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Analysis of the Avifauna Structure in the Alpine Belt of the Northwestern Putorana Plateau, Central Siberia

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Abstract—Ecological patterns of the spatial differentiation of bird fauna and populations in the alpine belt of the northwestern Putorana Plateau were analyzed at 730–1412 m above sea level. The survey was conducted by route counts along transects of unlimited width. The fauna of breeding birds was assessed using the species belonging to faunal complexes and zonal-landscape groups. The similarity of the avifauna of the areas and high-altitude zones compared was determined using the Sørensen faunal coefficient. To identify the differences in the bird populations at various sites, the population similarity coefficient was utilized. The taxonomic structure and species composition of the breeding avifauna in the alpine belt of the northwestern Putorana Plateau are quite common and amount to 33 species. Two species, the red-necked stint, *Calidris ruficollis* (Pallas 1776), and the long-tailed skua, *Stercorarius longicaudus* (Vieillot 1819), were first recorded breeding in the alpine belt in the Putorana Plateau at a distance of 600 and 200 km, respectively, away from the southern borders of their main distribution areas. The taxonomic structure of the breeding avifauna corresponds to the zonal and landscape features of the Arctic mountain regions with the dominance of species of Passeriformes and Charadriiformes, which together accounted for 80–88% of the overall diversity. The species of the Arctic faunal complex (52–62%) are the most significant in the formation of avifauna in the alpine belt of the Putorana Plateau. Zoogeographically, the avifauna of the alpine belt of the northwestern Putorana Plateau shows specific features due to Arctic–alpine (n = 5) and alpine (n = 1) species that are ecologically related to mountain landscapes. The avifauna of the alpine belt of the northwestern Putorana Plateau is formed within a system of general zonal-landscape and altitudinal belt patterns. The abundance and population density of birds in the alpine belt of the northwestern Putorana Plateau is much higher than in any other part of this belt. In the alpine belt of the northwestern Putorana Plateau, the species diversity, as well as bird population density and abundance, of most species decreases progressively with altitude. During the breeding season, 97% of species of local avifauna breed in the lower part of the alpine belt compared to 47% in its middle and lower parts. The population density of birds in the alpine belt in the northwestern Putorana Plateau is 264, 187, and 119 individuals per sq. km in its lower, middle, and upper parts, respectively.

Keywords: avifauna, population, distribution, species diversity, Putorana Plateau, alpine high-altitude belt, mountain tundra

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INTRODUCTION

This study deals with investigation of the spatial organization of the fauna and population of birds and is aimed at assessing the biodiversity of mountain areas of the continental Arctic. The Putorana Plateau was selected as a model area. Despite the summarizing ornithological studies on this region of Northern Eurasia (Romanov, 1996, 2013, 2015; Vartapetov et al., 2018), the patterns of the formation of the fauna and population of birds of mountain peaks of this vast area are still poorly studied. The avifauna of the alpine belt has not been studied purposefully, continuously throughout the entire breeding period, with a wide coverage of the territory. The studies conducted did

not set the main goal of studying the patterns of spatial (primarily high-altitude) differentiation of the fauna and population of birds within the alpine belt. The northwestern regions of the Putorana Plateau remained almost unexplored. All the above gives reason to believe that the avifauna of the alpine belt of the Putorana Plateau, similarly to other mountains of Northern Eurasia, has been studied unevenly, fragmentarily, and definitely insufficiently in general. It should be noted that, in terms of investigation of the biological diversity, knowledge of the faunal complexes of vast mountainous land areas is recognized as a relevant problem of modern ornithology (Baranov, 2007; Ruggiero and Hawkins, 2008; McCain, 2009; Vartapetov and Germogenov, 2011; Graham et al., 2014). An obvious contribution to its solution could be the identification of the patterns of the formation of the avifauna of the alpine belt on the tops of the Putorana Plateau. In the Pleistocene, the tops of the plateau were the centers of glaciation and were freed from glaciers later than the adjacent plains (Golubchikov, 1996). Therefore, a periglacial genesis in the appearance of the modern landscapes of the alpine belt of the Putorana Plateau can be traced (Matyushkin, 1976; Baranov, 2007; Romanov, 2013), and the avifauna here is probably younger than the avifauna of the adjacent plains, and its formation continues.

The main goal of this study was to identify the ecological and geographical patterns of the spatial differentiation of the avifauna of the alpine belt of the Putorana Plateau for its use in monitoring and for developing biodiversity conservation measures. In accordance with this, the main three objectives of the research conducted in 2010, 2013, and 2018 were (1) inventory of the species composition of the avifauna and determination of the residence status of species; (2) identification of the features of the distribution and abundance of species; and (3) determination of the altitudinal, latitudinal, and meridional differentiation of the fauna and population of birds.

MATERIALS AND METHODS

Study Area, Terms and Methods of Research, and Quantitative Indices of the Work Performed

The research conducted in the alpine belt of the northwestern Putorana Plateau in 2010, 2013, and 2018 for the first time covered the basins of four lakes: Bogatyr, Neralakh (Neralak on some maps), Negu-Iken, and Bogatyr-Khuolu. Geographically, the area of our field research on the plateau tops was approximately 1000 km^2 and lay within the region 69°35′–69°48′ N, 92°10′–92°40′ E. The length of the surveyed area was 35 km from north to south and 40 km from west to east. The study object was the avifauna of the alpine belt of the Putorana Plateau. In our analysis, we used the results of route counts of birds according to Ravkin (1967), which were performed at altitudes of 730–1412 m above sea level. The height of the terrain was determined using global positioning system (GPS) devices, and the length of the routes traversed was determined using large-scale maps. The total length of on-foot count routes in the mountain-tundra landscapes of the alpine belt was 657 km (227 km in 2010, 141 km in 2013, and 289 km in 2018). The number of aquatic and semi-aquatic bird species was determined by direct counts with subsequent recalculation of the number of individuals per unit length of the coastline. Observations were performed during the breeding period: from July 6 to August 5, 2010; from June 25 to July 26, 2013; and from June 18 to July 19, 2018. In 2018, at Bogatyr-Khuolu Lake, we also carried out surveys at the control plots laid down in the lower (830–900 m above sea level), middle (893–1065 m above sea level), and upper (1055–1245 m above sea level) altitude-landscape levels of the alpine belt. The reliability of breeding was assessed in accordance with the criteria recommended by the European Bird Census Committee (*The EBCC Atlas* ..., 1997). The similarity of the avifauna compared was determined by the faunal similarity coefficient (FSC), which can be calculated using the Sørensen formula (Pesenko, 1982; Chernov, 2008). To identify differences in the bird populations of different areas, the population similarity coefficient (PSC) was used (Naumov, 1964). The species were considered dominant and subdominant if their proportion in the total population density was more than 10% and 1–10%, respectively. Species with an abundance of 10–99 individuals/km^2 were considered abundant; 1–9, common; 0.1–0.9, rare; and less than 0.1 individuals/km^2, very rare. Species for which only single individuals were recorded were not included in the population density calculations. The fauna of breeding birds is characterized by the types of fauna (Shtegman, 1938) and in accordance with the concept of zonal-landscape (geographic-genetic) groups of birds (Chernov, 1975, 1978; Kishchinsky, 1977, 1988). In the category of faunal complexes, species with an extensive range and an unclear center of origin were regarded as widespread. In the category of zonal-landscape groups, species with an extensive range the current distribution of which coincides with several natural zones were considered widespread. In the nomenclature and in compiling the lists of birds, we followed the *Synopsis of the Avifauna of Russia and Adjacent Territories* (Stepanyan, 2003).

Physical and Geographical Characteristics of the Study Area

The description of the physical and geographical conditions of the alpine belt of the Putorana Plateau can be found in a number of monographs (Parmuzin, 1964, 1976; Gvozdetskiy and Golubchikov, 1987; Golubchikov, 1996; Kuvaev, 2006). For this reason, here we give only a brief description of the bird habitats. The vast territory of the northwestern Putorana

Plateau is representative of a slightly dissected (almost monolithic) mountain range. It harbors the mountain lakes Bogatyr (970 m above sea level), Neralakh (920 m above sea level), Negu-Iken (760 m above sea level), and Bogatyr-Khuolu (854 m above sea level). Their length is 9, 17, 12, and 6 km, respectively, with a width of no more than 0.5–1 km. The basins of these oligotrophic lakes have a tectonic origin, and the modern appearance of the surrounding low-mountain landscapes was formed under the influence of Late Pleistocene glaciation. Traces of ice expressed in modern orography and types of dominant geomorphological structures can be traced throughout the surveyed territory. A wide range of geomorphological structures (troughs, kars, glacier lake baths, lateral and terminal moraines, and cascades of lakes formed on morain-dammed watercourses) formed by glaciers are found on the tops of the plateau. Some of them resemble miniature copies of the structures that are usually formed by glaciers on plains (kames, eskers, and drumlins). The heterogeneity of the "rugged terrain" formed by glaciers is extremely important for the formation of the appearance of the modern fauna and bird population of the alpine belt, which was analyzed in a number of papers (Romanov, 2013). Glacial geomorphological structures create prerequisites for enrichment of the alpine belt avifauna with a "non-mountain" complex of species and, to a large extent, predetermine the spatial distribution of birds in the alpine belt. The relief of the surveyed lake basins is formed by steep-slope ranges of the plateau, rising above the surrounding space (in some cases with sharp alpine-type peaks), heavily eroded mountain ranges with smooth domed peaks and gentle terraced slopes, and table mountain plateaus with flat tops raised by an average of 900–1200 m above sea level. The mountain peaks of the Putorana Plateau are distinguished by particularly extreme climatic conditions (Golubchikov, 1996). Here, snow regularly falls in summer, and it can form a stable cover up to 15–20 cm deep for several days even in July. The radiation balance at the tops of the plateau is almost two times lower than in the valleys (Zemtsova, 1976). In years with cold summers, when the air temperature does not exceed 5°C, thick ice on the lakes remains almost unchanged throughout the summer (Parmuzin, 1976), and only narrow (2–15 m) ice holes are formed along the banks of the ice. This situation, for example, was observed on Bogatyr and Neralakh lakes in 2010. Such conditions largely determine the poverty and specificity of the avifauna of these landscapes, as well as the low abundance of almost all species. The alpine belt in the northern part of the plateau is located at an altitude of more than 500 m above sea level. Here, in the complete absence of trees and shrubs, areas covered with mountain tundra vegetation alternate with areas devoid of vegetation (Kuvaev, 2006). The projective cover in different parts of the surveyed territory is 25–100%. Moss–lichen–sedge, moss–lichen–subshrub, and moss–sedge–forb tundra is widespread immediately in the basins of Bogatyr, Neralakh, Negu-Iken, and Bogatyr-Khuolu lakes.

On the basis of the differences in the floristic composition, the structure and height of the vegetation cover, the projective cover indices, and the latitudes of the distribution of open stony surfaces and moisture, the alpine belt of the northwestern Putorana Plateau was conditionally vertically differentiated into the lower (730–950 m above sea level), middle (950–1100 m above sea level), and upper (1100–1412 m above sea level) parts.

The lower part is represented by moist small-tussock moss–willow–sedge mountain tundra with mountain avens. In floodplains of rivers and on gentle slopes of lake depressions tussock forb–meadow tundra with abundant mountain avens (*Dryas* sp.), Arctic sweetvetch (*Hedysarum arcticum* B. Fedtsch.), locoweed *Oxytropis* sp., *Polygonus* sp., and the arctic rose (*Novosieversia glacialis* (Adams ex Fisch.) F. Bolle) with a projective cover of up to 100% are widespread. The abundance of herbs makes the tussock tundra closer to meadow cenoses (Pavlov et al., 1988).

The middle part, where the projective cover does not exceed 60%, is dominated everywhere by moss–lichen, moss–sedge, and forbs–sedge tundra with arctic willow (*Salix arctica* Pall.), dwarf birch (*Betula nana* L.), and blueberry (*Vaccinium uliginosum* L.). The dry, gentle slopes of the alpine-belt lake basins abound in permafrost medallions and are covered with lichens, *Cassiope tetragona* (L.) D. Don, and mountain avens. Sand–gravel hills (late Pleistocene glacier moraines), overgrown with clumps of lichens, mountain avens, grasses, and forget-me-not plants (*Eritrichinum* sp.) in a patchwork manner, are widespread here. Hills alternate with vast flat waterlogged valleys of rivers and streams, the soddy shallow surface of which is covered with a dense vegetation cover formed by mosses, lichens, mountain avens, *Cassiope*, grasses, sedges, and dwarf willows. Numerous snowfields, stony placers (rock accumulations), and clusters of boulders are found everywhere.

The upper part of the alpine belt is characterized by extremely low values of the projective cover, which only in some sites reaches 40%. Terraced and steep slopes are occupied by almost completely lifeless cold alpine deserts (Kuvaev, 2006), where numerous mountain cliffs, outlier rocks, vast snowfields, patches of frozen soil, and stony placers with fragmentary interspersion of small tussocks of mosses, lichens, sedges, mountain avens, and the arctic rose alternate in a patchwork manner.

RESULTS AND DISCUSSION

General Structure of the Avifauna

The list of birds of the alpine belt of the Putorana Plateau known before the beginning of our studies

numbered 52 species, including 40 breeding ones (Romanov, 2013). Taking into account the data obtained in 2010, 2013, and 2018, this checklist of species was supplemented with 23 species—the red-throated loon (*Gavia stellata* (Pontoppidan 1763)), white-billed loon (*Gavia adamsii* (G.R,, Gray 1859)), white-fronted goose (*Anser albifrons* (Scopoli 1769)), bean goose (*Anser fabalis* (Latham 1787)), Bewick's swan (*Cygnus bewickii* (Yarell 1830)), Eurasian wigeon (*Anas penelope* (Linnaeus 1758)), common pintail (*Anas acuta* (Linnaeus 1758)), common shoveler (*Anas clypeata* (Linnaeus 1758)), greater scaup (*Aythya marila* (Linnaeus 1761)), common goldeneye (*Bucephala clangula* (Linnaeus 1758)), northern harrier (*Circus cyaneus* (Linnaeus 1766)), golden eagle (*Aquila chrysaetos* (Linnaeus 1758)), spotted redshank (*Tringa erythropus* (Pallas 1764)), common sandpiper (*Actitis hypoleucos* (Linnaeus 1758)), red phalarope (*Phalaropus fulicarius* (Linnaeus 1758)), red-necked phalarope (*Phalaropus lobatus* (Linnaeus 1758)), red-necked stint (*Calidris ruficollis* (Pallas 1776)), dunlin (*Calidris alpina* (Linnaeus 1758)), parasitic jaeger (*Stercorarius parasiticus* (Linnaeus 1758)), long-tailed jaeger (*Stercorarius longicaudus* (Vieillot 1819)), glaucous gull (*Larus hyperboreus* (Gunnerus 1767)), eastern yellow wagtail *Motacilla tschuschensis* J.F. Gmelin, 1789), and black crow (*Corvus* (*corone*) *orientalis* (Eversmann 1841))—and now includes 75 species. The list of reliably, probably, and possibly breeding species was supplemented with six species—red-throated and white-billed loons, common sandpiper, red-necked stint, long-tailed jaeger, and little bunting (*Ocyris pusillus* (Pallas 1776))—and now includes 46 species (Romanov and Golubev, 2011; Romanov et al., 2015, 2018). A total of 63 bird species were recorded in the surveyed sites ($n = 3$) (Table 1), including 33 species (52%) with confirmed, probable, or possible breeding (hereinafter, all of them are conditionally called breeding), which accounts for 72% of the breeding avifauna of the alpine belt ($n = 46$) and 24% of the breeding avifauna of the entire region ($n = 139$). Wandering species ($n = 30$) in the avifauna of the alpine belt ($n = 63$) account for 48%.

The taxonomic structure of the breeding avifauna in the surveyed sites ($n = 3$) corresponds to the zonal and landscape features of the part of Northern Eurasia considered, is generally retained throughout the area from the Bogatyr Lake basin in the west to the Negu Iken Lake basin in the east, and includes six orders. Only Anseriformes did not breed in the Bogatyr-Khuolu Lake basin in 2018. There were no behavioral signs that would allow such an assumption. In terms of the number of species represented, this area is dominated everywhere by Charadriiformes (11–13 species, 42–48%) and Passeriformes (11 species at each site, 38–42%), which are characteristic of the hypoarctic belt of the Palaearctic.

By the spatial distribution pattern, among the birds breeding in the alpine belt of the northwestern Putorana Plateau ($n = 33$), species with ubiquitous distribution ($n = 10$, 30%), species with local distribution ($n = 20$, 61%), and species with sporadic distribution ($n = 3.9$%) can be distinguished (Table 1).

Latitudinal and Meridional Differentiation of Avifauna

The avifauna of the alpine belt of the northwestern Putorana Plateau contains a significant proportion (49%) of plain–tundra species that are not found in other parts of this belt. The distribution of a number of species ($n = 35$) is associated exclusively with the northwestern part of the region within the alpine belt. These are the red-throated and yellow-billed loons, common ringed plover (*Charadrius hiaticula* (Linnaeus 1758)), wood sandpiper (*Tringa glareola* (Linnaeus 1758)), ruff (*Philomachus pugnax* (Linnaeus 1758)), little stint (*Calidris minuta* (Leisler 1812)), ruby-necked stint, common sandpiper, long-tailed jaeger, etc. This is explained by the presence of a complex of large glacial lakes, a rich food base, and a wide distribution of various plant associations resembling a zonal tundra (Pavlov et al., 1988). These habitats are optimal and sometimes the only ones available for the above species of birds under the conditions of the alpine tops of the plateau. The formation of such types of tundra is associated with the Late Pleistocene glaciation, which manifested itself to the maximum degree in the northwestern part of the Putorana Plateau. In the glacial valleys, after the destruction of glaciers at the turn of the Pleistocene and the Holocene, the ecological conditions turned out to be milder, more varied, and, in general, closer to the conditions typical for the zonal tundra than to the harsh mountain–Arctic conditions of "alpine plakors" (flat or slightly sloping well-drained sites in the tundra zone) (Romanov, 2013). This allowed a whole group of lowland species to penetrate and fragmentarily populate the periglacial areas of the mountain peaks of the northwestern Putorana Plateau. Thus, in the modern era, plain–tundra species are confined to habitats of glacial genesis. We assume that, when penetrating into the mountains, the plain–tundra species used the ecological conditions typical for them, which had formed in local areas of periglacial landscapes. They became part of the alpine avifauna by penetrating to the peaks of the mountains along the areas of the former location of glaciers as they melted (Romanov, 2013). Late Pleistocene glacial valleys, which occupy 25–30% of the area of mountain peaks on Putorana, are inhabited by approximately 70% of the alpine avifauna species (including almost 100% of plain–tundra species). The total abundance of birds in glacial valleys is 2–4 times higher than that in watersheds. Possibly, this is due to both the optimal modern ecological conditions in the valleys and the fact that glaciers could be a source of increased productivity of adjacent ecosystems. This is indicated by some modern studies, for example, in Alaska (Hood et al., 2009).

Table 1. Population of birds in the alpine belt of the northwestern Putorana Plateau during the breeding season (individuals/km^2)

Species	Neralakh and Bogatyr lakes				Negu-Iken Lake				Bogatyr-Khuolu Lake			
	abundance	proportion, %	status	distribution	abundance	proportion, %	status	distribution	abundance	proportion, %	status	distribution
Red-throated loon	–	–	–	–	0.2	0.02	+?	*	–	–	–	–
Arctic loon	0.2	0.3	+	**	0.8	0.8	+	***	0.1	0.04	+	*
Yellow-billed loon	–	–	–	–	0.04	0.04	+?	*	–	–	–	–
Greater white-fronted goose	–	–	–	–	–	–	–	–	0.02	0.01	■	*
Bean goose	C	C	■	*	0.2	0.2	■	*	0.3	0.1	■	*
Bewick's swan	–	–	–	–	–	–	–	–	C	C	■	*
European teal	–	–	–	–	0.2	0.2	■	*	–	–	–	–
Eurasian wigeon	–	–	–	–	–	–	–	–	0.3	0.1	■	*
Common pintail	–	–	–	–	0.02	0.02	■	*	0.02	0.01	■	*
Northern shoveler	–	–	–	–	–	–	–	–	C	C	■	*
Greater scaup	–	–	–	–	SG	SG	■	*	–	–	–	–
Long-tailed duck	0.04	0.06	+	*	0.6	0.6	+?	***	1.0	0.3	■	**
Common goldeneye	–	–	–	–	0.06	0.06	■	*	0.04	0.02	■	*
Black scoter	–	–	–	–	3.2	3.0	■	***	1.0	0.3	■	*
Velvet scoter	–	–	–	–	0.08	0.08	■	*	0.4	0.2	■	*
Red-breasted merganser	0.06	0.08	■	*	0.4	0.4	■	**	0.2	0.07	■	*
Common merganser	0.2	0.3	■	**	–	–	–	–	0.001	0.001	■	*
Northern harrier	–	–	–	–	–	–	–	–	SG	SG	■	*
Rough-legged hawk	0.02	0.03	+?	*	0.06	0.06	+?	*	0.01	0.002	+	*
Golden eagle	SG	SG	■	*	0.02	0.02	■	*	0.005	0.01	■	*
White-tailed eagle	SG	SG	■	*	SG	SG	■	*	0.004	0.01	■	*
Gyrfalcon	–	–	–	–	SG	SG	■	*	0.01	0.01	■	*
Peregrine falcon	SG	SG	■	*	–	–	–	–	SG	SG	■	*
Pigeon hawk	–	–	–	–	SG	SG	■	*	0.05	0.02	■	*
Rock ptarmigan	1.0	1.4	+	***	2.5	2.4	+	***	3.0	1.0	+	**
American golden plover	0.1	0.1	+	*	0.2	0.1	+	*	1.0	0.4	+	*
European golden plover	7.5	10.7	+	***	7.0	6.7	+	***	10.0	4.2	+	***
Common ringed plover	10.5	14.9	+	***	9.5	9.1	+	***	18.0	7.5	+	**
Eurasian dotterel	0.5	0.7	+	**	0.5	0.5	+	**	6.0	2.5	+	**
Wood sandpiper	SG	SG	■	*	0.5	0.5	+?	**	2.2	0.9	+	*
Spotted redshank	–	–	–	–	SG	SG	■	*	–	–	–	–
Gray-tailed tattler	1.5	2.1	+?	***	1.5	1.4	+?	***	2.0	1.0	+	*
Red phalarope	SG	SG	■	*	–	–	–	–	–	–	–	–
Red-necked phalarope	0.6	0.8	■	*	–	–	–	–	–	–	–	–
Common sandpiper	–	–	–	–	–	–	–	–	0.2	0.1	+	*
Ruff	0.3	0.3	■	*	0.5	0.5	+?	*	0.8	0.3	+	*
Little stint	1.5	2.1	+	*	0.2	0.1	■	*	–	–	–	–
Red-necked stint	2.5	3.5	+	**	1.0	0.9	+?	**	8.0	3.0	+	**
Temminck's stint	1.5	2.1	+?	**	4.0	3.8	+	***	10.0	4.0	+	***

Table 1. (Contd.)

Species	Neralakh and Bogatyr lakes				Negu-Iken Lake				Bogatyr-Khuolu Lake			
	abundance	proportion, %	status	distribution	abundance	proportion, %	status	distribution	abundance	proportion, %	status	distribution
Dunlin	SG	SG	■	*	0.1	0.1	■	*	–	–	–	–
Parasitic jaeger	–	–	–	–	–	–	–	–	0.04	0.02	■	*
Long-tailed jaeger	0.4	0.5	+	**	0.4	0.4	+	**	0.8	0.3	+	**
Little gull	0.4	0.5	■	*	0.02	0.02	■	*	–	–	–	–
Lesser black-backed gull	0.4	0.5	+?	***	1.4	1.3	+	***	0.3	0.1	+	**
Glaucous gull	SG	SG	■	*	–	–	–	–	–	–	–	–
Common gull	0.02	0.03	■	*	SG	SG	■	*	–	–	–	–
Arctic tern	1.0	1.4	+	**	1.4	1.3	+	***	0.2	0.1	+?	*
Common house matrin	0.05	0.1	+?	*	–	–	–	–	0.2	0.1	+?	*
Horned lark	2.0	2.8	+	***	4.0	3.8	+	***	17.6	7.5	+	**
Red-throated pipit	4.5	6.3	+	***	13.0	12.4	+	***	7.0	2.9	+	**
Buff-bellied pipit	11.0	15.6	+	***	16.5	15.8	+	***	48.0	20.4	+	***
Eastern yellow wagtail	–	–	–	–	0.5	0.5	■	*	–	–	–	–
Gray wagtail	0.05	0.1	+?	*	0.5	0.5	+	*	0.3	0.1	+?	*
White wagtail	0.5	0.7	+	**	3.5	3.3	+	**	7.0	3.0	+	*
Carrion crow	–	–	–	–	–	–	–	–	0.1	0.04	■	*
Raven	0.08	0.1	+?	***	0.6	0.6	+?	***	0.04	0.02	+?	*
Northern wheatear	2.0	2.8	+	***	6.0	5.7	+	***	13.3	5.6	+	**
Bluethroat	0.1	0.1	+	*	1.5	1.4	+	***	4.1	1.8	+	**
Common redpole	0.5	0.7	■	**	2.5	2.4	■	***	15.1	6.4	+	***
Arctic redpole	–	–	–	–	SG	SG	■	*	–	–	–	–
Little bunting	–	–	–	–	0.3	0.2	+?	*	–	–	–	–
Lapland bunting	6.5	9.2	+	***	19.0	18.3	+	***	44.0	19.0	+	***
Snow bunting	13.5	19.1	+	***	0.5	0.5	+	*	13.8	6.0	+	**
Total	71	100	–	–	105	100	–	–	237	100	–	–

+, Breeding species; +?, possibly breeding species; ■, wandering species; *, sporadically distributed species; **, species distributed locally throughout the study area; ***, ubiquitous species; SG, a single record of a single individual.

Widespread species such as the golden eagle, little gull (*Larus minutus* (Pallas 1776)), parasitic jaeger, and black crow are found exclusively within the alpine belt of the northwestern Putorana Plateau.

With allowance for our data for 2010, 2013, and 2018, it can also be stated that the most extensive of the two known fragments of the range of the snow bunting (*Plectrophenax nivalis* (Linnaeus 1758)) within the alpine belt of the Putorana Plateau is also located in the northwestern part of the region. The snow bunting, which is here ecologically tightly associated with the mountainous relief, is confined to the highest (1500–1700 m above sea level) parts of the plateau, both in the northwestern part, where it is widespread and ubiquitous, and in the northeastern part, where it is distributed narrowly locally.

It was found that, in the sites surveyed in 2010, 2013, and 2018 ($n = 3$), local breeding avifauna comprise 26 to 29 species, which significantly exceeds the species richness, represented by 5–14 (on average, 8) species of almost all other local breeding avifauna ($n = 10$) of the alpine belt of the Putorana Plateau. The only exception is the vicinity of Ondodomi Lake in the northwestern part of the plateau and Gusinye Lakes in the southwestern part, where 24 and 22, respectively, bird species breed (Rupasov and Zhuravlev, 2006; Romanov et al., 2007). The maximum species diversity of birds was recorded in the Negu-Iken Lake basin (Table 1), which is explained by the high diversity of

ecological conditions and, as a consequence, a very wide range of habitats for various bird species (including aquatic and semi-aquatic ones).

The percentage of the overall breeding avifauna of the alpine belt of the northwestern Putorana Plateau in some sites ($n = 3$) was 79–83%. A total of 27 bird species breed in all or nearly all areas ($n = 2$–3), which account for 82% of the local avifauna and form the general faunal core (rock ptarmigan (*Lagopus muta* (Montin 1776)), American golden plover (*Pluvialis fulva* (J.F. Gmelin 1789)), European golden plover (*Pluvialis apricaria* (Linnaeus 1758)), common ringed plover, Eurasian dotterel (*Eudromias morinellus* (Linnaeus 1758)), gray-tailed tattler (*Heteroscelus brevipes* (Vieillot 1816), Temminck's stint (*Calidris temminckii*, (Leisler 1812)), red-necked stint, horned lark (*Eremophila alpestris* (Linnaeus 1758)), red-throated pipit (*Anthus cervinus* (Pallas 1811)), buff-bellied pipit (*Anthus rubescens* (Tunstall 1771), northern wheatear (*Oenanthe oenanthe* (Linnaeus 1758), bluethroat (*Luscinia svecica* (Linnaeus 1758)), Lapland bunting (*Calcarius lapponicus* (Linnaeus 1758)), snow bunting, etc.). The majority of the species listed are widespread in the tundra zone and partly the forest–tundra zone of Eurasia. The coefficients of mutual commonality of local breeding avifauna of the surveyed areas ($n = 3$), obtained using the Sørensen formula, are 86–87%, which indicates the avifauna homogeneity within the alpine belt of the northwestern Putorana Plateau. Its modern qualitative composition, formed primarily by hemiarctic and boreal–hypoarctic elements, also has similar features within a single, much more extensive area. This area includes the mountain tundra of the northern part of the Putorana Plateau and the plain tundra of Taimyr, the coefficient of mutual commonality of breeding avifauna of which is 31%. The ability to disperse in these regions almost without obstacles was and is supported by a high level of similarity of the ecological parameters of the habitats of many bird species. Under the conditions of the spatial conjugation of mountain and lowland analogues of tundra landscapes throughout this region, many species have populated them everywhere, because they had no insurmountable barriers hampering their dispersal. In the three-dimensional section of the range of all species with a similar pattern of spatial distribution near the southern boundaries of the Taimyr Peninsula, a "shift" of the breeding range in the vertical direction is observed, which allows their further dispersal again along the horizontal surface, though within more highly echeloned landscapes. For example, the European golden plover, which is widespread in the tundra zone of the Taimyr Peninsula (Rogacheva, 1988), sharply increases the vertical level of its range near the northern slope of the Putorana Plateau and, at an altitude of approximately 1000 m above sea level, again is distributed along the alpine belt further southwards in the horizontal plane (Romanov, 2013). One of the likely causes for the wide distribution of some typical inhabitants of the zonal tundra in the northern part of the plateau is that the northern spurs of the Putorana Plateau are bordered at the foothills by sparse forests and shrub tundra, where these species are quite common and from where they can freely penetrate into the alpine belt.

Range Boundaries

In 2010, 2013, and 2018, we recorded a number of species ($n = 20$) the status of the presence and the pattern of the geographical distribution of which in the alpine belt of the Putorana Plateau were not known or were confirmed by single observations. Beyond the known boundaries of breeding ranges (Romanov, 2013), two breeding bird species (4% of the overall breeding avifauna of the alpine belt) were found for the first time in the alpine belt of the Putorana Plateau—the red-necked stint and the long-tailed jaeger. In all sites surveyed ($n = 3$), isolated breeding groups of both the two plain–tundra species and one Arctic–alpine species (snow bunting) were found far outside of their zonal range on the Taimyr Peninsula (Romanov and Golubev, 2011; Romanov et al., 2015, 2018). Whole communities of these species in the alpine belt of the Putorana Plateau were found at a distance of 200–600 km southwards of the nearest known breeding areas. Due to the spatial disunity of these areas, the range of such species becomes disjunctive and consists of plain and mountainous parts. The presence of the red-necked stint, long-tailed jaeger, and snow bunting on the Putorana Plateau on the scale of the northern part of Central Siberia has, in general, a clearly pronounced insular pattern. For these and some other (golden plover) species, the mountain tundra of the Putorana Plateau is the southern outpost of their breeding range in the northern part of Central Siberia, situated far beyond the zone of their main dispersal on plains. Similar island fragments of the range in northern Eurasia are also known for the snow bunting in the alpine belt of the Polousnyi Ridge in northern Yakutia (Romanov, 2013) and for the long-tailed jaeger in the thin alpine belt of the Polar and Subpolar Urals (Ryabitsev, 2014) and on the Verkhoyansk ridge (Shemyakin, 2015).

It was established that the Putorana Plateau is the southwestern outpost of distribution of the red-necked stint and that the boundary of the breeding range is located at the site with the coordinates 69°35′ N, 92°15′ E. Here, the breeding group of the species is isolated at heights of 850–1000 m above sea level and is located 600 km to the southwest from the nearest known reliable breeding sites in the Taimyr Peninsula. Our data obtained in 2010, 2013, and 2018 confirm the lack of accumulated knowledge about the general structure of the breeding range of the red-necked stint and are completely consistent with the concept of the objectively existing disjunctive distribution of this species. In addition, our observations are consistent with

the available information about its confinement to "foothill–low-mountain" habitats (Lappo et al., 2012). Since this species is not ecologically associated with vertically dissected relief, turbulent mountain streams, etc., there is no reason to classify it as a proper mountain (alpine) species. Nevertheless, the obvious confinement of the red-necked stint to the tundra–valley habitats in mountains and foothills determined the specificity of the latitudinal distribution of this species in some parts of the breeding range. For example, our observations showed that, within the northern part of Central Siberia, along the alpine peaks of the Putorana Plateau, the red-necked stint is able to penetrate much farther southwards of the boundaries of the zonal tundra and form isolated breeding areas in more southern latitudes of the boreal zone, within the zonal forest–tundra and northern taiga. In particular, the breeding sites found by us were located 250 km away from the southern boundary of the tundra zone on the Taimyr Peninsula.

The breeding group of long-tailed jaeger, first discovered on the Putorana Plateau, is isolated at altitudes up to 760–1100 m above sea level and is located 200 km south from the nearest known reliable breeding sites on the Taimyr Peninsula. This species inhabits mountain-tundra areas, which differ significantly from one another in their geomorphological features, indices of projective vegetation cover, moisture level, and the abundance of open stony surfaces. The most characteristic breeding habitats are small-tussock moss–sedge and moss–sedge–forb tundra and dry stony moss–lichen tundra with different proportions of mountain avens, *Cassiope,* and sedges, abounding in stony placers and permafrost medallions.

Until 2010, local small-area breeding foci of the snow bunting in the alpine belt of the Putorana Plateau were known near the northwestern and northeastern boundaries of this mountain country (Romanov, 2013). This mosaic Putorana part of the snow bunting range was supplemented with new fragments, which were first discovered by us on the tops of the mountains bordering the basins of Bogatyr, Neralakh, Negu-Iken, and Bogatyr-Khuolu lakes (69°35′–69°48′ N, 92°10′–92°40′ E), which are located 40 and 75 km away from the nearest known habitats near Ondodomi and Kapchug lakes, respectively (Morozov, 1984; Rupasov and Zhuravlev, 2006). On the territory examined in 2010, 2013, and 2018, the snow bunting was found to be a ubiquitous breeding species in the uppermost parts of the alpine belt (950–1412 m above sea level). Here, it is ecologically inextricably associated with steep massifs of the plateau (sometimes with sharp alpine-type peaks) and destroyed mountain massifs with steep precipitous slopes, abounding in rocks, heaps of basalt boulders, and stone fields (kurums). The main habitats of the species during the breeding season are located in the upper reaches of mountain rivers in narrow valleys with steep precipitous slopes, numerous cirques, and large snowfields. An integral element of breeding habitats of the snow bunting is the valleys of mountain streams fed by melting snowfields, the damp banks of which are fragmentarily covered with sedge–moss tussocks.

Formation of Vertical Heterogeneity of the Avifauna

In accordance with the prevailing type of altitudinal zonation within the Putorana Plateau, avifauna replacing each other with the altitude of the mountain-taiga, subalpine, and alpine belts have been differentiated. Species diversity decreases with increasing altitude. The breeding avifauna of the mountain-taiga, subalpine, and alpine belts numbers 129 (93%), 52 (37%), and 46 (33%) species, respectively. Similarly to other mountain systems of North Asia (Romanov, 2013), the species composition of the avifauna of the study region changes gradually with altitude. The avifauna of the alpine and subalpine belts, located adjacently, have many common species: the willow ptarmigan (*Lagopus lagopus* (Linnaeus 1758)), rock ptarmigan, European golden plover, Eurasian dotterel, red-throated and buff-bellied pipits, willow warbler (*Phylloscopus troechilus* (Linnaeus 1758)), Eversmann's warbler (*Phylloscopus borealis* (Blasius 1858)), bluethroat, Pallas' reed bunting (*Schoeniclus pallasi* (Cabanis 1851)), etc. Of the 46 bird species breeding in the alpine belt and 52 species breeding in the subalpine belt, 33 species are common to the avifauna of these belts. The faunal similarity coefficient of the alpine and subalpine belts is 67%.

However, the breeding avifauna of the alpine belt includes six specific species that are not found in other altitudinal belts. These are the red-necked stint and long-tailed jaeger, which were recorded breeding only in the northwestern part, as well as the American golden plover, little stint, horned lark, and snow bunting, which are more widespread within the alpine belt of the Putorana Plateau.

Purposeful study of the altitudinal differentiation of birds in the Bogatyr-Khuolu Lake basin showed that the avifauna of the lower part of the alpine belt, which occupies the bottom of this lake basin, the valley of the river of the same name, and the foot of the mountain slopes, is characterized by the highest species richness. Of the total number of species ($n = 36$) recorded in 2018 at the control plots, which were laid down near Bogatyr-Khuolu Lake at different heights, the avifauna of the lower part of the alpine belt is formed by 34 (97%) bird species (Tables 2, 3). With an increase in altitude, under conditions of decreased heat supply, a reduced duration of the snowless period, and fragmentation of the vegetation cover, the richness of the breeding avifauna decreases. Under extreme conditions of the middle and especially upper part of the alpine belt, where the environmental conditions on lifeless mountain peaks correspond to the conditions of the zonal arctic tundra and polar deserts,

Table 2. Vertical differentiation of the bird population of the alpine belt in the basin of Bogatyr-Khuolu Lake during the breeding period (individuals/km^2)

Species	Upper level (1055–1245 m above sea level)		Middle level (893–1065 m above sea level)		Lower level (831–900 m above sea level)	
	abundance	proportion, %	abundance	proportion, %	abundance	proportion, %
Arctic loon	–	–	–	–	0.7	0.3
Bean goose	–	–	–	–	0.03	0.01
Common scoter	–	–	–	–	6.7	2.5
Velvet scoter	–	–	–	–	2.8	1.1
Red-breasted merganser	–	–	–	–	1.7	0.6
Rough-legged	–	–	0.01	0.01	–	–
Rock ptarmigan	4.0	3.4	–	–	1.1	0.4
European golden plover	0.2	0.2	13.0	7.0	21.3	8.1
Common ringed plover	0.7	0.6	–	–	6.1	2.3
Eurasian dotterel	1.3	1.1	11.5	6.1	3.5	1.5
Gray-tailed tattler	–	–	–	–	1.8	0.7
Ruff	–	–	–	–	4.4	1.7
Red-necked stint	–	–	2.1	1.1	11.1	4.2
Temminck's stint	–	–	–	–	4.4	1.7
Long-tailed jaeger	–	–	SG	SG	1.5	0.7
Arctic tern	–	–	–	–	0.2	0.07
Horned lark	4.0	3.4	54.7	29.1	14.4	5.4
Red-throated pipit	4.0	3.4	–	–	15.6	5.9
Buff-bellied pipit	19.7	16.5	65.9	35.0	58.2	22.0
White wagtail	0.3	0.2	1.0	0.6	3.5	1.3
Carrion crow	–	–	–	–	0.6	0.2
Raven	0.02	0.02	0.3	0.2	0.06	0.02
Northern wheatear	9.3	7.8	18.9	10.1	4.4	1.7
Bluethroat	0.9	0.7	4.2	2.2	2.0	0.7
Common redpole	1.7	1.4	11.5	6.1	26.1	9.9
Lapland bunting	2.7	2.3	4.2	2.2	66.3	25.1
Snow bunting	69.8	58.6	–	–	5.1	1.9
Total	119	100	187	100	264	100

SG, a single record of a single individual.

a poorer avifauna is formed, which includes only 17 species (47%).

The species diversity of the avifauna of the alpine belt in the northwestern Putorana Plateau is maximum (94%) in its lower part, which accounts for only 17% of the living space of the belt in the vertical plane. The species diversity is minimum (47%) in the middle part of the alpine belt, which accounts for 83% of the living space of birds in the vertical plane.

A number of bird species are ecologically closely associated with the conditions that are formed at only one of these altitude levels and do not occur beyond it in neighboring habitats. According to observations in the Bogatyr-Khuolu Lake basin, the lowest part of the alpine belt in the northwestern Putorana Plateau limits the habitats of 10 species (16% of the local avifauna), including the breeding habitats of the Arctic loon (*Gavia arctica* (Linnaeus 1758)), the gray-tailed tattler, the ruff, Temminck's stint, the long-tailed jaeger, and th little bunting and the foraging habitats of the bean goose, the common scoter (*Melanitta nigra* (Linnaeus 1758)), the velvet scoter (*Melanitta fusca* (Linnaeus 1758)), the red-breasted merganser (*Mergus serrator* (Linnaeus 1758)), the Arctic tern (*Sterna paradisaea* (Pontoppidan 1763)), and the carrion crow (Tables 2, 3). A wider altitude profile is populated by 16 species (26% of the local avifauna). Of these, only the red-necked stint breeds simultaneously on two lower alti-

Table 3. Population of birds of aquatic and semi-aquatic habitats in the Bogatyr-Khuolu Lake basin (individuals/km of shoreline)

Species	Bogatyr-Khuolu Lake		Bogatyr-Khuolu River	
	abundance	proportion, %	abundance	proportion, %
Arctic loon	0.8	5.3	0.04	0.7
Bean goose	1.0	7.0	–	–
Eurasian wigeon	0.6	4.0	0.3	4.6
Common pintail	0.03	0.2	–	–
Northern shoveler	0.1	0.4	–	–
Long-tailed duck	1.0	7.0	0.04	0.7
Common goldeneye	0.1	0.9	–	–
Common scoter	3.3	22.8	–	–
Velvet scoter	0.8	5.3	–	–
Red-breasted merganser	0.3	2.0	0.8	11.7
Common merganser	–	–	0.5	7.5
Common ringed plover	1.8	12.6	1.6	24.2
Wood sandpiper	0.03	0.2	0.04	0.7
Gray-tailed tattler	0.2	1.3	0.1	1.6
Ruff	0.2	1.3	–	–
Little stint	0.1	0.9	–	–
Red-necked stint	1.0	7.0	1.0	15.3
Temminck's stint	1.2	8.1	0.8	11.7
Parasitic jaeger	–	–	0.04	0.7
Long-tailed jaeger	–	–	0.2	3.0
Lesser black-backed gull	1.0	7.0	0.5	7.5
Arctic tern	1.0	7.0	0.8	11.7
Total	14.5	100	6.8	100

tude-landscape levels. The remaining 14 species are distributed either at all three altitude levels (European golden plover, Eurasian dotterel, horned lark, buff-bellied pipit, northern wheatear, etc.), or at the lower and upper levels, being absent in the middle level (rock ptarmigan, common ringed plover, and red-throated pipit). The latter is explained by the negligible area of suitable biotopes in the middle part of the alpine belt, the distribution of which is limited by the local relief specificity with the widespread dominance of high, almost steep slopes abounding in rocky cliffs and talus areas. The breeding habitats of the snow bunting are limited to the uppermost part of the alpine belt of the northwestern Putorana Plateau, whereas the foraging biotopes of this species are partially located on the shores of lakes in the lower part of the alpine belt. Since mountain stony areas where the snow bunting builds nests are almost devoid of vegetation and are absolutely lifeless, many adult birds have to collect food for chicks in areas located 300–400 m lower. The ranges of the species dwelling in a wide range of altitudes have a distinct three-dimensional pattern.

An analysis of the degree of commonality of avifauna formed at different altitude levels ($n = 3$), which was performed using the Sørensen faunal commonality coefficient, revealed the following patterns. The maximum similarity is observed between the lower and middle levels (89%); a somewhat lower similarity, between the upper and lower levels (70%); and the minimum similarity, between the upper and middle levels (51%). The obtained digital data indicate a generally insignificant spatial vertical differentiation (disunity) of the avifauna of the alpine belt of the northwestern Putorana Plateau. The revealed differences between the avifauna of the upper and middle altitude–landscape levels are probably indicative of a certain autonomy of their formation.

Faunal and Zonal-Landscape Structure of Avifauna

The breeding avifauna of the alpine belt in the northwestern part of the Putorana Plateau is heterogeneous in origin (Table 4). It is formed by species of three types of fauna, the most significant of which in all surveyed sites ($n = 3$) are the elements of the Arctic

Table 4. Ratio of faunal assemblages in the breeding avifauna of the alpine belt of the northwestern part of the Putorana Plateau

Faunistic complex	Neralakh and Bogatyr Lakes		Negu-Iken Lake		Bogatyr-Khuolu Lake	
	species	%	species	%	species	%
Arctic	16	62	17	59	14	52
Siberian	3	11	4	14	4	15
Widespread	7	27	8	27	9	33

Table 5. Ratio of zonal-landscape groups in the breeding avifauna of the alpine belt of the northwestern Putorana Plateau

Zonal-landscape group	Neralakh and Bogatyr Lakes		Negu-Iken Lake		Bogatyr-Khuolu Lake	
	species	%	species	%	species	%
Alpine	1	4	1	4	1	4
Arctic-Alpine	5	19	5	17	5	18
Hemiarctic	9	35	10	35	7	26
Hypoarctic	2	8	3	10	2	7
Boreal–Hypoarctic	5	19	7	24	8	30
Widespread	4	15	3	10	4	15

faunal complex and the widespread species. Representatives of the Siberian type of fauna play a secondary role in local bird communities.

Despite the extreme environmental conditions, a fairly motley landscape-biotopic mosaic is formed in the vicinity of the surveyed mountain lakes Neralakh, Bogatyr, Negu-Iken, and Bogatyr-Khuolu, which attracts birds with significantly different requirements for the ecological parameters of habitats. This predetermines the heterogeneity of the avifauna in terms of the combination of representatives of the six zonal-landscape groups that form it, the most significant of which in all surveyed sites (n = 3) are Hemiarctic, Boreal–Hypoarctic, and Arctic-alpine bird species, which in total account for 73–76% of the local avifauna (Table 5). The proportion of alpine species (buff-bellied pipit) is not so significant in the formation of bird communities in the alpine belt. However, it is they that, along with the arctic-alpine species (rock ptarmigan, Eurasian dotterel, horned lark, northern wheatear, and snow bunting) and some other species that are ecologically closely associated with stony habitats on the banks of mountain water streams (gray-tailed tattler and gray wagtail), determine the mountain specificity of the avifauna of the alpine belt of the northwestern Putorana Plateau during the formation of its qualitative diversity.

Spatial Structure of the Bird Population

On the Putorana Plateau, the species richness, the bird population density, and the abundance of the absolute majority of species progressively decrease with altitude. The bird population density in the breeding season in the mountain taiga, subalpine, and alpine belts is 405, 164, and 62 individuals/km^2, respectively. Unlike the majority of other mountain regions of North Asia (Romanov, 2013), where the main decrease in the bird population density is observed upon the transition from the subalpine belt to the alpine one, the population density within the altitudinal profile of the Putorana Plateau decreases to the same degree (2.5 times) both upon the transition from the subalpine belt to the alpine one and upon the transition from the mountain-taiga belt to the subalpine one.

It was found that the population density of birds in the surveyed sites (n = 3) in the breeding season varies in the range 71–237 individuals/km^2 (Table 1), averaging 138 individuals/km^2, which significantly exceeds the average population density (62 individuals/km^2) throughout the alpine belt. The abundance of many bird species (n = 19) widespread throughout the alpine belt of the Putorana Plateau reaches its maximum in its northwestern part. For example, it was found that the abundance of the European golden plover, horned lark, buff-bellied pipit, and Lapland bunting is 8.2, 17.6, 25.2, and 23.2 individuals/km^2, whereas in the rest part of the region it does not exceed 2.7, 2.1, 19.2, and 1.1 individuals/km^2, respectively. The abundance of the snow bunting in the northwestern part of its range within the Putorana Plateau is also much higher (9.2 individuals/km^2) than in the northeastern part (2.5 individuals/km^2).

The similarity coefficients of birds population in the areas surveyed in 2010, 2013, and 2018 (n = 3) were

28–42%, which is much lower than the level of similarity of the corresponding avifauna.

Counts of birds in the Bogatyr-Khuolu Lake basin, purposefully conducted at different altitudes, showed that the bird population density is maximum (264 individuals/km^2) in the lowest part of the alpine belt, in the optimal habitats on lakeside terraces, and in river valleys (Table 2). With an increase in altitude in the middle part of the alpine belt, the bird population density decreased to 187 birds/km^2, gradually decreasing in the upper part to the minimum values (119 birds/km^2). A similar pattern was traced in the basins of Bogatyr, Neralakh, and Negu-Iken lakes. The decrease in the bird population density with altitude within the alpine belt of the northwestern Putorana Plateau corresponds to a general decrease in the productivity of animal communities from the foothills to the tops of mountains and demonstrates the relative independence of the bird population at each altitude-landscape level. The obtained population similarity coefficients indicate not only independence but also a pronounced autonomy of the formation of the bird population at different altitude-landscape levels: the population similarity at the lower and middle levels is 34%; at the middle and upper levels, 15%; and at the lower and upper levels, 13%.

In the Bogatyr-Khuolu Lake basin, against the background of a decrease in the total density of the bird population from the foothills to the peaks, three groups of species with different vectors of the vertical dynamics of abundance were identified (Table 2). With an increase in altitude, the abundance of the European golden plover, common ringed plover, red-necked stint, red-throated pipit, white wagtail (*Motacilla alba* (Linnaeus 1758)), common redpole (*Acanthis flammea* (Linnaeus 1758)), and Lapland bunting decreased, whereas the abundance of the rock ptarmigan and snow bunting increased. The abundance of species such as the Eurasian dotterel, horned lark, buff-bellied pipit, raven (*Corvus corax* (Linnaeus 1758)), northern wheatear, and bluethroat is maximum in the middle part of the alpine belt and gradually decreases both towards the peaks and towards the foot of the slopes.

The patterns of vertical differentiation of the bird population were also established when analyzing the corresponding values in the basins of Bogatyr (970 m above sea level), Neralakh (920 m above sea level), Bogatyr-Khuolu (854 m above sea level), and Negu-Iken lakes (760 m above sea level) (Table 1). The species in which the abundance definitely decreases (red-throated pipit, gray wagtail (*Motacilla cinerea* (Tunstall 1771)), and white wagtail) or increases (little stint and snow bunting) with increasing altitude are scanty. A group of species (n = 17) was identified, the abundance of which is maximum in the Bogatyr-Khuolu Lake basin (at average altitudes relative to other lakes) and decreases both in the direction of the higher Bogatyr Lake and in the direction of the lower Negu-Iken Lake. This group of species includes the rock ptarmigan, the American and European golden plovers, the common ringed plover, the Eurasian dotterel, the wood sandpiper (*Tringa glareola* (Linnaeus 1758)), the gray-tailed tattler, the ruff, the red-necked stint, Temminck's stint, the long-tailed jaeger, the horned lark, the buff-bellied pipit, the northern wheatear, the bluethroat, the common redpole, and the Lapland bunting.

Our data indicate that the altitudinal distribution of the majority of birds within the alpine belt of the northwestern Putorana Plateau is determined primarily by the boundaries of the distribution of optimal habitats rather than the absolute height of the terrain.

The population of birds of all sites surveyed in 2010, 2013, and 2018 (n = 3) was quantitatively dominated by the buff-bellied pipit. The group of dominant species in the basins of Neralakh and Bogatyr lakes also includes the snow bunting, the common ringed plover, and the European golden plover; the Negu-Iken Lake basin, the Lapland bunting and the red-throated pipit; and the Bogatyr-Khuolu Lake basin, the Lapland bunting. The subdominant species in the bird population of all sites surveyed (n = 3) are the horned lark, the northern wheatear, Temminck's stint, the rock ptarmigan, and the gray-tailed tattler. The subdominant species in the basins of Neralakh and Bogatyr lakes are also the Laplandian bunting, the red-throated pipit, the red-necked stint, the little stint, and the Arctic tern. The group of subdominant species of the Negu-Iken Lake basin also includes the common ringed plover, the European golden plover, the white wagtail, the common scoter, the common redpole, the bluethroat, the lesser black-backed gull (*Larus heuglini* Bree 1876), and the Arctic tern. The subdominants in the Bogatyr-Khuolu Lake basin are also the common ring plover, the common redpole, the snow bunting, the European golden plover, the red-necked stint, the white wagtail, the red-throated pipit, the Eurasian dotterel, and the bluethroat.

The lake–river system is the basis of the aquatic–semi-aquatic component of the landscapes of the alpine belt of the northwestern part of the Putorana Plateau. In the period from June 18 to July 19, 2018, we recorded 14 bird species with a population density of 6.8 individuals/km of coastline along the Bogatyr-Khuolu River and 19 species with a population density of 14.5 individuals/km on the lakeshore of Bogatyr-Khuolu Lake (Table 3). The quantitatively dominant species on Bogatyr-Khuolu Lake were the black scoter and the common ringed plover with an abundance of 3.3 and 1.8 individuals/km of shoreline, respectively; on the Bogatyr-Khuolu River, they were the common ringed plover, the red-necked stint, the Arctic tern, the red-breasted merganser, and Temminck's stint with an abundance of 1.6, 1.0, 0.8, 0.8, and 0.8 individuals/km of shoreline, respectively.

CONCLUSIONS

Detailed original information on the current state of the species composition as well as on the regional and altitude distribution of birds of the alpine belt of the northwestern Putorana Plateau was obtained, summarized, and analyzed. Previously unknown data on the structure of the fauna and population of birds are presented, which significantly expand the knowledge about the avifauna of the peaks of the most extensive mountainous region of the Asian Arctic.

In each of the sites (n = 3), we recorded 41 to 49 species (in total on the entire surveyed area, 63 species) of birds. The breeding avifauna of this territory numbers 33 species, among which two species were discovered here for the first time at a distance of 200 and 600 km southwards of the previously known boundaries of their breeding ranges on the Taimyr Peninsula.

The avifauna of the alpine belt of the northwestern Putorana Plateau contains a significant proportion of plain–tundra species (49%) that are not found in other parts of this belt. The distribution of a number of species (n = 35), including the red-throated and yellow-billed loons, the common ringed plover, the wood sandpiper, the ruff, the little stint, the red-necked stint, the common sandpiper, and the long-tailed jaeger, is associated exclusively with the northwestern part of the region within the alpine belt.

The proportion of the breeding avifauna of the alpine belt of the northwestern Putorana Plateau in some surveyed sites is 79–83%, and the level of faunal commonality is 86–87%, which testifies to the homogeneity of the avifauna of the mountainous area considered. The structure of the breeding avifauna corresponds to the zonal and landscape features of the part of Northern Eurasia considered, and its qualitative homogeneity in all surveyed sites is due to the widespread prevalence of representatives of the same orders (Charadriiformes 42–48%, Passeriformes 38–42%), the faunal complex (Arctic 52–62%), and the zonal-landscape groups (hemiarctic 26–35%, boreal–hypoarctic 19–30%, and arctic-alpine 17–19%).

The avifaunal structure commonality in the horizontal plane is maintained by species that are distributed simultaneously over all sites surveyed, whereas in the vertical plane it is maintained by the species that simultaneously inhabit two (usually adjacent) altitude–landscape levels. The majority of the bird species that simultaneously breed in all surveyed sites and that form a common faunal core are widespread in the tundra zone and partly in the forest–tundra zone.

The fauna and population of birds in the alpine belt of the northwestern Putorana Plateau are formed in a system of general zonal and altitudinal-belt patterns. The species richness, the bird population density, and the abundance of the absolute majority of species decrease with an increase in altitude. The avifauna of all surveyed sites, due to the identity of their prevailing ecological conditions, has a single pattern of altitudinal–landscape differentiation, in accordance with which the avifauna of the lower, middle, and upper levels of the alpine belt, replacing each other with height, are distinguished. The altitude distribution of the majority of birds within the area considered is determined primarily by the boundaries of the distribution of optimal habitats rather than the absolute altitude of the area.

Within the alpine belt of the northwestern Putorana Plateau, the maximum species richness is characteristic of the avifauna of the lower level. With increasing altitude, the avifauna becomes poorer. The similarity coefficient of avifauna of the lower and middle level is 89%; that of the middle and upper is 51%; and that of the lower and upper is 70%.

In the northwestern parts of the Putorana Plateau, the distribution of 41% of all bird species is limited to only one altitude level: 37% of species are limited to the lower level and 4% of species are limited to the middle level. As much as 59% of species dwell in a wide range of altitudes covering at least two altitude levels: two levels are populated by 22% of species and three levels are populated by 37% of species. The ranges of species dwelling in a wide (at least two altitudinal belts) range of altitudes have a pronounced three-dimensional pattern.

The bird population density in the surveyed sites is in the range of 71–237 birds/km^2 (on average, 138 birds/km^2). The bird population density decreases with altitude from 264 birds/km^2 at the lower level of the alpine belt to 119 birds/km^2 at the upper level.

The mountain specificity of the avifauna of the surveyed parts of the alpine belt of the northwestern Putorana Plateau is determined by the species that are ecologically closely associated with the terrestrial or aquatic–semi-aquatic elements of the alpine-type landscape throughout their range (gray-tailed tattler and buff-bellied pipit) or a significant part of it (rock ptarmigan, Eurasian dotterel, horned lark, gray wagtail, northern wheatear, and snow bunting).

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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