ANIMAL ECOLOGY

Natural habitats for the stable existence of wild boars (*Sus scrofa*) in the North

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Abstract

Wild boar *Sus scrofa* populations are actively expanding northwards. Their presence in the North is closely tied to anthropogenic activities, as wild boars are either fed, or find food and suitable habitat at farmlands. However, the nature reserves of the northern part of Russia show that wild boars are able to survive on their own even in a completely natural environment. In the taiga zone, there are habitats providing for their survival in winter: wetlands in mires and around large water bodies, and dense spruce forests. Continued northwards expansion of wild boar range is likely if pressure from hunting is reduced. Modelling based on climatic variables also shows that they could potentially inhabit vast areas in the North. The existence of wild boars in the North is interrelated with other species of relatively large mammals (beavers and roe deer) and partly supports the idea of "Pleistocene rewilding" in a boreal environment, i. e., the potential to increase the variety and numbers of megafauna representatives.

Keywords: wild boar, North, habitat, expansion, nature reserves.

Introduction

Northwards expansion of certain animal species is one of the expressions of the current global change of biosphere (Loarie et al., 2009; Shifting habitats, 2020). The wild boar Sus scrofa exemplifies this trend. Its native range covers most of the southern part of Eurasia, while the main part is located in a zone of warm climate. However, the rate and scale of the recent northwards spread of wild boars are surprising even after taking into account global warming. Initially it was believed that snow cover of about 40 cm limits their distribution (Formozov, 1946; Heptner, Nasimovich, and Bannikov, 1961), but wild boars quickly settled across the territory where the cover is much deeper; up to 80–100 cm within their new habitat. In the past the northern boundary of their range was around the 60th parallel in the Western part of Europe, and even farther south in the European part of Russia, but is now approaching the Arctic Circle. In Asia, the borders have also shifted, although not as significantly (Danilkin, 2002). A similar process is taking place in North America, where wild boar is an alien species (Snow, Jarzyna, and VerCauteren, 2017). The rate of wild boar expansion was traced, but they populate their new range unevenly, and the pattern of their distribution in the North is changing (Markov, Neifel'd, and Estaf'ev, 2004; Markov, Neifel'd, and McDonald, 2005; Markov, Pankova, and Filippov, 2019a; Markov, Pankova, and Morelle, 2019b; Markov et al., 2022; Kulpin, 2008; Danilov and Panchenko, 2012). In Russia, the expansion reached its maximum by the 1990s, then there was a retreat, and then another resettlement (Kulpin, 2008; Danilov and Panchenko, 2012). This expansion affected the neighboring territories of Finland, where they have also settled; after the first record made in 1956 the number of wild boars rapidly increased (Erkinaro et al., 1982). In Sweden and Norway, local wild boar populations were exterminated several centuries ago.

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In the 1970s, they were reintroduced to Sweden; in what follows they increased in number, and started to populate Norway (Rosvold and Andersen, 2008). The northern border of wild boar distribution shifted several hundred kilometers over the past few decades. However, it is still not entirely clear if they have settled stably in their new range and if their existence can be considered "natural". The question of the "natural" existence of wild boars in the North has been raised in Sweden (Magnusson, 2010). Boars were introduced there informally: they either escaped from farms, or were released intentionally by unauthorized individuals. After some debate, the Swedes came to the conclusion that wild boars are not an alien species. Analysis of the expert viewpoints over the whole Eurasia resulted in the conclusion that the northern Eurasian countries do not have a united approach to the challenge of wild boar expansion, and the factors that limit and promote the expansion in northern ecosystems are unknown (Markov et al., 2022). In the North, their ability to survive in winter is limited. Because of snow cover, it is difficult for them to get food and escape from predators. Moreover, the nutritive base in the North is poor, especially in the winter season. Forage limits the distribution of wild boars in the North more than cold temperatures (Rosvold and Andersen, 2008). Rapid northwards expansion became possible because wild boars find food in farmland. This was exhibited especially well throughout the northernmost habitats (in the Arkhangelsk Region): wild boars were found only near settlements and fields (Pleshak and Miniaev, 1986). The supplemental feeding provided by game managers also contributed to their expansion. In some areas of the northern part of the range, supplemental feeding is the primary determinant of the number of wild boars (Oja, Kaasik, and Valdmann, 2014). It is believed that in the North they have become a synanthropic species, they are completely dependent on anthropogenic influences, and therefore could disappear at any time after which their distribution would return to a previous state (Danilov and Panchenko, 2012). Since boar is a game animal, their spread was accelerated when the releases into new territories were carried out. Now to outline a counteracting trend: because of swine disease, wild boars are being extirpated, although experts oppose the practice (Danilkin, 2019). The question arises, are wild boars able to exist on independently in the North? Wild boar habitat in the North, absent farmlands or supplemental feeding, has been reported within a small area in Western Siberia (Markov, Pankova, and Filippov, 2019a; Markov, Pankova, and Morelle, 2019b). It was explained by the cumulative effect of a warming climate, and boar population growth in the neighboring southern territories due to the anthropogenic stimulus. We assessed a larger area with respect to the stability of the northern wild boar populations, focusing on their winter habitats. For this purpose, we studied the nature reserves of Russia. Any anthropogenic activity influencing the state of the environment is prohibited there, including the implementation of any measures that are taken to improve the state of ungulate populations, such as supplemental feeding or altering native vegetation. This means that if wild boar populations persist through the winter inside northern reserves, it follows that they are able to settle independently within their new range. These northern reserves can demonstrate the habitats necessary for such settlement. In the northern part of Russia, almost all nature reserves are large enough for such an assessment.

We evaluated the northward expansion of wild boars in the context of discussions regarding Pleistocene Park (Zimov, 2005) and Pleistocene rewilding (Donlan et al., 2006). In the Pleistocene, the north of Eurasia was inhabited by large numbers of various ungulates, despite the cold climate. Most of them have disappeared. Their descendants live on in warmer climates, but not as prosperously. The largest representatives are on the edge of extinction. A tempting idea arises to resettle them in the North, where vast unpopulated areas are available. Currently, an experiment on Pleistocene transformation is being carried out within one protected area in Yakutia (Zimov, 2005; Popov, 2020; Pleistocene Park, 2023). Ungulates were brought there from the South. They survive, but supplemental feeding is used to support their existence. It is expected that over time they will adapt to survive by themselves, meanwhile transforming the vegetation: instead of mires and unproductive coniferous forests a "tundra-steppe" will be formed. This habitat would be reminiscent of African savannah. The cold climate would be partly compensated by the fact that Northern summers are light around-theclock; this supports the rapid growth of grasses under favorable conditions. At present, the intensive growth of grasses is challenged by the dominance of mosses, lichens, and small shrubs, but if ungulates trample them, the area of meadow could increase. In this situation, the native moss cover is considered especially deleterious: its nutritional value is close to zero, mosses cover the soil with a heat-insulating layer that prevents its warming, and they suppress the growth of other plants. Since wild boars actively dig up the soil, they can contribute to the destruction of this "enemy of the Pleistocene". Information about their habitats in the North can provide new evidence on the prospects of Pleistocene transformation.

Methods

Literature search

We have collected information about nature reserves located to the north of the "initial" range of wild boar. The boundary considered "initial" was the one identified in the 1930s based on the role of snow cover (Formozov, 1946) (Fig. 1). Historically, wild boars hardly made their

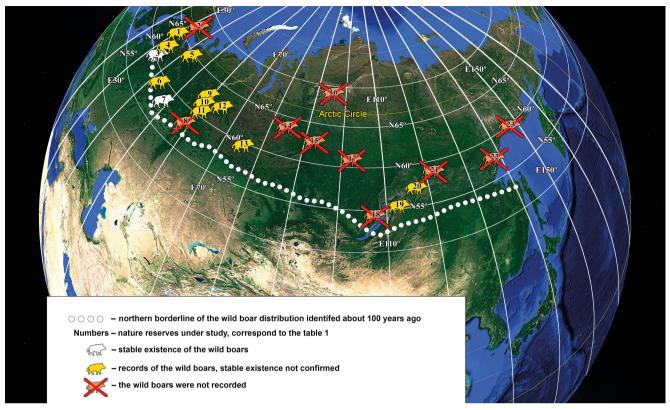


Fig. 1. Distribution of the wild boar in the nature reserves in the north of Russia.

way northwards, except for rare visits. Earlier, around 8000-9000 BCE during a temporary warming period, the border shifted slightly northward in the western part of the range (Ukkonen, Mannermaa, and Nummi, 2015). As the northern border of the assessment area, we considered the Arctic Circle, since the wild boar have almost reached it. However, they have not been reported north of the Arctic Circle, that is, in the Arctic, nor in the Kamchatka peninsula. Since all of the nature reserves keep a "chronicle of nature", we referred to these records using the database on protected areas of Russia (OOPT Rossii) and the official web sites of the nature reserves ("Basegi", "Denezhkin Kamen", Dzherginsky, Dzhugdzursky, Kandalakshky, "Kivach", "Kologrivsky Les", Magadansky, "Malaya Sosva", Nizhne-Svirsky, "Nurgush", Olekminsky, Pechoro-Ilychsky, Pinezhsky, Tsentralnosibirsky, Tungussky, Verkhne-Tazovsky, Vishersky, Vitimsky and Yugansky nature reserves). We searched for information on whether wild boars occur within the reserves, and if they do, then in what habitats, and how stably they exist.

Case Study — a survey of Nizhne-Svirsky Nature Reserve

The nature reserve is located at the eastern coast of Lake Ladoga and the lower reaches of the Svir River. It encompasses a large area and includes a variety of habitats: forests, swamps, meadows, rivers, and lakes. The reserve was established in 1980. A bird banding station exists there, which was founded in 1968. According to the communications of its founder, professor George Noskov (1937-2017), who worked there for almost 50 years, wild boars entered the area around the station several times, but when winters arrived, they were devoured by wolves. After several attempts, wild boars succeeded in settling in the central part of the reserve. There is no reason to disbelieve the anecdotes, nevertheless there is no supporting documentation of these events, and the professor's primary interest was in birds. Mammals had only been observed parallel to other studies, and without any specific goal or methodology. We assessed the situation based on observations, analysis of the "chronicle", publications, and reports from local residents. In the winter of 2021, we performed a focused search for wild boars within the reserve. In 2023, we repeated it and installed a camera trap (Bushnell Nature View) in the most promising site. It was in function continuously since 15 January up to 25 March.

Modelling distribution

Starting from identified points in the northern part of Russia, where the independent existence of wild boars is likely at the present time, we modelled their possible distribution using the maximum entropy method based on climatic variables for the period from 2000 to 2040 (Philips, Dudik, and Schapire, 2023; WorldClim).

Occurrence of wild boars in the nature reserves of the northern part of Russia

No	Name of nature reserve	Area, hectares	Co-ordinates of the center, N, E	Information on wild boars	
				Registration of occurrence	Stable existence
1	Kostomukshsky	49259	64°28'23" 30°16'27"	+	?
2	Kandalakshsky	70 530	67°04'34" 32°31'30"	-	-
3	Nizhne-Svirsky	41400	60°34'58" 33°00'24"	+	+
4	"Kivach"	10 930	62°16'02" 33°58'56"	+	?
5	Pinezhsky	51 890	64°40'36" 43°11'57"	+	-
6	"Kologrivsky Les"	58 939	58°56'41" 43°51'03"	+	?
7	"Nurgush"	23449,7	58°00'44" 48°27'24"	+	+
8	"Basegi"	37935	58°05' 58°03'	-	-
9	Pechoro-llychsky	721322	62°34'30" 58°15'30"	+	?
10	Vishersky	241200	61°29' 59°13'	+	-
11	"Denezhkin Kamen"	78 000	60°30'29" 59°29'35".	+	?
12	"Malaya Sosva"	225562	62°04'59" 64°05'47"	+	?
13	Yugansky	93893	59°39'21" 74°37'48"	+	-
14	Verkhne-Tazovsky	631308	63°30'14" 84°03'28"	-	-
15	Tsentralnosibirsky	1019899	62°21'25" 90°39'51"	-	-
16	Putoransky	1887251	68°52'34" 94°48'36"	-	-
17	Tungussky	296562	60°43'53" 101°58'03"	-	-
18	Baykalo-Lensky	659 919	54°13'35" 107°53'35"	-	-
19	Dzherginsky	238088	55°06'51" 111°27'32"	+	?
20	Vitimsky	585838	57°12'10" 116°48'28"	+	?
21	Olekminsky	847108	58°39'22" 122°15'28"	-	-
22	Dzhugdzursky	859 956	57°06'15" 138°15'26"	-	-
23	Magadansky	8838,17	59°38'31" 147°26'55"	-	-

Results

Wild boars in nature reserves

Wild boars have been registered in some nature reserves in the northern parts of Russia, but not in all of them, and information on the stability of boar populations is insufficient. Information regarding their winter habitats is also insufficient. Usually, only visits were reported (Table, Fig. 1). In some reserves, the pattern of wild boar occurrences resembles the above-mentioned scenario for Nizhne-Svirsky Nature Reserve. They settled in farmland at Pinega River valley near Pinezhsky Nature Reserve, then entered the reserve, but disappeared soon after, from predation and poaching. They also entered Vishersky Nature Reserve (in the Urals), but left it during winter. Through the warm winter of 2007, 6 individuals remained there, but only two survived, and later on, boars have not succeeded in colonizing this area. They

also entered Yugansk Nature Reserve, but did not settle there. In Pechora-Ilychsky Nature Reserve, several dozen registrations of wild boars have accumulated, but it is still unknown whether they live there stably.

Boars in Nizhne-Svirsky Nature Reserve

Wintertime occurrence of wild boars was first recorded in the Nizhne-Svirsky Nature Reserve in 1998. Since then, they have come to the attention of observers from time to time. Their numbers increased, and they became a common species in the reserve (Fig. 2). The locations of their winter registration indicate seven areas of wet habitat (Fig. 3). We examined these areas and found out in 2021 that boars had settled in one of them. It was the largest one located at the coast of Lake Ladoga. A herd of 18 individuals was observed there, but then two were eaten by wolves. The rest apparently survived the winter; in March the herd continued to wander there. The snow



Fig. 2. Wild boar in the Nizhne-Svirsky Nature Reserve.



Fig. 3. The location of winter habitats of wild boars in the Nizhne-Svisky Nature Reserve (white spots).





Fig. 4. Winter habitats of wild boars in the Nizhne-Svirsky Nature Reserve: a — swampy sparse forest; b — thickets of reeds and shrubs on wetlands

cover was much more than 40 cm all winter. In some areas it reached one meter. Despite the thaw, thick snow cover persisted and expanded until March 20th, then it began to melt rapidly, but remained in places until mid-April (within spruce forests and narrow stream valleys). From the end of March, wild boars began to actively move outside the wintering site. In 2023, we installed a camera trap at the center of this site and obtained similar results. From 1 to 10 individuals were recorded, the traces and trials made by boars were numerous in the surrounding area. Moreover, one adult boar was observed at the other site at the coast of Ladoga Lake. The main winter habitat of wild boars was located on the outskirts of the mire. It was a swampy sparse forest, in which dead tree trunks were numerous (Fig. 4a). Beavers (Castor fiber) greatly contributed to the formation of this biotope; they built dams on the small brooks, which is why a part of the forest was flooded. Another habitat represented thickets of reeds and shrubs near the lake shore near the mouth of a river (Fig. 4b), where beavers also took part in the transformation of the environment.

Modeling demonstrates that climate change would permit the spread of wild boar over large areas: the whole of European Russia (except for the Arctic islands), half of Western Siberia, a signifiacnt part of Eastern Siberia, the coasts of the Okhotsk Sea, Kamchatka, and even the southern part of Chukotka (Fig. 5).

Discussion

The observations from nature reserves demonstrate that wild boars somehow find habitat for wintering in the natural environment of the North. At least two types of biotopes were suitable for this: a flooded forest on the outskirts of mire, and wetland reed beds. They do not freeze over as much as other areas, which makes it possible for boars to dig and access water. The presence of water and moist food supports wild boar survival, be-

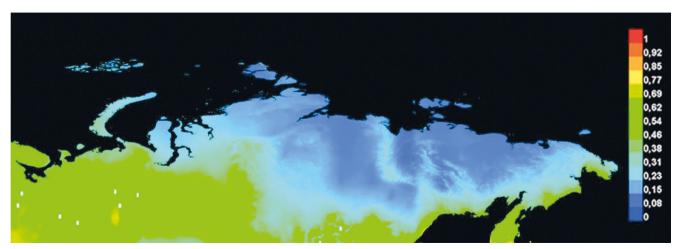


Fig. 5. Modelling of wild boar distribution area in the North, color scale shows the probability of occurrence.

cause in the winter dehydration is a problem; consuming snow and ice would lead to hypothermia and so cannot make up for the lack of liquid water. The large volume of dead tree trunks is likely important, because wild boars find food there: they eat insect larvae, tree fungi, and even the decomposed wood itself (Danilkin, 2002). The "assistance" of beavers is also likely important as they increase the area of wetlands. Beavers, like boars, also relatively recently settled to the North after almost complete extermination. It is quite possible that this was one of the contributors to the success of wild boars in their northward expansion.

It is probable that dense spruce forests also can act as winter habitat in addition to the habitats identified here. This is because when compared to other forests, in dense spruce forests the snow cover is thinner, the temperatures are higher, the shelter from winds is better; moreover, anthills are often numerous within spruce forests, and wild boars either feed there or occupy during rest (Kulpin, 2008). However, reports on such wintering practices do not contain much information on the movement of the boars, therefore it is not clear whether they spend all winter there, or come out sometimes to farmland or other habitats to find food.

It is likely that wild boars can settle on their own in the North without direct or indirect human support, but this requires some special circumstances. When the snow cover is thick, wild boars gather in herds and move along paths one after another, with the strongest individual in front. During rest, they gather in a "rookery" to keep warm. Their winter community must be numerous enough to resist cold and snow, as well as losses from predators or exhaustion. This means that in the North, if wild boars somehow become relatively numerous in one area, then their population may stabilize. This is possible inside reserves, but outside them they are hunted, and therefore are under continuous pressure. They may escape from predators, but not from humans. As history shows, even in the past they were defenseless against hunters. Over the past several hundred years, the extermination of the last wild boars has been documented in a number of countries. First in England, then Holland, then Scandinavian countries, and so on. The range of wild boars shrank; they remained in small pockets isolated from each other. A similar process took place in Russia and Central Asia (Heptner, Nasimovich, and Bannikov, 1961; Oliver, 1993). Extermination reached its culmination by the beginning of the 20th century, and only the strong regulation of hunting made restoration possible. At present, in the North of the range, where wild boars are few in number and are concentrated in small areas in wintertime, they are especially sensitive to the impacts of hunting. Hunters try to kill the largest individuals, while in the North the biggest individuals are particularly important for the survival of a group

(Danilkin, 2002). Thus, it turns out that even the smallest impact of hunting can be fatal for northern populations.

The survival of wild boars in "extreme" northern habitats partly supports the concept of a "Pleistocene Park". They demonstrate that in the North, large animals could become more numerous and diverse than at present, and that such increases may be ecologically related. The spread of wild boars is partly related to the spread of beavers, and the wild boars themselves can contribute to the spread of other ungulates. As one example, the roe deer Capreolus capreolus follow boars: in the North roe deer use wild boar trails in winter (Danilkin, 2002). In European Russia the recent changes of roe deer distribution are similar to those of wild boars (Danilov, Panchenko, and Tirronen, 2017). It turns out that at least three species can make up a complex relationship that contributes to their northward expansion. The concept of "Pleistocene transformation" is also focused on such relationships.

The current global warming trend can contribute to the spread of wild boars. Modelling has shown that they could colonize most of the territory of Russia in the foreseeable future. It does not mean that the entire indicated territory is suitable for them, but that they can populate some areas where suitable habitats are available. Perhaps other "additional" ungulates could follow them. However, natural spread is slow, and its acceleration through introductions is problematic. In the past, it was popular for human settlers to "enrich" the local fauna, but now the philosophy has reversed, and this practice is either discouraged or prohibited. In the case of wild boars, additional difficulties arise due to swine plague, because minimization of boar numbers is recommended to limit its spread. Recommendations to reduce the number of wild boars are also reasonable due to the ambiguity of their impact on the environment. They can cause damage to farmland (Thurfiell et al., 2009; Gren et al., 2020). In the wild, undesirable results are also possible, such as the destruction of bird nests (Carpio, Hillstrom, and Tortosa, 2016). Rooting activity affects the plants covering the soil as well as soil mesofauna, although both positive and negative impacts can result from this process (Barrios-Garcia and Ballari, 2012). On the one hand, soil disturbance is one of the natural processes of the environment, which is necessary for the stability of established ecosystems (Welander, 2000). On the other hand, excessive digging activity in poor soils leads to the depletion of vegetation (Pankova, Markov, and Vasina, 2020). Such situations usually justify a need to cull a part of the population. It turns out that at present, wild boars are vulnerable to anthropogenic impact and can disappear from the North at any time, and the main impact remains the constant pressure of direct extermination by humans.

Conclusions

Wild boars can live in the North even without direct or indirect assistance by humans. In the taiga zone, there are habitats providing for their survival in winter: wetlands in mires and around large water bodies, and dense spruce forests. Continued northwards expansion of wild boar range is likely if pressure from hunting is reduced. The existence of wild boars in the North is interrelated with other species of relatively large mammals (e. g., beavers and roe deer) and partly supports the idea of "Pleistocene rewilding" in a boreal environment, i. e., the potential to increase the variety and numbers of megafauna representatives.

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