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ORIGINAL PAPER

Wild boar (*Sus scrofa* L.) in the north of Western Siberia: history of expansion and modern distribution

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Abstract
We summarized the records of wild boar in the northern part of Western Siberia (Khanty-Mansy Autonomous Okrug–Yugra) for 1984–2016 to describe the expansion, modern distribution, and contribution of natural expansion and intentional release in establishing its population in the study area. We analyzed the spatiotemporal dynamics of the presence of wild boar using two parameters: minimum site occupancy and constancy of the presence of the species in various parts of the region. The relative importance of intentional release and natural expansion was assessed by comparing the distances to areas of releases and to the borders of neighboring regions. The wild boar naturally expanded from the southwestern regions to the northern Western Siberia, the role of release was insignificant. We suggest that river valleys were main pathways of expansion. The southern and central parts of the region (up to approximately 62° n.l.) are permanently inhabited by wild boar and can be treated as part of the species' geographical range.

Keywords *Sus scrofa* · Western Siberia · Expansion · Geographical range · Releases

Introduction

Wild boar is one of the most economically important ungulates and is distributed throughout the Palaearctic region, North Africa, and Southeastern Asia and has become naturalized in the New World and Australia (Singer 1981; Hone 1988; Danilkin 2002). In its area of distribution, the wild boar is an important part of the hunting economy (Massei et al. 2015). In many countries, it is recognized as a pest species that affects agriculture and local fauna (Massei and Genov 2004; Barrios-Garcia and Ballari 2012). Recently, wild boar was shown to contribute to the transmission of African swine fever (De la Torre et al. 2015).

Despite the economic importance of wild boar, its adaptation to new environments has been examined by few studies. Particularly, this subject has been analyzed in parts of North and South America (Bratton 1975; Waithman et al. 1999; Engeman et al. 2007; Pescador et al. 2009; Ballari et al. 2015; Skews 2015). Detailed studies on wild boar ecology in the early stages of expansion have been performed in Europe—e.g., in Scandinavia (Finland, Sweden) (Erkinaro et al. 1982; Lemel et al. 2003; Thurfjell et al. 2009) and the Russian Federation: central Russia (Fadeev 1973), the northwestern part of Russia in the 1970s–1980s (Rusakov and Timofeeva 1984), the northeast region of European Russia in the 2000s (Mashkin et al. 2008), and the Urals in the 1980s–1990s (Bolshakov et al. 2009; Markov 1997).

The area of distribution of wild boar has been expanding since the beginning of the twentieth century (Danilkin 2002). Primarily, the northern limit moved northward, and currently, wild boars inhabit areas that lie north of the 60th parallel. Several hypotheses have been proposed to explain the rapid expansion of this species in the northern and northeastern

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directions, including the development of the economy and agriculture in the Soviet Union after the Second World War, climate changes (warm winters), and a decrease in predator populations (Fadeev 1973; Danilkin 2002). The "agriculture hypothesis" has remained the most popular model, because wild boars actively use agricultural fields, especially during winter. However, the agriculture hypothesis does not explain the phenomenon of species expansion to those areas of the taiga zone in which agriculture is nearly absent.

This is exemplified by the expansion of wild boar to the north of Western Siberia—the area of the West Siberian plain that lies to the north from 59 n.l. Administratively, this region belongs to Khanty-Mansiysky Autonomous Okrug, or Yugra, and encompasses over 500,000 km^2. Wild boar in this area has been reported since the 1980s (Azarov and Dekov 1990), but no systematic analysis of species distribution and abundance has been performed, primarily because wild boars are rare and are treated as being only occasionally present in Yugra. However, recently, animals have begun to be reported annually in regular censuses, raising the following questions concerning the status of the species in the north of Western Siberia (Yugra):

1. What is the relative importance of natural immigration and releases in the establishment of this population?
2. Which part of Yugra region can be considered a stable part of the range of wild boar?

To address these questions, we analyzed the historical records of wild boar in the northern part of Western Siberia (Yugra region) and performed a quantitative analysis to separate parts of the region where the species is permanently present from those where it is only occasionally found. Delimiting the area of permanent presence is important for further analysis of ecological correlates of wild boar expansion to the Yugra region, since including spatially and ecologically marginal records in modeling species current and potential distributions could result in overestimating species niche and distribution when using ecological niche models (ENMs) (Soley-Guardia et al. 2014).

Study area

Geographical position Khanty-Mansy Autonomous okrug–Yugra occupies the central part of the West Siberian Plain (see Fig. 1). It stretches in the east-west direction for 1400 km (from Ural mountains to Ob'-Yenisey watershed, between appr. 60° and 86° on the eastern latitude) and in the north-south direction for approximately 800 km, situated between 58° 30′ and 65° 30′ northern latitude. The terrain is primarily a lightly dissected plain with an elevation of no more than 200 m above sea level; however, the mountain ridges of the Northern and Polar Urals are present in the western part of the region. The mountains stretch in the north-south direction for 450 km, and the width of mountainous area is approximately 30–40 km. The highest point is Narodnaya Mountain (1895 m above sea level). The main river is Ob', which flows in the south-north direction and divides the territory of Yugra into its western (situated closer to the Ural mountains) and eastern (West Siberian) parts. Irtysh is another large river that flows in from east to west and divides the eastern Yugra into its northern and southern parts.

Climate The climate is moderately continental. The average temperature in January varies within the region from − 18 to − 24 °C. The lowest temperature of − 62 °C was reported on January 21–22, 2016, in the central part of the region (basin of the Kazym River). Winter begins in the end of October and lasts until the end of April. The number of days with stable snow cover is 180–200 (during 40% of which the temperature is below − 20 °C), and the average depth of snow varies from 50 to 60 cm in the southern part of region to approximately 80 cm in its northern area. The vegetation period begins in the last week of May. The average temperature in July arise 15–18 °C, and the historical high is + 35 to 37 °C (Moskvina and Kozin 2001; Buligina et al. 2014a, b).

Landscape and vegetation According to Moskvina and Kozin (2001 with changes), the territory of Yugra region is divided into 16 landscape provinces, which are territories with one or several similar types of landscape, and similar orographic, lithological, and vegetation characteristics, situated typically within one natural zone (Fig. 1 and see Electronic Supplementary Material1 for brief description of the provinces). The westernmost province is the Ural Mountains. The southwestern part of the region is primarily lowland with a very high (up to 80%) proportion of bogs, marshes, and lakes. Upland plains lie in the northern and northeastern parts of the region. The typical tree stand consists of spruce (*Picea* sp.), Scotch pine (*Pinus sylvestris*), and Siberian pine (*Pinus sibirica*), with larch (*Larix siberica*) in the northern parts of the region (Moskvina and Kozin 2001, with changes). In most forest types, lichen and green moss dominate the herbaceous layer.

The human population density is extremely low and does not exceed 3.08 persons per square kilometer. The regional economy is based on oil and gas production and forestry, with almost no agricultural activity.

Methods

Mapping the wild boar records We used published data and information from the archives of local forestry and hunting services to map the records of wild boar in Yugra in 1984–2014. Particularly for the period 2014–2016, we used data of the

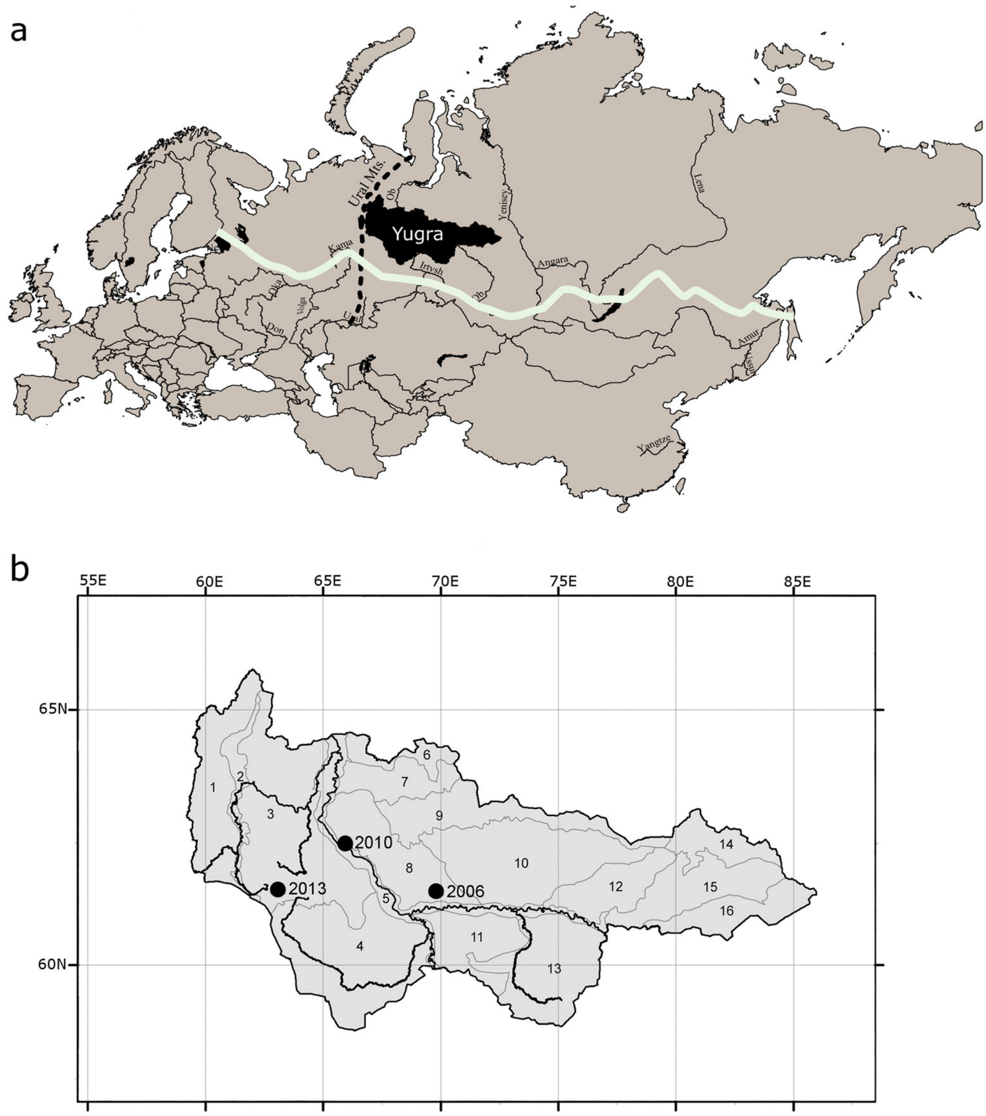

Fig. 1 Map showing **a** the geographical position of the study area (black polygon) in northern Eurasia, white solid line denotes the northern limit of geographical distribution of wild boar according to Danilkin (2002), and black dotted line denotes the Ural mountains; **b** localization of the landscape provinces, main rivers (bold black lines), and the places and years of wild boar releases (black circles with years) in Khanty-Mansiisky autonomous okrug–Yugra (Western Siberia)

official winter track counts (Stephens et al. 2006, Electronic Supplementary Material 2) Places in which animals had been found were mapped as precisely as possible. Data were summarized for 10-year periods (1984–1993, 1994–2003, 2004–2013) and we also included data for 2014–2016. The map of geographical points of records is presented in Electronic Supplementary Material 3. Here and below, all geographical measurements and analyses were performed using QGIS instruments (QGIS Development Team 2014).

The spatial distribution of locations of wild boar records is clearly uneven, which could have resulted from natural reasons and sampling bias. For example, some of the observations could be non-independent, when several points lie close to each other, resulting for example from observations of the same animal (or group of animals); thus, the observations become spatially autocorrelated (Dormann et al. 2007). Such observations could be reasonably approximated as a single point on the map. In this case, we face an issue with regard to the threshold distance for treating several records as one. Although the global Moran's I score for the entire dataset was insignificant (Moran's $I = 0.23$, z-score = 1.09, $p = 0.27$), there was still some sampling bias, because several records were made during the intentional collection of data on wild boar ecology in 2010–2016.

We addressed this problem based on two suggestions:

1) Because the source of the non-independence of records could be consecutive observations of the same animals being close to each other, we suggested that the threshold distance for combining records be less than 10,000 m. This value was chosen, based on literature (Spitz and Janeau 1990) and recent observations in the study area that the total daily distance that is traveled by wild boars rarely exceeds 10 km.
2) The distance between points of observations will change non-linearly when comparing non-independent and independent observations: series of non-independent

observations will be characterized by a large number of observations with short distances between points, but with independent points, we will observe a steep increase in distance between points and a decline in the total number of observations.

We analyzed the matrix of distances between points of observations that were situated less than 10 km from each other. The entire range of values was divided into twenty 500-m segments (0 to 500 m, 501–1000 m, etc.), and the number of observations was calculated for each segment. We observed two intervals of distances for which the number of observations decreased twice compared with the previous one: 2350–2870 and 5501–6000 m. Thus, the possible threshold between independent and non-independent records could lie within one of these intervals. We based our choice of the threshold value on literature data that the average daily movement of wild boar can reach 6 km or more, even in high-quality habitats (Spitz and Janeau 1990; Janeau et al. 1995; Keuling et al. 2008; Podgórski et al. 2013). This is also in agreement with mean home range span (largest diameter) which is 4–5 km in both native and non-native parts of species geographical range (Keuling et al. 2008, 2018 and references therein). Thus, we treated 6000 m as the threshold to distinguish independent and non-independent observations. We used the information on average but not total daily movement to balance type I (erroneously treating non-independent records as independent) and type II (erroneously treating independent records as dependent) errors. For records that were closer than 6000 m to each other, the median point was calculated, mapped, and used in subsequent analyses.

Analysis of historical dynamics and modern pattern of distribution We analyzed the dynamics of the distribution of wild boar for each of the landscape provinces (Fig. 1).

We used the approach previously described in the article by Markov with colleagues (Markov et al. 2005). The territory of each landscape province was divided into squares with 6000-m sides. We treated a unit as being sampled if the human settlement was situated within it or in one of the neighboring units (units were defined to be neighbors if they shared a side or corner) or if a species record was made in it or in one of the neighboring units. We also collected data on visited areas from nature reserves and hunting grounds and included them in the list of "sampled units." We calculated the site occupancy index by dividing the number of occupied units by the total number of "sampled" units (Manly et al. 2002). The number of occupied sites, obtained from mapping the locations of wild boar records, was considered as the *minimum number of occupied units*, because an animal could have been present but not detected. Thus, we computed the minimum site occupancy (MSO) as:

$$MSO = U_+/U$$

where U_+ is the number of occupied sites and U is the number of "sampled" units within the area that is under consideration.

The constancy of the presence of species in the area under consideration (CP) was estimated as:

$$CP = Y_+/Y$$

where Y_+ is the number of years in which wild boars have been detected within the area under consideration and Y is the total number of years within the period.

MSO and CP were calculated for each of the 16 landscape provinces. We removed 6 provinces from the analysis for which the proportion of "sampled" units to the total number of units was less than 0.1.

In the next step, landscape provinces were classified based on the matrix of MSO and CP. We used cluster analysis in PAST (Hammer et al. 2001). The grouping method was UPGMA, and the distance between clusters was measured as the Euclidian distance.

Analysis of the sources of wild boar expansion Here, the question to be answered was formulated as "What is the contribution of intentional releases and natural dispersion from previously settled regions of Urals and Western Siberia in the process of wild boar expansion in Yugra?" We hypothesized that the observations should be clustered around the possible source of expansion. Consequently, the average distance from the source to every point must be smaller than that between a random pair of points within the entire dataset.

We calculated the distances from each of the known places of releases (RP) to the points of wild boar records (WBRs) several years after their release. Because the first known release took place in 2006, the first dataset included observations that were made in 2007–2013 ($n = 61$). The second release occurred in 2010; thus, the dataset included observations for 2011–2016 ($n = 108$). The last point of possible release was where wild boars had been kept in fence since 2013; consequently, the last dataset included observations for only 3 years: 2014–2016 ($n = 91$). The average distance between a WBR and RP is further denoted RPD (release point distance). We also calculated the distance from every WBR in the same periods to the borders of the southern regions (Sverdloskaya oblast' and Tyumenskaya oblast'), which had been previously settled by wild boars and could be sources of natural dispersal. This index is further termed NRBD (neighboring regions' border distance). The third index that was used in this analysis was the average distance between WBRs within a given period (WBRD).

We used Shapiro-Wilks test (Shapiro et al. 1968) implemented in Statistica Software (StatSoft 2007) to test the distributions of distances in the samples for normality. The distribution of distances in all samples deviated significantly ($p < 0.05$) from the Gaussian; thus, Kruskal-Wallis median test was used to compare the median values of distances.

Results

The total number of wild boar observations in the dataset was 387. The first record was made in 1980: a female that was killed in the central part of Yugra (approximately 61° n.l. and 67° e.a.). The northernmost records were made at approximately 64° n.l. in the western (mountainous) part of the region, the most recent of which was dated in autumn 2016. Most records (approximately 55%) were made in the winter during the regular census of animals, based on snow track counts. Roughly 31% of records were made in the snow-free season or seasons with little snow cover (spring–autumn). The types of records were mainly footprints (69.85%), direct observations of animals (7.75%), and kills (3.6%).

MSO and CP varied over time (see here Table 1 and Fig. 2, and also Electronic Supplementary Material 4). At the end of the 1980s, only single records of animals were made in various parts of the region. In this period, landscape province (further denoted as "zone") 3 clustered separately from other zones, based on the highest values for MSO (0.006) and CP (0.2), although in absolute values, there were only two records in 10 years. Zones 4, 5, and 8 also clustered together with one record in 10 years; in other zones, wild boars were not found.

In the next decade (1994–2003), wild boars were reported primarily in the western part of the region. Again, zone 3 clustered separately from the others, with the highest values for MSO and CP. Areas with a moderate number of records were zones 2 (foothills of the Ural Mountains) and 8 (central part of the region). Areas with a low number of records (zones 4 and 11) were in the southern part of the area. The MSO in this period did not exceed 1%, and the highest CP score was 0.3. Generally, the distribution of records was similar to that in 1984–1993.

The distribution of records changed in 2004–2013. Zone 3 (western) clustered with zone 4 (southwestern) as the areas with the highest number of records; the other groups of areas with a moderate numbers of records included zones 5, 8, and 11 (central part of the region). Single records were made in the northern (zones 6, 7) and eastern (zones 10, 12) parts of the region and in the foothills of the Ural Mountains (zone 2).

In 2014–2016, the area of highest density of wild boar records was the southwestern part of the region (zone 4), whereas the central and southeastern provinces—zones 5 and 11—formed a cluster with moderate MSO and CP values. Animals were still found in the western part of the region (zone 3), but the MSO for the western areas in 2014–2016 was low compared with the southern and central parts of the region. Together with the northern (zones 6, 7) and eastern provinces (zones 10, 12), zone 3 was characterized by a low probability of recording animals in space and time in comparison with the southern and central parts of the region. This was rather due to the increase of the MSO and CP in the southern part of the region than due to the decrease of wild boar presence in other areas. In 2014–2016, the CP increased significantly over the entire region; in the southern part, wild boars were permanently present, and in the western areas, the index was 0.67 (Table 1).

A comparison of the distances of wild boar records to the borders of neighboring regions and places of releases showed that in all periods under consideration, the NRBD was significantly ($p < 0.01$) lower than the WBRD, indicating that records clustered in proximity to the borders of neighboring regions (see Table 2). In 2006–2013, the RPD (year of release, 2006) was also significantly ($p < 0.01$) lower than the WBRD, which demonstrates that the points of the records were clustered around the point of release. At the same time, the RPD was significantly ($p < 0.01$) higher than the NRBD, indicating that clustering around the borders of the southern region was stronger than around the point of release. In 2011–2016 and 2014–2016, the RPD was significantly ($p < 0.01$) higher than

Table 1 Spatial and temporal variation in the number of records (NR), minimum site occupancy (MSO), and constancy of presence (CP) for the landscape provinces of Yugra

Landscape province/year of observations	1984–1993			1994–2003			2004–2013			2014–2016		
	NR	MPO	CP	NR	MPO	CP	NR	MPO	CP	NR	MPO	CP
2	0	0.000	0.0	1	0.011	0.1	1	0.011	0.1	5	0.057	0.7
3	2	0.006	0.2	4	0.012	0.3	9	0.027	0.8	1	0.003	0.3
4	1	0.001	0.1	2	0.003	0.2	24	0.031	0.9	82	0.105	1.0
5	1	0.002	0.1	0	0.000	0.0	11	0.020	0.6	9	0.016	1.0
6	0	0.000	0.0	0	0.000	0.0	0	0.000	0.0	0	0.000	0.0
7	0	0.000	0.0	0	0.000	0.0	1	0.015	0.1	0	0.000	0.0
8	1	0.004	0.1	1	0.004	0.1	5	0.022	0.5	4	0.017	0.7
10	0	0.000	0.0	0	0.000	0.0	2	0.010	0.1	0	0.000	0.0
11	0	0.000	0.0	2	0.007	0.2	9	0.031	0.6	10	0.034	1.0
12	1	0.010	0.1	0	0.000	0.0	0	0.000	0.0	0	0.000	0.0

Data for the landscape provinces that are included in the analysis (proportion of sampled units more than 0.1) are shown

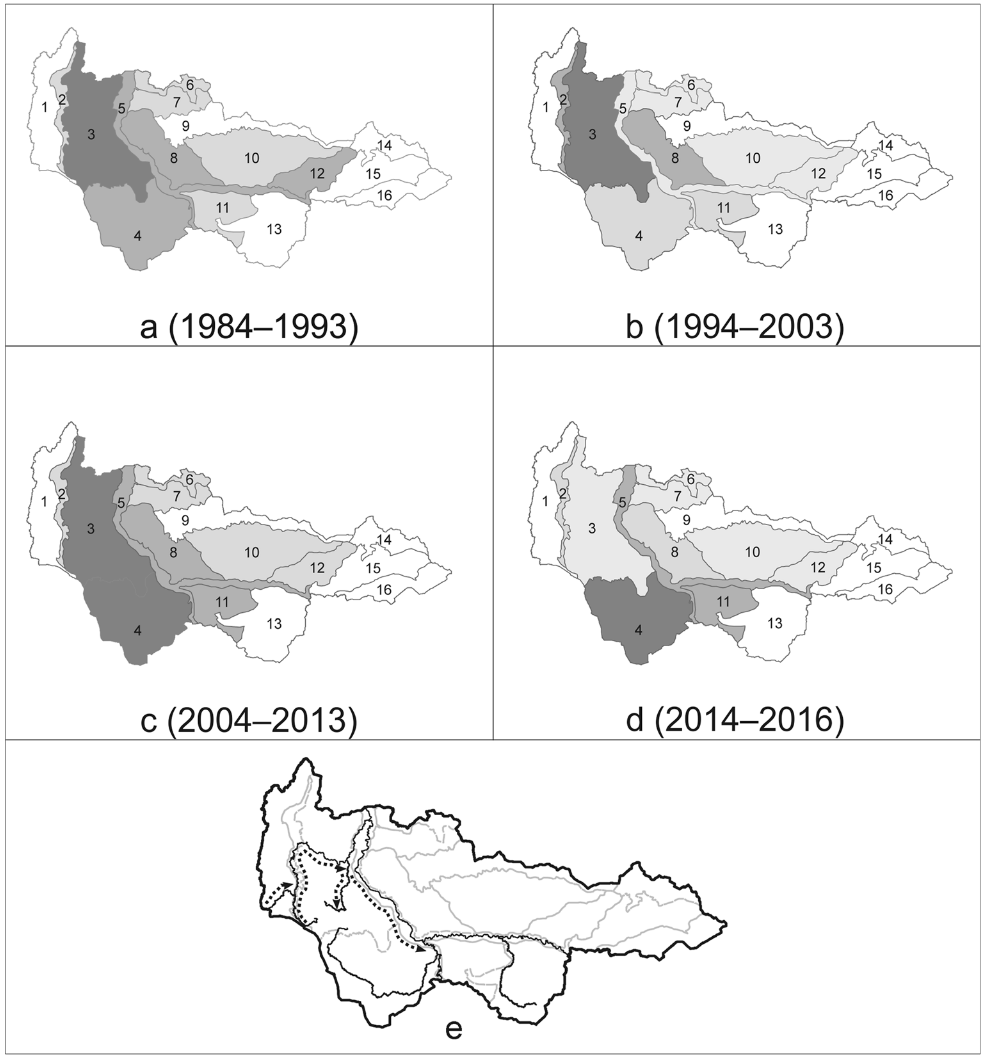

Fig. 2 Spatiotemporal variation in wild boar presence in the landscape provinces of Yugra. Colors illustrate the results of the cluster analysis. Non-colored areas denote the provinces excluded from analysis due to a low proportion of sampled units. The darker colors denote higher values for MSO and CP. **a** 1984–1993. **b** 1994–2003. **c** 2004–2013. **d** 2014–2016. **e** Possible routes of wild boar expansion (dotted lines with arrows) along the main rivers

Table 2 Summary of comparisons of distances between wild boar records (WBRD), distance to the borders of neighboring regions (NRBD), and distance to places of wild boar release (RPD)

Year of release	Period of records	WBRD	NRBD	RPD
2006	2006–2013			
	WBRD (276.1 km)	–	***	**
	NRBD (125.02 km)		–	***
	RPD (195.7 km)			–
2010	2011–2016			
	WBRD (226.2 km)	–	***	***
	NRBD (60.6 km)		–	***
	RPD (291.9 km)			–
2013 (possible escapes)	2014–2016			
	WBRD (199.6 km)	–	***	***
	NRBD (48.06 km)		–	***
	RPD (249.7 km)			–

Because the distribution of values in the sample deviated significantly (at $p < 0.05$) from the normal, the median values for the samples of distances are shown in parentheses

$^{**}p < 0.1$; $^{***}p < 0.01$

the WBRD and NRBD, indicating that the WBRs were not clustered around the points of release.

Discussion

According to the observed spatiotemporal changes in MSO and CP, wild boars became regularly detected in the north of Western Siberia (Yugra region) only at the beginning of the twenty-first century, when, for some parts of the region, the MSO exceeded 0.01 and the CP for most of the region exceeded 0.5. Thus, wild boars settled in the Yugra region only 10 years after stabilization of the species distribution area in the southern neighboring regions (Azarov and Dekov 1990; Bolshakov et al. 2009; Markov 1997). Notably, the area with the most frequent records shifted in a southwestern direction—i.e., in the early stages of expansion, animals were found mainly in the western and northwestern parts of the region, whereas in the beginning of 2000s, the highest number of records was in the southern and central areas.

This pattern could be related to the hypothesis that river valleys serve as "ecological corridors" (Gallé et al. 1995) along which wild boars can disperse. Particularly, river valleys were reported to be main routes of wild boar expansion to the northern part of European Russia (Fadeev 1975; Pleshak and Minyaev 1986). The southern part of Yugra is covered with sphagnum bogs that provide little food or shelter for wild boar, so animals probably could not disperse directly from southern regions through the sphagnum bogs. On the other hand, in the western part of the region, there are rivers that generally flow in the south-north direction and that can provide a suitable habitat for animals. However, these habitat could work as ecological traps (Kokko and Sutherland 2001) providing good habitat in snow-free season but not able to maintain a stable population in winter because of relatively deep snow and low temperatures. Such "ecological traps" effect could be especially pronounced for sink populations in the peripheral parts of species geographical range (Kirkpatrick and Barton 1997; Remeš 2000). Thus, we argue that, in the first stages of expansion, wild boars could disperse through zone 3 to settle southern (zones 4 and 11) and central (zone 5) parts of the region. The dispersal of animals first to the north and then back to the central and southern parts of the region could explain the observed spatiotemporal variation in the frequency of records (Fig. 2). It is not possible to confirm or explicitly reject this hypothesis, but it is a reasonable explanation for these observations.

In this study, we performed a retrospective analysis of the role of releases and natural dispersal of wild boar in settling a new area. The exact places from which wild boars were taken for introduction are unknown; most probably they were brought from the neighboring regions of Urals and Southern Siberia or from the European part of Russia. Modern genetic instruments—for example, microsatellite markers—could theoretically distinguish sources of animals' expansion. However, several years after their release, animals that are brought from distal regions could crossbreed with those that naturally arrived from neighboring territories; thus, a genetic analysis could produce non-relevant results. Thus, we had to use an indirect method for assessing the roles of natural dispersal and intentional release with regard to the expansion of wild boar in the northern part of Western Siberia. Despite many articles on the natural expansion and release in establishing and re-establishing wild boar populations in new areas (Merino and Carpinetti 2003; Vernesi et al. 2003; Pescador et al. 2009; Danilov and Panchenko 2012; Saito et al. 2012), none of them (to our best knowledge) has addressed the question of the comparative role of these processes.

Our results showed that natural dispersal was likely the main source of wild boar expansion to the study area, but one of the releases (in 2006) into the region could also have contributed to the establishment of the wild boar population. We did not observe clustering of wild boar records around the place of release in 2010 or around a wild boar farm that was established in 2013, despite a number of species records being made in these parts of the region (landscape provinces). Thus, we conclude that expansion of wild boar to the north of Western Siberia is a natural process that differs from that in Urals and South of Western Siberia, where releases played a major role in establishing species' populations (Azarov and Dekov 1990; Markov 1997).

Discussing the possible reasons for wild boar expansion to the north of Western Siberia, we first address the hypothesis of the increase of the areas for agriculture that could result in supplementary food for wild boars. According to the official hunting statistics for the Yugra region, no supplementary feeding for wild boar has been provided in 1980–2016. The proportion of agriculture lands in Yugra in 2016 did not exceed 1.2% of the territory. Most of these were pastures and haymaking areas that could not provide supplementary food sources for wild boars especially in winter. Thus, most probably, the land use could not significantly affect the rate of animals' expansion. On the other hand, the increase in the amount of supplementary food took place in the 2000s in the regions neighboring Yugra from the south: Sverdlovskaya and Tyumenskaya oblast'. This resulted in wild boar population growth in these regions (Bolshakov et al. 2009; Status 2007, 2011) which could enhance animals' expansion to the north.

The other factor that could explain wild boar expansion to the north of Western Siberia is the climate change. In the end of the twentieth century, the increase in mean annual temperature for Siberia was about 0.34 °C/10 years, the duration of no-frost period in Western Siberia increased 2.3 days/10 years, and the precipitation decreased in cold period of the year (Ippolitov et al. 2008; Groisman and Gutman 2013). Thus, the climate change could favor expansion of species typical for more southern ecosystems. We think that the decrease of precipitation in winter time and increase of the duration of no-frost period could play a more important role in promoting wild boar dispersal than the increase of annual temperature, because they affect the availability of natural food sources for animals.

We excluded the decreased predation by carnivores and decreased hunting pressure from the list of factors that could promote wild boar expansion to the north of Western Siberia since both the hunting pressure and the abundance of wolves and brown bears increased in the Urals and Western Siberia in the end of the twentieth and the beginning of the twenty-first century (Bolshakov et al. 2009; Status 2007, 2011).

Thus, the climate change and the increasing of species populations in the neighboring region (particularly due to supplementary feeding) seem to be the main factors promoting wild boars expansion to the north of Western Siberia in the beginning of the twenty-first century.

Based on our analysis of the spatial and temporal dynamics of wild boar records in the northern part of Western Siberia (Yugra region), we concluded that presently the wild boar permanently inhabits the southern part of the region and is found regularly in the central and western parts. The mountainous part of the region (northern and subpolar Urals) and the eastern parts of it (particularly, the uplands of Siberian ridges) are not inhabited by the species. Further studies on the dynamics of the wild boar population and a prediction of its expansion using, for example, the species distribution models (Elith et al. 2011) should be based on an analysis of the impact of environmental factors on the areas of permanent and regular presence of the species in the region.

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