences between them were manifested only in series. We are aware of the fact that even for professional ornithologists, not engaged in the problem of hybridization in a specific pair of species, it is very difficult to have a clear picture of the subtleties of coloration of the hybrids, especially given the fact that different specialists interpret the coloration variants differently, attributing them either to hybrids or to the manifestation of an intraspecific polymorphism (Stepanyan, 1983). On the other hand, on the basis of our own data, the level of hybridization between the yellowhammer and the pine bunting is susceptible to significant changes in different parts of the contact zone (see above); therefore, the existence of populations where hybridization is completely absent is quite feasible.

Revealing the nature of the relationship and, in particular, the level of hybridization between the yellowhammer and pine bunting in the forested steppe Trans-Urals in comparison with the other parts of the zone of contact and recreating a picture of their relationship are, in general, the main tasks of this work.

MATERIALS AND METHODS

The material on the nesting biology of two bunting species in the forested steppe Trans-Urals was collected in the course of an avifaunistic survey of this region in 1999–2015. Work was carried out at seasonal stations and at points of short-term research, including route ones, predominantly in Kurgan oblast, as well as in its immediate vicinity. In some years, in different places of the region, the density of the nesting of buntings was determined. In order to do this, an absolute counting of birds on test plots was performed by mapping the mating territories (according to Gudina, 1999). Plots with distinct contours served as the test sites (groves, felling sites, clearings, glades, etc.); their area was calculated using the space pictures of the terrain available in open access. The dimensions of the sites varied from 4 to 50 hectares, in total, in different years from 1.4 to 2.0 km². Each site was visited a minimum of two times. The data on 26 nests of the yellow-

hammer and 16 nests of the pine bunting were analyzed.

The dates of oviposition were calculated by the degree of their incubation, which, in turn, was determined by the method of flotation of eggs and by the age of the chicks. For both species, the duration of incubation was accepted to be 13 days and the duration of chicks staying in the nest was considered to be 12 days (Ryabitsev, 2008). The average timing of the beginning of nesting was calculated by the first clutches, which in turn were determined using the curve of the normal distribution that characterizes the first wave of nesting. Repeat and second clutches were not reflected in that curve, and hence they were not taken into account. In addition, the dates of the first sightings of flitting chicks were taken into account ($n = 3$ for the yellowhammer and $n = 2$ for the pine bunting), taking their age to be 17 days.

To identify the nature of hybridization in the yellowhammer and pine bunting in the forested steppe Trans-Urals, in the period from May 10 to May 22, 2014, we examined two localities in Kurgan oblast: Ketovskii district 30 km to the southeast of Kurgan (55.2° N, 65.3° E) and the vicinity of the village of Bugrovoe in the Zverinogolovskii district (54.7° N, 64.9° E) located about 80 km southwest of the first locality. From May 20 to May 27, 2015, we examined the surroundings of the Belozersk Nature Reserve in the Armizonskii district of Tyumen' oblast (55.8° N, 67.8° E) 170 km to the northeast of Kurgan (Fig. 1). Territorial males were attracted for recording of their song, and their phenotype was described by looking through binoculars with a 12-fold increase or photographing with a Nikon D7100 digital camera with the Nikkor Af-S300F4 telephoto lens. Some of the males described were caught for a more detailed description of the phenotype and blood sampling for further genetic analysis. The males were captured using a mist net made by Ecotone with a height of 2.5 m and a length of 3 m with a mesh size of 16 mm, beckoning them using a recorded song (sound trap method). The songs of some males were recorded using a Sennheizer K6/ME67 ("long gun") directional microphone and a Marantz PMD661 digital recorder (16 bits, 44.1 kHz) for the subsequent comparative analysis. To construct and analyze the sonograms, we used the SpectraLAB V4.32 program with a frequency and resolution of 43.066 Hz and 5.8 ms, respectively. In total, the phenotypes of 90 males were described, 21 of them were caught, and the songs of 36 males were recorded. The material was statistically processed in the Statistica 10 program; to compare the sampling, the Student's *t*-test, Fisher's test, chi-square test, and nonparametric Mann–Whitney test were used. For analysis of the quantitative characteristics of the song, factor analysis was used. In assessing the reliability of the statistical hypotheses, a 5% significance level was adopted.

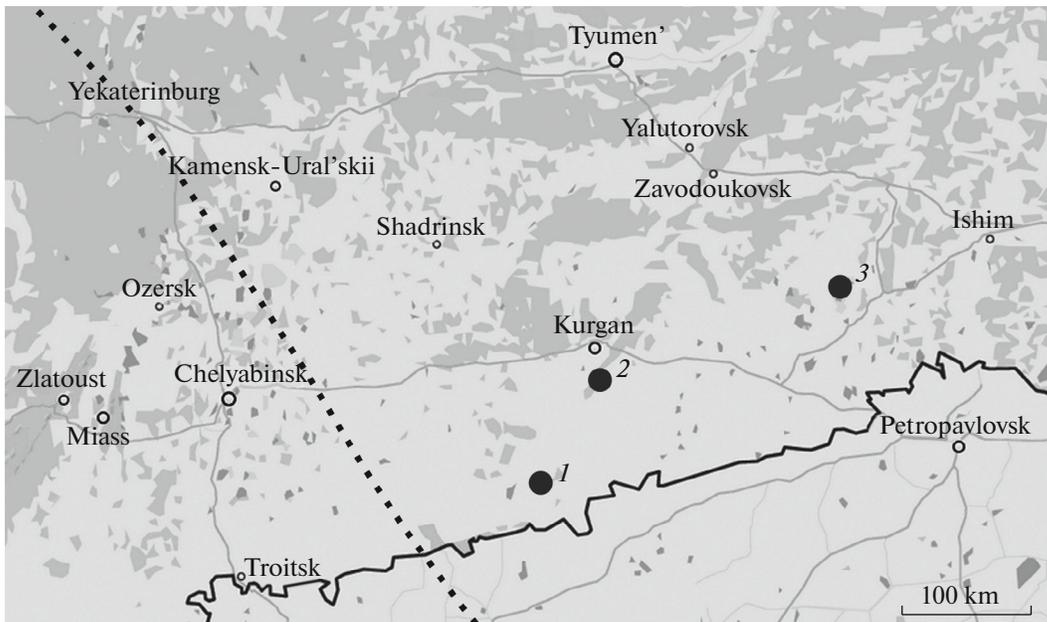


Fig. 1. The position of the key sites for studying the nature of hybridization of the yellowhammer and pine bunting: (1) Bugrovoe village, (2) Kurgan, (3) Armizonskoe village. The dotted line indicates the western boundary of the nesting range of the pine bunting (Ryabitsev, 2008).

To describe the phenotype of the captured males, we used three coloration parameters, each of which was ranged on an eight-point scale (Table 1), after which each male was placed into one of the eight categories (Table 2). When describing the phenotype of a male using binoculars or a photo, we used six categories: the phenotypic classes 1, 2 and 7, 8 were combined into “citrinella” (CT = PC + SC) and “leucocephala” (LC = PL + SL), respectively, due to the impossibility of identifying the differences between them.

RESULTS

Distribution and Abundance of the Yellowhammer and Pine Bunting in the Study Area

The forested steppe of the Trans-Urals is located in the center of the nesting range of the yellowhammer and at the western edge of the pine bunting’s range. Nowadays, the area of the latter continues to expand in the southwesterly direction. In the mid-20th century, it was distributed to the west of the Urals ridge (Danilov, 2003), and in the second half of the 20th century it “stepped over” the range and appeared nesting in the Permskoe Prikam’ye (Shepel’ et al., 2010). However, south of the latitude of Sverdlovsk, in the forested steppe zone, its range was located to the east and did not reach the Ural Mountains. In the 1980s, its was registered during the periods of migration in different places of the southern Trans-Urals, but during the nesting time it was only found in some places in the southern part of Tyumen’ oblast (Blinova and Blinov,

1997). Apparently, at that time, in the forested steppe of northern Kazakhstan, it did not yet nest there either (Vilkov, 2010). In the late 20th–early 21st century, this bunting assimilated the eastern half of Kurgan oblast. In 2001–2002, we found it very common in the Tobol-Ishim interfluvium (Tarasov et al., 2001) and in the Tobol valley in the southern part of the oblast (Ryabitsev et al., 2002), and later, in the forested steppe parts of northern Kazakhstan as well (Tarasov and Davydov, 2008). Over 25 years, the western border of the pine bunting expanded by approximately 350 km over the forested steppe and now passes along the eastern part of Chelyabinsk oblast (Kuz’mich et al., 2005; Tarasov and Bainov, 2009), where it is still very rare. With its advance to the east, its numbers are noticeably increasing (Table 3). In the central part of Western Siberia, it already dominates over the yellowhammer: in the forested steppe of Omsk oblast, the population density of the pine bunting in 1996–2004 in boggy birch stands was 35.3 ± 1.3 pairs/km². In dry valley stands, it varied from 5.7 ± 1.1 to 57.1 ± 1.1 , while the population density of the yellowhammer in swamped tree stands was 2.2 ± 0.5 and in the dry valley stands varied from 0 to 8.7 ± 0.9 pairs/km² (Kolkakova, 2005). In the Tobol-Ishim interfluvium, the abundance of pine buntings increased by an average of 15 times over 30 years (from the 1980s to the 2010s) and that of the yellowhammer decreased by four times. As a result, the pine bunting almost equaled the yellowhammer in abundance in this area (Table 3). Such growth in the numbers of pine buntings in the forested steppe of the Trans-Urals is consistent with the expansion of its

Table 1. Description of the phenotypic variability of hybrids of the yellowhammer and pine bunting: ranging the coloration traits

Point	Coloration trait		
	brown color on the throat	brown color on the brow	yellow color in the plumage
0	Absent	Absent	Bright yellow
1	Thin spotted moustache or brown spots on the sides of the throat	Around half of the feathers of the periorbital ring are brown	Lemon yellow, some parts (ears, forehead) are lighter than others
2	Thin but distinct short moustache	The periorbital ring is brown, the rest of the brow plumage is light	Light yellow, some parts (ears, forehead) are almost white
3	Thin and long or short and wide moustache	A small area of plumage around the eye is brown	Yellow hue over a large part of the head plumage
4	Wide brown moustache close in a thin stripe on the chin	About 30–40% of the brow plumage is brown (usually the lower part next to the eye)	Yellow hue on some parts of the head (throat, top of the head)
5	Wide brown moustache and a stripe on the chin, the throat is light	About half of the brow plumage is brown	The bend of the wing and/or edges of remiges are yellow, the rest of the plumage is white
6	Short brown throat (brown color continues past the ear coverts)	A small part of the brow plumage remains light (usually near the forehead and the top of the head)	Yellow tint on the wing bend or the edges of remiges
7	As in the pine bunting	The brow is entirely brown as in the pine bunting	Purely white, no yellow color anywhere

Table 2. Description of the phenotypic variability of the hybrids of the yellowhammer and pine bunting: phenotypic classes

Name (designation)		Coloration traits (points)		
		brown color on throat	brown color on brow	yellow color in plumage
Pure citrinella	(PC)	0	0	0
Almost citrinella	(SC)	1–2	0–2	0–2
Citrinella	(CT) = PC + SC	0–2	0–2	0–2
Citrinella-hybrid	(CH)	3–4	0–3	0–2
Yellow hybrid	(YH)	5–7	4–7	0–3
White hybrid	(WH)	0–3	0–3	3–7
Leucocephala-hybrid	(LH)	4–5	4–5	4–7
Almost leucocephala	(SL)	6–7	6–7	4–7
Pure leucocephala	(PL)	7	7	7
Leucocephala	(LC) = SL + PL	6–7	6–7	4–7

range in the southwesterly direction in recent decades. The decrease in the abundance of yellowhammers may have occurred as a result of competition and hybridization with the pine bunting.

Features of the Nesting Biology

The pine bunting in the forested steppe of the Trans-Urals is a migratory species, the yellowhammer is a partially wintering one. On March 7, 2004, in the vicinity of Dalmatovo, on a field near the curb of an asphalted road, a flock of over 100 yellowhammers was

found; in 2009, the same small group of these birds was observed on February 27; and on April 3, 2010, the singing males were already common there. In other years, we observed singing males from the very beginning of our field seasons: April 20, 2005; April 17, 2009; April 15, 2011; and April 18, 2013. Apparently, they began to sing even earlier. The first worrying specimens were registered on May 11, 2006.

Pine buntings appear in the 2nd half of April (about two weeks later than in the central forested steppe of Omsk oblast; Kolpakova, 2005). The first singing

Table 3. The density of the nesting population of the yellowhammer and pine bunting in forested habitats of the forested steppe Trans-Urals, individuals/km²

Place	Year	Yellow-hammer	Pine bunting	Source
West: Chelyabinsk oblast, Kunashakskii district	1978–2004	112–141	0	Korovin, 2004
"	2001–2005	74–103	0–11	Kuz'mich et al., 2005
"	2006	57	0	Our data
Center: Kurgan oblast, Ketovskii district	2004	55	10	"
Kustanaiskaya oblast, Mendykarinskii district	2008	155	6	"
East: Tyumen' oblast, Armizonskii district	1983	51	1	Blinova and Blinov, 1999
"	2012	7	21	Our data
Kurgan oblast, Makushinskii district	1984	76	3	Blinova and Blinov, 1999
"	2001	110	45	Tarasov et al., 2001
"	2002	52	33	Our data
"	2015	37	19	"
North Kazakhstan oblast, Zhambylskii district	2008	78	132	"

males were marked on May 3, 1999; May 9, 2008; and May 8, 2010, in the Dalmatovskii district, and on May 10, 2005, we still observed flying flocks of 10–20 individuals.

In most nesting parameters, the two species compared do not differ (Table 4). The differences are observed only in terms of nesting (the pine buntings begin to nest approximately four days later than usual) and egg size (on average, the eggs of pine buntings are longer and more variable in this feature). It should be noted that the terms of the onset of spring differed in different years, as well as in the number of nests found, which was used to estimate the beginning of breeding. To eliminate the “noise” introduced by the timing of the onset of spring and to compare the two species, we tried to link the dates of their breeding with a certain phenological phenomenon. The closest date to the beginning of breeding of both species was the date of flowering of the bird cherry. However, when we use this method of comparison, the differences between species disappear (on average, both begin egg-laying at the same time as the flowering starts) do not form a normal distribution of the sampling. Their dispersion does not decrease but, on the contrary, increases. Therefore, the way to estimate the date of the beginning of nesting by linking it to phenology proved to be not more but less reliable. The terms of nesting of the yellowhammer are more extended than those of the pine bunting: fresh clutches (evidently, the second ones) were found at the beginning July, whereas clutches of the pine bunting were only found until mid-June.

Kolpakova (2005) notes that, even in the conditions of a lack of biotopic segregation, the buntings nest in clusters in which individuals of one species gravitate toward each other. This is consistent with our observations: in 2007, in the Kazanskii district of Tyumen' oblast, in copses near Gusinoe Lake, out of the 15 singing males examined, one proved to be a hybrid, the rest were pine buntings. Near Zotkino Lake, on the contrary, of the six males considered, five were yellowhammers and one was a pine bunting (Tarasov et al., 2007). In 2015, in the Armizonskii district of Tyumen' oblast, the number of buntings was relatively low, and in some areas, where in previous years the buntings were numerous, they were not observed, while other similar sites were occupied by bunting colonies numbering up to 10–15 pairs.

As differences in the breeding biology of the two species compared, it should also be mentioned that the pine bunting places its nests a little farther from the clearings than the yellowhammer and, unlike the yellowhammer, does not arrange nests in glades.

The Phenotypic Composition of the Populations and the Biotopic Preferences

The breeding biotopes in the forested steppe Trans-Urals are similar for both species. These are mainly birch groves and copses among the fields, clearings of aspen–birch and pine forests, overgrown felling sites, and shrubby floodplains of rivers with birches and poplars. Pine buntings tend to nest in taigalike (pine or aspen) forests cluttered with brushwood. The birds of

Table 4. Nesting parameters of the yellowhammer and pine bunting in the forested steppe Trans-Urals, $M \pm m$ (min–max; n)

Parameter	Yellowhammer	Pine bunting
Nest diameter, mm	103 ± 11 (90–130; 4)	110 ± 12 (80–130; 4)
Nest height, mm	75 ± 6 (65–80; 3)	78 ± 18 (65–90; 2)
Tray diameter, mm	67 ± 4 (60–75; 4)	70 ± 8 (60–90; 4)
Tray depth, mm	51 ± 3 (45–55; 4)	50 ± 5 (40–60; 4)
Distance from the nest to the edge of the clearing (outmost trees), m	18 ± 7 (2–70; 11)	37 ± 15 (10–100; 6)
Date of laying the first egg*	May 9 ± 1 day (April 28–May 26; 23)	May 13 ± 2 days (April 30–May 27; 16)
Size of the clutch, number of eggs	4.52 ± 0.13 (3–5; 23)	4.60 ± 0.20 (3–6; 15)
Egg length, mm**	20.81 ± 0.12 (18.4–23.4; 56)	21.49 ± 0.25 (18.7–24.3; 33)
Egg diameter, mm	16.02 ± 0.09 (14.2–17.4; 56)	16.11 ± 0.10 (14.8–17.1; 33)

The parameters in bold indicate statistically significant differences between the samplings.

* Nonparametric Mann–Whitney test.

** Student's and Fisher's parametric tests.

Table 5. Phenotypic composition of the yellowhammer and pine bunting populations in various locations and habitats

No.	Locality, habitat	CT	CH	YH	WH	LH	LC	n
1.	Kurgan	23 (72%)	2 (6%)	1 (3%)	2 (6%)	3 (9%)	1 (3%)	32
2.	aspen–birch groves	13	2	–	1	2	1	19
3.	clearings of a pine forest	10	–	1	1	1	–	13
4.	Zverinogolovskoe	8 (44%)	1 (6%)	5 (28%)	–	3 (17%)	1 (6%)	18
5.	clearings of a pine forest	6	1	2	–	–	–	9
6.	felling sites in pine forest	2	–	3	–	3	1	9
7.	Kurgan + Zverinogolovskoe	31 (62%)	3 (6%)	6 (12%)	2 (4%)	6 (12%)	2 (4%)	50
8.	Armizonskoe aspen–birch groves	17 (43%)	4 (10%)	2 (5%)	4 (10%)	1 (3%)	12 (30%)	40

both species avoid solid forest massifs. Mapping the mating territories of males of different species showed that they do not overlap. The males of the same species treat both the males of their own and other species as rivals and protect their territories from invasions equally strictly.

In 2014–2015, the yellowhammer and pine bunting were found by us in three types of habitats. (1) Small aspen–birch groves, often bogged in the center and dry around the edges. (2) Aspen–birch edges of pine forests. (3) Cluttered felling sites in pine forests with heaps of dead fallen trees and a weak grass cover. The results of counting the phenotypes of the territorial males in different locations and habitats are presented in Table 5. An analysis of the data presented allows us to conclude the following.

(1) The phenotypic composition of the populations inhabiting the clearings and groves is identical:

a comparison of samplings [2] and [3]: $\chi^2 = 0.48$, $df = 2$, $p = 0.79$.

(2) The phenotypic composition of the Kurgan and Zverinogolovskii populations is also the same: a comparison of samples [1] and [4]: $\chi^2 = 3.72$, $df = 2$, $p = 0.16$; a comparison of samplings [3] and [5]: $\chi^2 = 0.28$, $df = 1$, $p = 0.60$.

(3) Birds with the appearance of the pine bunting more often occur on felling sites, and the differences in the phenotypic composition of the populations from felling sites and clearings are statistically significant: a comparison of samples [5] and [6]: $\chi^2 = 6.0$, $df = 2$, $p = 0.05$; a comparison of samplings [1] and [6]: $\chi^2 = 7.64$, $df = 2$, $p = 0.022$.

(4) Farther to the southwest, the phenotypic composition of populations also varies (comparison of samplings [7] and [8]: $\chi^2 = 16.7$, $df = 5$, $p = 0.005$): the proportion of pine buntings is sharply reduced and the

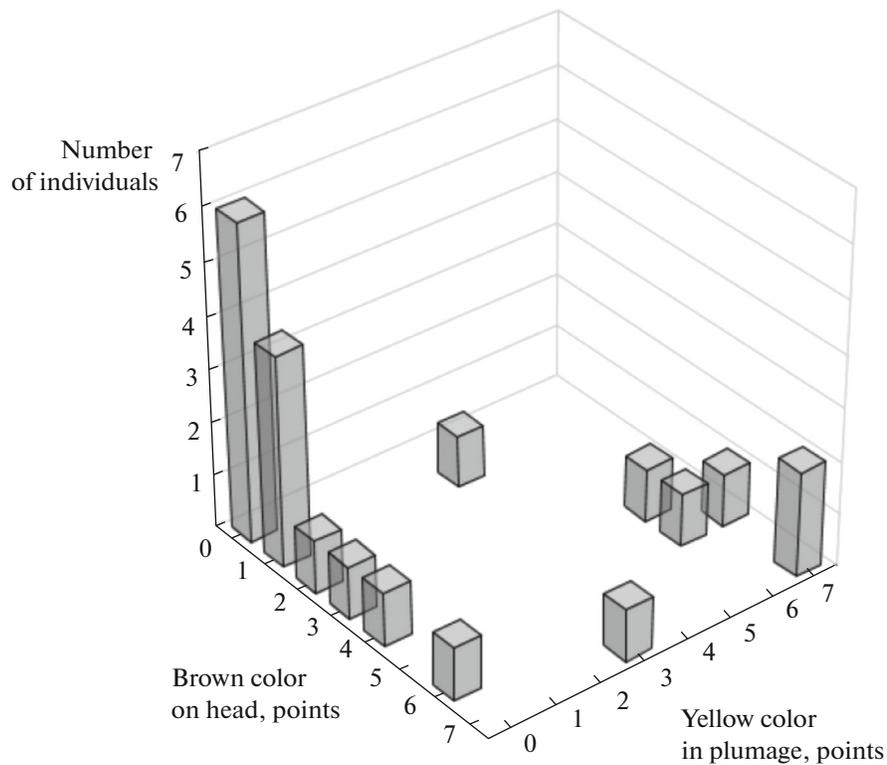


Fig. 2. The diversity of the phenotypic variability of males in the hybrid population of the yellowhammer and pine bunting in Kurgan oblast ($n = 21$).

share of pine bunting hybrids (LH) increases, while the total proportion of birds with a pine bunting's appearance (LC + LH) does not change considerably (the differences do not reach the level of statistical significance: $\chi^2 = 3.38$, $df = 1$, $p = 0.066$). However, the share of hybrids of the remaining phenotypic classes (WH, YH, CH) remains on the same level (25 and 22%, respectively), the differences in the ratio of different phenotypic classes of hybrids between the two locations is statistically insignificant ($\chi^2 = 2.77$, $df = 2$, $p = 0.25$).

(5) With a more formal approach, the total share of phenotypic hybrids (CH + YH + WH + LH) is maximum at the southwestern boundary of the sympatry zone (sampling [4], 50%) and significantly decreases farther away from it (sampling [1], 25%; sampling [8], 28%), although the differences do not reach the level of statistical significance, which can probably be explained by the insufficient volume of the samplings: comparison of samplings [4] and [1]: $\chi^2 = 3.21$, $df = 1$, $p = 0.073$; comparison of samplings [4] and [8]: $\chi^2 = 2.78$, $df = 1$, $p = 0.095$.

In 2014, in Kurgan oblast, 21 males were caught by us, which allowed us to perform a more detailed analysis of their coloration. Earlier, we (Panov et al., 2003) showed that the signs of chestnut coloration of the throat and eyebrows correlate quite strongly ($r = 0.6$), while the sign of yellow color in the coloration of the

contour feathering does not depend on the first two. This allowed us to merge the first two traits into one by calculating the arithmetic mean between them. The results of the analysis are shown in Fig. 2. The graph shows that the frequency distribution of findings of individuals in the space of the two coloration traits is bimodal: the individuals with hybrid traits are grouped around two centers, phenotypically pure yellowhammer and pine bunting. This indicates the limited nature of hybridization: the forming hybrids, apparently, participate in back crossings with the birds of the parental phenotypes, which prevents further increase in the level of hybridization.

Variability of the Song

The nature of the variability of the song, terms used.

The songs of the yellowhammer and pine bunting are similar in structure and represent short trills with a duration of 2.5–3 s, consisting of the initial *series of homotypic signals* and one or two long *end notes* (Fig. 3). The signals in the initial homotypic series are composed of one, two, or three notes and are performed in the course of a series strictly stereotypically or with a small frequency or time modulation. In relatively rare cases, in the course of performance of a homotypic series, the configuration and/or the mutual the posi-

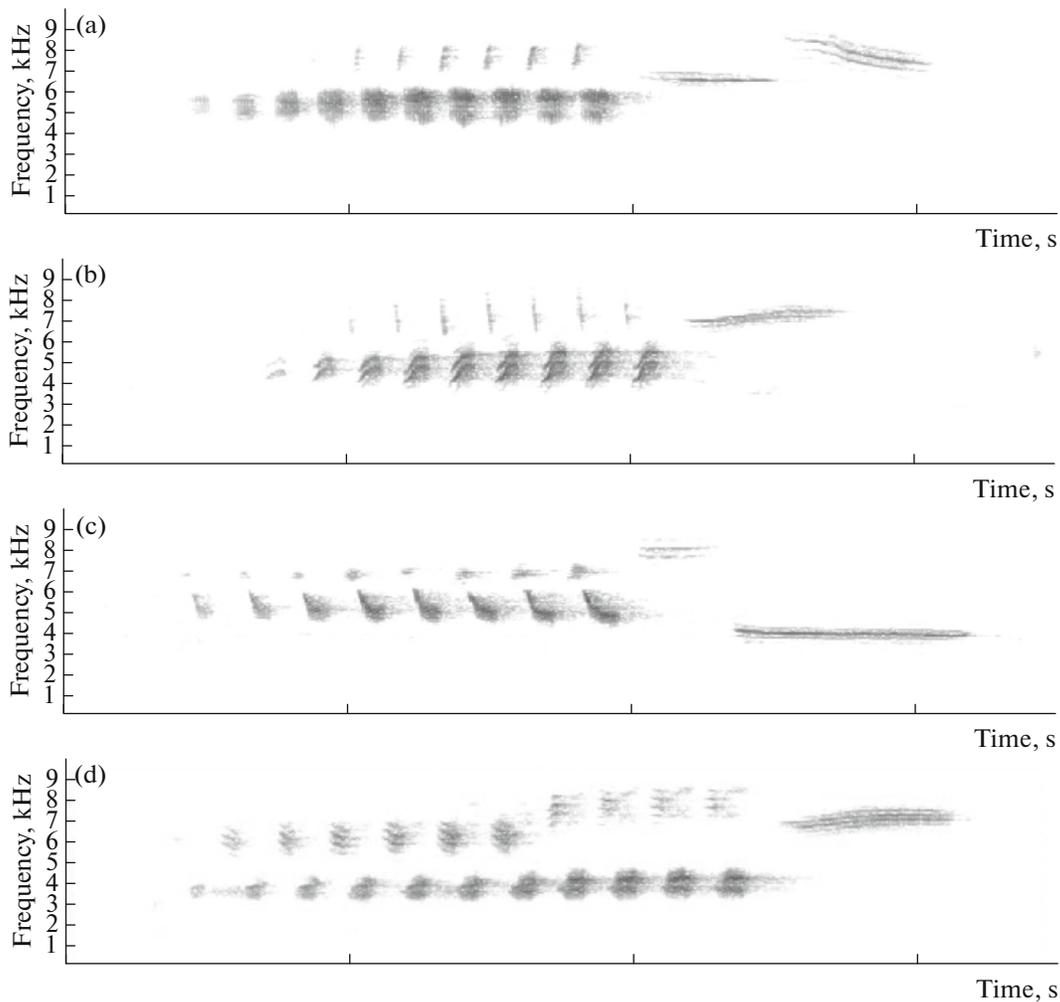


Fig. 3. Examples of sonograms of the songs of yellowhammers and pine buntings in Kurgan oblast: (a) “tii-zi-i” tune (yellowhammer), (b) “zii” tune (yellowhammer), (c) “zi-tii” tune (pine bunting), and (d) example of a song with a varying structure of signals of a homotypic series.

tion of notes in the signal change, in which case the homotypic series itself consists of two parts (Fig. 3d).

The repertoire of every male includes two or three (rarely more) *variants* of the song differing in the configuration and the relative arrangement of notes in the signal of the homotypic series. The songs of one variant are performed by a male strictly stereotypically: only minor variations are observed in the number of signals in a homotypic series (± 1). In addition, the male may not sing the song to the end, by omitting one or both of the end notes, which, probably, reflects the emotional state of the bird. This makes it possible to analyze not all the songs of a given male, but only one of each variant. Different males have similar, often completely identical versions of the song. We define similar individual variants of the song performed by different males as belonging to the same *type of song*.

Different combinations of end notes of a song form various *tunes*. There are three types of end notes,

which in the English language literature (Cramp and Perrins, 1994) are called according to their sound “tii,” “zi,” and “zii.” The name of the tunes is composed of the names of notes forming it (Fig. 3). The variability of tunes has the nature of song dialects: usually in one population all birds sing only one tune, each dialect has its own area of distribution, and in the populations located on the boundaries of dialect ranges, the birds perform different tunes corresponding to two dialects. This was the situation we observed in the forested steppe Trans-Urals. Since in this case we are talking about an intrapopulation rather than geographic variability, we consider that the term “dialect” in this context is not entirely justified.

Variety of tunes. In the research area, we recorded three tunes, two of which were described earlier (Rubtsov, 2007). The “tii-zi-i” (Fig. 3a) tune corresponds to the south Ural dialect, which was found in the allopatric populations of yellowhammers in Chel-

Table 6. Use of various tunes by the yellowhammer and pine bunting males

Phenotype	Kurgan oblast				Tyumen' oblast			
	tii-zi-i	zi-tii	zii	<i>n</i>	tii-zi-i	zi-tii	zii	<i>n</i>
CT	14 (58%)	1 (4%)	9 (38%)	24 (9)	2 (16%)	5 (42%)	5 (42%)	12 (7)
LC + LH	—	11 (85%)	2 (15%)	13 (6)	—	9 (90%)	1 (10%)	10 (5)
CH + YH + WH	5 (50%)	—	5 (50%)	10 (5)	2 (25%)	1 (13%)	5 (62%)	8 (4)

yabinsk and Orenburg oblasts. The “zi-tii” tune (Fig. 3c) corresponds to the Siberian dialect, which covers the central (Novosibirsk, Barnaul, Altai) and eastern (Sayan mountains, Baikal) parts of the sympatry zone, where this dialect is performed by males of both species.

The third tune was not previously described by us. It contains only one end note, similar to on the note “zi,” but approximately two times longer and with an increasing frequency modulation (Fig. 3b). We designated this note and the corresponding tune as “zii.” We assume that this tune has a very limited area of distribution and is found only in the region of overlapping of the “ranges” of dialects “tii-zi-i” and “zi-tii.” The “zii” tune itself can be interpreted as transitional between these two dialects. This point of view is confirmed by the fact that we have found a tune, which is intermediate between the tunes “zii” and “zi-tii”: in the songs of four males, after the note “zii” there was the note “tii,” but the first note retained its characteristic features, which distinguished these songs from the “zi-tii” tune.

Table 6 shows the data on the frequency of using these three tunes in the repertoire of males depending on their phenotype and locality. It can be seen from the table that birds with the appearance of the pine bunting predominantly used the “zi-tii” tune, while yellowhammers and hybrids used the two other tunes. The differences in the repertoires of the yellowhammer and pine bunting males are statistically significant for both locations: for Kurgan oblast: $\chi^2 = 39.3$, $df = 6$, $p = 1 \times 10^{-6}$; for Tyumen' oblast: $\chi^2 = 19.6$, $df = 6$, $p = 0.003$. The repertoires of the pine buntings from Kurgan and Tyumen' oblasts are similar, whereas the repertoires of yellowhammers undergo significant changes: with the advancement to the east, the share of the “tii-zi-i” tune decreases, while that of the “zi-tii” increases. The differences are statistically significant: $\chi^2 = 10.3$, $df = 3$, $p = 0.016$.

Individual variants of the song. The diversity of individual variants of the song is extremely large, but at the same time, different males have similar, often completely identical variants. Earlier we showed that the number of similar song variants in the two populations compared is inversely proportional to the distance between them (Rubtsov, 2007). Obviously, this similarity cannot be explained by random reasons and they are “inherited” by males from each other as a

result of imprinting. In this case, the number of similar variants of the song among different phenotypic classes in a hybrid population can be used as an indirect estimation of the assortativeness of mating and, accordingly, of the intensity of hybridization: in the same way as a male can learn a song from a male of another species, a female can capture the appearance of a heterospecific sexual partner. For both localities studied, the number of repetitive individual song variants in birds of different phenotypic classes does not differ significantly from that theoretically expected, calculated on the basis of an assumption about the random nature of their distribution (Table 7): Kurgan oblast: $\chi^2 = 6.6$, $df = 5$, $p = 0.25$; Tyumen' oblast: $\chi^2 = 6.1$, $df = 5$, $p = 0.29$.

The differences in the quantitative parameters of the song. To identify the differences between the parental species and in the quantitative parameters of the song, 76 individual songs from 36 males were analyzed by 14 parameters (Table 8). Since in the area of research, the songs of the species under study can be reliably distinguished by the configuration of end notes, this analysis was used only for the initial homotypic series of signals. Using the method of principal components with the scree criterion, four new variables were distinguished (factors) explaining in total 59% of the general variability. To simplify the structure of the factors, they were “varimax normalized.” For each of the four factors selected, we evaluated the significance of the differences between the songs of yellowhammers and pine buntings using Student's *t*-test. For the identification of the songs of the yellowhammer and pine bunting, factors 1 and 3 are suitable: only for these factors were significant differences in the mean values between the samplings observed. The correlation coefficients between the factors and the initial characteristics can serve to interpret the nature of the factors. Factor 1 can be called a factor of frequency song modulation: in the songs with a low value of this factor, the initial and final signals of the homotypic series are executed at the same frequency, at high values of the factor, the frequency of the signal increases as the song progresses. Factor 3 is negatively correlated with the duration of pauses between the signals in series: at lower values of the factor the pauses are longer. As Fig. 3 shows, although on average the songs of the yellowhammer are more frequency-modulated than those of the pine bunting and the pauses between the

Table 7. Number of similar variants of song among the males of different phenotypic classes in two localities of the forested steppe Trans-Urals

Pairs of phenotypic classes	Kurgan oblast		Tyumen' oblast	
	expected	real	expected	real
citr-citr	7.1	7	3.2	4
hybr-hybr	1.2	0	1.4	1
leuc-leuc	4.3	8	2.2	0
citr-hybr	5.8	8	4.3	8
citr-leuc	11.1	8	5.3	4
hybr-leuc	4.5	3	3.6	3
<i>n</i>	34	34	20	20

(citr) Yellowhammer (CT), (leuc) birds with the pine bunting's appearance (LC + LH), (hybr) other phenotypic hybrids (CH + YH + WH).

signals are shorter, these differences are extremely unreliable for the identification of their songs.

DISCUSSION

Earlier, we (Panov et al., 2003) showed that the relations between the yellowhammer and pine bunting in the area of contact are of a dynamic nature. Over 100 years, the zone of sympatry has extended to the east by about 1 thousand km, and over the last 30 years of the 20th century, in the environs of Novosibirsk and the northwestern foothills of the Altai (Zmeinogorsk), the once numerous pine bunting population has completely disappeared, and the share of phenotypic hybrids reached 45%, the maximum among all studied populations in the contact zone. Given these facts, it can be assumed that hybridization between the yellowhammer and pine bunting has intensified recently, probably not more than 250–300 years ago, due to anthropogenic influence on their habitats (Rubtsov, 2010). The results outlined in this paper, which are, in general, in agreement with this conclusion, significantly expand and complete the overall picture.

The zone of sympatry between the species studied expanded not only through the expansion of the yellowhammer in the easterly direction, but also as a result of the dispersal of pine buntings to the west. At the end of the 20th century, this species was only sporadically encountered during the breeding period in the southern Tyumen' and eastern Kurgan oblasts, but over the last 10–15 years, it has become a common nesting species in the area by expanding its range to the west by approximately 350 km. It is logical to assume that in the past the pine bunting was also absent in Omsk oblast, and the contact zone of the species studied occupied the eastern extremity of the West Sibe-

rian plain, being probably localized in the northwestern foothills of Altai and Kuznetsk Alatau. In fact, judging by the regional ornithological reports, the pine bunting was absent in the vicinity of Omsk in the late 19th century (Finsch, 1879; Slovtsov, 1881; Morozov, 1898, quoted by Solov'ev, 2005), but in the 20th century it became a common species, even exceeding the yellowhammer in abundance (Kots, 1910; Lavrov, 1925).

The hybridization between the two species studied increases in the conditions of the rarity of specific partners, for example, at the border of the range of one of the species. But even in this case, the positive assortativeness of mating seems to persist: the hybrids are involved mainly in back crosses with newly arriving individuals of the assimilating species, thereby preventing an increase in the level of hybridization. In this respect, a comparison of the phenotypic composition of the mixed populations in the southern part of Tyumen' and Kurgan oblasts is of interest. With the advance to the southwest, the number of pine bunting hybrids abruptly increases, while that of pine buntings decreases, whereas the total share of these phenotypic classes in mixed populations does not change significantly (Table 5). The highest proportion of hybrids of various phenotypic classes (50%) is observed in the southern part of Kurgan oblast, near the boundary of the pine bunting's range, whereas farther from the border deeper into the zone of the sympatry, their proportion is much smaller (25–28%). It is likely that with the advance to the east their share will continue to decrease. Not surprisingly, in Omsk oblast, Kolpakova (2005), having passed 205 km of survey routes and having captured 92 individuals, could not find them at all, although a complete absence of phenotypic hybrids appears improbable. It should be noted that,

Table 8. Results of factor analysis of the songs by quantitative parameters: the coefficient of correlation of the distinguished factors with the initial traits and their significance for species discrimination

Initial trait	Factor 1	Factor 2	Factor 3	Factor 4
1. Duration, s	0.679576	-0.263889	0.387710	-0.170890
2. Minimum frequency, kHz	-0.692892	0.206018	0.256368	-0.009129
3. Maximum frequency, kHz	0.621893	0.113438	0.159618	0.169696
4. Main frequency, kHz*	0.064596	0.169379	-0.099461	0.607778
5. Number of signals of the variant	0.306101	-0.877252	0.168504	-0.062935
6. Number of notes in the signal	0.277733	0.432076	-0.068748	0.396536
7. Average duration of the signal	0.051121	0.882594	0.107359	-0.147944
8. Coefficient of variation of signal duration	-0.212850	-0.447693	0.328882	0.487785
9. Coefficient of correlation of the signal with its number in the series	-0.170039	-0.180529	0.359191	0.599421
10. Average duration of the pause between the signals	-0.130854	0.091694	-0.834392	0.216832
11. Coefficient of variation of the duration of the pause	0.031803	0.031257	0.811896	0.172767
12. Coefficient of correlation of the duration of the pause with the number of the signal in the series	-0.071753	0.085820	0.055833	-0.561885
13. Coefficient of variation of the signal frequency	0.674075	-0.052046	0.064467	0.008575
14. Coefficient of correlation of the signal frequency with its number in the series	0.718686	0.200243	-0.038997	-0.012177
The proportion of the explained variability	0.183906	0.155818	0.135530	0.114329
The level of significance of the differences between the parental species, <i>t</i> -test (<i>p</i>)	0.0003	0.69	0.036	0.106

In bold: (1) coefficients of correlation of the factors with the initial traits, the values of which are higher than 0.6; (2) probability values lower than 0.05. The initial traits belong only to the series of homotypic signals. Since in this region, the songs of buntings differ in the type of end notes, their parameters were not taken into account in this analysis.

* The frequency that has the maximum value of total energy.

in the populations of the forested steppe Trans-Urals, the decrease in the proportion of phenotypic hybrids occurs mainly due to a sharp decrease in the number of pine bunting hybrids, whereas the proportion of hybrids of the other phenotypic classes remains at the level of 22–25%. It is approximately in this ratio that the hybrids were found in most of the previously studied populations in the zone of sympatry, while the minimum share of phenotypic hybrids did not fall below 7–10% (Panov et al., 2003, 2007).

The limited nature of hybridization is attested to by the fact that even at the border of the range, in the conditions of an increasing level of hybridization, the pine bunting retains its bio-logical features: while the yellowhammer is partially sedentary, the pine bunting is a migratory species; the eggs of the pine bunting are

slightly larger. The latter fact appears to be a little unexpected, given that these two species hardly differ in body size (Panov et al, 2003). Taking into account that in the forested steppe Trans-Urals the length of the eggs of pine buntings is larger not only in mean values but also in terms of variance (Table 3), it is possible to presume that this species is subjected here to the pressure of driving selection (as a settling species), and on the border of the range, a selective advantage is enjoyed by the individuals bearing larger eggs. The increase in the size of eggs in this case can only be due to their length, as their diameter is limited by the size of the oviduct. However, this hypothesis requires more detailed verification, in particular, comparing the sizes of eggs from other populations.

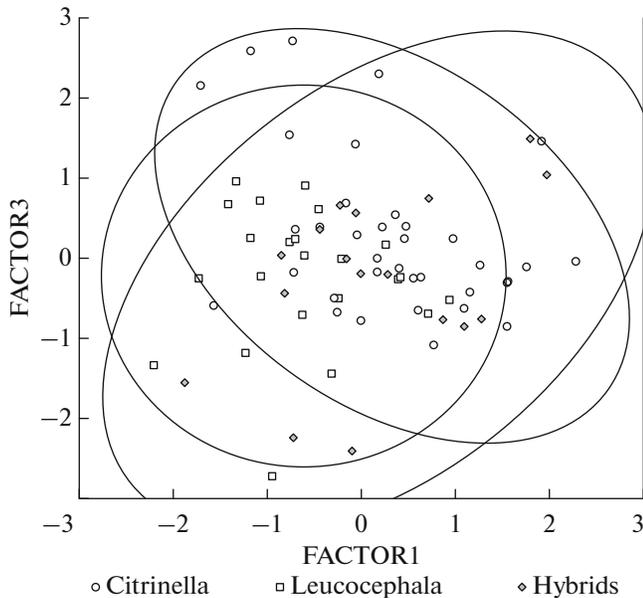


Fig. 4. Distribution of songs of the yellowhammer and pine bunting in the space of two factors: results of factor analysis by the quantitative parameters of the song.

The limitation of hybridization is facilitated by the partial biotopical segregation. In the previous studies, we (Panov et al., 2003, 2007) showed that in a mountainous and hilly area pine buntings prefer to occupy larch forests of mountain slopes, and the yellowhammer inhabits shrub thickets and floodplain forests of river valleys. In this paper, we showed that partial biotopical segregation persists on the plain as well: the pine bunting willingly occupies forest felling sites, which the yellowhammer tries to avoid. It is possible that precisely because biotopical segregation is more strongly expressed in the forest zone, the movement of the pine bunting to the west is faster in the northern areas. According to our observations, insignificant biotopical segregation exists in the forested steppe zone as well: pine buntings more willingly settle in the aspen groves littered with fallen wood, whereas yellowhammers prefer birch groves. So far, we have not been able to confirm this conclusion statistically.

The main isolating mechanisms, which limit the hybridization between the yellowhammer and pine bunting, are the ethological factors, first of all, the sharp differences in the mating color of males. Unfortunately, we do not have sufficient data on the composition of the mating couples to assess directly the assortativeness of mating in mixed populations. However, data on the number of similar song variants of the males of different phenotypes allow us to make an indirect assessment of the assortativeness of mating: to the same extent as young females can capture the image of the “wrong” partner (or choose a pair contrary to the image), young males can learn to sing a song from a heterospecific male. Previously, we

(Rubtsov, 2007) showed the effectiveness of this method: in the Baikal region, where both species are present in approximately equal proportions and the proportion of phenotypic hybrids is low (30%), no similar versions of the song between the males of different species were found; in Altai, where the share of the phenotypic hybrids is maximum (60%), the distribution of similar variants of the song does not differ from accidental; in the vicinity of Barnaul, the share of hybrids is 45%, and the pine bunting occurs about three times less frequently than the yellowhammer. The share of similar variants of the song in conspecific males is higher here than expected (although the differences do not reach the level of statistical significance). In the forested steppe Trans-Urals, the distribution of similar variants of the song does not differ from random (Table 6). For Kurgan oblast, as expected, this result confirms the conclusion that the level of hybridization intensifies near the border of the pine bunting’s range. However, in Tyumen’ oblast, we would have to observe some deviations from the random distribution. The fact that this does not happen can probably be explained by the proximity of the two populations studied to each other and the intensive exchange of individuals between them.

The differences in the structure of songs, apparently, do not play a decisive role in the recognition of conspecific individuals in the two species, which would be comparable with the signs of mating coloration (Panov et al., 2003). The songs of the yellowhammer and pine bunting have the same organization and cannot be reliably diagnosed even with the help of powerful tools of multidimensional statistical analysis, although the differences in the average values are preserved over the entire contact area (Rubtsov, 2007), including the study area (Fig. 4). However, each local mixed population has its own additional parameter, which allows us to determine the species status of a bird by its song sufficiently reliably (Rubtsov, 2007). In the forested steppe Trans-Urals, it is a combination of end notes that form various tunes. As noted above, the variability of tunes in different populations of the species under study has the nature of song dialects. In Kurgan oblast, yellowhammers mainly perform the (“tii-zii-i”) tune, which corresponds to the south Ural dialect, while pine buntings perform a “zi-tii” tune (Siberian dialect). In the eastern regions, yellowhammers also perform the songs of the Siberian dialect (Rubtsov, 2007), so there is nothing surprising in the fact that in Tyumen’ oblast many yellowhammers also have this dialect. As for the third tune (“zii”), which is also performed mainly by the yellowhammer males, as we believe, it exists only in the zone of contact between the Siberian and South Ural dialects of the yellowhammer and is, probably, the product of their interaction.

Thus, summarizing the above, we can state that mixed populations of the yellowhammer and pine bunting in the forested steppe Trans-Urals formed at

the end of the 20th century as a result of the settlement of the pine bunting in the westerly direction. This colonization is accompanied by hybridization, which is quite intensive due to the rarity of the settling species but which dies away rapidly when its numbers increase. As a result, hybridization has no significant effect on the phenotypic originality of the species, probably because hybrids are mainly involved in back crossings with parental species, which is indirectly confirmed by the analysis of their phenotypic variability (Fig. 2).

As for longer prospects of the coexistence of the yellowhammer and pine bunting in a wide area of contact with limited regular hybridization, we consider this situation unstable: the natural fluctuations in population numbers will lead to an increase in the level of hybridization, which will ultimately lead to the disappearance of one of the species. This assumption is based on observations in the central part of the sympatric zone (Novosibirsk oblast and Altai krai), where hybrid populations have existed for a longer period of time (Panov et al., 2003, 2007). In that region, the pine bunting, which was once numerous throughout the forested steppe, has completely disappeared in the last 40 years. This species is preserved in insignificant numbers only along belt forests (Panov et al., 2007), obviously, due to more pronounced biotopical segregation in the forest zone. We cannot say definitely why the yellowhammer is proving to be a more competitive species. It may be associated with its partially settled way of life, as a result which it appears in the nesting grounds slightly earlier than the pine bunting.

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