Spatial Heterogeneity of Bird Communities in the Natural Landscapes of the Southern Taiga of the Ob–Yenisei Interfluve and the Chulym River Valley (Tomsk Region)

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Abstract The study area covers the Ob-Yenisei interfluve in the southern taiga zone of Western Siberia within the Tomsk region. On this territory in 2012, 2013 and 2017, the spatial heterogeneity of bird communities in the summer on routes stretching more than 350 km was studied. Thirty-nine habitats in the taiga, forest and swamp landscapes of the rivers and floodplains of large and medium rivers, as well as lesopolye landscapes of agricultural lands were surveyed. When analyzing the data, all of them are combined into 12 main types of landscape tracts, reflecting the diversity of natural conditions of the study area along the gradient from southeast to northwest along the Chulym river valley. Significant differences in population density, species richness and composition of the dominant bird species were established. In taiga and forest habitats there was a significant decrease in these indicators from north to south, which correlates with the overall productivity of cenoses and a variety of forest vegetation conditions. In floodplain intrazonal landscapes, spatial variability of bird communities is not associated with latitudinal differences, but is determined by such environmental factors as water encroachment onto territories, forest cover and population density within landscape tracts.

1. Introduction
Study of the spatial structure and heterogeneity of animal populations has been the subject of much research carried out within the framework of landscape or factorial zoogeography. Such research has been actively developed by Siberian scientists since the mid-1970s [1]. Detailed materials on the summer population of birds of the Tomsk Prichulymye, collected in 1998–2002, are presented in Blinova and Samsonova [2]. Our research aims to identify a possible trend in the spatial changes of bird communities from the southeast to northwest along the Chulym river valley in the main taiga, forest, forest-meadow and marsh landscapes of the Ob-Yenisei interfluve within the Tomsk region (the total length of the gradient is about 700 km). According to the spatial-typological classification of the bird population in the central region of Northern Eurasia, this district is classified as forested, with subtypes of southern taiga, subtaiga forests, including forest-meadow floodplains of large rivers, and raised bogs, as well median plains rivers, channels, freshwater lakes and salt lakes [3].

2. Materials and methods
Bird counts on regular routes were conducted in May–July 2012, 2013 and 2017 in Teguldetsky, Zyryansky and Molchanovsky districts of Tomsk region. Recalculation of the number of individuals encountered per species per unit area (abundance, in individuals per km²) was carried out according to the average detection distance; the total population density is the sum of the abundance of all the bird species encountered in a particular habitat [1 and 4]. Of particular interest were the districts of Tongulsky (Kiya-Chulym interfluve) and Verkhne-Sorovsky (Ob-Chulym interflue in the lower reaches of the Chulym River) zoological reserves and key bird territories of federal importance Middle Prichulymye [5]. The least studied so far in terms of ornithology is the Ulukh-Chayakh swamp system in the upper Prichulymye, included in the Russian list of especially valuable wetlands promising for expanding the network of wetlands of international importance [6], as well as the inter-river swamp-forest array Chelbak. For more complete coverage of the studied area, use was made of materials collected by other authors in 1994 in the inter-river landscapes of the Teguldetsky district in the neighborhood of the village Chet-Countorka [7]. A total of 32 habitats were surveyed, combined into 12 types of landscape tracts, reflecting the diversity of natural conditions, according to which averaged or interval data are analyzed. The total length of hiking routes was more than 350 km, and the total length of boat routes amounted to more than 300 km.

3. Results and discussion

The observation period covers the arrival and nesting periods of most birds. It is the numerous and typical breeding species that make up the group of dominant (% of total density) and background (more than 1 individual per km²) species that determine to the greatest extent the appearance of bird communities, differences in species composition and total numbers, and also reflect the connections of birds with productivity, forest vegetation, fodder, protective and other conditions in different habitats. Therefore, it is legitimate to speak of nesting population density, both of individual species and communities as a whole.

In the dark coniferous forests along the gradient from south to north, most birds were in the Upper Prichulymye, fewer were in central part of the Yaya-Chulym interfluve in the Zyryansky region and even fewer in the Lower Prichulymye on the Ob-Chulym interfluve (537, 373 and 236 individuals per km²) a gradual decrease in species diversity (Table 1). This was even more clearly illustrated in dark-coniferous forests of the Kiya-Chulym interfluve, growing south-west and representing the taiga landscapes of the northern spur of the Kuznetsky Alatau, with arrays of indigenous taiga dominated by fir and various varieties of the dark coniferous forests along the Kiya, Chet and Tongul river valleys. In 1994 the abundance of birds in such forests on the watersheds reached 615, and in the riverbed part of the valleys in the fir – 909 individuals/km² [7]. Absolute domination (9–14%) by the willow tit Parus montanus (Bald.) was observed in every location, with an abundance of more than 100 individuals/km²; only in the dark coniferous forests of the Lower Prichulymia was it 2–3 times less. The group of co-dominants included the chiffchaff Phylloscopus collybita (Vieill.), Chaffinch Fringilla coelebs (L.), bramble finch Fringilla montifringilla (L.), coal tit Parus ater (L.), pallas’s warbler Phylloscopus proregulus (L.), olive-backed pipit Anthus hodgsoni (L.), nuthatch Sitta europea (L.), hazel grouse Tetrastes bonasia (L.), in some years (except for the Lower Prichymya) goldcrest Regulus regulus (L.) and blue nightingale Larivora cyan (Pall.), and in the marshy valley areas there was also the song thrush Turdus philomelos (L.), long-tailed tit Aegithalos caudatus (L.) and greenish warbler Phylloscopus trochiloides (Sund.). Only in 1994 did the abundance of the seldom observed rustig bunting Emberiza rustica (L.), red-flanked bluetail Tarsiger cyanurus (L.) and mugimaki flycatcher Muscicapa-mugimaki (Temm.) reach 10 or more individuals/km² [7].

In mixed coniferous-deciduous and birch-aspen forests, a trend towards a reduction in the bird population density and species diversity from south to north was maintained: in coniferous-deciduous forests from 715 individuals/km² in the Upper Prichulymye to 395 in the Lower Prichulymye, and in birch-aspen forests, from 681 to 450 correspondingly. In mixed and secondary aspen-birch forests of the Kiya-Chulym interfluve, located to the south, the abundance of birds was not inferior to that observed in the Upper Prichulymye (693 and 672 individuals/km²) with very similar species richness.
The group of dominants (5–10%) also included the willow tit, chaffinch, chiffchaff and hazel grouse, but the willow tit is no longer the prevailing species, giving way to the chaffinch, garden warbler *Acrocephalus dumetorum* (Blyth) or tree pipit *Anthus trivialis* (L.). In addition to them, the great dominant taiga species of birds in dark-coniferous forests were the great tit *Parus major* (L.), fieldfare *Turdus pilaris* (L.), great spotted woodpecker *Dendrocopos major* (L.), in some years the redstart *Phoenicurus phoenicurus* (L.), pied flycatcher of *Ficedula hypoleuca* (L.), Siberian rubythroat *Luscinia calliope* (L.), redwing *Turdus iliacus* (L.) and willow warbler *Phylloscopus trochilus* (L.).

Table 1. Density (individuals per km²) and species richness of the summer bird population Southern taiga of the Ob-Yeniseisky interfluve

| №  | Types of landscapes, landscape tracts                                      | Upper Prichulymye, Teguldetsky district, 2017 | Yaya-Chulym Interfluve, Zyryansky District, 2012, 2017; Teguldetsky district, 1994 | Lower Prichulymye, Ob-Chulym interfluve, Molchanovsky district, 2013 |
|----|--------------------------------------------------------------------------|-----------------------------------------------|----------------------------------------------------------------------------------|---------------------------------------------------------------------|
| 1  | Dark coniferous (spruce-cedar-fir) semi-logged forests                    | Population density 537                        | Population density 373–615                                                          | Population density 236                                             |
|    |                                                                          | n^b^n^c                                       | 58–65^c                                                                         | 36–42^c                                                          |
| 2  | Mixed coniferous-deciduous forests                                       | Population density 715                        | Population density 524–693                                                          | Population density 395                                             |
|    |                                                                          | n^b^n^c                                       | 57–77^c                                                                         | 35–51^c                                                          |
| 3  | Aspen-birch grass forests                                                 | Population density 681                        | Population density 626–672                                                          | Population density 450                                             |
|    |                                                                          | n^b^n^c                                       | 56–69                                                                         | 41–48                                                             |
| 4  | Pine forests                                                             | Population density 335                        | Population density 262                                                             | Population density 192                                             |
|    |                                                                          | n^b^n^c                                       | 39                                                                           | 30                                                               |
| 5  | Suhodolny meadow-groves on deposits                                      | Population density 421                        | Population density 406                                                             | Population density 292                                             |
|    |                                                                          | n^b^n^c                                       | 66                                                                            | 39                                                               |
| 6  | Semi-forested floodplain meadows                                        | Population density 633                        | Population density 527–902                                                          | Population density 284–470                                        |
|    |                                                                          | n^b^n^c                                       | 66–74                                                                         | 43                                                               |
| 7  | Open floodplain meadows                                                  | Population density 765                        | Population density 607–742                                                          | Population density 47                                             |
|    |                                                                          | n^b^n^c                                       | 55–63                                                                         | 42–45                                                             |
| 8  | Forest fields with agrocnoses                                            | Population density 332                        | Population density 234                                                             | Population density 172                                             |
|    |                                                                          | n^b^n^c                                       | 49                                                                            | 48                                                               |
| 9  | Marsh birch trees (Chelbak bog)                                          | Population density 172                        | Population density 48                                                              | Population density 33                                              |
|    |                                                                          | n^b^n^c                                       | 27                                                                            | 17                                                               |
| 10 | Medium pine ryama                                                        | Population density 230^c                       | Population density 43                                                              | Population density 50                                             |
|    |                                                                          | n^b^n^c                                       | 33                                                                            | 33                                                               |
| 11 | Transitional birch-shrub bogs                                             | Population density 170                        | Population density 123                                                             | Population density 49                                             |
|    |                                                                          | n^b^n^c                                       | 49                                                                            | 49                                                               |
| 12 | Upland bogs                                                              | Population density 86                         | Population density 32                                                              | Population density 35                                             |
|    |                                                                          | n^b^n^c                                       | 32                                                                            | 35                                                               |

^a. [7] Toropov, Shor, 2012.

^b. total number of bird species.

^c. number of background bird species (with an abundance of more than 1 individual per km²).

Among the forest habitats, the least number of birds was found in the pine forests of the riverbed terraces and interfluves with a nearly twofold decrease in population density from south to north from 335 individuals/km² in the Upper Prichulymye to 192 in the Lower Prichulymye. At the same time, the
species composition of bird communities of pine forests was very similar, but much poorer than all other types of forest tracts. The total number of numerous (more than 10 individuals/km²) birds in all pine forests did not exceed 7–11 species. The willow tit (12–21%) was the absolute dominant. The number of other co-dominants, which included the olive-backed pipit *Anthus hodgsoni* (L.), redstart, bramble finch, chaffinch and nuthatch *Sitta europea* (L.), was 1.5–4 times lower. In some years, the chiffchaff, tree pipit, coal tit, red-flanked bluetail and spotted flycatcher *Muscicapa striata* (L.) were also numerous.

In the majority of semi-forested and open inter-river and floodplain habitats under consideration, as well as in open and forested marshes, there is no obvious trend of changes from south to north. On the one hand, this can be explained by the insufficiently complete set of landscape tracts along the gradient under consideration and the uniqueness of some of the surveyed areas. These include, for example, the Chelbak bog massif located in extensive farmland in the forest-field landscape of the Zyryansky region, and the near-channel semi-forested part of the Ulukh-Chayakh bog system in the Teguldetsky region [8]. On the other hand, in various floodplain landscapes of large and medium-sized rivers, the formation of the species composition of bird communities and bird population dynamics are determined to a greater extent by factors other than forest communities, the magnitude of the flood, the length of floods, the degree of flooding of the territory in different seasons, diversity stations, etc. In the marshes, the leading factors are forestation, marshiness and trophicity of different types of marshes. Therefore, the majority of floodplain and marsh landscapes of the southern taiga zone of Western Siberia are, in fact, intrazonal and do not correlate with changes in the productivity of cenoses established for different geographical zones and altitudinal belts [3].

Among forest-meadow and open floodplain habitats, most of the birds were found in a variety of semi-forested floodplain willow meadows and in open floodplain meadows. In such tracts of the forest-meadow wide Chulym river floodplain, the total bird population density reached 633–902, and in floodplain meadows – 607–742 individuals/km². The species diversity of bird communities in floodplain habitats was sometimes even lower than in productive forest communities. In areas of narrow semi-forested floodplains of the Yaya, Kiya and Chet rivers on the Yaya-Chulym interfluve and in the weakly pronounced flood plain of the river channel on the left bank of the lower reaches of the Chulym river the abundance of birds was 1.5–3 times lower (284–527). Such differences in the total population density are associated with differences in the numbers of only three or four of the most widespread bird species. Thus, the abundance in different years of yellow wagtail *Motacilla flava* (L) in the forest meadow floodplain (22–146) and in open floodplain meadows (42–192) is associated, at least, with the duration of spring-summer floods on the Chulym river in different years and the lack of extensive floodplain meadows in the valleys of medium and small rivers in the inter-river watersheds preferred by this type. The abundance of the sand martin *Riparia riparia* (L.) in willow meadows (19–175) and in open meadows (31–102) was completely determined by the presence or absence of large colonies along the banks of rivers. The number of the singing warbler *Locustella certhiola* (Pall.) in all floodplain habitats (32–94) is associated with the presence of their most preferred habitats – watered or waterlogged sedge-grass lowlands. More or less stable numbers in different floodplain lands and in different years (21–58) were noted in the garden warbler, starling *Sturnus vulgaris* (L.), fieldfare, corncrake *Crex crex* (L), snipe *Gallinago gallinago* (L.), individual biotopes were found in stonechat *Saxicola torquatus* (L.), willow warbler, dusky warbler *Phylloscopus fuscatus* (L.) and sedge warbler *Acrocephalus schoenobaenus* (L.).

In dry meadow-groves on deposits that are not represented at all in the Lower Prichulymye in the Ob-Chulym interfluve, there were 1.5–2 times fewer birds than in the floodplain (slightly more than 400 individuals/km²). Dominate birds (10–12%) were the yellow wagtail, tree pipit, fieldfare and garden warbler. Slightly less common were the lanceolated warbler *Locustella certhiola* (L.), starling, whitethroat *Sylvia communis* (L.) and common rosefinch *Caprodacus erythrinus* (L.) in some biotopes. Even fewer birds (234–332) were encountered in forest-field areas with agrocenoses and fields of spring crops, which are located only near settlements on high terraces of the Chulym River and between the rivers of the Zyryansky district. Discounting bogs, here is also the poorest composition of
numerous and background bird species. Only a few species dominated (6–10%): the tree pipit, fieldfare, yellow wagtail, starling *Sturnus vulgaris* (L.). Less abundant were the jackdaw *Corvus monedula* (L.), starling, yellowhammer *Emberiza citrinella* (L.) and stock dove *Columba oenas* (L.).

In forested and semi-forested swamps of various types, the total population density, as a rule, did not exceed 123–230 individuals/km$^2$ with similar low species diversity. Very productive lowland forested swamps of riverbed floodplains, in which the bird population density can reach 470 [7] did not come within the bounds of our study. In the surveyed marsh habitats, there were only 6–8 numerous species, constituting up to 50–70% of the total population density. The willow warbler, tree pipit, willow tit, chifchaff, yellow wagtail and lanceolated warbler dominated in the birch boggy areas in the Chelbak bog massif. In middle pine forests and hummock-ridge complexes, the olive-backed pipit, Bramble finch, chaffinch were the most marked: the redstart, green sandpiper *Tringa ochropus* (L.) and the cuckoo *Cuculus canorus* (L.). The transitional mesotrophic birch-shrub marshes were dominated by yellow wagtail, willow warbler, snipe, lanceolated and singing warbler, and along the edges of the marshes also by the tree pipit, citrine wagtail *Motacilla citreola* (Pall.), dusky warbler and black grouse *Tetrao tetrix* (L.).

The poorest bird communities were found in large open upland bogs, where only 14–17 background species were encountered and the total abundance of birds did not exceed 80–90 individuals/km$^2$. A number exceeding 10 was observed only for tree pipit, yellow wagtail and snipe, and common species were citrine wagtail, singing warbler and lance isolated warbler.

In the analysis of materials collected by other ornithologists in similar habitats of Tomsk Prichulymye in the months May–July between 1998–2002 [2], the considered trend of depletion of bird communities from the south-east to north-west in forest landscapes also was confirmed. Moreover, the areas of these studies included the valley and inter-forest forest landscapes of the Middle Prichulymye (Pervomaisky district) and the northernmost Nizhnechelyumsky area not far from the confluence of the Chulym river into the Ob river (Molchanovsky district), which were absent from our observations, thus increasing the latitudinal gradient of spatial changes in bird populations. So, from the Upper Prichulymye to the Lower Prichulymye, the total population density of birds in the dark coniferous taiga declined from 562 individuals/km$^2$ to 564, in mixed coniferous deciduous forests from 518 to 276, in clean furs and with green moss from 488 to 170, in pine forests and mixed grass forests from 509 to 317, and even up to 220 on the terraces of the Chichka-Yul river of the Chulym-Yenisei interfluve, located substantially east of the gradient under consideration.

In the semi-forested and open meadows of the Chulym river floodplain, latitudinal changes were not traced, but even more significant differences were observed in the total abundance of birds (from 352 to 1047), also associated primarily with changes in the number of the most widespread species. Thus, in different years and in different habitats of the forest-meadow floodplain, the numbers of yellow wagtails changed 9 times (43–372), the sand martin from complete absence in places where there were no colonies nearby, up to 283, the singing warbler from 9 to 120, the yellow-breasted bunting *Emberiza aureola* (L.) from 1 to 116. It should be noted that 15–20 years ago the yellow-breasted bunting was one of the most widespread birds in the floodplain landscapes of Tomsk Priroby and Tomsk Prichulymye, where its nesting density reached 200 and more per km$^2$ [2 and 7]. In 2013 and in 2017 even in the most optimal floodplain biotopes, it was observed very rarely or not at all, and its abundance did not exceed 4–6. This once again justifies the inclusion of the yellow-breasted bunting in the IUCN Red List in the “Threatened Species” group in the CR category “Critically Endangered” [9].

For another species from the IUCN Red List in the VU category (Vulnerable) [10] – the rustic bunting – there has also been a noticeable decline over the last twenty years in the number observed in the Tomsk Prichelymye. In 1994, on the Ob-Yenisei interfluve (Teguldyetsky district), the nesting density of the bunting in wetland mixed forests reached 52–90 individuals/km$^2$. It was numerous in dark-coniferous taiga, small-leaved forests, in forested lowland marshes (15–8) and common in pine forests, tall ryam and floodplain mixed forests (6–7) [7]. In 1998–2002 in the entire Tomsk Prichulymye it was observed only once in a birch-pine forest [2]. In June 2012, we occasionally
observed the rustig bunting in cedar-small-leaved forests in the valley of the Chet River (0.1). In May–July 2017, it was observed in the Zryansky region only in the coniferous-deciduous forest of the Chelbak swamp massif (0.5) and in the Teguldetsky region in dark-coniferous swamp forests on the ridges of the Ulukh-Chayakh swamp system (2). Only in 2013 was this species common in various boggy dark coniferous and coniferous-deciduous forests, as well as in tall ryam in the territory of the Verkhne-Sorovsky zoological reserve (5–9).

In addition, in similar habitats over the last 10–15 years, a significant decrease up to 2–4 times in the lanceolated warbler and redstart was observed, and a corresponding increases in the Bramble finch and blue nightingale.

4. Conclusion

Therefore, it can be stated that in the formation of the spatial heterogeneity of bird communities in the nesting period, even within the same subzone of the southern taiga of Western Siberia, there is a clear downward trend in species richness and overall population density from south to north in forests of the same type. In taiga and forest landscapes, in general, territorial differences in bird populations are largely related to the place of growth (inter-river, riverine, floodplain forests), the composition of the tree layer, the thickness and structure of the grass cover and the total water content of the territory. In intrazonal floodplain landscapes, spatial differences in bird communities are determined by the degree of forestation and subsistence of habitats, the length and diversity of plant stations within the designated tracts, and are also largely associated with water encroachment (the degree of flooding) and the total water content of the territories.

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