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Review paper

The structure, territorial relationships and ecology of birds in high-mountain Daghestan

Vilkov Evgeny

Precaspian Institute of Biological Resources of the Daghestan Federal Research Centre of the Russian Academy of Sciences

*email: evberkut@mail.ru

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Abstract

In this paper the results of the bird counting during the period of 1998-2017 in High-mountains of Daghestanhas been presentd. The species composition and ecological structure of the avifauna from the study area has been described for the first time. Using cluster analysis I found that the avifauna patterns of the most key sites have similar features. In this areas, high heterogeneity of biotopes and the faunal diversity can be seen which formed under the conditions of sufficient moisture. Data showed that high-grass meadows in the south-eastern highlands are used by some species as a substitute of the forest habitats, typical for the forested central and north-western parts of the high-mountainous province.

Keywords: Avifauna, birds' community, ecological structures, high-mountain Daghestan.

Introduction

The High-mountain region of Daghestan occupies an axial part of the Greater Caucasus and is formed by the Lateral and Watershed ridges with the trenches enclosed between them. The social tension in the period of the Caucasian wars made this remote mountainous territory inaccessible to researchers until the 19th century. Only by the end of the 19th century, the Caucasus, including High-Mountain Daghestan, became relatively open for ornithologists. The pioneer researchers included E. Ménétries (1832), G. I. Radde (1884), K. N. Rossikov (1884, 1885), N. Ya. Dinnik (1886, 1887, 1905), S. I. Bilkevich (1893) and some others. In the 20th century, the studies were continued by K. A. Satunin (1912), L. B. Böhme (1932, 1950), R.L. Böhmeand D.A. Banin (2001) and other scientists.

Despite the rich but variegated retrospective material, the summarized analytical works on the fauna and distribution of birds of the Daghestan highlands have not yet been written. However, the need for up-to-date information on the bird population of this mountainous area has recently become especially acute. This is due to the fact that, firstly, the avifauna of the Caucasus, historically formed in a relative isolation (Polivanova 1990), includes three neoendemic taxa (Neoendemics of the Caucasus, including High-mountain Daghestan, are represented by *Lyrurus mlokosiewiczi* Taczanowski 1875, *Tetraogallus caucasicus* Pallas 1811, and *Phylloscopus lorenzii* Lorenz 1887), which status in the rapidly changing conditions of Daghestan mountain ecosystems requires constant monitoring. Secondly, the specificity of the region orography generated a number of transitional landscapes inhabited by bird communities, typical not only for the High-mountain, Intra-mountain and Piedmont regions of Daghestan, but also for the plains of the republic. The structure of these communities and the principle, according to which they are formed, still remains to be revealed. Thirdly, the border of the 20th and 21st centuries with its global warming (Baranov

2007) and socio-economical transformations has induced qualitative changes in the natural environment of many mountainous areas of Daghestan due to a sharp decrease in arable lands, felling of forests, decline in the number of livestock and expansion of various kinds of anthropogenic pressure. All of that consequently affected avifauna, very sensitively responding by their number dynamics and species composition to the integrated impact of regulatory factors.

The above-mentioned trends have determined the priority goals and objectives of our research as to identify the species composition of birds, their status, abundance, ecological structure and territorial relationships in High-mountain Daghestan.

Proceeding from the formulated goals and objectives, a series of avifauna studies was launched in 1996 in Daghestan highlands (Vilkov 2001, 2009 a,b, 2010a, b, 2011a,b,c, 2014). The collected material was used to prepare a summarized report on the fauna and distribution of birds in the High-mountain Province, the most hard to reach of the three mountain provinces of the republic. To avoid discrepancies, the data on the species composition of birds, their residence status, abundance and territorial distribution are based only on the author's material.

Material and methods

The paper summarizes the results of long-term (1998–2017) ornithological counts carried out in 13 key sites, located within six administrative districts of High-mountain Daghestan (Fig. 1). The altitude of the study area ranges between 1300–3000 m a.s.l. (hereinafter simply m). A total of 66 ornithological counts were made, including 309 observation hours and 505.5 km of walking routes (5–22 km per census day in different landscapes). Most of the counts were carried out from the second half of July to the third decade of August, since it is a steady period of relatively fair weather in High-mountain Daghestan. This is also the time when not only adults (breeding pairs) still remain within their nesting areas but their fledglings as well.

This is due to the fact that in severe bioclimatic conditions of mountains birds select particular habitats with an optimal set of conditions and preferred resources, mostly staying there until the autumn migration (migratory and nomadic species) or even remaining for winter (synanthropic and partly conventionally synanthropic birds). Given that during 1.5-2 months after leaving nests a significant part of fledglings (weak individuals, predator pressure, etc.) is eliminated, it is the period from the third decade of July to the third decade of August when the most viable individuals can be found in their occupied areas. This part of the population consequently makes up the core of the bird population, most of which will start reproducing next year. Thus, the data on the bird abundance obtained in the second half of the summer can be regarded as a reliable assessment of the real bird population density, whereas the counts conducted in the first half of the summer are inaccurate since they record those individuals at the beginning of the post-breeding period which will be subsequently eliminated and will not take part in reproduction.

The counts were made from 7 to 17–00 hrs, excluding the time spending for rest, hiding or taking photos, etc. The only exception was the ornithological counts conducted in October 2012 in Tlyaratinsky District (Vilkov 2013) and in January 2015 and 2017 in Charodinsky District (Karanub Village and Tlyarosh Village). The winter census data are not included in the table to avoid errors when calculating the bird population abundance.

The physical-geographical characteristics of the region are based on Ataev (1996). Bird counts were carried out along transects with unlimited width, recalculating the size of the area in accordance with the mean group detection distances (Ravkin 1967). For flying birds, the corrections were made for the average flight speed (Ravkin and Dobrokhotov 1963). Bird

taxonomy is given according to L.S. Stepanyan (2003). The avifauna was classified according to the average abundance of birds and their species diversity in key sites using cluster analysis based on the data matrix (Table). The data were processed with Statistica v. 5.5 and Excel software.

To characterize ecologically different species of birds, the author's classification was used (Vilkov 2010b), distinguishing the birds by their occurrence in preferred habitats that allowed the identification of 11 bird communities (Fig. 2). The birds, found in the air above the upper boundary of the vegetation (birds of prey, airborne birds), were subdivided into bird communities of hoverers and airborne birds, while the air environment, being a feeding place of airborne birds and a location from where the hoverers view the surroundings in search of their victims, is conventionally treated as "habitat". The use of the above-mentioned methods allows us: 1) to identify the whole set of birds in each bird community; 2) to identify the total average abundance of the species in each bird community; 3) to determine the percentage of each species in the corresponding bird community and identify the top three most abundant species by means of which the relationship between bird populations of the compared key sites is provided.

Study area

High-mountain Daghestan is formed by the Main Caucasian (Watershed) Ridge and independent massifs of the Lateral Ridge with strongly compressed folds. Between them lies a longitudinal valley with a complex of trenches, isolated by smaller transverse ridges. The climate of the region is less continental and more humid than in the other part of the republic. Winter temperatures are low. The coldest month is February with an average temperature up to -4 °C in the valleys, and up to -12 °C in the alpine area. Summer is warm in the valleys, and cool in the alpine area. The average temperature in July–August is + 20°C in the valleys and + 5°C in the alpine zone. The annual precipitation increases with the altitude from 400 to 100–1,200 mm, characterizing by a summer maximum. Due to the continental climate, the snow boundary lies high (3,500–3,600 m), and the area of glaciers is insignificant. Mountain-meadow landscapes are dominant and extend up to 2,800–3,000 m. Slopes of ridges and valleys up to 2,500 m are covered with subalpine meadows, higher – with alpine meadows and lawns. A mountain-steppe belt lies on the slopes of southern exposures and in river valleys up to 2,000 m with typical steppe associations of upland xerophytes. Deciduous, pine and pine-birch forests, uncontrolled felling of which led to the replacement of trees by shrubs, are widespread in the valleys and at the lower parts of slopes. Above 3,000 m a narrow strip of mountains is occupied by the subnival belt, deprived of continuous grass and soil cover. Natural landscapes, including large summer pastures, still remained in the province. The territory of arable land is small, occurring only in the river valleys and on the gentle slopes around villages.

Natural and territorial differences allow distinguishing three physical-geographic regions within the province: 1) The region of the Lateral Ridge, which unites five ridges considerably exceeding the altitude of the watershed Ridge. There can be found traces of ancient glaciers with interspersed tarns. The climate is characterized by a cold long winter with a stable snow cover and a short wet summer. Prevailed subalpine and alpine meadows are used as summer pastures. In the subnival zone, there is no continuous vegetation cover. Above 3600–3700 m the nival belt dominates; 2) The region of intermountain trenches is located between the sections of the Lateral and Watershed ranges and is represented by four large trenches. The climate is characterized by a warm summer with an average temperature of July – August + 20°C. The average temperature in January in the valleys ranges from -4 to -6°C. Deciduous, pine and pine-birch forests grow in the river valleys. Along the riverbeds and streams there are well-developed thickets of the sea buckthorn. Intermountain trenches are the area

of the highest concentration of the human population of High-mountain Daghestan. Artificial terraces with fields, orchards and vegetable gardens are common; 3)The region of the Watershed Ridge is the southernmost area of High-mountain Daghestan and has a more humid climate. Mountain-meadow landscapes, used for summer pastures, dominate in the region.

Results

In a mountainous terrain, characterized by diverse natural landscapes, representatives of various faunas are equally considerably isolated and united, forming very peculiar species compositions. High-mountain Daghestan, being a wetted region with the contrasting orography enhanced by a complex of intermountain trenches, is particularly intricate in this respect. The absence of clear faunal boundaries and fragmentation of bird ranges are induced by strong discontinuities of the terrain, where similar habitats are mosaically distanced or, on the contrary, are immediately close to each other due to the inversion of geobotanical zones. For example, the mountain steppe is located above the forest belt, or the mutual penetration of habitats is observed. Consequently, some birds, inhabiting diffusely dispersed habitats, occur at different altitudes and at a significant distance, while others are brought together and located at the same altitude. The formation of the vertical zonal inversion is based on the abiotic process - the runoff of cooled air masses over the intermountain trenches, shifting the altitude belt along the gradient (Irisov 1997). As a result, stable mesoclimatic conditions are formed on the local parts of the mountains provoking the development of the biota not typical for a given altitude. This bioclimate mosaic is especially common for sharp forms of relief and expressed individually for each of the mountain ridges being enhanced by the difference in exposures of each of the mountain slopes. In High-mountain Daghestan this resulted in the development of many transitional habitats with varying bioclimate conditions, where formed local communities of plants and birds. At the same time, the mountain biota is constantly exposed to the impact of extreme environmental factors (high levels of ultraviolet radiation, dramatic daily and seasonal temperature fluctuations, strong winds, precipitation) that reduces the period of biological activity in birds, forcing them to select habitats with the optimal set of conditions and preferred resources. In this regard, the role of suboptimal habitats is reduced, while the connection of birds with optimal habitats increases due to the development of specific adaptations arisen during the long process of changes in many generations controlled by natural selection in the same type of habitat. Such phenomena lead to the formation of narrowly specialized and usually territorially isolated micropupulations (Micropopulation is an assemblage of individuals of the species occupying a homogeneous part of a small area. An ecological micropopulation is distinguished from the other neighboring micropopulation by distribution in a different habitat, its morphophysiological and ethological features) (Naumov 1963) inhabiting the same habitat for many years. Basically, this applies not only to the resident communities of typical mountain birds, but also to the nesting in the mountains adapted populations of migratory birds of the plains (Vilkov 2010b).

For 19 years of research in High-mountain Daghestan (Fig. 1), 115 species of birds were recorded (Appendix 1), constituting 32% of the total republic avifauna (365 species). Among them 56 species were sedentary, 36 nesting migrants, eight supposedly nesting migrants, six transit species, and seven accidental or rare visitors.

The presented list of birds is not final and will probably be supplemented in the course of further studies. Thus, it did not include species, the absence of which during the counts did not allow evaluating their species abundance. Not neglected, they were combined into a "shadow list" of 14 species, including the Large Egret

Egrettaalba Linnaeus 1758, Purple Heron *Ardea purpurea* Linnaeus 1766, Mute Swan *Cygnus olor* Gmel. 1789, Whooper Swan *C. Cygnus* L. 1758, White-fronted Goose *Anser albifrons* Scopoli 1769, Greylag Goose *A. anser* Linnaeus 1758, Mallard *Anas platyrhynchos* Linnaeus 1758, Teal *A. crecca* Linnaeus 1758, Garganey *A. querquedula* Linnaeus 1758, Common Crane *Grus grus* Linnaeus 1758, Black-winged Stilt *Himantopus himantopus* Linnaeus 1758, and Lapwing *Vanellus vanellus* Linnaeus 1758, periodically penetrating into the highlands (Vilkov 2010a, b; 2011c). The list can be also supplemented by accidental visitors, such as the Black-throated Diver *Gaviaartica* Linnaeus, 1758 and the Black-winged Pratincole *Glareola nordmanni* J.G. Fischer, 1842, photographed by local residents in 2011–2017 in High-mountain Daghestan.

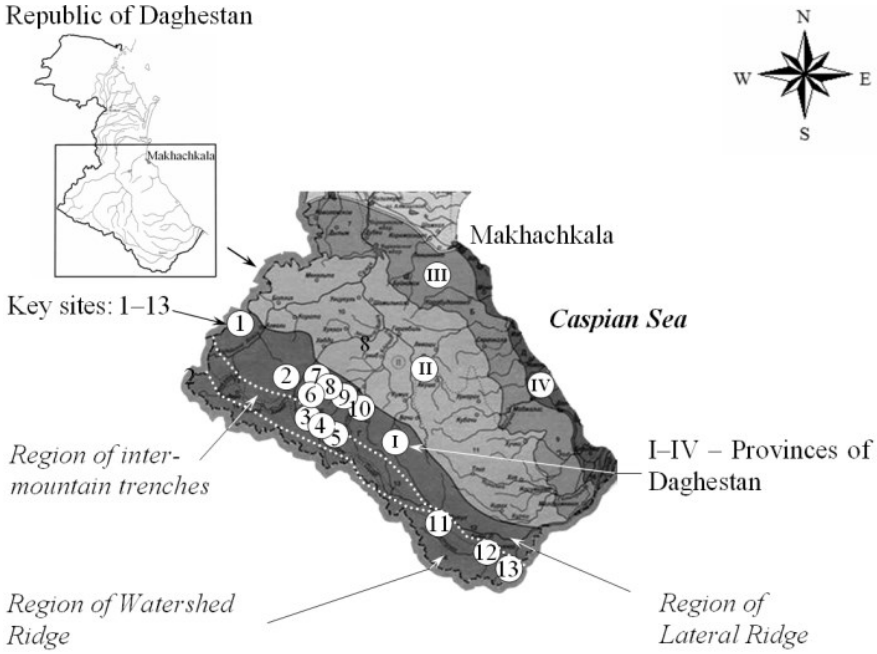
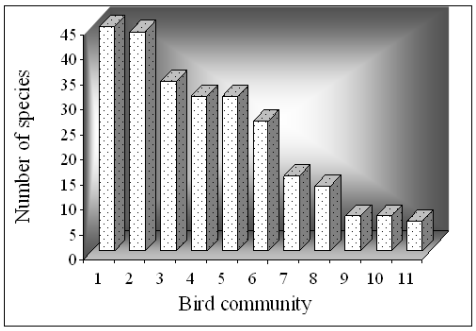


Figure 1. Scheme showing zonation of Daghestan (Ataev 1996), key sites, altitudes and timing of counts.
Notes: I–IV – Daghestan provinces: I – High-mountain, II – Intra-mountain (middle-mountain), III – Piedmont, IV – Coastal lowland. Key sites: 1) Tsumadinsky 1,700–2,200 m (the centre – VerkhneeGakvari Village, 18–19 Aug 2003); 2) Tlyaratinsky 1,300–3,000 m (centre – Koshob Village, 13–16 Jul 1998); 3) Tlyaratinsky 1,500–2,200 m (centre – Takhota Village, 23–26 Jul 2001); 4) Tlyaratinsky 1,800–2,500 m (centre – Salda Village, 18–20 Jul 2012); 5) Tlyaratinsky 1,700–2,750 m (centre – Gortnob Village, 17–20 Oct 2012); 6) Charodinsky 2,100–2,200 m (centre – Gochob Village, 21–22 Aug 2011); 7) Charodinsky 1,830–2,200 m (centre – Urukh-Sota Village, 23–25 Aug 2017); 8). Charodinsky 1,550–2,200 m (centre – Tlyarosh Village, 9–11 Aug 2006; 29 Jul – 2 Aug 2008; 20–24 Jul 2009; 12-17 Aug 2010; 9–10 Jan 2017); 9) Charodinsky 2,050–2,200 m (centre – Moshob Village 18–20 Aug 2015); 10) Charodinsky 2,000–2,850 m (centre – Karanub Village: 23–24 Aug 2011; 24–27 Aug 2012, 7 Jan 2015); 11) Rutulsky 1,334–2,200 m (centre – Rutul Village, 23–25 Sept 2015); 12) Akhtynsky 1,700–1,800 m (centre – Jaba Village, 8 Oct 2010); 13) Dokuzparinsky 2,510–3,000 m (centre – Kurush Village, 11–14 Aug 2004).

To simplify the analysis and identification of the avifauna structure of the High-mountain Province, an ecological classification was used (Vilkov 2010b), listed in the table above. The essence of the latter lies in the differentiation of birds by their occurrence in the preferred habitats, on the basis of which 11 ecologically different bird communities have been identified (Fig. 2).

The used algorithm not only enabled the determination of ecological appearance of the avifauna of the studied mountain province, but also reflected the entire spectrum of landscape and habitat differences expressed through the heterogeneity of the bird population. It is also

taken into account that a number of bird species belong to different avian communities. This peculiarity, on the one part, reflects the ecological plasticity of individual species and availability of suitable ecological niches in different habitats (except for hoverers and aerobionts), and on the other hand, determines the ecological relationships of birds between territorially disjunctive faunal communities. In addition, the applied approach made it possible to identify not only a complete set of birds participating in the formation of each of ecological bird communities, but also established the priority level of each of them in the avifauna structure of the study area. Hence, it is axiomatic that the higher the bird species diversity in the avian community, the greater its stability and priority in the faunal community of High-mountain Daghestan.



Legend to Fig. 2:
1. forest birds – 45 species (39 %);
2. birds of subalpine meadows – 44 species (38 %);
3. birds of agrolandscapes (fields, orchards, vegetable gardens) – 34 species (30 %);
4. birds of cliffs and rock outcrops – 31 species (27 %);
5. birds of synanthropic (conventionally synanthropic) and anthropogenic landscapes – 31 species (27%);
6. birds of tree-shrub vegetation – 26 species (23%);
7. birds of alpine meadows – 15 species (13%);
8. hoverers– 13 species (11%);
9. subnival-nival birds – 7 species (6%);
10. waterbirds – 7 species (6%);
11. airborne birds – 6 species (5%).

Figure 2. The ecological structure of birds recorded in High-mountain Daghestan

Basing on the data for the entire population of birds (matrix, table), we performed a cluster analysis. As a result, 3 groups of relevant key sites were distinguished (Fig. 3).

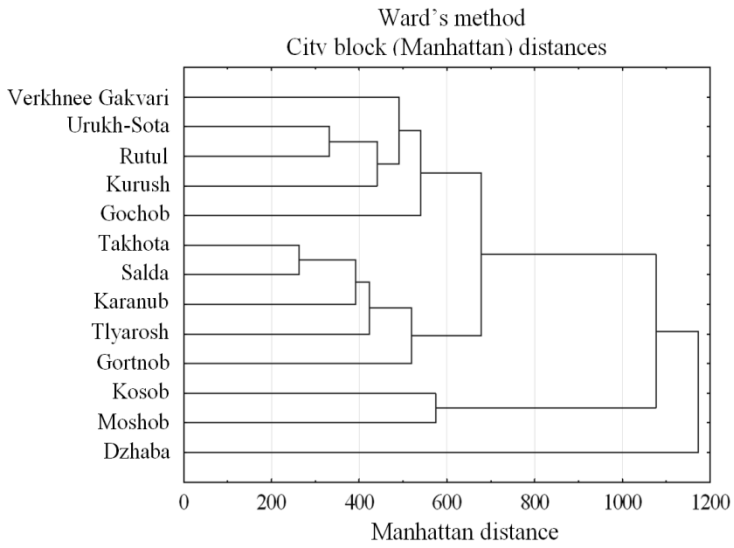


Figure 3. Dendrogram of similarity of bird communities of High-mountain Daghestan

Discussion

The resulting dendrogram shows the similarity of the bird population in all key sites, not taking into account their subdivision into ecological bird communities. To detail the faunal similarity, we again returned to the above-mentioned ecological classification (Vilkov 2010b), which enabled not only the identification of ecological relationships of birds between different habitats in each of 3 groups of clustered key sites, but also

characterized it according to similar ecological specificity.

Thus, the interpretation of Figs. 2, 3 and the table data shows that the first group of birds from corresponding them key sites, located in the north-west (Verkhnee Gakvari) and the central (Gochob, Urukh-Sota) parts of the high-mountain province, is adjoined by rather unexpected faunal communities from the south-east of the high-mountain zone (Rutul and Kurush). It is interesting that despite the considerable difference in altitudes (1,334–3,000 m), territorial disjunction and significant landscape-habitat differences (Kurush and Rutul are situated in treeless southern highlands dominated by subalpine and alpine meadows, whereas the centres of forest vegetation are present only on slopes of the northern exposures of lateral gorges) between the compared faunal communities we find many common species belonging to forest and tree-shrub birds. This is explained by the fact that high-grass meadows in the south-eastern highlands are used by some species as a substitute of the forest habitats, typical for the forested central and north-western parts of the high-mountain province. In this context, it is quite understandable the presence of more numerous group of birds of agrolandscapes, cliffs and rock outcrops, subalpine and alpine meadows, hoverers, airborne birds and birds of aquatic habitats, since the presence of the latter is possible due to the availability of rivers, small streams and marshy lawns. At the same time, a number of birds of anthropogenic landscapes (Jay, Magpie, Hooded Crow) are absent in the settlements of the southern highlands, as in the most of high-mountainous villages the tree-shrub vegetation is not very pronounced.

The second place in faunal similarity was occupied by the quite expected bird community of the intermountain trenches (Takhota, Salda and Gortnob), adjoined by bird communities from the central part of High-mountain Province (Karanub and Tlyarosh). The similarity of their faunal structure is explained by their proximity of these study areas and insignificant altitude variation (1,550–2,850 m) that consequently determines the relative uniformity of typical habitats. Moreover, the compared sites are united by the same orographic structure and joined by river valleys with a similar set of bioclimatic conditions. It also enhances the similarity of their faunal structure, giving them the appearance of a trench-like formation. A distinctive feature of these sites is the dominance of sharp landforms and extensive forest areas determining the prevalence of forest and tree-shrub birds. For this reason, birds of cliffs and rock outcrops, subalpine meadows, hoverers and airborne birds predominate here. In turn, the similarity by the synanthropic and conditonallysynanthropic bird groups is explained by the fact that the compared sites have the largest concentration of the human population in the High-mountain Daghestan with well-developed anthropogenic infrastructure. A significant percentage of agrolandscape birds are associated with the availability of vast subalpine meadows and open areas (fields, hay meadows) with horticultural complexes. Instead, birds of alpine meadows, nival-subnival areas and waterbirds are rather scanty in these sites, because of other preferred altitudes and also inaccessibility of mountain waterways for research.

Finally, the third group of key sites with structurally close fauna communities located in the north-west (Kosob) and in the central (Moshob) part of the highlands, including a similar bird community in the south-east of the High-mountain Province (Dzhaba), is also characterized by territorial disjunction with a significant altitude range (1,300–3,000 m). In this case, the similarity between the compared bird communities is based on the birds of open areas, since the first two sites, in addition to forests, have extensive subalpine meadows apparently prevailing in the south-east of the High-mountain Daghestan. For the same reason, there is observed the dominance of the birds of agrolandscapes, subalpine meadows,

cliffs and rock outcrops. As for the representatives of birds from other communities only a weak relationship is found among three groups of compared key sites.

The analysis allows us to conclude that the faunal similarity of the compared key sites is based on the difference in the absolute altitudes of the localities, their orographic configuration (trench-like form) and landscape-habitat differences, which together determine not only the ecological appearance and abundance, but also the spatial typological structure of the bird population of High-mountain Daghestan.

Conclusion

For the first time a list of birds of the High Mountain Daghestan including 115 species is presented, which can be additionally supplemented with 14 species from the "shadow list". The latter were not included in the main list due to the impossibility of identifying their abundance, since these birds were not recorded during the surveys, though repeatedly seen by local residents or other researchers in different years in the study area.

The cluster analysis has established that the faunal similarity of the compared key sites is based on the difference in the absolute altitudes of the localities, their orographic configuration (trench-like form) and landscape-habitat differences, which together determine not only the ecological appearance and abundance, but also the spatial typological structure of the bird population of High-mountain Daghestan.

The avifauna ecological structure of the High-mountain Daghestan has been identified using the method of ecological differentiation of birds by their occurrence in the preferred habitats, on the basis of which 11 bird communities are distinguished. The use of the original classification makes it possible to establish a complete set of birds participating in the formation of each of the bird communities, and reveal their ecological relationships between different habitats in each of 3 groups of clustered key sites. The application of this method is especially important when characterizing the avifauna ecology in large territorial areas with a high number of species, as each of the bird communities with a complete set of birds can be characterized by similar specific features of their ecology, establishing their priority in the avifauna structure of the study area.The analysis of the collected material provides not only a picture of the species diversity and territorial distribution of birds, but also helps to understand the avifauna resource capacities of the High-mountain Daghestan.

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