

WILLOW AND ROCK PTARMIGAN MONITORING IN RUSSIA: AN HISTORIC OVERVIEW

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ABSTRACT.—The Willow Ptarmigan (*Lagopus lagopus*) and Rock Ptarmigan (*L. muta*) are among the most numerous species of ptarmigan in Russia. Their ranges cover most of the tundra zone and the alpine zone of some mountains. Willow Ptarmigan also breed in the bogs found in forest and forest-steppe zones of Russia and adjacent countries. During the Pleistocene, their ranges were much larger and extended as far south as 40°N, and in the Holocene, the ranges of both species experienced several episodes of shrinkage and expansion. Range shrinkage is currently evident in many areas of Russia; for example, several southern enclaves recently ceased to exist. The density of Willow Ptarmigan is substantial in the tundra zone, and the current advancement of shrubs to the north, evident throughout the Arctic, makes the habitat even more hospitable. In general, the effect of global warming on habitat appears beneficial for ptarmigan in the northern Palearctic. Current global climate predictions suggest that snow cover depth will be decreasing in the European part of Russia, and increasing in northeast Asia in the coming decade. This means that overwintering conditions for ptarmigan would be somewhat favorable in the European north because shrub parts would be more accessible. Deeper snow predicted for northeast Asia might cover most of the shrubs and limit the numbers of ptarmigan there. Ptarmigan were monitored in various localities throughout their range in Russia, but these efforts came to an end in the early 1990s with the cessation of the fur trade and the demise of the monitoring agencies. New restructured agencies have no monitoring schemes in place, or they exist only on paper and are not supported by funds and trained personnel. *Received 1 March 2011, accepted 31 May 2011.*

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THE *LAGOPUS* PTARMIGAN have been an important food source for people dwelling in the vast spaces of Eurasia since early Paleolithic times. During the early stages of the Industrial Revolution, ptarmigan were continuously seen in the markets of large cities in Russia. In the days of the USSR, *Lagopus* ptarmigan were harvested commercially in many places, and in the second half of the 20th Century were monitored in several locations. Technically this monitoring is in place now, but poor training of personnel as well as a lack of funding make this monitoring scheme highly inaccurate. In addition, the majority of reports are scattered across a collection of papers, and are not indexed by abstracting companies. The purpose of this paper is to provide a brief summary of the *Lagopus* ptarmigan monitoring effort throughout Russia from these reports and other sources.

EARLY HISTORY OF *LAGOPUS* PTARMIGAN IN RUSSIA

The earliest fossils of ptarmigan were found in Southwest Europe (Poland and Bulgaria), and were dated as 3.1–4.2 million years ago (Bochenski 1991, Boev 1995). Within Russia, as well as in other sites of Eurasia, the paleontological evidence was dated from much later periods. The more easterly a finding is located, the earlier the date (Potapov et al. 2003). The remains of ptarmigan are most common in the layers of the late Pleistocene. By the end of the Pleistocene, ptarmigan reached the eastern fringes of the Palearctic, and then spread into North America. Because of a plethora of late-Pleistocene findings, it is possible to conclude that Willow Ptarmigan (*L. lagopus*), and to a lesser degree Rock Ptarmigan (*L. muta*), were abundant in the tundra-steppe landscape. The latter was spreading across the entire northern part of the Palearctic from the Atlantic to the Pacific. Almost every Paleolithic, Mesolithic and Neolithic archeological site contains a fair number of ptarmigan bones. The most favorable times for ptarmigan were the last two glaciations, known as Riss and Würm. The

ptarmigan distribution was at its maximum, stretching from the Atlantic to the Pacific, and south to the Iberian, Appenine and Crimean Peninsulas. At the time there were no statistical differences between the fossil bones of Willow and Rock Ptarmigan throughout this entire range. The first study which managed to separate Willow from Rock Ptarmigan was carried out in Britain (Stewart 2000) and the separation dated back to Britain 450,000 BP. In all other sites up to the end of the Pleistocene, the differentiation between Willow and Rock Ptarmigan was and still is difficult.

The end of the Pleistocene and the beginning of the warmer Holocene period was caused by abrupt changes in the global climate. In a relatively short time, the climate caused a gigantic transformation of fairly uniform tundra-steppe into climatically differentiated biomes. From the west to the east, a new forest zone, soon to be a boreal forest biome, cut the tundra-steppe zone apart. The southern belt of the grasslands transformed into the steppe and forest-steppe biomes. Many species of the tundra-steppe formed disjunct ranges on both the southern and northern parts of the boreal forest, while others survived either on the northern or southern side of the boreal forest. For some species, the newly formed biome was fatal. For Willow Ptarmigan, this process forced the formation of four types of habitat adaptations for raised bogs, moors and river valleys, forest-steppe, and mountainous habitats. The latter, usually fenced by the forest belt below, as well as isolated enclaves in the southern fringes of their former range, are the direct descendants of their ancestral forms living together with the mammoth megafauna. Massive orogenesis elevated these relict habitat areas up to 1000 m or more asl, where they are still preserved in the alpine and sub-alpine zones of mountains of the southern Palearctic. Rock Ptarmigan have not survived in the flat forest-tundra steppe, but only in those areas of mountains isolated by vast areas of forested plains, or, as in Western Siberia, on semi-isolated or interconnected mountain tops.

All these processes, which happened from the end of the Pleistocene until now, affected the distribution of both species. Most importantly, the ranges shrank. The first to split was the range of the Rock Ptarmigan, a species most adapted to a cold climate and hilly landscapes. The largest enclaves of this species are located in the most northern regions of the Northern Hemisphere: northeastern Asia and the northern part of North America. The third block of the previously continuous range is in Greenland. Here, Rock Ptarmigan were forced to survive on the fringes of the Greenland ice-sheet. The fourth are the isolates in the Arctic and Atlantic Oceans: Iceland, the British Isles, Svalbard, the Kola Peninsula and the Northern Urals. And finally, the southern-most group of isolates survived in Eurasia associated with the Pyrenees, Alps, to some extent the mountains of Kamchatka, Chukotka, Yakutia, and Japan, and Central Asian mountains: Altay, Sayan, Tarbagatai, and Khangai. In the north, the survival of Rock Ptarmigan is limited by the cold (Pleistocene-like) climate, and in the south, by the same Pleistocene-like climate on elevated mountains. The Rock Ptarmigan subspecies living in the Kuril Islands, Commander Islands and the Aleutians are very interesting isolates. Previously these islands were mountain ranges bordering Beringia. The islands in the Arctic Ocean with a flat landscape (Wrangel and Novosibirskie islands) do not have Rock Ptarmigan. So far, there are no big changes in the range of the Rock Ptarmigan in the Palearctic that can be linked to climate change as a result of global warming.

The range of Willow Ptarmigan is much bigger and has a relatively smaller number of isolates. It stretches across the continental plains northwards from 50°N latitude in Eurasia and 52–54°N in North America. The main part of its range is located within Russia, occupying all of the biomes: tundra, forest-tundra, taiga, forest-steppe and sub-alpine zones of Siberia and north-east Asia. If, at the end of the Pleistocene, the range occupied almost all of Europe, by the end of the Holocene it had

shrunk significantly in the forest and forest-steppe zone, and the western border started to move east. There were a number of reasons for such a change: global warming, as well as increasing pressure from humans, most notably manifested in deforestation and converting lands in forest and forest-steppe zones into agriculture. After prehistoric times, the species ceased to exist in Ukraine, East Prussia, Poland, Lithuania and a larger part of Byelorussia. The species is dramatically waning in numbers in the current western parts of the range: Estonia, Pskov, Leningrad, Novgorod and Smolensk districts of the Russian Federation. In the 1950s–80s, the decline was mostly driven by a directive to convert raised bogs into arable lands, and/or peat extraction. No attention was given to the fact that these bogs sustain many species, such as Willow Ptarmigan, Western Capercaillie (*Tetrao urogallus*), Blackgrouse (*Lyrurus tetrix*), many migratory waterfowl, and maintain water balance or large drainage areas. The mild winters of 1990–2008 were devastating for this species. The white winter plumage of the Willow Ptarmigan was visible for large distances in periods without snow. Byelorussian ornithologists were first to note their visibility while counting game animals from helicopters. Unfortunately, in the majority of cases they were recording fresh kills, mostly by Goshawks (*Accipiter gentilis*) and Golden Eagles (*Aquila chrysaetos*). Currently the number of Willow Ptarmigan has gone down in the diet of these raptors. For example in the diet of the Golden Eagle the proportion of Willow Ptarmigan went from 2.3% in 1972–84 to 0.2% in 1985–2002 (Ivanovskiy and Kovalenok 2002).

Recent winters (2009–2011) were cold, without significant thaw periods, and had enough snow. This offers hope that the numbers of Willow Ptarmigan might start to increase. However there is a need for several such cold and snowy winters. It is not plausible that these cold winters will avert the eastward movement of the western border of the species' range.

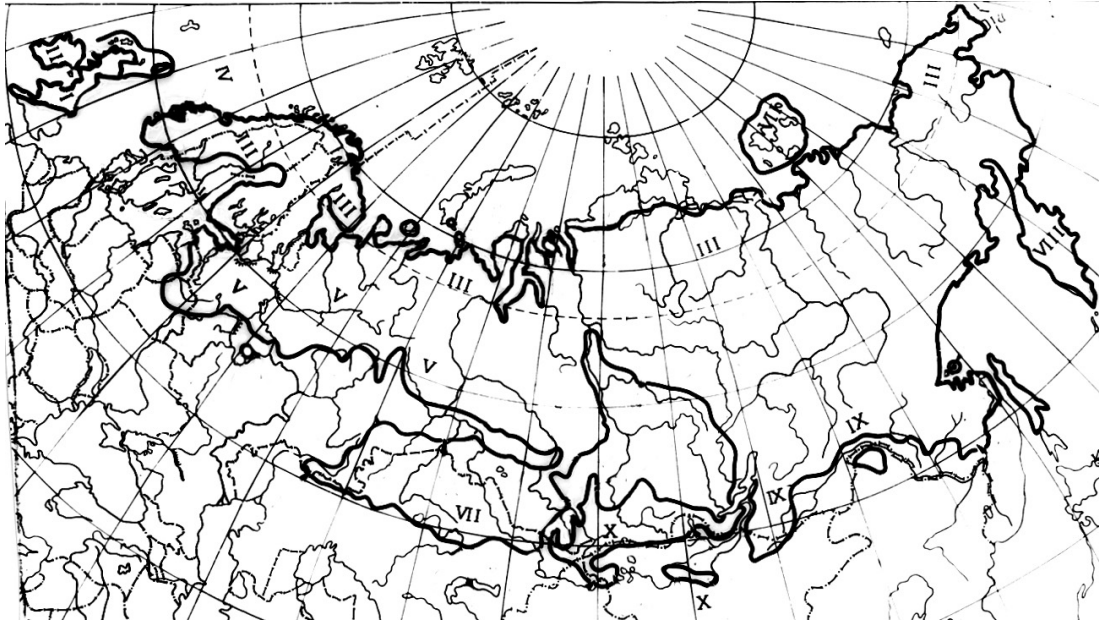


Figure 1. Range of Willow Ptarmigan in Palearctic (from Potapov 1985 with changes and additions). Numbers denote subspecies: I – *L. l. scoticus*, II – *L. l. hibernicus*, III – *L. l. lagopus*, IV – *L. l. variegatus*, V – IV – *L. l. pallasii*, VI – *L. l. major*, VII – *L. l. kamchatkensis*, VIII – *L. l. serebrowskyi*, IX – *L. l. brevirostris*.

Abundant paleontological records do not allow even an approximate estimate of the density of the Willow and Rock Ptarmigan in pre-historic times. Only one thing is definite: that early dwellers of Eurasia were eating ptarmigan on a regular basis. It took about 10,000 years of evolution of the human civilization before it was plausible to monitor resources in nature. The counts became economically feasible, as well as useful. Large concentrations of humans in cities needed resources which exceeded those of small rural settlements. Commercial activities and an improved infrastructure (communications, roads, etc.) caused an increase of exploitation of natural resources.

In Russia, the first reliable data on the number and distribution of ptarmigan appeared from the end of the 19th Century, and were mostly from the European part of the country. The numbers of the ptarmigan were determined by rule of thumb and usually given as “very abundant,” “abundant,” “common,” and “rare” (Menzbier

1902, Sabaneev, 1902). More accurate counts were used from the 1920's. By the end of the 20th Century, the Russian Federation had a functioning department for the conservation and development of the game resources. It had the Control-Analytical Center for the Game Animals and their habitats. One of the branches of this center is the Stage Game Counts Service. In the years 2000–02, this service made an attempt to make a standardized All-Russia Winter Game Survey (ARWGS) following the methods of Kuzyakin et al. (1990). The counts were carried out by the rangers, who were not properly trained, and tended to overestimate. Besides, many of them were not able to tell the difference between the Black-billed Capercaillie (*Tetrao parvirostris*) and Western Capercaillie, and most importantly, the Rock Ptarmigan from the Willow Ptarmigan. In the regions where only one species occurred, the results of the survey had great value. For the regions where both species occurred, we had to rely on the data from old literature. Ptarmigan were part of this

Table 1. Density of Willow Ptarmigan in different Tundra areas, given in individuals per 10 km², unless stated differently.

Place	Year	Season	Birds per 10 km ²	Reference
Bolshezemelskaya Tundra, North	1939	August	181–422	Skrobov 1968
Bolshezemelskaya Tundra, South	1939	Aug, Sept	650–2149	Skrobov 1968
Bolshezemelskaya Tundra, South	1940	May	29–162	Skrobov 1968
Malosemelskaya Tundra	1938	Spring	444–660	Mikheev 1948
Malosemelskaya Tundra, 67°N	1985	Spring	66	Voronin 1995
Timanskaya Tundra	1950	June	200–300 nests per 10 km ²	Mikheev 1952
Yamal, North	1989–94	Spring	206–350, average 286	Tarasov 1995
Taimyr peninsula, shrub tundra 69–73°N	1965	June	20	Pavlov 1975
	1966	June	32	Pavlov 1975
	1967	June	35	Pavlov 1975
	1968	June	15	Pavlov 1975
Taimyr, Dudypa estuary, 72°N	1960–62	Summer	120–140 pairs	Krechmar 1966
	1963	Summer	20–30 pairs	Krechmar 1966
Taimyr, Pura lakes, 73°N	1965	August	55 broods	
Taimyr, Pura lakes, 73°N	1967	August	70	
Taimyr, Mokritto Lake, 73°N	1968	Spring	30 pairs	Pavlov 1975
Novosibirskie Islands, Kotelnii Island	1968	March-April	15	
Novosibirskie Islands, Lyakhovskiy Island	1968	March-April	5	Kishinskiy 1975
Khromo-Indigirka lowlands, Yakutia, 70–72°N	1961	Spring	74	Perfiliev 1975
Khromo-Indigirka lowlands, Yakutia, 70–72°N	1961	Fall	180	Perfiliev 1975
Khromo-Indigirka lowlands, Yakutia, 70–72°N	1962	Spring	46	Perfiliev 1975
Anabar, Yakutia	1962–64	Spring	200–320 pairs	Uspenskiy 1965
Koryak Mountains	1960	June	250 pairs	
Kamchatka tundra	1965–67	Spring	20 pairs	Gizenko 1968
Parapol depression, Kamchatka	1976	Summer	30–110 pairs	Lobkov 1986

survey, and some transects recorded good numbers (Mezhnev 2000, 2002). Below we provide the density and numbers available to date by species and by different biological zones.

WILLOW PTARMIGAN (*LAGOPUS LAGOPUS L.*)

Tundra and Forest-tundra.—The northern boundary of this zone is set by the Arctic Ocean, the southern boundary is set by the timberline. In general Willow Ptarmigan are very abundant here, especially in the shrub sub-

zone, in all the tundra areas from Kola to the Chukchee Peninsula. Willow Ptarmigan populations have a cyclic pattern in many places, but it appears that the cycles are not synchronous across the continents.

Kola Peninsula, Pasvik Nature Reserve. In the period 1993–2007, the total number of individuals seen on 10 km of transect reached a maximum (>5 individuals) in 1994, 1999, and 2001, an average number (3 individuals) in 2004 and 2005; and a minimum (<1 individu-

als) in 1997, 2002, 2006. There was 4–5 year period between the absolute minima (Khlebosolov et al. 2007).

Kolguev Island (5020 km²), c. 75 km north of the Malozemelskaya Tundra. This island supports a very high density of Willow Ptarmigan (94–219 birds per km²) (Kurvits et al. 2009). All Willow Ptarmigan move to the mainland in the fall. Local people bag about 1000 individuals per fall (Kondratiev 2006).

Nesting is reported from the entire Bolshzemelskaya Tundra. Fall numbers were estimated not less than 5 million. Only 20% were harvested by commercial hunters (1962–65). The numerical estimates are given in Table 1.

Overall numbers of the Willow Ptarmigan in the Khroma-Indigirka tundras were estimated at 200,000 birds. Similar extrapolations for the Alaseya Tundra, Yakutia, for roughly the same area was given as 22,000 birds (Perfiliev 1975).

The density of Willow Ptarmigan in the Kolyma Tundras was studied in the 1970s–1980s by Andreev (1988). He concluded that the ptarmigan population there has a 10-year cycle governed by the production of 1–2 year twigs by the dominant shrub (*Salix pulchra*, *S. glauca* and *S. kolymnensis*). The density was measured by area occupied by territorial cocks. It was as low as 2.3 ha per territorial male in the peak years to 69 ha per territorial male during low density years. The peaks were reported in various regions of the Kolyma plain in 1980–81 and 1987, and a depression was reported in 1979.

Northern Taiga.—The data on density of Willow Ptarmigan in various regions of the Northern Boreal Forest (Taiga) is given in Table 2. In general, the densities of this species were much lower than in the tundra zone. The estimated total number of Willow Ptarmigan was given for the Sverdlovsk District (area c. 194,800 km²) as 17.5 to 25 thousand individuals (Romanov 1975). Western Siberia (up to 62°N)

had an estimated total number of 300–800 thousand individuals by the end of a typical summer, with fluctuations in density from 0.5 to 6.0 individuals per km². In winter the total number of birds in this region increased 1.5 times because of an influx of birds arriving from the forest-tundra subzone (Vartapetov 1998).

In Eastern Siberia, Willow Ptarmigan are rather common in bogs and sparse forests. In Yakutia, the best habitats for this species are in the lake hollows (Yakutian name: alas) covered with shrubs, sparse larch tree forest and vast areas of bogs. The numbers fluctuate, but the nature of these fluctuations is not properly understood. In the Far East, Willow Ptarmigan concentrate along river valleys where they find willow shrub. In Kamchatka, Willow Ptarmigan also occur in the coastal plains covered with Siberian Dwarf Pine (*Pinus pumila*). The density in these regions is very low (1–2 pairs per km²) (Kishninskiy 1975).

Southern Taiga.—The southern taiga subzone is occupied by the Middle-Russian subspecies of Willow Ptarmigan (*L. l. pallasi* Portenko 1972). It is distributed from the southern timber-line to c. 64°N (Potapov 1985). In contrast to the tundra and north taiga ptarmigan, this subspecies does not have significant seasonal movements; it is sedentary.

In the Pskov District, Willow Ptarmigan survived only in some isolated upland bogs. The surveys of 1997–98 estimated that the total number of this species in the district did not exceed 500 individuals (Fetisov et al. 1999).

In 2005–2010, Willow Ptarmigan almost disappeared in the Leningrad District. Perhaps a few pairs (1–2 per 10 km²) survived on upland bogs in the east of the District. It was listed in the Red Data Book of the Leningrad District (Potapov 2004). A similar situation exists in Byelorussia, where only a handful of reports from the northern part of the country exist and the species is listed in the Red Data Book of Byelorussia (Red Data Book 2006). It ceased

Table 2. Density of Willow Ptarmigan in different parts of the Northern Taiga, given in individuals per 10 km², unless stated differently.

Place	Year	Season	Birds per 10 km ²	Reference
Karelia, North	1957–64		31–67	Ivanter 1974
Karelia, South	1957–64		18–22	Ivanter 1974
Karelia	1960–70	Winter	1.7–82.6, average 24.3	Ivanter 1974
Karelia	1960	Winter	8.3–8.5	Karpovich 1963
Archangelsk District	1960s	Winter	10.8–14.7	Karpovich 1963
Komi Republic	1960s	Winter	4.9–13.4	Karpovich 1963
Komi, Navishera River, 63°N	1963–65	Fall	4–28	Sevastianov 1974
Komi in Voronin 1995	1950–53	Winter	48–300	Maslov 1972, cited
Komi, Mezen River 64–65°N	1973	Fall	40	Voronin 1995
Komi, Mezen River 64–65°N		Spring	18	Voronin 1995
Komi, Vym' River		Fall	9.0 – 51.1	Voronin 1995
Komi, Vym' River		Spring	19.4 – 42.6	Voronin 1995
Northern Ural mountains	1954–57	Summer	1–1.1	Romanov 1975
Larch forests, western Putoran, 69°N	1958–59, 1964	Summer	40–80 pairs	Krechmar 1966
Eastern Siberia	1960s	Summer	6–63	Syrocheckovskiy and Rogacheva 1968
Evenkia, Kataramb lakes	1955	August	5–145	Fedosenko and Belozarov 1968
Yakutia, Forest zone	1960–70s	Fall	80	Perfiliev 1975
Yakutia, Forest zone	1960–70s	Summer	4–6	Perfiliev 1975
Kamchatka			10–20	Kishinskiy 1975

to exist in Mordovia, Chuvashia, Udmurtia, Mari-El, Ryasan and Tula Districts, and is almost extinct in the Moscow District (Romanov and Kozlova 2001). The situation was alarming even in earlier periods, when local hunters unanimously were citing the disappearance of this species. There were attempts to re-introduce the bird into Moscow, Leningrad, Yaroslavl, and Vladimir districts. In 1960, there were 2893 birds released there. (Romanov and Kozlova 2001). The re-introduction efforts failed because of poor preparation and lack of basic feasibility studies.

At the beginning of the 1980s, the southern border of the subspecies distribution crossed Smolensk, Moscow, Vladimir, Nizhniy Novgorod and Perm Districts up to the Urals. The standardized All-Russia Winter Game Surveys from 2000–2002 (Mezhnev 2002) did not record a single individual of this species in the Smolensk, Moscow, Vladimir, or Nizhniy Novgorod Districts. This species is impossible to miss on the snow as it makes unmistakable tracks. Therefore, the southern boundary of this subspecies' range is not currently known, but it has moved north since the 1980s. In the Perm District, the counts in 2000–2002

Table 3. Density of Willow Ptarmigan in different parts of the Southern Taiga, given in individuals per 10 km², unless stated differently.

Place	Year	Season	Birds per 10 km ²	Reference
Leningrad District	1866–1909	Spring	15	Rodionov 1969
Leningrad District	1949	Summer	16 birds on 1.5 km ² bog	R. Potapov, unpublished data
Leningrad District	1960	Summer	3.3 broods	Rodionov 1969

Table 4. Numbers of Willow Ptarmigan in the Western Siberian Districts recorded during the All-Russia Winter Game Counts 2000–2002 (Mezhnev 2002) and their overall density (individuals per 10 km²).

Total number/density	2000	2001	2002
Kurgan District	14,700/2.1	21,900/3.1	19,300/2.7
Tumen' District	28,400/0.2	24,100/0.2	15,900/0.1
Omsk District	82,900/5.9	61,000/4.3	67,000/4.7
Novosibirsk District	76,500/4.3	75,400/4.2	56,900/3.2

recorded 25.2, 21.9 and 24.8 thousand individuals (Mezhnev 2002).

Currently there is a propagation project in the Kerzhanets State Nature Reserve, Nizhniy Novgorod District. In 2009, five birds raised in captivity were released within the reserve (Korshunova and Korshunov 2010).

Central Urals and Western Siberia.—The southern timberline crosses the Ural Mountain Ridge at c. 59° 40' N. The density of Willow Ptarmigan here is very low and during the breeding season is 1 or rarely 3–5 individuals per 10 km². In the 1970s, the total summer numbers of Willow Ptarmigan in the taiga zone (85,000 km²) of the Sverdlovsk District (total 194,307 km²) was 17.5–20 thousand individuals (Danilov 1975). In the All-Russian Winter Survey (ARWS) in 2000, 2001, 2002 this figure was 80.9, 171.2 and 159.7 thousand individuals respectively (Mezhnev 2002). This large difference in numbers may be explained by the influx of migratory ptarmigan coming from the tundra zone in winter.

There is no data on the numbers of Willow Ptarmigan in the southern taiga subzone. In

Western Siberia, there is a large area between the taiga and forest-steppe which does not have Willow Ptarmigan. In the narrowest place the gap is 100–120 km (Danilov 1975). In contrast, the abundance of bogs between the Ob and Irtysh Rivers suggests that a high density of ptarmigan could occur here. There were only winter counts done in the area in 1964–67, which recorded 1.5–50 individuals per 10 km² (Gyngazov and Shubin 1968). The number of Willow Ptarmigan recorded during the All-Russia Winter Game Counts 2000–2002 (Mezhnev 2002) in Western Siberian Districts are provided in Table 4.

Eastern Siberia.—This area has a very different type of southern taiga subzone. A lack of upland bogs, presence of permafrost-underlain lake depressions (alas) covered with shrub and grass vegetation, and less dense forest favors Willow Ptarmigan. The nominate subspecies lives here in an ultra-continental climate (Dfd, Dwd in Köppen-Geiger classification, meaning dry and relatively hot summers, and dry and extremely cold in winter (Peel et al. 2007). The numbers here fluctuate out of sync with various other regions, and the mechanism

behind these fluctuations is not well understood (Isaev 2011 in this volume).

Amur River Regions.—Neither the distribution nor biology of the local population of Willow Ptarmigan has been studied here, but it is here where the southeastern boundary of this species' range in Eurasia is located. The range included lowlands of the Amur River estuary (Evron, Udył, Kizi lake depressions). There are no breeding records further south from here, but there are some winter records (Potapov 1985). At the end of the 19th Century, the numbers here were enough to harvest ptarmigan commercially, but now the species' density is extremely low. In the bogs of the Udył lake depression in 1968, there were 10 pairs per 10 km² (Potapov, unpublished data).

Sakhalin Island.—In the 19th Century (Suprunenko 1890) and in the first half of the 20th Century, Willow Ptarmigan were abundant and were commercially harvested (Gizenko 1955). The numbers declined from the mid-20th Century, to the extent that the commercial harvest was no longer viable. Currently in the most favorable places, the breeding density of Willow Ptarmigan is 1–2 pairs per km². Breeding habitats are similar to that of the Amur District – bogs with sparse forest, larch-tree forest with tundra patches and small patches of the Siberian Dwarf Pine, and rarely on gentle slopes with sparse forests. Extensive logging reportedly moved the boundary of the species' range slightly to the south (Voronov et al. 1975), but later this trend was not confirmed (Nechaev 1991).

Forest-steppe Zone.—The most significant changes in the range of Willow Ptarmigan were observed in this zone where the species' southern limit is located. In this zone, the species lives in a wide network of isolated patches of forest, shrubs, and wetlands surrounded by steppe. In the past several decades, the species has shown a tendency for local declines and extinctions in this zone. Although it is not clear what exactly caused the decline,

possibilities include human interference, or changes in insect fauna, which play an important role in the diet of chicks, or changes in the vegetation, but it was not global warming. The Willow Ptarmigan populations in this region managed to adapt to climate changes in the past 16,000 years which fluctuated from very cold conditions to hot and then back again to interglacial moderate climates. There are several factors which facilitated these adaptations. Firstly, the changes at the southern fringes of the range were developing for 10,000 years through the Holocene, which makes it possible for natural selection to work. Secondly, this forest-steppe zone, which originated from the mammoth megafauna populated tundra-steppe, was located in the middle of a huge Eurasian continent; so, no matter what the temperature of summer and winter was, and we know that both were swinging up and down, the climate was always continental, as this place is too distant from the oceans. Winters were cold and dry, sometimes with little or no snow, but cold enough for ptarmigan. Thirdly, climate change left the shrub vegetation unchanged as it remained dry. This belt of the southern fringes of the Holocene taiga, stretching from the British Isles to the South Urals, was populated by Willow Ptarmigan which could have survived to this day if humans hadn't taken over the forest-steppe areas by converting them to pasture and arable fields.

Among the interesting adaptations of Willow Ptarmigan facing winters without snow is the complete loss of white winter plumage in Red Grouse (*L. l. scoticus*) in Scotland and partial loss in Ural-Siberian forest-steppe. It is apparent that the white plumage is retained in the genes, despite the deep local climate change, since 1 in 1000 individuals molt into white plumage in the fall (Hudson pers. comm., Figure 2). This leads us to conclude that throughout the Pleistocene, with its deep swings between glacial (cold) and interglacial (warm) periods, the Willow Ptarmigan did lose and gain again its white winter plumage (Potapov et al. 2003). One of the great illustrations of



Figure 2. White plumage of Red Grouse and Red Grouse bagged at Scottish Moors. This rare photo shows that the sub-species which has 'lost' white plumage still keeps it in the genes. Note black and white primaries. Photo by Peter Hudson.

this statement was an experiment carried out by A. Barry-Garfoldt in Belgium. He initially introduced Red Grouse to his collection, then later added some Willow Ptarmigan which he imported from Russia. The latter differed from the Red Grouse by molting into white winter plumage, but later lost this winter plumage altogether. This interesting story he told the editor of French "Chasse Perche" magazine (Trutovskaya 1905).

Currently, the distribution of the Forest-Steppe Willow Ptarmigan (*L. l. major*) is limited in the west by the River Ilel (53°30' E) and to the east by the Altai foothills (up to 86°E). The southern border of this subspecies is identical to the species' southern border and follows the southern border of the forest-steppe along 52°N, sometimes going south to 49–50°N in places in Kazakhstan (Potapov 1985). Boggy wetlands with lavish grasslands and shrubs are the most preferred habitats here. They also like birch and alder patches. The density is typically 2–4 pairs per 10 km², and only in exceptional circumstances reaches 30–40 pairs per 10 km². The shrinking of the range at this southern edge has been noted for decades: by 1940 it ceased to exist at the Karakalinsk (49°30' N, 75° 30' E), Kazakhstan (Kuzmina

1975); by the end of the 1960s it disappeared from several places in the Orenburg District (51° 46' N, 55°05' E) (Khmelevskiy 1968).

Sub-alpine Zone (Mountains).—The main feature of this zone is the total dominance of shrubs in the vegetation. Such areas cover most of the mountains of south Siberia. The upper altitude limit of this belt is the alpine zone which does not have shrubs. In all mountain systems where this species is present, Willow Ptarmigan exist as isolated populations. At the moment there are two such mountain systems, and each has its own subspecies.

1. *Altay-Sayan Mountain System.* This region is populated by the Short-billed Willow Ptarmigan (*L. l. brevirostris*). Its range covers most of the Altay Sayan system from the western border (Ivanovsky Range) 83°30' E, Kazakhstan, to the Tunkinskiy Golets (102° E) and includes all the ranges of the Russian and Mongolian Altay (up to 47°N), and the main ridges of the Sayan, Khangai (including Kuznetskiy Alatau, Tannu Ola and mountains around Hubsugul Lake, and Khentey Mountains). The numbers of ptarmigan are not very high: in Eastern Sayan, 50 pairs per 10 km² in spring (Izmailov and Tarasov 1968); in Kuznetskiy Alatau, 14 pairs per 10 km² (Zinoviev 1968); in Central Altay, in the winter seasons of 1940–1950, from 50 to 200 birds per 10 km², in July 1947, 1949, from 20 to 50 broods per 10 km² (such concentrations are very rare), and in August from 100 to 120 birds per 10 km² (Dulkeit 1975).

2. *Mountain Ranges of Eastern Siberia and Russian Far East.* This region includes the mountain ranges of Baikal, Khमार-Daban, Olekmo-Chara highlands, Stanovoy, Dzhug-Dzhur, Yam Alin, Duse-Alin, and Aldan-Uchur ranges. The breeding habitats here are patches of mountain tundra above the forest line. This region is populated by the Siberian Willow Ptarmigan (*L. l. serebrowsky*). Moving further northwards, the bond between the ptarmigan and the elevated tundra becomes

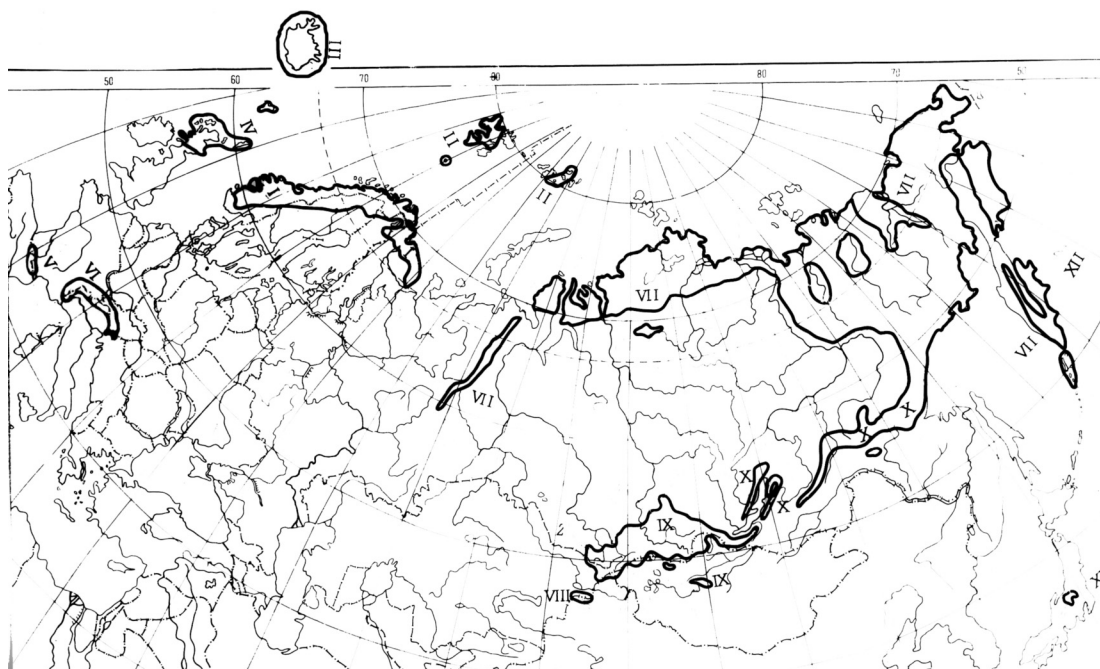


Figure 3. Range of Rock Ptarmigan in Palearctic (from Potapov 1985 with changes and additions). Numbers denote subspecies: I – *L. m. muta*, II – *L. m. hyperboreus*, III – *L. m. islandorum*, IV – *L. m. milliaisi*, V – *L. m. pyrenaica*, VI – *L. m. helveticus*, VII – *L. m. comensis*, VIII – *L. m. pleske*, IX – *L. m. krasheninikowi*, X – *L. m. macrofynchus*, XI – *L. m. nadazdae*, XII – *L. m. transbaicalicus*, XIII – *L. m. japonicus*, XIV – *L. m. ridgwayi*, XV – *L. m. kurilensis*.

less powerful. Nevertheless this attachment to the mountains is evident to the northernmost boundary where this subspecies intergrades with the nominate subspecies. The density of this subspecies is comparable to that of the Short-billed Willow Ptarmigan. At the Yablon Range one can find up to 40 broods per 10 km² (Pavlov 1948). In the Khamar-Daban range the numbers were 13 individuals per 10 km² in 1958–1959. In the sub-alpine zone in the winter of 1963, the density was 2–3 individuals per 10 km² (Izmailov and Pavlov 1975). There are evident, but little studied, vertical seasonal movements; in winter the ptarmigan move from the sub-alpine zone to the bottom of the river valleys.

ROCK PTARMIGAN (*L. MUTA*)

In contrast to Willow Ptarmigan, Rock Ptarmigan are attached to vertically structured relief: undulating or rolling hills in the polar zone, and elevated mountains in the temperate zone. Information on the species' distribution and abundance is sparse:

- Kola Peninsula: rare, did not see it during transect surveys (Khlebosolov et al. 2007).
- Northern Urals, Dezhkin Kamen': 10 broods per 10 km² (Danilov 1975).
- Syn' River tributaries, fall 1975: one flock of 25 birds on territory in 400 ha (Potapov 1985). The area suitable for this species in the Urals is c. 13,000 km², which gives potential numbers of 40,000 – 50, 000 individuals.

Table 5. Estimates of Willow Ptarmigan for the winter 2006 (Potapov, unpublished data) and estimates given for the same territory by the ARWS (Mezhnev 2002).

Territory	2006, Potapov, unpublished	2001, Mezhnev 2002
Karelia	300,000	274,000
Leningrad and Novgorod districts	10,000	(50,900+18,600)
Pskov District	500	1500

- Putoran Plateau: No density data. Considered to be rare, but not so rare in the central and western parts of the Plateau (Romanov 2004).
- Yamal, Gydan, Taimyr: No precise data available. It was mentioned that the total numbers were several times lower than that of Willow Ptarmigan. From the past commercial harvest in the 1970s, it was known that in the annual bag of 150,000 ptarmigan, Rock Ptarmigan constituted only 10–15% (Pavlov 1975).
- Yakutia: No accurate counts. It was known that in the Kolyma-Alazeya plain the numbers of Rock Ptarmigan were lower than Willow Ptarmigan by 40–50 times; in the Khroma-Indigurka plain they were 100 times lower (Perfilev 1975).
- Far-East, Okhotsko-Kolyma Highlands: In 1963, 10–30 pairs were recorded per 10 km² of suitable habitat (Perfilev 1975).
- Koryak Highlands: In 1961, 10–30 pairs were recorded per 10 km² of suitable habitat (Perfilev 1975).
- Kamchatka: In 1967 in the Parapol depression (plain tundra), up to 20 pairs per 10 km² were recorded (Lobkov 1986). Five broods were recorded in 1 km² (Voronov 1968). Along the Kambalnaya River, on slopes above 400 m asl, the density was 40–60 individuals per 10 km² (Gizenko 1968).
- Commander Islands: In 1960, 50–100 pairs per 10 km² were recorded. Total numbers on the Beringa and Medniy Islands were estimated at 9,000 to 10,500 birds (Marakov 1962).

- Kuril Islands: The species was common here. Maximum density up to 100 birds per 10 km². On the islands of Paramushir and Shumshu in 1967 there were 20,000 birds wintering (Velizhanin 1968). On Paramushir in 1960, 3–4 broods were recorded on a 1 km transect (Voronov 1968).

TOTAL NUMBER OF PTARMIGAN IN RUSSIA

The ARWS estimated the total numbers of Willow and Rock Ptarmigan (combined) for the years of 2000, 2001, and 2002 respectively as 34965.9, 18705.4 and 10471.3 thousand individuals. We suspect that these are overestimates. Compared to our data for Willow Ptarmigan that we estimated for the Karelia, Pskov, Novgorod, and Leningrad Districts (Table 5), the official statistics provide a more or less accurate estimate for the districts with a high density of ptarmigan, whereas in the districts with moderate or low density of birds, the official figures tend to overestimate the real numbers. Evidently, the official counts are too optimistic for overall counts, but they are better than nothing.

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