ISSN 1995-4255, Contemporary Problems of Ecology, 2016, Vol. 9, No. 1, pp. 86–97. © Pleiades Publishing, Ltd., 2016.
Original Russian Text © Yu.S. Ravkin, I.N. Bogomolova, S.M. Tsybulin, T.K. Zheleznova, K.V. Toropov, L.G. Vartapetov, S.P. Milovidov, V.A. Yudkin, V.S. Zhukov, S.P. Gureev, I.V. Pokrovskaya, E.Sh. Kasibekov, A.A. Ananin, E.N. Bochkareva, 2016, published in Sibirskii Ekologicheskii Zhurnal, 2016, No. 1, pp. 103–116.

Spatial-Typological Heterogeneity and Environmental Organization of the Summer Population of Birds in the Middle Region of Northern Eurasia

Yu. S. Ravkin, I. N. Bogomolova, S. M. Tsybulin, T. K. Zheleznova, K. V. Toropov, L. G. Vartapetov, S. P. Milovidov, V. A. Yudkin, V. S. Zhukov, S. P. Gureev, I. V. Pokrovskaya, E. Sh. Kasibekov, A. A. Ananin, and E. N. Bochkareva

Institute of Animal Systematics and Ecology, Siberian Branch of the Russian Academy of Sciences, ul. Frunze 11, Novosibirsk, 630091 Russia

Tomsk State University, Siberian Branch, Russian Academy of Sciences, ul. Lenina 36, Tomsk, 630091 Russia

e-mail: zm@eco.nsc.ru

Received May 21, 2015; in final form, July 29, 2015

Abstract—The area under study covered the West Siberian Plain from the Urals to the Yenisei River and the same band to the southern borders of the former Soviet Union in 1991, including a part of the Altai-Sayan mountain country, Kazakhstan, Uzbekistan, Turkmenistan, and the whole of Kyrgyzstan and Tajikistan. The results of ornithogeographic surveys carried out on routes with a length of 63000 km in 3140 habitats from May 16 to July 31 in the period from 1936 to 2013 were analyzed for this territory. More than 110 specialists took part in the study. The collected data were averaged according to the contours of natural-geographical maps. The subsequent cluster analysis revealed the presence of three systems (series) of bird communities in undeveloped and developed lands, as well as in water and riparian areas. Eight types of communities were distinguished within the first system: 1—tundra type; 2—forest-tundra type; 3—forest type; 4 and 5—West Siberian meadow-steppe and semidesert-steppe types; 6 and 7—Middle Asian northern desert-steppe and southern desert types; 8—high-mountain type. The borders of their distribution do not coincide with the zonal borders. Seven and six types of communities were distinguished in the second and third systems, respectively. A part of them was divided into 29 subtypes in total. The revealed heterogeneity of bird communities is largely determined by 12 environmental factors. The greatest correlation was detected for forestation, buildup, and watering. The multiple correlation of the bird population variability with all the identified environmental factors amounted to about 54 ± 1% of variance in the similarity matrix, which approximately corresponds to the correlation coefficient of 0.74.

Keywords: density, species richness, avifauna, cluster analysis, factors, correlation, classification

DOI: 10.1134/S1995425516010121

INTRODUCTION

The West Siberian Plain and the entire territory to the south of it up to the borders of the Soviet Union in 1991 are conditionally included by us in the Middle Region of Northern Eurasia, by analogy with the Middle Region of the Soviet Union (*Perspektivnye*..., 1978; *Priroda*...., 1980). Thus, our research area covers the whole of West Siberia and then a larger part of Kazakhstan, Uzbekistan, Turkmenistan, as well as the whole of Kyrgyzstan and Tajikistan. Since this region is very irregularly covered by bird counts, the results of this (second in order) attempt to analyze its population can be regarded as preliminary according to the level of examination for 2013.

MATERIALS AND METHODS

The materials collected in the databank of the laboratory of zoological monitoring at the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences were used for the analysis. In their collection, 110 ornithologists took part. Bird counts were carried out in the period from 1936 to 2013 from May 16 (from June 16 in tundras and forest tundra and from June 1 in northern taiga) to July 15 (to July 31 in tundras). In total, information on bird communities was taken from 3140 habitats, collected on routes with a total length of about 63000 km.

In addition to the authors of this and previous reports (Ravkin et al., 1991), the collection of the materials was carried out with the participation of A.F. Belyankin, O.Ya. Garms, K.V. Grazhdan, E. Davranov, I.F. Zhimulev, N.V. Klimova, A.B. Kurmankulov, I.P. Lebyazhinskaya, S.G. Livanov, G.A. Lunina, N.P. Malkov, A.N. Malkova, O.B. Mitrofanov, A.A. Odintseva, V.Yu. Petrov,

I.B. Preobrazhenskaya, M.M. Samsonova, D.R. Khaydarov, E.E. Shukurov, and B.V. Shcherbakov. A number of published data were also included in the calculations.

A large volume and significant heterogeneity of the collected materials dictated the specificity of their processing in comparison with the standard (Pavkin and Livanov, 2008). Thus, all variants of populations were averaged according to the contours of regional maps (*Rastitel'nost' Zapadno-Sibirskoi ravniny*, 1976; *Atlas Kirgizskoi SSR*, 1987; *Landshaftnaya karta...*, 2001). As a result, the number of average estimates obtained for bird communities was 749, and the number of estimates for developed lands and water and riparian objects was 188 and 259, respectively. According to the information gathered in the same territory before 1989, these systems (series of latitudinal measurements) had been traced earlier on the basis of the similarity graph (Ravkin et al., 1991). Therefore, the indicated arrays were subjected in this work to a cluster analysis separately. After this, 60 clusters were formed for undeveloped lands. They were in turn repeatedly aggregated into 17 groups using the same program (Trofimov and Ravkin, 1980). After their composition was analyzed, representative groups were supplemented with unrepresentative ones. For this purpose, the latter were included among the former, relying upon the similarity of landscape characteristics. This procedure is called idealization. As a result, all its particularities, deviations, and exceptions were eliminated by averaging with retention of only the major, most representative joined cluster groups that reflected the concept of bird community heterogeneity developed in this process. Eight joined cluster groups of this type were distinguished for undeveloped lands. They were considered as community types. The simple average abundance indicators were estimated on their basis for all 477 bird species registered during the counts (without regard to the areas occupied by individual habitats). The major characteristics of communities were calculated for these averages: density, species and background richness, faunal composition (based on the total abundance of the representatives of the marked faunal types according to Shtegman (1938, with additions)), and also the matrix of similarity coefficients for quantitative traits (Jaccard, 1902; Naumov, 1964). The same method was used to process the data on bird communities of developed lands and water and riparian habitats. Three graphs that reflect the structure of major changes for the indicated groups of ornithocomplexes (systems (supertypes) of bird communities) were constructed on the basis of these coefficients by the method of correlation pleiads (Terent'ev, 1959) at the selected threshold of significance for intergroup relationships.

The force of relationship with ecologically significant environmental factors was estimated for the marked-out gradations using the linear qualitative approximation of correlation matrices, which is a qualitative analog of the regression model (Ravkin et al., 1978). Owing to the software restrictions on the volume of analyzed data, the calculations were performed six times based on half of all averages chosen using a random number generator in order to assess the integral information value of the classifications and multiple correlation with all factors and regimes.

The names of bird species were given according to Ivanov (1976).

RESULTS AND DISCUSSION

The Spatial—Typological Structure of Communities

Undeveloped lands. The similarity graph illustrates the presence of one series of changes (Fig. 1) and one deviation from it. The changes in this series correspond to the growth in heat supply from the north to the south. The upper part of the series, which consists of types 1–4 and deviation (the eighth type) can be regarded as macrohumid, and the remaining part (types 5–7) can be considered as macroarid. The trend from Arctic tundras to deserts is accompanied first by the increase in bird population density from 244 to 500 ind./km^2 in the meadow-steppe type and then by the decrease in drier landscapes to 329 ind./km^2. The indices of the species richness of ornithocomplexes change in the same way (from 78 to 333 species and then to 172 species), but the maximum values are immanent to the forest community type rather than to the meadow-steppe type. The number of background species changes almost in the same way (it grows from 31 to 83 species and then decreases to 46 species). Admittedly, the total bird abundance and the number of background species in the seventh type grow to 1166 individuals/km^2 and 69 species. This is due to the fact that the ornithocomplexes of all southern desert landscapes, including comparatively rich riparian woodlands, orchards, and vineyards, were related to this type by similarity. In comparison with the forest bird community type, all the mentioned indices were noted to decrease for the high-mountain type.

The species that are leading for the community types are very specific for the corresponding vegetation types, although the species such as tree pipit, common rosefinch, yellow wagtail, and skylark are among the leaders simultaneously in two or three types of ornithocomplexes. The faunal composition of the bird communities prevalent in abundance in the tundra community type is predominantly Arctic (84%); the forest-tundra community type includes only 14% representatives of this faunal type, and the bulk consists of Siberian and Trans-Palearctic species. The representatives of the Siberian faunal type are among the species prevalent in the forest and high-mountain types (25 and 18%). The share of Trans-Palearctic species is the highest in the meadow-steppe and semidesert-steppe West Siberian types (42 and 44%) and is smaller in the remaining types (10–23%). The participation of

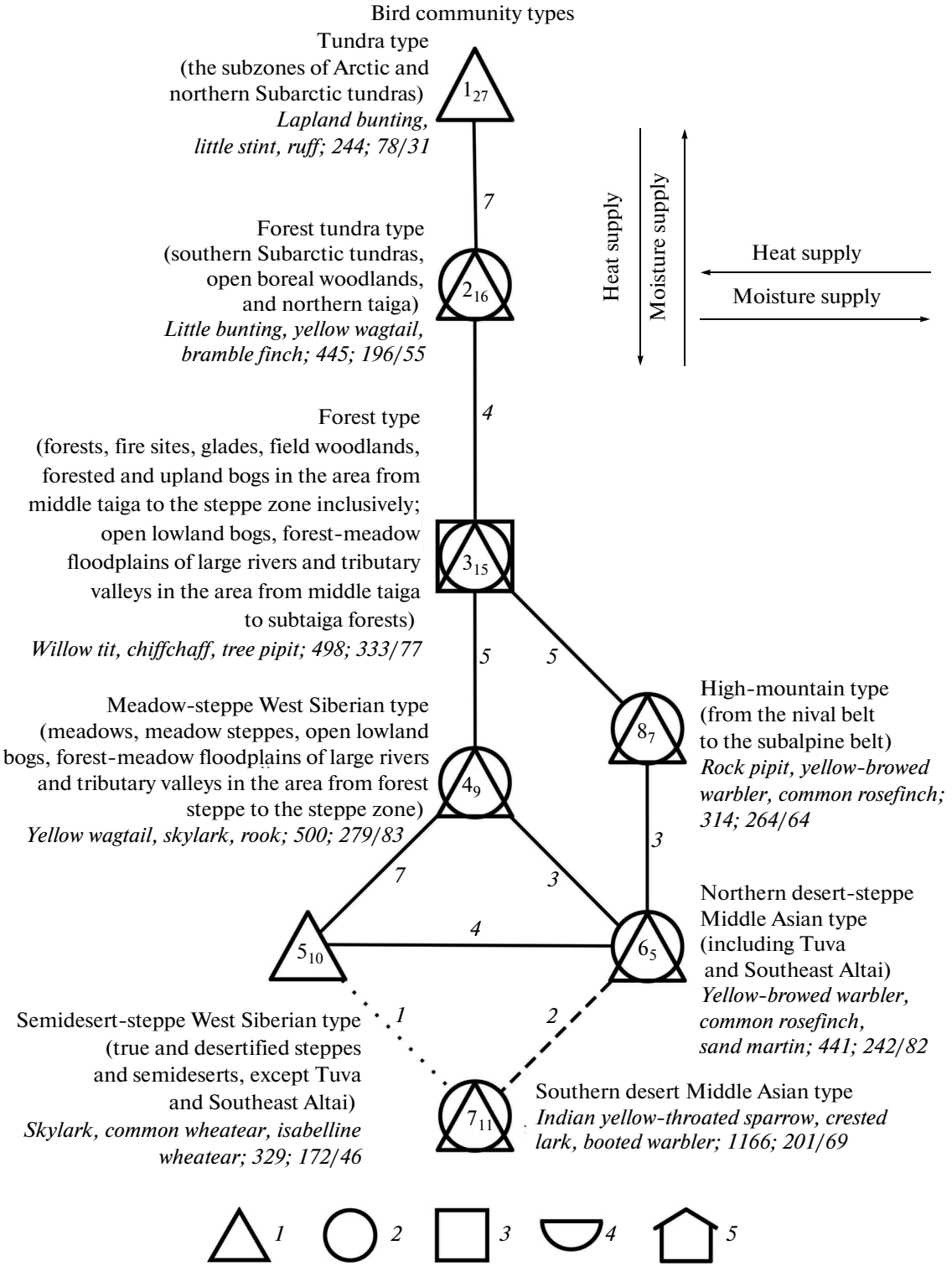

Fig. 1. Spatial-typological structure of bird communities in the undeveloped part of the Middle Region of Northern Eurasia. Figures 1–3 show the following habitats: (*1*) open habitats; (*2*) mosaic habitats; (*3*) wooded habitats; (*4*) water-riparian habitats; (*5*) built-up habitats. The solid line shows significant ties, and the dashed line shows maximum ties in the absence of significant ones; the dotted line indicates additional ties; the scores of ties are near them; the ciphers in the icons indicate the numbers of types and subtypes according to the classification; the following information is indicated near the icons: the names of types or subtypes, the three most abundant species, the population density (individuals/km^2), the total number of encountered species, and the number of background species in which abundance is not less than 1 individuals/km^2 (after the slash).

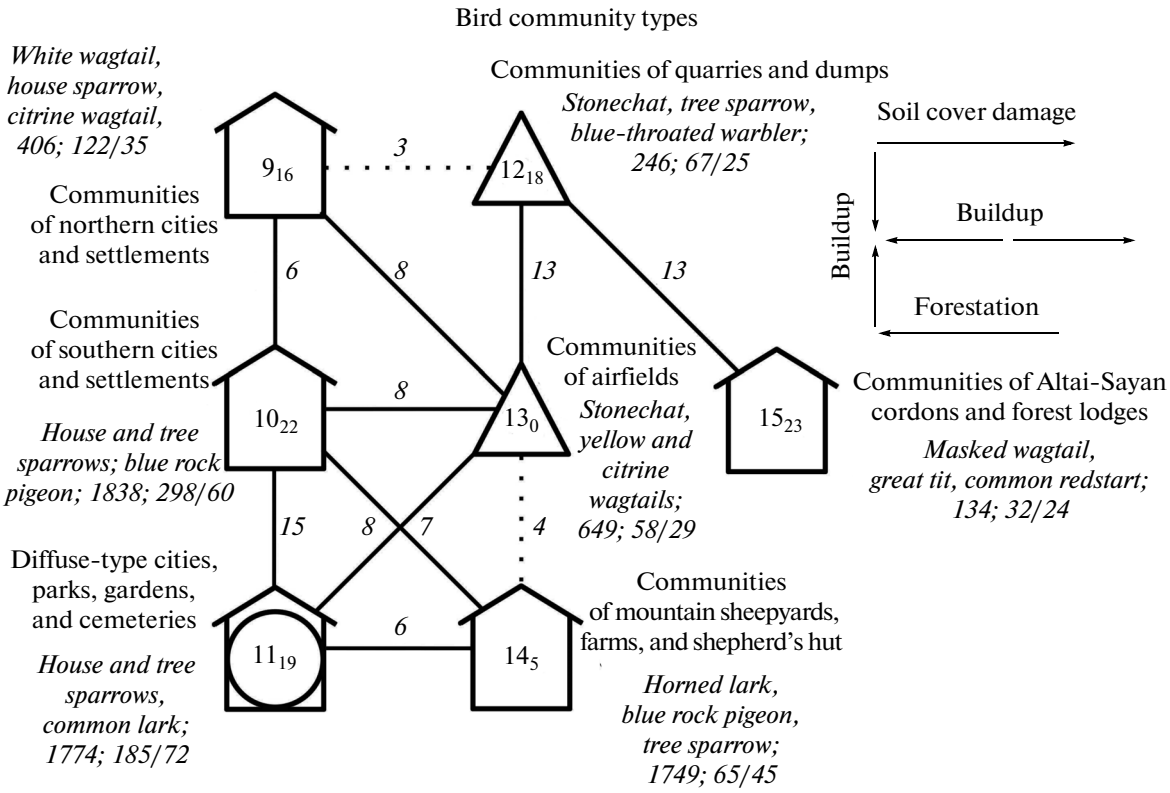

Fig. 2. Spatial-typological structure of bird communities in the developed territories of the Middle Region of Northern Eurasia.

European forms is maximal in the forest type (41%) and noticeably smaller in the meadow-steppe, high-mountain, northern desert-steppe, and southern desert types (15–28%). The share of the Chinese faunal type is significantly smaller (11–16%) in the forest, high-mountain, semidesert-steppe West Siberian, and northern desert-steppe Middle Asian types (11–16%), and the share of the Mongolian and Tibetan faunal types is also lower (29 and 11% in the two latter community types and 16% in the high-mountain type, respectively). Mediterranean forms with a prevalent percentage in the population are typical only of the northern desert-steppe and southern desert types (17 and 66%).

Developed lands. The structural graph of changes in the similarity and distinction of communities in residential, industrial, and recreation habitats traces two series and one deviation (Fig. 2). The series represented by types 9–11 consists of the ornithocomplexes of residential territories with all-round development (northern and southern) and predominantly recreation zones. The latter of these types includes communities of diffusive-type cities, where apartment areas include interblock forests, as well as those of parks, built-up gardens, and cemeteries. The right series is represented by bird communities of industrial territories (quarries, dumps, airfields, and areas with constructions of agricultural purpose). Deviations from this series include bird communities in isolated developed areas: cordons in reserves and forest lodges.

The community types represented in the left series feature an approximately twofold growth in the total abundance, species richness, and the number of background species from the north to the south. The partly developed recreation and forest southern territories are characterized by somewhat smaller values than completely developed areas. These distinctions are due to the decrease in heat supply and density of development to the north and in recreation zones and, correspondingly, to the decreased density of the human population and amount of anthropogenic fodder. The formation of the second series is due to the damage of the soil and plant cover, almost complete absence of anthropogenic fodder in landing strips of airfields, and abrupt reduction of development and amount of anthropogenic fodder around cordons and lodges, and to a lesser extent, near mountain cattle-breeding constructions.

Water—riparian communities. Bird communities in these habitats can be represented as a reticular graph with a very high idealization according to the results of the cluster analysis (Fig. 3). This graph can easily trace two vertical and three horizontal typological series. The first vertical series consists of three ornithocomplex types of rivers and channels (16, 18, and 20). The first of these types includes the northern plain community types in the area from tundras to northern taiga

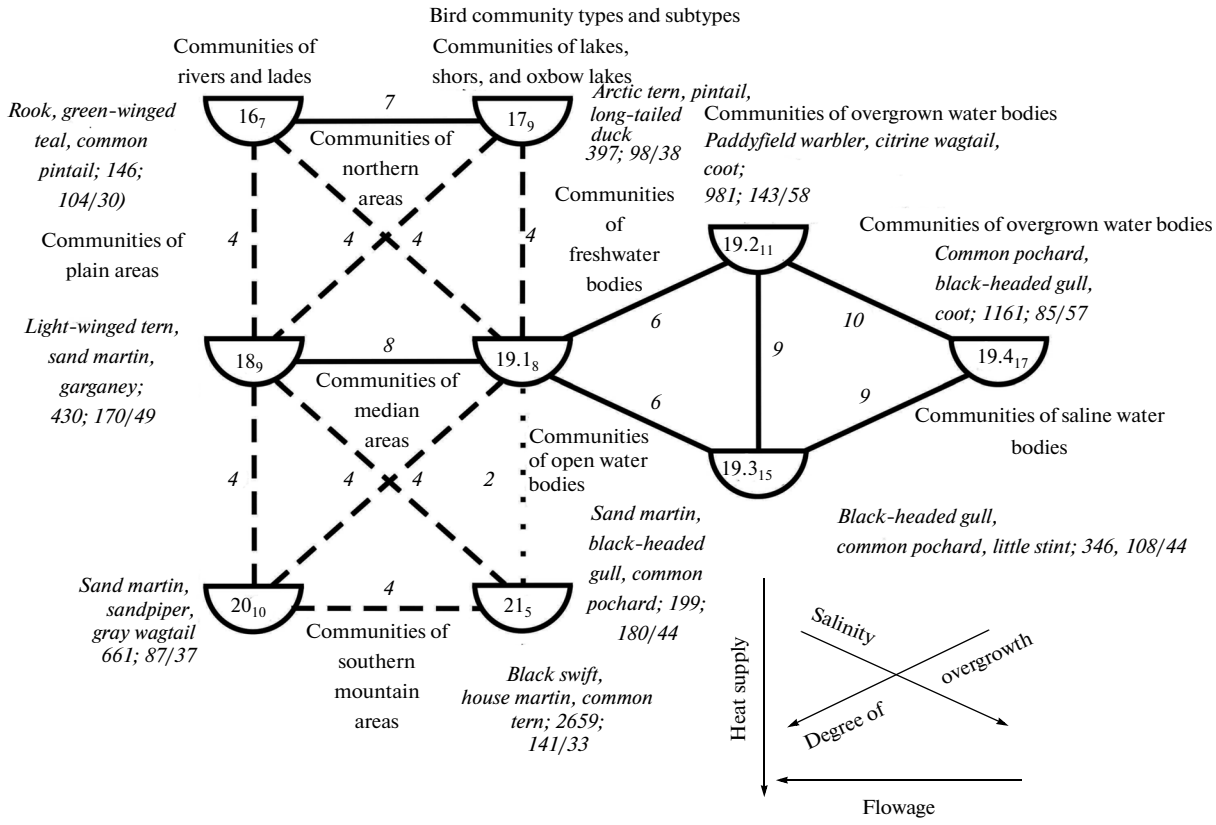

Fig. 3. Spatial-typological structure of ornithocomplexes of water—riparian habitats in the Middle Region of Northern Eurasia.

inclusively, the second one includes median plain types in the area from middle taiga to steppes inclusively, and the third one is formed by those of southern mountain rivers and channels.

The second vertical series is formed by the ornithocomplexes of lakes, shors, reservoirs, and oxbows in the same zonal bands. This being the case, the median communities can be divided into four community subtypes, respectively, in combination with fresh, saline, open, and overgrown water bodies. The species and background richness is maximal in median water bodies and watercourses, just like the population density, although the greatest number of birds for rivers and channels, as well as for all water-riparian ornithocomplexes as a whole, is immanent to southern mountain ecosystems. The median plain ornithocomplexes of open water bodies have lower indices than the overgrown ornithocomplexes (on average, by a factor of almost 4 for abundance, by 30% for background species, and almost equally higher for the species richness). The bird population is almost 30% larger at saline water bodies in comparison with fresh ones, the values for background species are almost equal, and the total number of species is almost 70% higher. It must be noted that the similarity between community types and subtypes is 6–10% in the northern and median horizontal series (on average, 8), and the similarity between the series is 4%, just as in the southern mountain horizontal series. This suggests that the zonal and altitudinal zonal distinctions in heat supply are more significant in comparison with flowage, salinity, and degree of overgrowing.

All three distinguished bird community systems are significantly interrelated on the joint graph, although the total number of such relationships is small. Thus, the ornithocomplexes of built-up and recreational areas, quarries and dumps have a superthreshold similarity to the communities of the forest tundra type and those of northern cities and settlements, as well as communities of the forest type and those of diffusive-type cities, parks, cemeteries, and gardens. Water and riparian ornithocomplexes are interrelated through bird communities of northern lakes and oxbows with the tundra type of the land community system.

Consequently, the analysis of the spatial-typological heterogeneity of the summer bird communities in the Middle Region of Northern Eurasia traced the influence of zonality, which nevertheless does not coincide with the landscape geographical division into zones and subzones. Thus, the first of the types includes the ornithocomplexes of Arctic and northern Subarctic tundras. The second (forest tundra) type includes the bird communities in the area from southern Subarctic tundras to northern taiga inclusively; the forest type is

formed by the bird communities in the area from middle taiga to subtaiga forests as well as forest steppe and steppe zones, except for ornithocomplexes of meadow steppes, fields, meadows, forest-meadow floodplains of large rivers and tributary valleys, which are included in the following meadow-steppe West Siberian type. The remaining communities of the West Siberian Plain form the semidesert-steppe community type. It must be noted that the communities in the same habitats of Southeast Altai and Tuva are not included in the latter two types. The high-mountain type is formed by the bird communities in an area which spreads from the nival belt to alpine and subalpine meadows and sparse forests in the Altai-Sayan mountain country and Middle Asia, and the latter two types include the corresponding ornithocomplexes of Middle Asia, Tuva, and Southeast Altai.

CLASSIFICATION OF ORNITHOCOMPLEXES

The composition of bird community types and the main characteristics are presented below and in Fig. 4 in more detail than in the graphs.

1. The tundra community type (subzones of the Arctic and northern Subarctic tundras in the West Siberian Plain; the leaders in abundance are as follows, %: Lapland longspur *Calcarius lapponicus* (L.) (18), little stint *Calidris minutus* (Leisl.) (13), ruff *Philomachus pugnax* (L.) and red-throated pipit *Anthus cervina* (Pall.) (9 for both species), red-necked phalarope *Phalaropus lobatus* (L.) (5) / the leaders in biomass were as follows: white-fronted goose *Anser albifrons* (Scop.) (29), white ptarmigan *Lagopus lagopus* (L.) (8), ruff (7), long-tailed duck *Clangula hyemalis* (L.) (6), king eider *Somateria spectabilis* (L.) (5); the population density was 244 individuals/km^2 / the biomass was 41 kg/km^2; the number of encountered species was 78/including 31 background species; the percentage of the representatives of fauna types with prevalent abundance was 84% for the Arctic type[1]).

Subtypes:

1.1—communities of the subzones of Arctic tundras (little stint (21), Lapland longspur (15), horned lark *Eremophila alpestris* (L.) (8), ruff (6), dunlin *Calidris alpina* (L.) (5) / white-fronted goose (41), long-tailed duck (6), white and tundra *Lagopus mutus* (Mont.) partridges and king eider (5 for each species); 189/43; 66/27; 93 for the Arctic fauna type);

1.2—communities of the subzones of northern Subarctic tundras (Lapland longspur (20), red-throated pipit and ruff (11 for each of them), little stint (10), red-necked phalarope (5) / white-fronted goose (20), ruff (10), white ptarmigan (9), long-tailed duck, and pomarine skua *Stercorarius pomarinus* (Temm.) 6; 283/39; 68/33; 80 for the Arctic fauna type).

[1] Below, these indices are given in the same order without naming them.

2. The forest tundra community type (the southern subzones of Subarctic tundras, open boreal woodlands and northern taiga in the West Siberian Plain; little bunting *Emberiza pusilla* Pall. (13), western yellow wagtail *Motacilla flava* L. (10), bramble finch *Fringilla montifringilla* L. (7), redpoll *Acanthis flammea* (L.) (6), willow warbler *Phylloscopus trochilus* (L.) (5) / pintail *Anas acuta* L. (12), white ptarmigan (7), capercaillie *Tetrao urogallus* L., tufted duck *Aythya fuligula* (L.) and whooper swan *Cygnus cygnus* (L.) (4 for each species); 445/32; 196/55; 44 for Siberian fauna type; 23 for the Trans-Palearctic types, and 14 for both the European and Arctic types).

Subtypes:

2.1—communities of the bands of dwarf-shrub tundras (linnet, Lapland longspur (12 for each species), red-throated pipit (8), citrine wagtail *Motacilla citreola* Pall. (7), little bunting (6) / white ptarmigan (32), long-tailed duck (8), pintail (6), scaup *Aythya marila* (L.) (5), ruff (4); 311/28; 84/36; 42 for the Arctic type, 27 for the Siberian type, 14 for the Trans-Palearctic type, and 10 for the European type);

2.2—communities of the bands of shrub tundras and tundra, pretundra, and northern taiga polygonal and hilly bogs (western yellow wagtail (23), little bunting (11), red-throated pipit (9), linnet (7), Lapland longspur (5) / white ptarmigan (12), herring gull *Larus argentatus* Pontopp. and pintail (8 for each species), whooper swan and teal *Anas crecca* L. (5 for each species); 494/38; 113/44; 37 for the Trans-Palearctic fauna type, 26 for Arctic type, and 24 for the Siberian type);

2.3—communities of the subzones of open boreal woodlands and northern taiga, except hilly bogs (little bunting (14), bramble finch (10), western yellow wagtail (7), willow warbler and Arctic warbler *Phylloscopus borealis* (Blas.) (6 for each species) / pintail (14), wood grouse (6), tufted duck (5), gray crow *Corvus cornix* L. and whooper swan (4 for each species); 457/31; 185/57; 51 for the Siberian fauna type, 20 for the Trans-Palearctic type, and 17 for the European type).

3. The forest community type (forests, burned areas, glades, field woodlands, wooded and upland bogs in the area from the middle taiga to the steppe zone of the West Siberian Plain and from the submountain region of the Altai-Sayan mountain country to its middle-mountain region; open lowland bogs and forest-meadow floodplains of large rivers and tributary valleys in the area from middle taiga to subtaiga forests of the West Siberian Plain and from the submountain region of the Altai-Sayan mountain country to its middle-mountain region; willow tit *Parus montanus* Bald. and chiffchaff *Phylloscopus collybita* (Vieill.) (7 for each species), tree pipit *Anthus trivialis* (L.) (6), rosefinch *Carpodacus erythrinus* (Pall.) (5), garden warbler *Acrocephalus dumetorum* (Blyth) (4)/hazel grouse *Tetrastes bonasia* (L.) (6), gray and black *Corvus corone* L. crows (5 and 4, respectively); fieldfare *Turdus pilaris* L. (4), magpie *Pica pica* (L.) (3); 498/26;

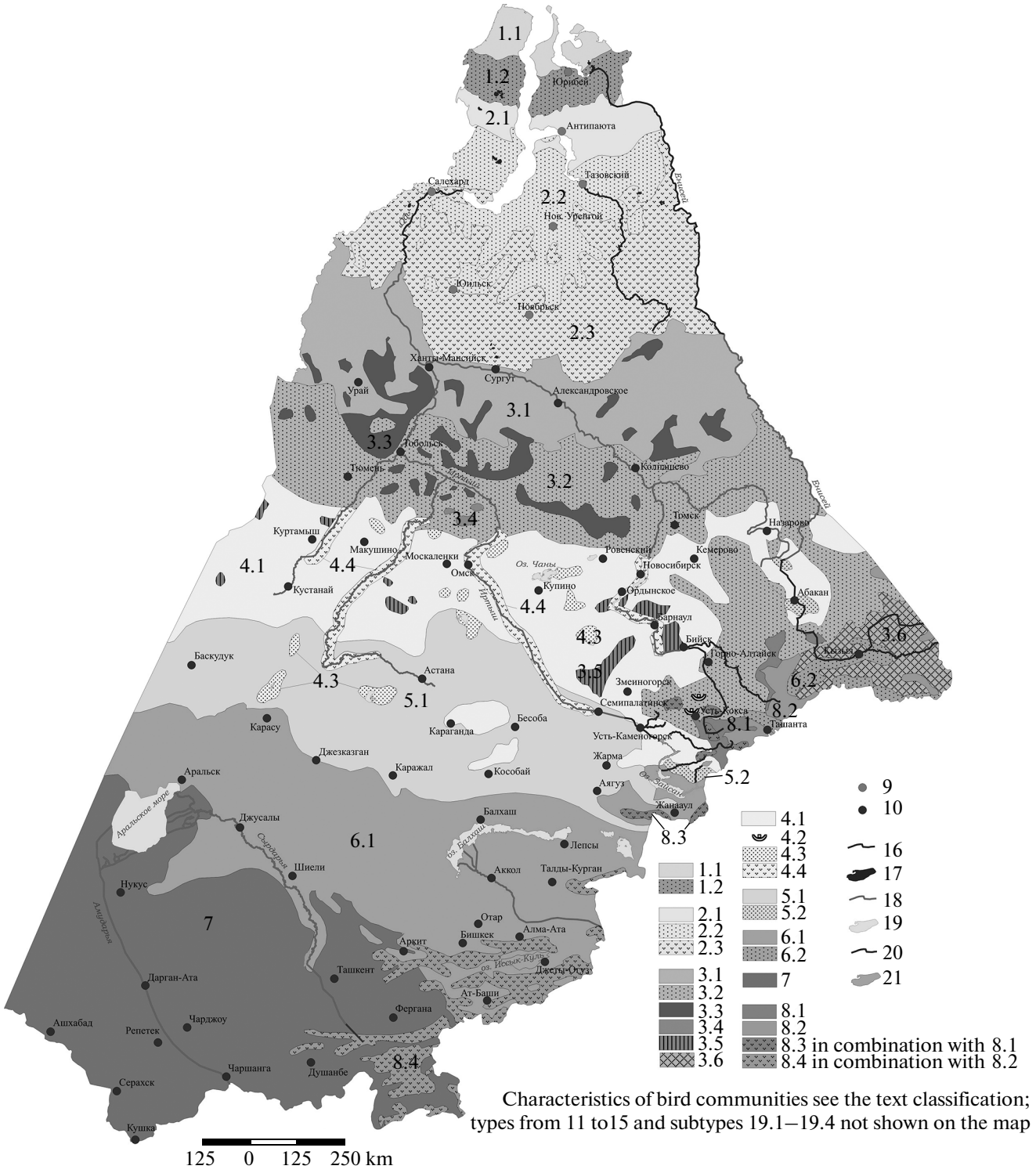

Fig. 4. Spatial-typological heterogeneity of summer population of birds in the Middle Region of Northern Eurasia.

333/77; 41 for the European fauna type, 25 for the Siberian type, 14 for the Trans-Palearctic type, and 12 for the Chinese type).

Subtypes:

3.1—communities of middle taiga (except upland bogs; bramble finch (8), willow tit (7), golden bunting *Emberiza aureola* Pall. 5, chiffchaff (4), sedge warbler *Acrocephalus schoenobaenus* (L.) (3) / wigeon *Anas penelope* L. (6), hazel grouse, pintail, and gray crow (5 for each species), wood grouse (4); 317/23; 226/64; 38 for the Siberian fauna type, 27 for the European type, 20 for the Trans-Palearctic type);

3.2—communities of southern taiga and subtaiga forests (except upland bogs), nonpine forest steppe and steppe forests in the West Siberian Plain and the Altai-Sayan mountain country (except Tuva and Southeast Altai; chiffchaff and willow tit (7 for each species), tree pipit and rosefinch (6 for each species), garden warbler (4) / hazel grouse (7), gray and black crows (5 for each species), 4 fieldfare (4), common blackbird *Turdus atrogularis* Pall. (3); 535/27, 307/81; 42 for the European fauna type, 25 for the Siberian type, 13 for both Trans-Palearctic and Chinese types);

3.3—communities of upland bogs in middle and southern taiga (tree pipit (23), golden bunting (9), yellow wagtail and pine bunting *Emberiza leucocephalos* (8 for each species), little bunting (4) / black grouse *Lyrurus tetrix* (L.) (15), pintail (7), wood grouse and tree pipit (6 for each species), white ptarmigan (5); 133/11, 167/26; 36 for the European fauna type, 27 for the Siberian type, 22 for the Trans-Paleactic type, and 11 for the Chinese type).

3.4—communities of subtaiga, forest-steppe, and steppe upland bogs (pine bunting (23), willow warbler (19), tree pipit (10), gray warbler *Sylvia communis* Lath. and accentor *Sylvia curruca* (L.) (6 and 5, respectively / gray duck *Anas strepera* L. (14), gray crow and garrot *Bucephala clangula* (L.) (9 for each species), pine bunting (8), gray crane *Grus grus* (L.) (7); 311/25; 104/33; 51 for the European fauna type, 28 for the Siberian type, and 14 for the Trans-Palearctic type);

3.5—communities of plain and mountain forest-steppe and steppe pine forests and field woodlands (tree pipit and magpie (8 for each species), chaffinch *Fringilla coelebs* L. (7), starling *Sturnus vulgaris* L. (6), black swift *Apus apus* (L.) (5) / gray crow (15), magpie (13), oriental turtle *Streptopelia orientalis* (Lath.) (6), silver gull (5), rook *Corvus frugilegus* L. (4); 317/41; 120/50; 61 for the European fauna type and 18 for the Trans-Palearctic type);

3.6—communities of Tuva and Southeast Altai (garden bunting *Emberiza hortulana* L. (8), tree pipit and yellow-browed warbler *Phylloscopus inornatus* (Blyth) (7 for each species), tree sparrow *Passer montanus* (L.) and chiffchaff (6 for each species) / mallard *Anas platyrhynchos* L. (20), common merganser *Mergus merganser* L. (10), roody shelduck *Casarca ferruginea* (Pall.) (8), black crow *Corvus corone* L. (7), magpie (4), 577/36, 111/60; 38 for the European fauna type, 23 for the Trans-Palearctic type, 17 for the Siberian type, and 14 for the Chinese type).

4. The West Siberian meadow-type community type (meadows, meadow and true halophytic steppes, fields, open lowland bogs, forest-meadow floodplains of large rivers and tributary valleys in the area from forest steppe to the steppe zone in the plain, in forest and forest-steppe belts of the Altai-Sayan mountain country except Southeastern Altai and Tuva; yellow wagtail and skylark *Alauda arvensis* L. (9 for each species), rook (4), starling and stonechat *Saxicola torquata* (L.) (3 for each species) / rook (11), gray goose *Anser anser* (L.) (9), mallard (6), garganey *Anas querquedula* L. and coot *Fulica atra* L. (4 for each species); 500/67; 279/83; 41 for the Trans-Palearctic fauna type, 30 for the European fauna type).

Subtypes:

4.1—communities of plain and mountain fields (except Central Altai areas), non-halophytic meadow steppes and true steppes and meadows (skylark and yellow-tail (10 for each species), garden warbler and rook (6 for each species), great tit *Parus major* L. (4) / rook (21), roody shelduck (10), avocet *Recurvirostra avosetta* L. (5), garrot and common pochard *Aythya ferina* (L.) 4; 410/45; 213/60; 35 for both the Trans-Palearctic and European types);

4.2—communities of meadow and true steppes, meadows, fields and open bogs in Central Altai (skylark (18), isabelline wheatear *Oenanthe isabellina* (Cretzschm.) (14), ortolan (10), stonechat (9), common wheatear *Oenanthe oenanthe* (L.) (4) / skylark and demoiselle crane *Anthropoides virgo* (L.) (10 for each species), black crow (8), lapwing *Vanellus vanellus* (L.) (7), isabelline wheatear (6); 270/17; 104/36; 41 for the Trans-Palearctic fauna type, 26 for the Mongolian type, 19 for the European type);

4.3—communities of halophytic meadows and halophytic-meadow steppes (skylark (23), yellow wagtail (15), rook (8), starling (7), migrating red-throated pipit (6) / rook (21), gray goose (10), silver gull (7), skylark (6), mallard (5); 434/64; 182/45; 58 for the Trans-Palearctic type and 22 for the European type);

4.4—communities of open lowland and transitional bogs, floodplains of large rivers and tributary valleys within the forest steppe and steppe zones (yellow wagtail (9), Indian warbler *Acrocephalus agricola* (Jerd.) (6), sedge warbler and starling (5 for each species), golden bunting (4) / gray goose (13), mallard (10), coot and garganey (6 for each species), pink pelican *Pelekanus onocrotalus* L. (4); 853/139; 229/90; 40 for the Trans-Palearctic fauna type, 31 for the European type).

5. The West Siberian semidesert steppe community type (except Tuva and Southeast Altai, semideserts, fields, and desertified and true steppes except halophytic ones; skylark (22), common wheatear (8), isabelline wheatear and tree sparrow (7 for each species), yellow wagtail (6) / rook (16), skylark and roody shelduck (10 for each species), rock pigeon *Columba rupestris* Pall. (5), jackdaw *Corvus monedula* L. (4); 329/26; 172/46; 52 for the Trans-Palearctic fauna type; 21 and 12 for the Mongolian and European types, respectively).

Subtypes:

5.1—communities of the West Siberian Plain (skylark (22), common wheatear (8), isabelline wheatear and tree sparrow (7 for each species), yellow wagtail (6) / rook (35), skylark (20), pale harrier *Circus macrourus* (Gm.) (3), white-winged lark *Melanocorypha*

leucoptera (Pall.) and yellow wagtail (2 for each species); 313/23; 126/29; 68 for the Trans-Palearctic fauna type, 13 for the European type, and 12 for the Mongolian type);

5.2—communities of the Altai-Sayan mountain country (isabelline wheatear (14), tree sparrow (13), common wheatear (11), horned lark (7), pied wheatear *Oenanthe pleschanka* (Lepechin) (5) / roody shelduck (18), rock pigeon (10), black crow (8), jackdaw (7), silver gull (6); 344/28; 109/45; 38 for the Trans-Palearctic fauna type, 29 and 11 for the Mongolian and European types, respectively).

6. The Middle Asian northern desert community type, including Tuva and Southeast Altai (steppes, semideserts, northern deserts and meadows, fields and sparse forests and shrubs within their limits; yellow-browed warbler, common rosefinch, and sand swallow *Riparia riparia* (L.) (5 for each species), red-headed bunting *Emberiza bruniceps* Br. and horned lark (4 for each species) / blue rock pigeon *Columba livia* L. (10), pheasant *Phasianus colchicus* L. (9), black crow (7), rook (6), magpie (5); 441/30, 242/82; 25 for the European fauna type, 17 for both the Trans-Palearctic and Mediterranean types, 11 for both the Mongolian and Chinese types).

Subtypes:

6.1—communities of areas within the Turan Plain and Tien Shan (yellow-browed warbler (6), sand swallow, common rosefinch, red-headed bunting, and gray warbler *Sylvia communis* Lath. (5 for each species) / blue rock pigeon (11), pheasant (10), black crow and rook (7 for each species), magpie (6); 537/37, 210/87; 28 for the European fauna type, 20 for the Mediterranean type, 17 for the Trans-Palearctic type, and 13 for the Chinese type);

6.2—communities of areas within the Tuva and Southeast Altai basins (horned lark (23), common wheatear and skylark (10 for each species), mountain linnet *Cannabina flavirostris* (L.) (8), isabelline wheatear (6) / horned lark (14), demoiselle crane *Anthropoides virgo* (L.) (10), steppe eagle *Aquila nipalensis* (Hodgs.) (7), skylark (5), chough *Pyrrhocorax pyrrhocorax* (L.) (4); 205/12; 122/33; 37 for the Mongolian fauna type, 23 for the Arctic type, and 22 for the Trans-Palearctic type).

7. The Middle Asian southern desert community type (southern deserts and semideserts, meadows, fields, riparian woodlands, orchards, and vineyards within their limits; Indian sparrow *Passer indicus* Jard. et Selby (17), crested lark *Galerida cristata* (L.) (9), chat *Hippolais caligata* (Licht.) (8), olivaceous warbler *Hippolais pallida* (Hempr. et Ehr.) and pastor *Pastor roseus* (L.) (5 for each species) / pheasant (30), see-see partridge *Ammoperdix griseogularis* (Br.) (7), Indian sparrow, crested lark, and pastor (6 for each species); 1166/79, 201/69; 66 and 15 for the Mediterranean and European fauna types, respectively).

8. The highland community type (tundras, tundra steppes, alpine and subalpine meadows, sparse forests in Middle Asia and the Altai-Sayan mountain country, including relatively moist habitats in Tuva and Southeast Altai; rock pipit *Anthus spinoletta* (L.) (8), yellow-browed warbler (7), common rosefinch and greenish warbler *Phylloscopus trochiloides* (Sund.) (5 for each species), tree pipit (4) / black crow (12), Himalayan snowcock *Tetraogallus himalayensis* Gray (8), chough (6), white ptarmigan (5), rock pipit (3); 314/19, 264/64; 19 for the European fauna type, 17 for the Siberian type, 16 for both the Chinese and Tibetan types, 13 for the Trans-Palearctic type).

Subtypes:

8.1—communities of tundras, tundra steppes, and alpine meadows of the Altai-Sayan mountain country (except Tuva and Southeast Altai; rock pipit (15), yellow-browed warbler (6), horn-bird (5), common rosefinch and bluethroat *Cyanosylvia svecica* (L.) (4 for each species) / white ptarmigan (11), buzzard *Buteo buteo* (L.) (8), rock pipit and rock ptarmigan (6 for each species), black kite *Milvus corschun* (Gm.) (5); 264/26; 156/51; 19 for the Tibetan fauna type, 16 for the European, Siberian, and Mongolian types, 14 for the Trans-Palearctic types, 11 for the Chinese type);

8.2—communities of tundras, tundra steppes, and alpine meadows of the Tien Shan Mountains, Tuva, and Southeast Altai (rock pipit (12), bluethroat (6), yellow-browed warbler, citrine wagtail and common wheatear (4 for each species), golden bunting (3) / black crow (23), chough (9), Himalayan snowcock (5), white ptarmigan (4), magpie (3); 291/23; 178/58; 24 for the Tibetan fauna type, 21 for the Trans-Palearctic type, 15 for the European type, and 12 for the Chinese type);

8.3—communities of subalpine meadows of the Altai-Sayan mountain country (rock pipit (14), common wheatear (10), ortolan bunting (8), Himalayan reel and pied wheatear (5 for each species) / black kite (16), black crow (11), magpie (9), gray heron *Ardea cinerea* L. (7), white ptarmigan (5); 228/16; 84/42; 24 for the European fauna type, 20 for the Tibetan type, 19 for the Trans-Palearctic type, 14 for the Mongolian type, and 10 for the Chinese type);

8.4—communities of subalpine meadows of the Tien Shan (Himalayan reel (7), common blackbird *Turdus merula* L., gold-fronted finch *Serinus pusillus* (Pall.), and common rosefinch (5 for each species), linnet (4) / Himalayan snowcock (34), chough (7), chukar *Alectoris kakelik* (Falk), eastern turtle dove, and common blackbird (6 for each species); 336/29; 125/52; 30 for the European faunal type, 21 for the Trans-Palearctic type, 18 for the Tibetan type, and 14 for the Mongolian type).

8.5—communities of subalpine woodlands (yellow-browed warbler (13), greenish warbler (10), common rosefinch and tree pipit (9 for each species),

chiffchaff (6) / common blackbird and nutcracker *Nucifraga caryocatactes* (L.) (10 for each species), white ptarmigan (6), common rosefinch and tree pipit (5 for each species); 355/13; 164/39; 31 for the Siberian faunal type, 25 for the Chinese type, and 21 for the European type).

Bird community types:

9—communities of tundra, forest-tundra, and northern-taiga towns and villages (white wagtail *Motacilla alba* L. (24), house sparrow *Passer domesticus* (L.) (17), citrine wagtail and sand martin (7 for each species), yellow wagtail (5) / gray crow (30), silver gull (11), white wagtail and house sparrow (10 for each species), common gull *Larus canus* L. (3); 406/22; 122/35; 65 for the Trans-Palearctic faunal type and 14 for the Arctic type);

10—communities of cities (except diffusive-type cities) and plain and mountain settlements in the area from middle taiga to deserts (house and tree sparrows (42 and 13), blue rock pigeon (12), starling (6), rook (3) / blue rock pigeon (42), house sparrow (15), rook (13), starling (5), gray crow (4); 1838/156; 298/60; 64 for the Trans-Palearctic faunal type, 17 for the European type, and 14 for the Mediterranean type);

11—communities of diffusive-type cities, parks, gardens, and cemeteries (tree and house sparrows (17 and 14), starling (8), great tit (6), magpie (5) / gray crow (23), magpie and blue rock pigeon (15 for each species), starling (9), house sparrow (6); 1774/130; 185/72; 46 and 37 for the European and Trans-Palearctic faunal types, respectively);

12—communities of quarries and dumps (stonechat (18), tree sparrow (13), bluethroat (11), masked wagtail *Motacilla personata* Gould. (9), tree pipit (6) / rook and rock pigeon (17 for each species), horned lark (15), myna *Acridotheres tristis* (L.) (10), magpie (7); 246/7; 67/25; 64, 42, and 16 for the Trans-Palearctic, European, Tibetan faunal types, respectively);

13—communities of airfields (stonechat (24), yellow and citrine wagtails (16 for each species), tree sparrow (13), skylark (6) / gray crow (20), rook (17), magpie (10), starling and stonechat (7 for each species); 649/30; 58/29; 64, 16, and 15 the Trans-Palearctic, Tibetan, and European faunal types, respectively);

14—communities of mountain sheepyards, farms, and shepherd's huts in Middle Asia (horned lark (26), eastern rock pigeon, tree and house sparrows, and myna (9 for each species) / rook (24), eastern rock pigeon (22), myna (9), black crow and horned lark (8 for each species); 1749/211; 65/45; 20, 17, and 10 for the Trans-Palearctic, European, and Chinese faunal types, respectively);

15—communities of Altai-Sayan cordons and lodges (masked wagtail (20), great tit (14), white-fronted redstart *Phoenicurus phoenicurus* (L.) (8), tree sparrow (7), barn swallow *Hirundo rustica* L. (6) / blue rock pigeon (23), black crow (20), eastern rock pigeon (11), masked wagtail (10), demoiselle crane *Anthropoides virgo* (L.) (6); 134/7; 32/24; 42 and 17 for the European and Trans-Palearctic faunal types, respectively).

Community types:

communities of northern plains (the area from tundra to northern taiga)

16—communities of rivers and channels (ruff (17), green-winged teal (9), pintail (8), wigeon (7), white wagtail (5) / pintail (15), wigeon and white-fronted goose (10 for each species), whooper swan (7), green-winged teal (6); 146/69; 104/30; 33, 32, and 29 for the Arctic, Trans-Palearctic, and Siberian types, respectively);

17—communities of lakes, shors, and oxbows (Arctic tern *Sterna paradisaea* Pontopp. (14), pintail (12), long-tailed duck (9), wigeon and black-throated diver *Gavia arctica* (L.) (7 for each species) / black-throated diver (30), pintail (16), long-tailed duck (10), wigeon (8), tufted duck (5); 397/238; 98/38; 34 for both the Arctic and Siberian faunal types, and 29 for the Trans-Palearctic);

Communities of median plains (the area from middle taiga to the steppe zone)

18—communities of rivers and channels (light-winged tern *Chlidonias leucoptera* (Temm.) (13), sand martin (10), garganey (9), common pochard and yellow wagtail (4 for each species) / garganey and mallard (12 for each species), common pochard (11), coot (9), common shoveler *Anas clypeata* L. (6); 430/139; 170/49; 58 and 28 for the Trans-Palearctic and European faunal types, respectively);

19—communities of lakes, shors, oxbows, and reservoirs (common pochard and paddy-field warbler (7 for each species), black-headed gull *Larus ridibundus* L. and coot (6 for each species), yellow-headed wagtail (4) / common pochard (14), coot (11), whooper swan, gray goose, and mallard (5 for each species); 430/181; 203/60; 51 and 17 for the Trans-Palearctic and European faunal types, respectively).

Water bird community subtypes:

19.1—<u>communities of surface freshwater bodies</u> (sand martin (8), black-headed gull (5), common pochard, coot and light-winged tern (4 for each species) / common pochard (9), coot (8), tufted duck (7), mallard (6), garrot (4); 199/81; 180/44; 57 and 17 for the Trans-Palearctic and European faunal types, respectively);

19.2—<u>communities of fresh overgrown water bodies</u> (paddy-field warbler (12), citrine wagtail and coot (8 for each species), black-headed gull and reed bunting *Emberiza schoeniclus* (L.) (5 for each species) / coot (20), common pochard (11), black-headed and silver gulls and garganey (5 for each species); 981/295, 143/58; 15 and 12 for the European and Mediterranean faunal types, respectively);

19.3—<u>communities of surface saline water bodies</u> (black-headed gull (13), common pochard (8), tran-

Force of the relationship between environmental factors and heterogeneity of summer bird communities in the Middle Region

Factor, regime	Taken into account the dispersion, %
Forestation	18
Buildup	9
Watering	9
Moistening	8
Flooding regime (the degree of flooding)	8
High-altitude zone	6
Latitudinal zonality and subzonality	5
Altitudes	5
Provinciality in the Altai-Sayan mountain country	1
Mineral nutrition of bogs	0.3
Lake salinity	0.1
Degree of lake overgrowing	0.1
All factors	40*
Classification regimes	42
structural regimes	41
total	44
All factors and regimes	54*

* Because of the software restrictions on the amount of analyzed data, the assessments of the integral information value of the classifications, as well as multiple correlation with all factors and regimes, were calculated in six replications based on half of all averages chosen by a random number generator. The obtained results were averaged. The remaining assessments were obtained for the entire sample based on 1199 averages.

sient little stint and little gull *Larus minutus* Pall. (7 for each species), rook (4) / transient white-fronted goose (17), whooper swan (13), common pochard (12), black-headed and silver gull (6 for each species); 346/199; 108/44; 49 for the Trans-Palearctic faunal type, 18 and 16 for the European and Arctic types, respectively);

19.4—communities of saline overgrown water bodies (common pochard (17), black-headed gull and coot (8 for each species), garganey and wigeon (5 for each species) / common pochard (21), gray goose (14), coot (9), wigeon and pink pelican (5 for each species); 1161/765; 85/57; 47 and 21 for the Trans-Palearctic and European faunal types, respectively).

Community types:

Southern mountain communities

20—communities of rivers and channels (sand martin and common sandpiper *Actitis hypoleucos* (L.) (16 for each species), gray wagtail *Motacilla cinerea* Tunst. (15), magpie (7), black crow (6) / black crow (25), magpie (9), common merganser (8), pintail (7), common sandpiper (5); 661/106; 87/37; 64 and 18 for the Trans-Palearctic and European faunal types, respectively);

21—communities of lakes, oxbows, and reservoirs (black swift 72, house martin *Delichon urbica* (L.) (18), common tern *Sterna hirundo* L. and black-headed gull (2 for each species), common merganser (1) / black swift (33), common merganser (15), white-winged velvet scoter *Melanitta deglandi* (Bp.) (9), great-crested grebe *Podiceps cristatus* (L.) (6), black-headed gull (5); 2659/236; 141/33; 72 and 25 for the European and Trans-Palearctic faunal types, respectively).

Environmental Relationships of Heterogeneity of Ornithocomplexes, Environmental Factors, and Natural-Anthropogenic Regimes

Analysis of the hierarchical classification and similarity graph obtained while studying bird communities showed that there was a correlation between the heterogeneity of ornithocomplexes and variability of 12 environmental factors. In addition, the common boundary related to the presence or absence of permafrost was revealed between northern and middle taiga for all bird community systems. However, the division into taxons according to the degree of permafrost influence was tracked by no means always and was estimated for this factor at 4% of the variance of the matrix of similarity coefficients for bird communities. The presented table does not mention this factor, since its influence was correlated with other more significant natural regimes. Changes in bird communities are most closely interrelated with forestation (18% of the variance). A twofold smaller influence is exerted by the degree of development and watering of territories, and a somewhat less effect is made by moistening and flooding. The interrelation of the heterogeneity of bird communities with high-altitude zone in mountains is three times smaller, and the interrelation with zonality (subzonality) in plains and altitude marks is even lower. The provincial distinctions within the Altai-Sayan mountain country account for only 1% of the variance; the mineral nutrition in swamps and also salinity and overgrowing of lakes are even less significant as factors of spatial differentiation. About 40% of the variance is due to all the aforementioned factors. The total information value of separately taken classifications is 42% of the variance, and that of graphs is 41% (taken together, they account for 44%). All factors and regimes can account for 54% of the variance, which is equal to the coefficient of multiple correlation of about 0.74.

CONCLUSIONS

The cluster analysis of the collected materials has shown that the ecological influence of zonal and altitudinal zonal distinctions in heat and moisture supply is prevalent in the formation of bird community heterogeneity in the Middle Region of Northern Eurasia. This being the case, the boundaries of natural geo-

graphical zones and belts do not coincide with the types (bands) of ornithocomplexes, which were distinguished by similarity. Thus, the tundra community type includes the bird communities of only Arctic and northern Subarctic tundras, whereas the ornithocomplexes of southern Subarctic tundras together with the communities of open boreal woodlands and northern taiga are included in the forest tundra type. At the same time, the forest community type includes the communities of more or less wooded habitats within the area which extends from the middle taiga to the steppe zone and those of analogous areas in the West Siberian mountain territories. The bird communities open habitats of West Siberia are divided into two types: the meadow-steppe and semidesert-steppe types. The ornithocomplexes of Middle Asiatic territories are also divided into two types: the northern desert-steppe and southern desert types. The latter includes the analogous communities of Tuva and Southeast Altai. The eighth bird community type includes the communities of all high-mountain regions.

The ornithocomplexes in the developed lands form an individual bird community system. Only two zonal residential community types can be distinguished within its limits: these are the northern and southern types with the boundary between northern and middle taiga. The formation of the other four types is due to the distinctions in the degree of greening and economic use of areas (industrial, transport, or agrarian). The bird communities of water—riparian habitats can be divided into three bands. The northern and median latitudinal bands are divided by the boundary between the northern and middle taiga. The median band includes the ornithocomplexes of water bodies and rivers in the area, which extends from the middle taiga to plain steppes. The third band is represented by southern and mountain water—riparian communities.

Consequently, it can be stated that zonality is dominant in the formed territorial heterogeneity of ornithocomplexes as a phenomenon determined by the latitudinal changes in hydrothermal conditions, but there is a significant inconsistency between the ideas of the boundaries drawn by the researcher for bird communities and the boundaries of natural geographical zones. This inconsistency leads to the fact that the variation in bird communities is most strongly correlated with the spatial distinctions in forestation, development, and watering of a territory, whereas latitudinal zonality (including subzonality) in plains and altitudinal zonality in mountains account for a much smaller portion of the variance of the similarity matrix for ornithocomplexes.

ACKNOWLEDGMENTS

We are sincerely grateful to T.V. Kotova and O.N. Nikolayeva for reviewing the article prior to its publication and a number of valuable comments on the map. The research that served as a basis for this study were supported by the Russian Foundation for Basic Research, project no. 13-04-00582, and partly implemented within the framework of the "Program for Increasing Competitiveness of the Tomsk State University."

REFERENCES

Atlas Kirgizskoi SSR (Atlas of Kirgiz Soviet Republic), Moscow: Glav. Uprav. Geodez. Kartogr., 1987, vol. 1.

Ivanov, A.I., *Katalog ptits SSSR* (Catalogue of the Birds of Soviet Union), Leningrad: Nauka, 1976.

Jaccard, P., Lois de distribution florale dans la zone alpine, *Bull. Soc. Vaud. Sci. Nat.,* 1902, vol. 38, pp. 69–130.

Landshaftnaya karta Altae-Sayanskogo ekoregiona, Masshtab 1 : 2250000 (Landscape Map of Altai-Sayan Ecological Region, Scale 1 : 2250000), Moscow: WWF Russia, 2001.

Naumov, R.L., The birds in the foci of tick-born encephalitis, *Extended Abstract of Cand. Sci. (Biol.) Dissertation,* Moscow, 1964.

Perspektivy orosheniya v Sredinnom regione SSSR (Prospects of Irrigation in the Central Region of Soviet Union), Moscow: Nauka, 1978.

Priroda Sredinnogo regiona SSSR (v svyazi s problemoi perebroski rechnogo stoka) (Nature of the Central Region of Soviet Union Related to the Problems of Regulated River Run-Off), Moscow: Mosk. Gos. Univ., 1980.

Rastitel'nost' Zapadno-Sibirskoi ravniny, Masshtab 1 : 1500000 (Vegetation of West Siberian Plain, Scale 1 : 1500000), Moscow: Glav. Uprav. Geodez. Kartogr., 1976.

Ravkin, Yu.S., Kupershtokh, V.L., and Trofimov, V.A., Spatial organization of bird community, in *Ptitsi lesnoi zony Priob'ya* (The Birds of Forest Zone of Ob' Region), Novosibirsk: Nauka, 1978, pp. 253–269.

Ravkin, Yu.S. and Livanov, S.G., *Faktornaya zoogeografiya* (Factor Zoogeography), Novosibirsk: Nauka, 2008.

Ravkin, Yu.S., Vartapetov, L.G., Milovidov, S.P., Tsybulin, S.M., Pokrovskaya, I.V., Fomin, B.N., Adam, A.M., Yudkin, V.A., Toropov, K.V., Zhukov, V.S., Ananin, A.A., Blinov, V.N., Burskii, O.V., Panteleev, P.A., Blinova, T.K., et al., Spatial-typologic structure of summer communities of birds in the Central region of Soviet Union, in *Mater. 10-i Vses. Ornitologicheskoi konferentsii* (Proc. 10th All-Union Ornithological Conference), Minsk, 1991, part 1, pp. 133–134.

Terent'ev, P.V., The method of correlation pleiads, *Vestn. Leningr. Gos. Univ.,* 1959, no. 9, pp. 137–141.

Trofimov, V.A. and Ravkin, Yu.S., Express analysis of relationship between spatial heterogeneity of living population and environmental factors, in *Kolichestvennye metody v ekologii zhivotnykh* (Quantitative Methods Applied in Animal's Ecology), Leningrad: Nauka, 1980, pp. 113–115.

Shtegman, B.K., Principles of ornitho-geographical division of Palaearctic, in *Fauna SSSR. Ptitsy* (Fauna of Soviet Union: Birds), Moscow: Akad. Nauk SSSR, 1938, vol. 1, no. 2.

Translated by L. Solovyova