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Regularities of Spatial Differentiation of Fauna and Bird Population on the Putorana Plateau

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Abstract—The spatial differentiation of the bird population on the Putorana Plateau has been analyzed. One hundred and thirty-seven bird species nest in the region. Species diversity, bird population density, and abundance of most species decrease with altitude. The largest decrease in bird population density occurs during the transition from the subalpine belt to the alpine belt; a little less significant one occurs during the transition from the forest belt to the subalpine belt. Most bird species inhabit a wide range of altitudes, which usually involves at least two altitude belts. The bird population density at the level of alpine, subalpine, and forest altitude and landscape belts decreases in the direction from west to east (from the Putorana Plateau to Koryak Upland). The spatial dynamics of the bird population density and abundance of most background species of the Putorana Plateau has a tendency to increase from the highest internal regions of mountain countries towards the periphery. At the Putorana Plateau, the communities of birds from the forest belt are more diverse, stable, and homogeneous in space and time when compared with the alpine and subalpine belts. In addition to high values of the population similarity coefficient, minimal amplitudes of species diversity and bird population density, and a relatively even distribution of more than half of the species composition along the region territory, insignificant provincial differences in the composition of leaders were detected here.

Keywords: avifauna, bird population, the Putorana Plateau, Asian subarctic mountains, distribution, number, nesting, altitude belt

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INTRODUCTION

The results of the presented investigations are in the field of studying the spatial organization of the bird population and are directed at estimating the biodiversity of birds in Asian subarctic mountains using the example of the Putorana Plateau as a model region. Geographical aspects of the development of the fauna and bird population in this land area are still poorly studied. The main purpose of the work by Yu.I. Chernov (1978) devoted to the structure of the subarctic animal population was not the detection of mountain–subarctic ecosystem specifics. Ornithological studies by A.A. Kishchinskii (1988) involved part of northwest Asia and can be considered base studies for the analysis of avifauna of the more extensive and diverse (in natural respect) mountain range of northern Asia. The ornithofaunistic regionalization and classification of birds by the similarity of distribution (developed for Northern Eurasia) (Blinova and Ravkin, 2008, 2009; Vartapetov and Germogenov, 2011) are extremely generalized. At the same time, the cognition of ways and mechanisms of the development of faunistic complexes and bird population of extensive mountain regions is recognized as one of the topical questions of modern ornithology in the field of biological diversity (Baranov, 2007; Germogenov and Vartapetov, 2010). The detection of regularities of the development of spatial differentiation of fauna and population in Asian subarctic mountains can make an obvious contribution to its decision using the example of a model region (the Putorana Plateau).

The main aim of the study is a complex analysis of the bird population in the Putorana Plateau in the light of ecological and geographical regularities of its spatial differentiation for use during the monitoring and development of measures for the maintenance of biological diversity in all Asian subarctic mountains.

MATERIALS AND METHODS

The results of studies conducted on the Putorano Plateau in 1988–2008 form the basis of the present work (Romanov, 1996, 2003, 2013). All main peculiarities of physical and geographical environment typical for all Asian subarctic mountains are expressed within the Putorana Plateau, which makes it possible to consider it a model region for the detection and cognition of general regularities of bird population differentiation in mountain subarctic ecosystems. The object of the study was the fauna and population of the largest mountain region in northern Asia, which is located within the subarctic of the Putorana Plateau. The subarctic concept is accepted in interpretation that is widespread among geographers and biologists (Chernov, 1978; Golubchikov, 1996; Kuvaev, 2006) and is determined as a type of physical and geographical environment, territorially corresponding to a subzone of southern tundra, forest–tundra, and northern outskirts of the north taiga subzone. The nesting population of birds in the Putorana Plateau was analyzed as compared with the nesting populations of birds from other Asian subarctic mountain regions, within which alpine, subalpine, and forest altitude and landscape belts are expressed. Koryak and Kolyma Uplands, mountains in Yakutia (Verkhoyanskii, Cherskogo, Kular and Polousnyi ranges), the Anabar Plateau, and the Circumpolar and Polar Urals are among these regions. The results of ornithological studies in 135 scientific works of different authors were involved in the analysis (Romanov, 2013). The similarity of avifauna in compared mountain systems was determined by the faunistic community coefficient calculated according to Sørensen's formula (Pesenko, 1982; Chernov, 2008). The population similarity coefficient (PSC) was calculated according to the formula

$$\mathrm{PSC} = \frac{a}{(b+c)-a} \times 100\% \text{ (Naumov, 1964)},$$

where a is a sum of the lowest (of two) indices of the species abundance (common for two compared regions); b and c are the total abundance of birds from the first and second regions. This coefficient was used for the detection of provincial differences in the bird population in different regions of the model mountain region (the Putorana Plateau). The statistical treatment of the materials was conducted using variation statistics methods (Lakin, 1990), taking into account recommendations by Doctor of Biology S.P. Kharitonov. We followed L.S. Stepanyan (2003) in nomenclature and while compiling lists of birds.

RESULTS

Taxonomic structure. One hundred and thirty-seven bird species nest at the Putorana Plateau, which accounts for 70% of nesting avifauna of Asian subarctic mountains ($n = 197$ species). The taxonomic structure of nesting avifauna from the Putorana Plateau corresponds to zonal and landscape peculiarities of the considered northern Asia region with the dominance of 4 orders typical for boreal and hypoarctic belts of Palaearctic, including perching birds (51 species, 43%), Charadriiformes (26 species, 19%), Anseriformes (23 species, 17%), and Falconiformes (12 species, 9%). In total, these orders account for 88% of reported species at the Putorana Plateau (almost the same as in all other Asian subarctic mountains (85%)).

Latitudinal and meridional differentiation of avifauna. The Putorana Plateau in the range of Asian subarctic mountains is a center of specific diversity. The specific diversity of avifauna decreases by 10% (nesting decreases by 6%) to the west of the Putorana (towards the Circumpolar and Polar Urals); by 15% (nesting, by 3–5%) to the east of the Putorana (towards Verkhoyanskii and Cherskogo ranges and Kolyma Upland); and by 26% (nesting, by 22%) further at Koryak Upland. An increased specific diversity of avifauna at the Putorana Plateau corresponds to its location within Yenisei zoogeographical border, which was formed along the line of estimated glacial rupture of faunistic complexes and areas of species (Matyushkin, 1976; Rogacheva, 1988). This avifauna includes species and subspecies that are typical members of taiga and tundra faunistic complexes prevailing to the west or to the east of Yenisei border and do not spreading further from it. The process of settlement of species that had considerably broader areas before glaciation, receded during the glacial period, and currently settle in their aboriginal territories probably starts influencing the increase of specific diversity of the Putorana avifauna (Matyushkin, 1976). Such an assumption is fair for a number of species that have a very-noticeable "southern deflection" of the northern border of the areas within average part of the Asian subarctic mountain range (the Putorana Plateau, mountains in Yakutia) (the *Anas clypeata* shoveler (Linnaeus, 1758), *Mergus albellus* magpie diver (Linnaeus, 1758), *Falco subbuteo* hobby falcon (Linnaeus, 1758), *Falco tinnunculus* common kestrel (Linnaeus, 1758), *Larus ridibundus* black-headed gull (Linnaeus, 1766), *Dendrocopos major* greater spotted woodpecker (Linnaeus, 1758), *Dendrocopos minor* lesser spotted woodpecker (Linnaeus, 1758), *Anthus hodgsoni* Indian tree pipit (Richmond, 1907), *Phylloscopus trochiloides* greenish warbler (Sundevall, 1837), *Pyrrhula pyrrhula* common bullfinch (Linnaeus, 1758), *Emberiza rustica* rustic bunting (Pallas, 1776), *Emberiza aureola* golden bunting (Pallas, 1773)). The insufficient number of observations does not allow one to make representative conclusions about the positive trends of the dynamics of northern borders of their distribution and the restoration of preglacial areas. However, for example, the registration of the first facts of the repeated nesting of common kestrel, greenish warbler, and rustic bunting on the territory of the Putorana in 2006–2007 (that we succeeded to find for the first time at the nesting site in four qualified studied before the Putorana Plateau regions) indicate the correctness of such an assumption (Romanov, 2013). It is unlikely that these birds could be "missed" during extensive and, in a number of cases, long-term studies that are quite sufficient for the detection of typical and rather noticeable species.

The maximally high level of similarity (85%) of the Putorana Plateau avifauna is revealed with avifauna of mountains in Yakutia. This is probably due to the fact that reorganizations of ecosystems of Yakutia mountain systems in pleistocene were less catastrophic than in ecosystems of other Asian subarctic mountains. This caused in general the relatively more stable development of local avifauna, which (probably, mainly as a donor) in turn ensured the possibility of the species exchange with the nearest regions and among others favored the development of increased species diversity of avifauna at the Putorana Plateau. The homogeneity of avifauna of the Putorana Plateau and mountain regions of Yakutia is also supported by the similarity of modern ecological conditions (Romanov, 2013).

Avifauna of the Putorana Plateau has a clearly designed common faunistic nucleus. The species that are widespread in northern taiga and forest tundra, particularly in southern tundra, and simultaneously are members of avifaunas of almost all regions from the Urals to the Koryak Upland form approximately half of the nesting avifauna of both the Putorana Plateau and all other Asian subarctic mountains.

The development and spatial dynamics of avifauna from the Putorana Plateau is determined by including patterns of a latitudinal–zonal character. For example, when moving in a northern direction, the total species diversity of nesting avifauna within the plateau reduces from 137 species at the southern outskirts to 105 species at the northern outskirts. Plain and tundra species (the *Clangula hyemalis* long-tailed duck (Linnaeus, 1758), *Calcarius lapponicus* Lapland bunting (Linnaeus, 1758) and arctic–alpine species (*Plectrophenax nivalis* snow bunting (Linnaeus, 1758)) penetrate along bald peaks of the Putorana Plateau much further south (at a distance reaching 500 km) than the borders of their zonal area. There is also an opposite phenomenon: some bird species penetrate along the lower (forest) part of large mountain river valleys much farther to the north than along the plain river valleys and, moreover, plain watershed. This is rather clearly expressed in the north of Middle Siberia. The highest bonitet forests in this region are timed to mountain valleys of the Putorana Plateau, where they enter almost 2° further north than at adjacent plains or Anabar Plateau (Golubchikov, 1996; Kuvaev, 2006; Chernov, 2008). Therefore, for example, the *Bombycilla garrulus* waxwing (Linnaeus, 1758), *Prunella montanella* mountain accentor (Pallas, 1776), *Phylloscopus inornatus* browed warbler (Blyth, 1842) *Fringilla montifringilla* mountain finch (Linnaeus, 1758), *Loxia leucoptera* white-winged crossbill (Gmelin, 1789) that are common or even numerous in forests of the Putorana Plateau become extremely rare and are found sporadically in more depressed Anabara forests located at the latitude of Putorana forests. Species such as the *Accipiter gentilis* northern goshawk (Linnaeus, 1758), *Accipiter nisus* sparrow hawk (Linnaeus, 1758), *Sterna hirundo* common tern (Linnaeus, 1758), *Aegolius funereus* boreal owl (Linnaeus, 1758), *Jynx torquilla* wryneck (Linnaeus, 1758), *Dryocopus martius* black woodpecker (Linnaeus, 1758), *Ficedula parva* red-breasted flycatcher (Pallas, 1764), *Tarsiger cyanurus* bluetail (Pallas, 1773), and *Pinicola enucleator* pine grosbeak (Linnaues, 1758) find a northern limit of their distribution in forests of the Putorana river valleys (Romanov, 2013).

Development of vertical heterogeneity of avifauna. The ratio of taxonomic groups that compose the basis of avifauna from alpine, subalpine, and forest belts of the Putorana Plateau remains in general over the entire altitude profile. Perching birds (43–57%), Charadriiformes (18–28%), Anseriformes (12–14%), and Falconiformes (8%) are the most important. The specific weight of Charadriiformes increases from the foot of a mountain to its peak (from 18 to 28%) (particularly of sandpipers, from 14 to 23%), approaching the structure of avifaunas of mountain and plain tundra.

In the presence of specific species in avifauna of each vertical belt of the Putorana, avifaunas of two adjacent belts have many common species in their composition. Out of 129 bird species that nest in the forest belt and 52 species that nest in the subalpine belt, 48 species are common for avifaunas of both belts. Out of 52 bird species that nest in the subalpine belt and 40 species that nest in the alpine belt, 30 species are common for avifaunas of these belts. Moreover, due to the decreased location of the "snow line," the living space is here considerably narrower than in mountains of more southern latitudes (for example, in mountains of the south of the Palearctic. Due to this, birds of different faunistic complexes that have specific adaptations to life in the taiga, tundra, or mountains appear in a close proximity to each other at the Putorana Plateau (like in other Asian subarctic mountains). In the presence of appropriate ecological preconditions, they have the possibility of not only rather rapidly moving from belt to belt, but also generating combined "mixed grouping." This allows the continuity and maximal efficiency of the development and transformation of avifauna according to the direction of space-time changes of environmental conditions to be maintained (Romanov, 2013).

Analysis of the degree of community of alpine, subalpine, and mountain–forest avifaunas, conducted using Sørensen's formula (Pesenko, 1982; Chernov, 2008), detected that the large homogeneity of the main part of the species composition is typical for mountain–forest avifauna and considerably smaller part for subalpine and alpine avifauna. Mountain–forest avifauna was developed in a single area of northern Asia with the prevalence of northern taiga forests and hypoarctic light forest occurring everywhere. Under conditions of continuity of forest landscapes and the widespread contingency of mountain and plain forest types, the vast majority of species master them everywhere, since they do not have insurmountable barriers that prevent settlement. Fragmentation, mutual remoteness, and isolation of subalpine and alpine belt regions in combination with more diverse and unstable ecological conditions caused a smaller mutual similarity of regional avifaunas at the level of each of these belts.

Regions with a maximally high level of mutual community were detected for mountain–forest, subalpine, and alpine avifaunas. The location of these

Table 1. Bird population density in different altitude belts of Asian subarctic mountains, individuals/km^2

No.	Altitude–landscape belt	Circumpolar and Polar Urals	The Putorana Plateau	Anabar Plateau	Mountains of Yakutia	Kolyma Upland	Koryak Upland	At average
1	Alpine	149	47	42	–	14	–	63
2	Subalpine	194	164	147	–	55	–	140
3	Forest	420	405	185	–	145	–	289

(–) Data are absent.

regions is different in the range of Asian subarctic mountains. The most homogenous (83–84%) mountain–forest avifauna was developed at the Putorana Plateau, the mountains of Yakutia, and Kolyma Upland. This is consistent with the unity of taiga Siberian fauna, in which the establishment of the role of a rather specific east Siberian (Angarsk) faunistic complex is especially large (Chernov, 1975). The similarity of avifaunas of regions that simultaneously cover the mountain–foothill and plain territories of northern Asia (55–58.3%) (Chernov, 1975) is smaller than mountain–taiga avifaunas of Asian subarctic mountains (83–84%). This indicates the higher homogeneity of avifauna of mountain–taiga regions and provides a basis for considering the development of avifauna of Asian subarctic mountains as an original process which flows in a single relatively independent ecological and zoogeographical space (Romanov, 2013).

The subalpine avifauna of the Putorana Plateau does not have any considerable qualitative similarity to subalpine avifaunas of other Asian subarctic mountains due to the depletion of its species composition and faunistic "facelessness." The mutually most similar (61–65%) subalpine avifaunas are developed in Koryak Upland and in the mountains of Yakutia and Koryak Upland adjacent to it. It is probably closely associated with the formation of the so-called Bering forest–tundra and its mountain derivatives, which is very typical for the indicated territory, especially its eastern part (Kishchinskii, 1988).

The most homogenous (63%) alpine avifauna is developed in the northern area of the Asian subarctic mountain range at the Putorana Plateau and Yakutia mountains (closest from the east) and the Circumpolar and Polar Urals (closest from the west). This region occupies the median transitional (from the point of view of the interpenetration of species) part of the Eurasian subarctic, the avifauna of which unites elements of European and Asian northern biomes (Rogacheva et al., 1995). Many of these elements (inhabitants of plain tundra) penetrate subarctic mountains on the entire interval from the Urals to the Verkhoyanskii range, maintaining an increased similarity of alpine avifaunas of indicated mountain countries (Romanov, 2013).

Spatial structure of bird population. The species richness, bird population density, and abundance of the absolute majority of species progressively decrease with altitude at the Putorana Plateau, as well as in other Asian subarctic mountains (Table 1).

Considerable differences between bird populations in three altitude belts of the Putorana Plateau, detected using the population similarity coefficient (Naumov, 1964), indicate a high degree of autonomy of the process of its development within each of the belts. Thus, the level of population similarity of forest and subalpine belts does not exceed 29% at the Putorana Plateau, for the subalpine and alpine this level is 18%, and for forest and alpine it is only 2%. With the rise on each 100 m, the bird population density reduces at the average ($n = 4$) by 28 individuals/km^2. The main decrease of the bird population density at the Putorana Plateau (as well as in most other mountain regions) occurs during the transition from the subalpine belt to the alpine belt; a slightly less considerable decrease occurs during the transition from the forest belt to the subalpine belt.

Four groups of species, which have different vectors of vertical abundance dynamics, were detected at the Putorana Plateau within a decrease of total bird population density from the foot to the peak. (1) Progressively reducing the abundance with the altitude (the *Falco columbarius* merlin (Linnaeus, 1758), *Lagopus lagopus* white grouse (Linnaeus, 1758), *Motacilla cinerea* gray wagtail (Tunstall, 1771), *Motacilla alba* white wagtail (Linnaeus, 1758), *Phylloscopus borealis* Arctic warbler (Blasius, 1885), *Turdus eunomus* brown thrush (Temminck, 1831), *Acanthis flammea* mealy redpoll (Linnaeys, 1758), *Emberiza pusilla* little bunting (Pallas, 1776)). (2) Progressively increasing the abundance with altitude (the *Oenanthe oenanthe* common chat (Linnaeus, 1758)). (3) Maintaining stable abundance in the forest and subalpine belts and reducing it only in the alpine belt (the *Gallinago stenura* pin-tailed snipe (Bonaparte, 1831), *Motacilla citreola* yellow-headed wagtail (Pallas, 1776), *Phylloscopus trochilus* willow warbler (Linnaeus, 1758)). (4) Having maximal abundance in the sublalpine belt and reducing it towards peaks and slop foots (*Heteroscelus brevipes* Siberian gray-tailed tattler (Viellot,

Table 2. Significance of correlation between longitude and bird population density

Altitude–landscape belt	n	r (correlation coefficient between longitude and bird population density)	P (correlation coefficient significance)
Alpine	4	–0.89	0.10
Subalpine	4	–0.92	0.07
Forest	4	–0.94	0.06

1816), *Cuculus canorus* common cuckoo (Linnaeus, 1753), *Asio flammeus* marsh owl (Pontoppidan, 1763), *Anthus cervinus* red-throated pipit (Pallas, 1811), *Luscinia svecica* bluethroat (Linnaeus, 1758), *Carpodacus roseus* Siberian rosefinch (Pallas, 1776), *Emberiza pallasi* Pallas' reed bunting (Cabanis, 1851). Due to regional specifics of ecological conditions, directions of the spatial change of abundance of the same species can differ in different Asian aubarctic mountains. For example, Arctic warbler and mealy redpoll in Kolyma Upland reach maximal abundance not in the forest belt (like at the Putorana Plateau), but in the subalpine belt (Kishchinskii, 1968). The most extreme forms of such tendencies can manifest in the fact that some species that inhabit most of Asian subarctic mountains, mainly (or including) in the forest belt, "leave" the limits of the forest belt at the east and inhabit only overlying subalpine belt. These are, for example, pin-tailed snipes in Koryak Upland or bluethroat in Kolyma Upland (Kishchinskii, 1988).

Within the range of Asian subarctic mountains, the bird population density at the level of all altitude–landscape belts reduces from the Putorana Plateau in the eastern direction up to the Koryak Upland. This is consistent with a decrease in the same direction of the total productivity of the plant cover (National Strategy and Plant of Action Plant for Conservation of Biodiversity of Russia, http://www.sci.aha.ru/biodiv/npd/ind1.htm). The correlation between a decrease in the bird population density and longitude is close to the significance for population density indices within the alpine, subalpine, and forest belts (Table 2).

The bird population density in the alpine belt decreases ten times in the eastern direction from the Putorana Plateau; the decrease is not as severe for subalpine (3.5 times) and forest (3 times) belts.

A similar composition of leading species was detected at the Putorana Plateau and in other Asian subarctic mountains, indicating not only the community of the nucleus of their avifaunas, but also the certain unity of ecological and zoogeographical regularities of the development of the basis of the bird population in these regions. The spatial continuity of the bird population in the horizontal plane is maintained by species leading in regards to abundance in several regions of Asian subarctic mountains simultaneously and that in vertical space is maintained by those leading in two (usually adjacent) altitude–landscape belts. Seven species, out of which four (Arctic warbler, mountain finch, mealy redpoll, and little bunting) are common, lead in the forest belt of the Putorana Plateau (as well as in larger part of the Asian subarctic mountain range). Arctic warbler and mealy redpoll lead in the bird population in the subalpine belt of the Putorana Plateau and in other mountain regions of Asian subarctic. Common chat in different combinations with five other species (usually members of the *Anthus* genus) leads almost everywhere in the alpine belt of the Putorana Plateau, as well as in other Asian subarctic mountains. These are the *Anthus pretensis* meadow pipit (Linnaues, 1758) and red-throated pipit (Estaf'ev, 1977, 1981; Golovatin, Paskhal'nyi, 2005) in the western part of the Asian subarctic mountain range, the Urals, and the *Anthus rubescens* buff pipit (Tunstall, 1771) and red-throated pipit (Kishchinskii, 1980; Romanov, 2013) at the Putorana Plateau and to the east.

Intraregional variability of density and structure of bird nesting population. The huge size and complex orography of Asian subarctic mountain countries predetermine the intraregional (provincial) peculiarities of the bird population. The Putorana Plateau was a model region, where peculiarities of intraregional differences in the density and structure of the bird population were detected using the population similarity coefficient (Naumov, 1964).

The most significant intraregional differences were detected in the bird population of the subalpine belt of the Putorana Plateau. The lowest indices of minimal (3%) and maximal (49%) population similarity were in the subalpine belt. The total level of absolute PSC values was also considerably lower than in alpine and forest belts; the similarity of the bird population does not exceed 20% in more than a half of the compared pairs of regions; in total, the population similarity slightly exceeds 30% in 10 out of 55 compared pairs of regions. A pronounced provinciality of subalpine bird communities when compared with alpine or, moreover, forest communities is caused by heterogeneous and less stable ecological conditions, as well as the almost complete absence of species adapted to them.

Provincial differences of the bird population within the alpine belt of the Putorana Plateau are not as contrasted as in the subalpine belt. There is quite a significant amplitude between minimal (8%) and maximal (67%) index of the population similarity coefficient in the alpine belt (as well as in subalpine belt). However, their absolute values (as well as the total level of PSC absolute values) are higher than in the subalpine belt; the similarity of the bird population exceeds 30% more than in half of compared pairs of regions; the similarity of population is lower than 20% only in 9 out of 67 compared pairs of regions. Ecological conditions in the alpine belt are more extreme and simultaneously more stable than in subalpine belt. The portion of alpine and arctic–alpine species (well adopted to conditions of subarctic mountain peaks) is significant in the bird population of the alpine belt. All this provides the large total spatial–temporal resistance of the bird population in the alpine belt (Romanov, 2013).

Provincial differences of the bird population are expressed much less in the forest belt of the Putorana Plateau than in alpine and subalpine belts. The amplitude between minimal (36%) and maximal (67%) indices of the population similarity coefficient is smaller. Absolute PSC values, as well as the total level of absolute PSC values, are higher than in alpine and, moreover, subalpine belts. The similarity of the bird population exceeds 50% more than in a half of the compared pairs of regions. The similarity of population is lower than 40% only in 4 out of 45 compared pairs of regions. In general, high absolute values of the population similarity coefficient are typical for all compared pairs of regions. This indicates a rather stable and equivalent mutual influence of bird communities even in mutually distant regions at the level of the forest belt. The bird communities of the same regions in alpine and subalpine belts result in a much greater spread of PSC values during their pairwise comparison.

Detected vectors of the population density change and abundance of most background species indicate that their spatial dynamics at the Putorana Plateau has a concentrically centrifugal character. These indices have a tendency towards an increase from the highest internal regions of the mountain country (where their values are minimal) to the periphery (Romanov, 2013). This regularity is especially clearly manifested in the bird population of the lowest and highest parts of the altitude profile (in forest and alpine belts).

Provincial differences within all altitude–landscape belts of the Putorana Plateau are typical both in total indices of the bird population and in specifics of spatial changes of the abundance of certain species. It was found that regularities of provincial differences in the density of bird population are rather specific in the forest, subalpine, and alpine belts of the Putorana Plateau. In the forest belt of the Putorana Plateau, provincial differences of the population density are determined by different compositions of main forest-forming breeds and by the bonitet of forests depending on the geographical latitude of the locality and climate continental. The presence of two equivalent trends of a decrease in this index (from south (566–673 individuals/km^2) to north (295–309 individuals/km^2) and from west (364–488 individuals/km^2) to east (251 individuals/km^2)) is explained by it. In the subalpine belt of the Putorana Plateau, the spatial irregularity of the development of bushes and elfin wood zone (associated, first and foremost, with the level of climate continental) should be recognized as the main factor determining provincial differences in the population density within a separate mountain system. In the subalpine belt of the Putorana, this is confirmed by the presence of only one reliably detected trend of a decrease in the population density (from west (196–388 individuals/km^2) to east (71 individuals/km^2)). No dependence between the population density and the locality latitude was detected within the subalpine belt of the Putorana. In the alpine belt of the Putorana, provincial differences of the population density are determined by the character of prevailing mountain–tundra types of vegetation, mainly associated with absolute locality altitude (which explains the presence of trends to an increase in this index from the highest middle part of the plateau (30 individuals/km^2) to lower southern (43–46 individual/km^2) and northern (102–115 individuals/km^2) outskirts. An increased density of the bird population in the alpine belt of the most northern parts of the Putorana Plateau is caused not so much by proper geographic latitude as by their direct contact with zonal tundra and forest tundra, which are rather densely populated by birds, and maintaining as a "donor" a rather high level of abundance of a number of species in the alpine belt (Romanov, 2013).

The bird communities in the forest belt of the Putorana Plateau are more diverse, stable, and homogenous in space and time when compared with the alpine and subalpine belts. In addition to small provincial differences (detected according to the population similarity coefficient), this is indicated by a minimal excess of species richness indices and population density in different regions of the forest belt, even distribution on the territory of the region of more than 50% of the species composition, and insignificant provincial differences in the composition of leaders, the main part of which is found in this capacity in the forest belt almost everywhere.

Provincial differences in the bird population of the Putorana Plateau (diagnosed using PSC) are unequal at the level of each of the considered altitude–landscape belts. Altitude–belt specificity of provincial differences of the main parameters of the population (species composition, density, and composition of leading and background species), and in some cases of regularities that determined their spatial trends, is also typical. This indicates in favor of a rather high level of autonomy of the development of the bird population at different altitudes of the Putorana Plateau (Romanov, 2013).

Spatial differentiation of nesting bird population within homogeneous landscape. General regularities of the development of spatial variability of the bird population within a homogeneous landscape largely depend on abiogenous factors (particularly, on lithogenic basis (absolute altitude of the locality, surface angle, slope exposition, and mechanical composition of the soil)). The bird population density at the Putorana Plateau considerably increases in mouth and flood habitats (808–1324 individuals/km^2) and on slopes of southern exposition (570–780 individuals/km^2) and glacial geomorphological structures

(79–200 individuals/km^2); it decreases at plane regions of intermountain valleys (236–260 individuals/km^2), slopes of northern exposition (89 individuals/km^2), and mountain watersheds without traces of activity of late pleistocene glaciers (8–30 individuals/km^2) (Romanov, 2013).

The local placement of many bird species at the Putorana Plateau is maintained by a mountain–depression type of locality and is increased by the disposition of a number of noncolonial species to generate microassociations. One to two territorial pairs of three to five species (perching birds) generate polyspecific associations at the Putorana Plateau in one small area, around which there are no such species at a considerable distance (0.3–20 km) within absolutely similar conditions. Such associations are generated by small perching bird species, none of which acts as a protector relative to others. All members are equally vulnerable in case of danger. They are united by a compact location of habitats that are the most appropriate for nesting and forage. As was demonstrated in our studies at the Putorana Plateau, such polyspecific associations ($n = 447$) are found more than three times more frequently than monospecific associations ($n = 131$). The difference in favor of polyspecific associations is highly significant ($P = 0.0001$). In the forest belt, polyspecific microassociations are usually composed of mountain accentor, brown thrush, Arctic warbler, browed warbler, and mountain finch; in subalpine and alpine belts they are made up of willow warbler, bluethroat, and Pallas' reed bunting (Romanov, 2013). It is possible to assume that the reason for the preferential development of polyspecific associations consists of the existence of certain self-organization of bird communities, including a tendency to maintain ecologically (and then, apparently, evolutionarily fixed) population density and a certain combination and intensity of interaction between different species even at a minimal amount of individuals under conditions of "under population" of subarctic mountain landscapes. One more aspect of the regularity detected at the Putorana Plateau is not excluded. Mountain–subarctic landscapes are probably more actively developed by whole bird communities than by separate species under conditions of extremely low population (far from potentially possible) and, consequently, upon an almost complete absence of interspecies competition.

Regularities of vertical differentiation of nesting bird population within altitude belt. At the Putorana Plateau, differences in total bird population density and abundance of many species are found at relatively small vertical displacement within a homogenous landscape of any of altitude–landscape belt (Romanov, 1996). The bird placement along the vertical profile within the forest belt conforms to an important regularity (their concentration in lower parts of the belt). Within the subalpine belt, vertical differentiation of the species placement is associated with ecological specifics of two main preferred habitats. The upper subalpine belt of the Putorana (characterized by maximally sparse forest stand and shrub vegetation) is inhabited by species of open tundra spaces of the alpine belt, including the *Lagopus mutus* rock ptarmigan (Montin, 1781), *Eudromias morinellus* common dotterel (Linnaeus, 1758), *Pluvialis apricaria* golden plover (Linnaeus, 1758), buff red-throated pipits, and common chat. The species mostly associated with shrubs and mainly inhabiting forest landscapes of the Putorana are strongly attached to the lower zone within the subalpine belt (which are immediately adjacent to the forest belt located below). The *Perisoreus infaustus* Siberian jay (Linnaeus, 1758), bluethroat, Arctic warbler, brown thrush, mealy redpoll, Pallas' reed bunting, and little bunting are among them (Romanov, 2013). The progressive transformation of the plant cover with altitude underlies the vertical variability of the bird population within the alpine belt of subarctic mountains. At the Putorana Plateau, richer species composition and maximal bird population density was detected in the lower zone of the alpine belt, which accounts for only 18% of their living space in a vertical plane. Eighty percent ($n = 16$) of all species composition of birds from the alpine belt are presented here, and the population density (79 individuals/km^2) are more than twice as high as average (35 individuals/km^2) in this altitude belt. A sharp decrease in both indices occurs with altitude (8 species; 22.5 individuals/km^2), and they reach minimal values in the most spacious upper part of the alpine bet (5 species; 8 individuals/km^2), which accounts for almost 60% of the living space of birds in a vertical plane. Due to the special extremity of ecological conditions of mountain peaks, only 20% of bird species (that form avifauna of the alpine belt) penetrate here, and the population density is more than 4 times as low as the average density in this altitude belt (Romanov, 2013).

Regularities of differentiation of the nesting-bird population in a lake–river system. Vectors of changes in the bird population density, associated with an increase in the absolute altitude, are different in land and water habitats of the Putorana Plateau. The bird population density of water and near-water habitats gradually increases from the forest belt (6 individuals per 1 km of coastline) to the subalpine belt, where it reaches a maximal value (10.3 individuals per 1 km of coastline). Further, with an increase in absolute altitudes of the locality, it steadily decreases in the alpine belt, but reaches values here (5.4 individuals per 1 km of coastline) that are only slightly inferior to appropriate indices of the forest belt. A decrease in the abundance of a number of background (or leading) species from the subalpine belt towards the forest and alpine belts allows one to assume that optimal habitats in vertical component of the area of these species are located in the subalpine belt and suboptimal habitats are in the forest and alpine belts. At the Putorana Plateau, these are long-tailed duck, the *Melanitta nigra* black scoter (Linnaeus, 1758), *Melanitta fusca* common scoter

(Linnaeus, 1758), Siberian gray-tailed tattler, and the *Sterna paradisaea* Arctic tern (Pontoppidan, 1763). For the Siberian gray-tailed tattler, such a situation indicates its close ecological relations with specific conditions of Asian subarctic mountain peaks. Long-tailed duck, black scoter, common scoter, and Arctic tern, being ecologically closely related to zonal hypoarctic landscapes, also mainly master mountain analogs of these landscapes (prevailing in the subalpine belt) under conditions of Asian subarctic mountains.

At the Putorana Plateau, the *Mergus merganser* merganser (Linnaeus, 1758), Siberian gray-tailed tattler, *Larus minutus* little gull (Linnaeus, 1758), *Larus argentatus* herring gull (Pontoppidan, 1763), and Arctic tern lead in the bird population of water and near-water habitats of the forest belt; long-tailed duck, black scoter, common scoter, *Tringa glareola* wood sandpiper (Linnaeus, 1758), Siberian gray-tailed tattler, and Arctic tern lead in the subalpine belt; and the *Charadrius hiaticula* ringed plover (Linnaeus, 1758), Siberian gray-tailed tattler, *Actitis hypoleucos* fiddler (Linnaeus, 1758), *Calidris minuta* little stint (Leisler, 1812), *Calidris temminckii* Temminck's stint (Leisler, 1812), and Arctic tern lead in the alpine belt. Thus, 13 species lead in water and near-water habitats of all belts at the Putorana Plateau; out of them, only 2 species are common, and all 11 other species are specific only for one altitude belt.

The maximal density of the bird population of water and near-water habitats at the Putorana Plateau exceeds the minimal density only 1.9 times, while it exceeds it 8.6 times in land habitats. In water and near-water habitats of the Putorana, the similarity of population of the forest and subalpine belts (determined using the population similarity coefficient (Naumov, 1964)) is 26%; that of subalpine and alpine is 25%; and that of forest and alpine is 40%. The amplitude between minimal (25%) and maximal (40%) PSC indices in water and near-water habitats is much smaller than in land habitats (2% and 29%, respectively), and absolute PSC values are higher. All this indicates that bird communities of intrazonal (extrabelt) water and near-water habitats are more resistant, stable, and homogenous in the space than of land habitats (Romanov, 2013).

CONCLUSIONS

The spatial differentiation of the fauna and bird population of the Putorana Plateau is caused by a system of common zonal–landscape and altitude–belt regularities.

The species diversity, bird population density, and abundance of the absolute majority of species progressively decrease with altitude at the Putorana Plateau. The main decrease in the bird population density occurs during the transition from the subalpine belt to the alpine belt (and a slightly smaller decrease occurs during transition from the forest belt to the subalpine belt).

The species that are widespread at the space from the Urals to the Koryak Upland form half of the avifauna of the Putorana Plateau. The community of the bird population structure in the Putorana Plateau and other mountains is maintained in horizontal plane by species leading in abundance simultaneously in several mountain regions of the Asian subarctic; in the vertical plane it is maintained by species simultaneously leading in two (usually adjacent) altitude–landscape belts. Avifauna of the Putorana Plateau is the most similar to avifauna of mountains in Yakutia and the Kolyma Upland.

At the Putorana Plateau, most bird species inhabit a wide range of altitudes, usually including at least two altitude belts. The wide vertical distribution of many bird species determines the large total biodiversity even in altitude belts with extreme conditions and, as a consequence, preserves the high potential possibility of the successful evolutionary development of mountain communities and development of mountain avifauna in general.

Among Asian subarctic mountain systems, the center of species diversity is located at the Putorana Plateau, which corresponds to its location within the Yenisei zoogeographic border formed along the line of glacial rupture of avifaunistic complexes and species areas. The process of settlement of species that had significantly wider areas before glaciation influences the increase in the species diversity of the Putorana Plateau avifauna.

The Putorana Plateau, having a significant vertical differentiation of landscapes, forms an altitude echeloned system of differently directed ways of spatial distribution of many bird species. Due to it, the mutual penetration of northern forms to the south (and southern forms to the north) occurs by the appropriate cenoses of different altitude belts, which influences the increase in the level of species richness of fauna and bird population density.

Most (80%) species that penetrate from adjacent plains into mountain landscapes of the Putorana Plateau develop the basis of nesting bird population. Plain elements qualitatively approach avifaunas of different altitude belts and landscapes of foothills. This determines the high level of similarity of adjacent plain and the Putorana Plateau avifaunas, and provides a more plain ecological character to avifauna of the latter. Almost no mountain birds leave to the foothills. The plain avifauna acts as a "donor" relative to the Putorana Plateau avifauna, and mountain fauna only acts as a "recipient" relative to the plain fauna.

At the Putorana Plateau, a larger similarity of the species composition is typical for mountain–forest avifauna (and considerably smaller for subalpine and alpine avifauna). Under conditions of forest landscape continuity and the conjugation of mountain and plain forests occurring everywhere, most species master them all the time. The fragmentation and isolation of subalpine and alpine belt regions caused the development of more regionally specific avifaunas in each of these belts.

The location of areas with a maximally high level of community of mountain–forest, subalpine, and alpine avifaunas is different in the Asian subarctic mountain range. The spatial isolation of these areas, as well as different values in the level of community of appropriate avifaunas, indicate the autonomy of the development of avifauna at the level of each altitude belt. Homogenous mountain–forest avifauna was most qualitatively developed at the Putorana Plateau, at mountains in Yakutia, and in the Kolyma Upland. The most homogenous alpine avifauna is developed in the northern area of Asian subarctic mountains (the Putorana Plateau, the Circumpolar and Polar Urals, and mountains in Yakutia).

The bird population density at the level of alpine, subalpine, and forest altitude–landscape belts is decreased in the direction from west to east (from the Putorana Plateau to the Koryak Upland). This is consistent with a decrease in the total productivity of vegetation cover in the same direction. The correlation between a decrease in the bird population density and longitude is close to significant for the population density indices within all altitude belts.

The spatial dynamics of the bird population density and abundance of most background species at the Putorana Plateau has a concentrically centrifugal character. These indices have a tendency towards an increase from the highest internal areas of the region (where their values are minimal) in the direction to the periphery.

At the Putorana Plateau, the communities of birds from the forest belt are more diverse, stable, and homogenous in space and time when compared with alpine and subalpine belts. In addition to the high values of the population similarity coefficient, minimal amplitudes of the species richness and bird population density, a relatively even distribution along the regional territory of more than half of the species composition, and insignificant provincial differences in the composition of leaders were detected here.

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