

Using spatial data on habitat suitability in estimation of wild boar (*Sus scrofa* L.) resources in Russia

ALEXANDER V. ECONOMOV¹, VYACHESLAV V. KOLESNIKOV^{1,2},
VICTOR I. MASHKIN² AND ANDREY A. LISSOVSKY^{3*}

¹ Russian Research Institute for Game Management and Fur Farming, Preobrazhenskaya str. 79, Kirov, 610000, Russia

² Vyatka State Agricultural Academy, Oktiabrskii prosp. 133, Kirov, 610017, Russia

³ Zoological Museum, Moscow State University, Bolshaya Nikitskaya 6, Moscow, 125009, Russia

* Corresponding author: andlis@zmmu.msu.ru

Economov, A.V., Kolesnikov, V.V., Mashkin, V.I. and Lissovsky, A.A. 2020. Using spatial data on habitat suitability in estimation of wild boar (*Sus scrofa* L.) resources in Russia *Baltic Forestry* 26(2): 193–201. <https://doi.org/10.46490/BF486>.

Received 9 April 2020 Revised 2 August 2020 Accepted 26 October 2020

Abstract

The wild boar is one of the most important hunting game species in Eurasian boreal and temperate forests. In Russia, these animals inhabit a large part of the country; however, official bodies do not allow public access to relevant and unbiased regional statistics. In parallel with official figures, such statistics have been kept for decades by VNIIOZ (Russian Research Institute for Game Management and Fur Farming): the resource is estimated using the indirect method of recalculating multiple scores from independent respondents. We compared the VNIIOZ long-term datasets with the wild boar habitat suitability distribution within the Russian territory to assess the reliability of these figures and to carry out a pilot evaluation of the need for their adjustment. Our results show a good correlation between the abundance assessment by VNIIOZ and habitat suitability (about 0.7); we also identified several regions where wild boar abundance indicators are sharply dissonant with the existing environmental capacity.

Keywords: *Sus scrofa*, distribution, abundance, SDM

Introduction

The wild boar is one of the most important hunting game species in Eurasian boreal and temperate forests. They inhabit permanently a large part (about 38%) of the Russian territory in its 76 federal members (Danilkin 2002). In the ranking of socially significant species in Russia, these animals take the second position after the moose (Zarubin et al. 2012). Unique features of the wild boar's biology are its environmental plasticity, vast distribution, high reproductive ability and consumption by them of a wide range of feed items, together with commercial products delivered through hunting on wild boars, which makes them a valuable species in hunting industry. These values have given rise to an interest in the accurate evaluation of their resources and the structure of their population distribution throughout the country.

The modern methodological apparatus allows for calculations of habitat suitability on the basis of analysis of spatial distribution of environmental predictors and species

occurrence localities; such studies were carried out on wild boar in several regions across Europe (Belda et al. 2012, Bosch et al. 2014a, 2014b, Acevedo et al. 2019, Vargas Amado et al. 2020). The habitat suitability affects the number of animals that can feed in the given territory; therefore, we can evaluate the game species resources. Similar studies have already been successfully carried out for wild boar in Europe (Bosch et al. 2012, Acevedo et al. 2019, 2020) and for moose in Russia (Razenkova et al. 2020).

At the modern stage, the studies evaluating correlation between habitat suitability and wild boar abundance are absent for the entire Russian territory. Moreover, the data on wild boar number are collected by the Federal Centre of Hunting Industry Development (FGBU Tsentri Okhot Kontrol) and the final figures have restricted public access. These publicly available data are published with considerable delays; sometimes such data are not complete. According to the data of the FGBU Tsentri Okhot Kontrol (2013–2017), recent information about the wild boar resources in Russia

dates to 2015. The FGBU Tsentr Okhot Kontrol figures include no data by regions of the country. Regional data by federation members of the Russian Federation are partially available in individual ‘governmental reports’ of federation members ‘On the State of the Environment...’. Therefore, such data hardly can be used for the investigation of correlation between habitat suitability and wild boar abundance.

The purpose of this paper is to assess the state of wild boar resources in Russia, considering the spatial distribution and suitability of habitats calculated based on Earth remote sensing and climate models. We used long-term datasets collected using the method developed at the Russian Research Institute for Game Management and Fur Farming (VNIOZ) (Glushkov et al. 2007).

Materials and methods

We used wild boar resource estimates for the period from 1994 to 2019 obtained by the ‘harvest’ service of the VNIOZ monitoring system (Figure 1, Table 1s). We used ‘official’ (FGBU Tsentr Okhot Kontrol) data only to compare the annual census fluctuations countrywide (Lomanov et al. 1996, Lomanov et al. 2004, Gubar et al. 2008, Min-Prirody Rossii 2003–2018).

To assess the validity of estimates by VNIOZ, we built a model of wild boar habitat suitability within the Russian territory and compared the overall suitability of habitats (i.e. proportional to habitat capacity) to the overall wild boar resources according to the VNIOZ data within each of the 76 federation members of the Russian Federation inhabited by wild boar. Additionally, to verify the resulting linear model, we made the same comparisons within 11 hunting grounds that counted wild boar within their territories, using various methods.

Data on the wild boar registration localities in the Russian Federation were obtained from the database ‘Mammals of Russia’ (Lissovisky et al. 2018, Mammals of Russia 2017–2020), where, in turn, such data were transferred both from the VNIOZ ‘harvest’ service archives and from various zoological museums and from observations by zoologists and amateurs confirmed by photos, etc. In total, at the initial stage, we collected 938 registration localities in the Russian Federation (Sluzhba urozhaia 2020). The complete observation dataset contained spatial aggregations. Therefore, we filtered the initial dataset, selecting one ob-

servational locality per 50×50 -km square. The resulting dataset, which was used in the further analysis, contained 496 observations (Figure 1s).

We additionally invoked the data on meetings of different Cervidae species (*Alces*, *Cervus*, *Capreolus*) totaling 2,210 localities of wild boar and deer. Based on this data, we created a spatial layer (a bias file) that described the territory exploration in terms of the composition of ungulates. For this purpose, the territory of the Russian Federation was assigned the value 1, and the 5-km circumference buffer around each of the localities the value 10.

The spatial frame of the analysis included a grid of 2-km resolution in the Mollweide equidistant projection. We used 86 environmental variables: WorldClim 19 ‘bioclimatic’ variables (Hijmans et al. 2005; WorldClim 2020), altitude, slope curvature and steepness, snow depth (Brown and Brasnett 2010) and 63 MODIS generalised average monthly data layers (nine months of 2004 per seven spectral bands; UMIACS 2020) as model predictors. We did not remove correlations among environmental variables, since MaxEnt has robust internal algorithms of feature selection (Elith et al. 2011). Modelling was performed in MaxEnt, version 3.4.1 (Phillips et al. 2018). We used default values for feature types, raw output and 5000 iterations (the run converged after 800 iterations) and the bias file as described above. Regularisation multipliers of 0.5, 1 and 5 were selected to check different levels of model complexity. Additionally, we repeated the analysis 50 times (subsampling), randomly removing 20% of training sample each time to evaluate the model spatial stability.

Given that the species distribution boundary is generally a complex multifactor function, including time and population density, it is not easy to show such a boundary in a picture. For a species, some populations of which are supported by special human activities, this is even more difficult to do. To give a general idea of the location of the wild boar population attenuation zone in geographic space, without using of any arbitrary information thresholds, we used the following approach. We highlighted on the map a zone located between two threshold values that were sensible (Liu et al. 2013) and often markedly different in their value: 10 percentile training presence and maximum training sensitivity plus specificity.

To assess the correlation between the wild boar habitat suitability (capacity) and abundance, we had to use aggregate values per federation member of the Russian Federation, as the VNIOZ statistics are recorded at this level. Here, we faced two methodological peculiarities: 1) Simple summarising of all habitat suitability raster cells values by federation member led to a noticeable bias in the results. As the MaxEnt result corresponds to relative, rather than absolute, suitability, the zero position being unknown (Guillera-Arroita et al. 2015), the raster cells included a very small value, even in the far-north regions. However, summing these values by very large regions gave the total suitability, which was markedly different from zero. There-

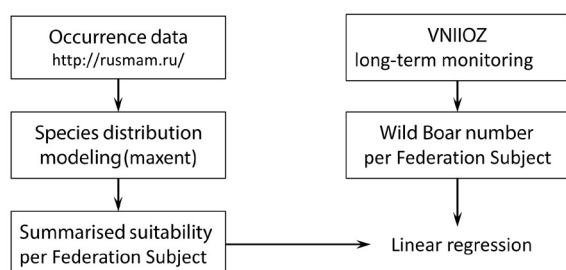


Figure 1. Scheme of the methods used in the study

fore, we subtracted a small value (0.0001, which was obviously lower than any value in the wild boar distribution range) from all the raster cells. Varying this value did not change the correlation analysis result; 2) The habitat capacity corresponds to a certain equilibrium number of animals that can support life in the given territory. However, without having a clear idea of the wild boar number dynamics, it was not possible to determine this equilibrium state; therefore, we used the maximum long-term abundance as a reflection of one of the population dynamics phases. A similar approach has been used earlier (Acevedo et al. 2019). The linear regression was calculated using STATISTICA software package, version 13.0 (Dell 2015) based on two datasets: including all federation members of the Russian Federation and excluding outlier members (see *Results*).

As we compared the habitat capacity with the VNIIOZ forecast data rather than with real figures, a reference point to verify the reliability of the VNIIOZ estimates was lacking. For this purpose, we used long-term data on wild boar numbers based on winter census data (winter route censuses and censuses in feeding grounds) in 11 hunting grounds within the European part of Russia, which we believe to be reliable. Linear regression was built up in a similar way for the maximum abundance of wild boar in hunting grounds and the overall capacity of the same hunting grounds.

Description of the VNIIOZ method (Glushkov et al. 2007)

The basis of the long-term monitoring conducted by VNIIOZ is the survey method involving voluntary regular hunter-respondents, dating back to 1935. Questionnaires adapted to the regions are sent to respondents twice a year. As a result, data is accumulated covering the species abundance, the availability of feed in hunting grounds, animal migrations, deaths and diseases, hunting, reproduction success and other indicators. It is assumed that the estimates provided by private respondents do not depend on the economic and political situation in the relevant hunting ground.

The animal species abundance is evaluated on the following scale: ‘few’, ‘medium’ and ‘many’ within the area monitored by each respondent. Long-term datasets and many respondents within each region allow assessment of the relative abundance dynamics in the regions. There is no doubt that this information does not allow for the quantification of resources, which is necessary for their sustainable management.

The emergence of the state hunting census system in the 1950s and regular publication of census results for many mammal game species in absolute terms facilitated comparison of the series of two indicators (the relative VNIIOZ data abundance and the absolute abundance figures) and finding a relationship between them. Based on various data on absolute wild boar abundance from 1995 to 2003, individual conversion coefficients have been developed for each federation member of the Russian Federation (Glushkov et al. 2007). To calculate these coefficients,

graphs of linear regression equations were built for each region, where the abscissa was the relative score according to the ‘harvest’ service data, and the ordinate was information on the number of animals taken from various sources. For each case, in addition to linear function parameters (the slope ratio and the free term), the determination coefficient (R^2) was calculated. The threshold, after which the linear function was considered successful, was R^2 equal to 0.7. If R^2 was less than 0.7, no linear function was used; rather, the score ‘value’ was calculated (as the product of the average number of wild boars for a certain period and the average value of one score in the same year). Therefore, it was possible to directly recalculate scores in a resource indicator. After 2003, census data have no longer been used for resource calculation, and abundance datasets were calculated based only on the average scores from respondents together with regional conversion factors. Accordingly, data on the wild boar census before 2001 was obtained by retrospective calculations using conversion coefficients.

Results

The wild boar resource dynamics in Russia based on the VNIIOZ data and comparison to the FGBU Tsentr Okhot Kontrol data for the period 1994 to 2019 are shown in Figure 2. The wild boar resources are distributed within the national territory in a relatively irregular manner (Table 1).

The spatial structure of wild boar suitable habitats is shown in Figure 3. Habitat suitability is probably underestimated for the Omsk, Novosibirsk, Kemerovo and Irkutsk regions, the republics of Tuva and Khakassia and the Transbaikal Territory.

Comparison of environmental capacity and the VNIIOZ wild boar resource estimates by region showed that, in some regions, the number of wild boars is clearly inconsistent with the general trend (figure not shown). Thus, in Karelia, the Arkhangelsk and Vologda regions and the Perm Territory (the northern border of the species distribution in the European part), the environmental capacity far exceeded the predicted wild boar resources. In contrast, in the Amur Region, the Khabarovsk Territory and the Transbaikal Territory (the northern distribution boundary

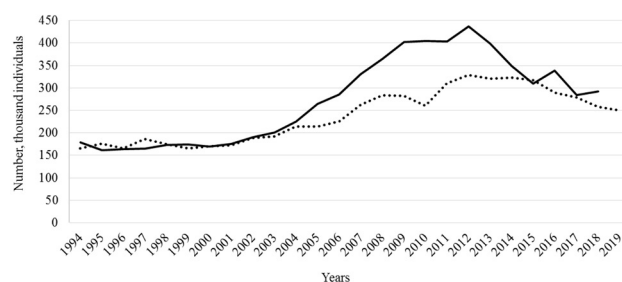


Figure 2. Dynamics of wild boar resources in Russia

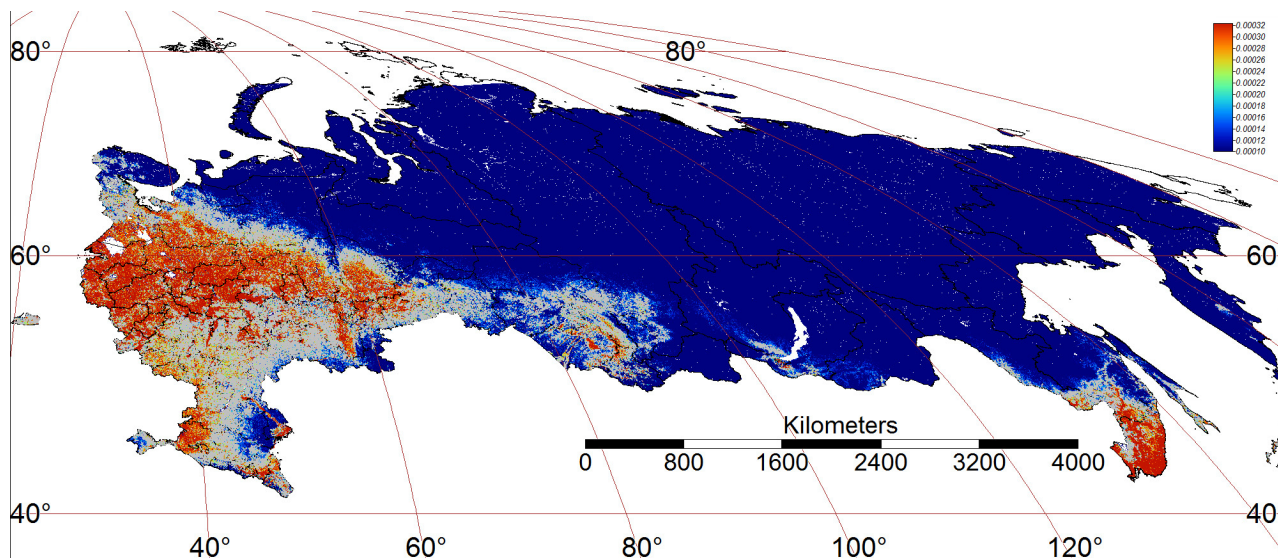
Note: Solid line represents data of the FGBU Tsentr Okhot Kontrol (2013–2017). Dotted line represents data of Russian Research Institute for Game Management and Fur Farming.

Table 1. Population dynamics of wild boar in Russia over the last 5 years (thous. animals)

Area	2015	2016	2017	2018	2019
The North-West of European Russia	36.21	29.38	27.77	20.92	18.67
Central Russia	71.15	45.57	40.43	25.63	22.25
Volga region	74.62	65.9	54.33	47.10	45.83
The South of European Russia	12.15	7.32	7.47	7.52	9.25
Northern Caucasus	3.05	4.80	4.36	4.97	6.61
Ural	38.45	41.4	39.2	42.62	40.52
Siberia	37.45	44.6	51.33	51.71	49.50
Russian Far East	43.8	50.85	54.15	57.35	57.65
Russia (in total)	316.88	289.82	279.04	257.82	250.28

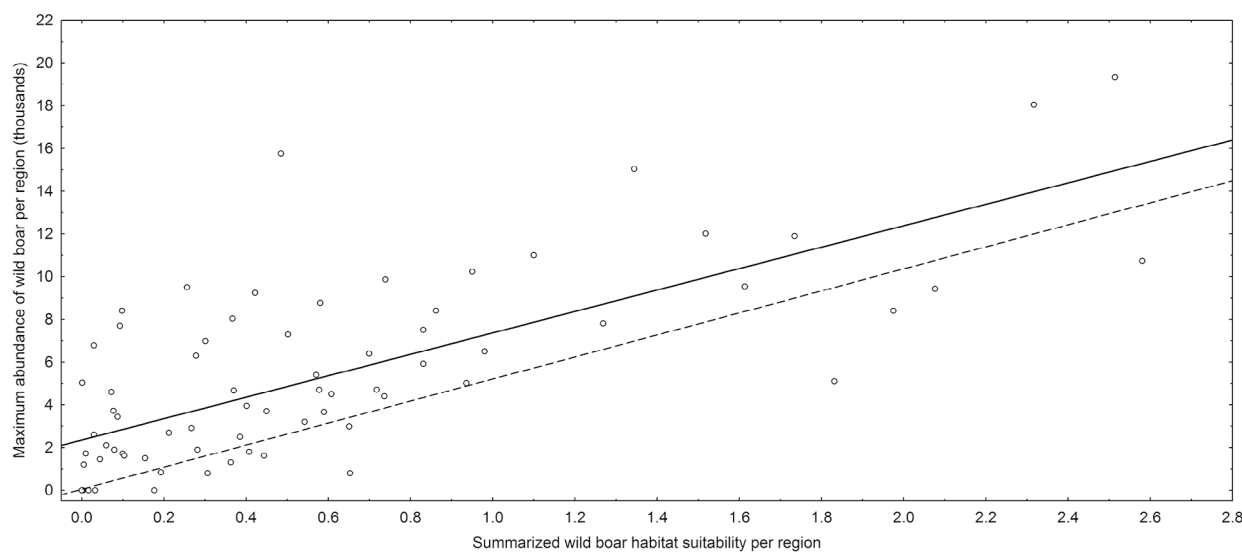
Note: Population dynamics of wild boar in Russian regions during 1994–2019 (thous. animals),

Figure 3. Spatial distribution of wild boar habitat suitability according to the species distribution model, calculated in MaxEnt



Note: Colours from blue to red (in the direction of increasing habitat suitability) code habitat suitability values; grey colour indicates the ‘border’ of wild boar distribution areas, namely the area situated between two MaxEnt threshold values: 10 percentile training presence and maximum training sensitivity plus specificity.

Figure 4. Distribution of federation members of the Russian Federation in the space of total wild boar habitat suitability, calculated from the species distribution model, and maximum long-term abundance of wild boar according to the VNIIOZ estimates



Note: Solid line is a regression plot calculated based on data from the constituent territories. Dashed line is a regression plot calculated based on data from hunting grounds.

in the east), the predicted resources exceeded the capacity many times. Assuming that these deviations are due to errors in collecting information for these regions, we excluded them from the linear model calculations. We also excluded the Primorsky Territory, where both the capacity and the predicted resources exceeded the same indicators for other regions by 2–3 times or more; therefore, an error in the predicted resource value for the Primorsky Territory would have a stronger effect on the line slope than other localities. As a result, the correlation coefficient of the environmental capacity and the predicted wild boar resources by region was 0.72 (Figure 4); regression line was maximum abundance = $2.515 + 4.928 \times$ habitat suitability.

In the analysis of 11 hunting grounds, the correlation factor was 0.78. The slope of the two regression lines was the same, but the intercepts of the linear functions were different (Figure 4). The regression based on the VNIIOZ forecast data overestimates the number of wild boars by 2.5 thousand compared to the regression based on hunting-ground records. It should be noted that, although the wild boar abundance in the Primorsky Territory was excluded from the calculations, it exactly matched the regression line.

Varying the model complexity did not change the correlation notably; however, the greater correlation corresponded to more complex models. The standard deviation of values in each raster cell after 50 runs was highly correlated with the corresponding model values ($R = 0.87$) indicating equal model stability in different geographic parts of the model.

Discussion

In general, spatial structure of wild boar suitable habitats (Figure 3) obtained in our study is consistent with our expert opinion and previous publications (Danilkin 2002, Smirnov 2014, Danilov 2017) on the wild boar distribution in Russia. Wild boar resource estimates by VNIIOZ have similar dynamics with the FGBU Tsentri Okhot Kontrol figures, however difference in numbers is notable (Figure 1). The most probable reason for such difference lies in the way of collection of the ‘official’ (FGBU Tsentri Okhot Kontrol) statistics. Pursuant to Order No. 344 dated September 6, 2010 (MinPrirody Rossii 2010), hunting grounds should submit data on the number and distribution of hunting resources to the competent authority. Then, data collected in individual hunting grounds are summarised in a consistent manner at the level of administrative districts, the federation members and federal districts. As a result, we get an official evaluation of species resources nationwide.

Different methods are used for monitoring wild boar groups. Pursuant to Order No. 963 dated December 22, 2011 (MinPrirody Rossii 2011), activities ‘for counting of the number and distribution of wildlife items’ shall be carried out in accordance with ‘accepted methods’, and, by default, in accordance with the existing scientific approaches. Generally, wild boar is counted using the meth-

od approved at the governmental level: the winter route census method (MinPrirody Rossii 2012). Nevertheless, in the southern regions of the country, where the snow cover is unstable, such a winter route census is impossible; therefore, animals are counted at feeding grounds and in localities of concentration, as well as by the drive census (Glushkov et al. 2007). It is essential to remember that there is no perfect census technique; each of such methods, along with positive aspects, has its drawbacks, leading to bias in the final result (Glushkov et al. 2007, Keuling et al. 2018b). Besides, census methods are subject to periodic changes. This complicates comparison of the results of long-term datasets and data obtained from geographically remote regions, affecting the final quality of information about the census dynamics.

Therefore, currently available the FGBU Tsentri Okhot Kontrol data about the wild boar resource distribution within the Russian territory are based on the use of heterogeneous methods and depend completely on the managers of hunting grounds, who can be interested in increasing or decreasing such numbers according to the situation. There is no independent audit of these figures.

Our model (Figure 3) allows, for the first time, introduction of a spatial structure of suitable habitats into the calculations of the regional wild boar abundance in Russia. This is an important methodological aspect, which should eventually increase the accuracy of population indicator calculations, as required for game management. However, our results reveal many methodological issues that should be resolved in the future. Strengthening the correlation between the habitat capacity and the wild boar abundance in more complex models (reducing the weight of general ecological pattern and increasing the weight of local patterns) reflects the regional specifics in the distribution of resources of this species. The regional specifics is also likely to be reflected in the relatively low habitat suitability in southern Siberia (Figure 3), where we had relatively poor data (Figure 1s); in other words, the ecological pattern found in the data-rich regions did not fully reflect the interpolated habitat suitability in southern Siberia. In order to study and strengthen regional specifics, we should collect additional data on the wild boar distribution in poorly explored areas, especially in Siberia and the Amur River region, which would allow us to build and compare independent models for different parts of the distribution range.

The ‘bordering’ wild boar distribution area is interesting and requires further study (Figure 3). On the one hand, it is intuitively clear that each species should have an area of suboptimal natural conditions, where it does not live permanently, entering therein from adjacent, more suitable territories or where it forms minimal population densities (Danilkin 2002, Kulpin 2008, Rosvold et al. 2008, Markov et al. 2019). On the other hand, when collecting information about wild boar habitats it was unknown which populations survived only due to special biotechnical measures. Therefore, our data sample most likely included localities

lying beyond the natural wild boar distribution (some obvious examples are shown in Figure 1s). Such localities should affect the threshold value as calculated based on original data sample characteristics (10 percentile training presence). Without special research, it is impossible to distinguish between the natural distribution localities and those of artificially created populations (Pavlov 1999, Danilkin 2002, Danilov 2017, Markov et al. 2019).

The coincidence of the slope of the regression lines as calculated using the direct counting results in hunting grounds and from the VNIOZ estimates (Figure 4) allows us to state both the appropriate quality of the VNIOZ estimates and the general success of habitat suitability modelling (Bosch et al. 2012, Acevedo et al. 2019, 2020). Nevertheless, a correlation factor of 0.7 suggests a notable variation in the ratios of habitat capacity and abundance in different regions. The reasons for such deviations from the single trend may be different. On the one hand, they may be due to imperfections of the model itself. As described above, the model may lack regional specificity, whereas environmental preferences of wild boar in the European part of Russia may differ from those in Siberia. Such hypothesis agrees with recent findings in taxonomic structure in wild boar (Keuling et al. 2018a). Another reason for such mismatch between habitat capacity and abundance may be proactive biotechnological activities aimed at maintaining the wild boar population at a level that allows for its intensive economic use. A change in the intensity of such local activities can result in a change in the respondents' scores, such changes being unrelated to the trends existing in the rest of the population. Another possible reason is the unevenness of the respondent network, which could distort the correction coefficient (see *Methods*) due to an erroneous identification of the territory inhabited by the wild boar. Moreover, the habitat suitability in the localities of different respondent observations is not considered at present. Therefore, changes in abundance in optimal and suboptimal habitats are assigned an equal weight.

It is of interest that the VNIOZ evaluations overestimate the wild boar abundance by approximately 2.5 thousand animals compared to the direct counting results in hunting grounds (Figure 4). This is hardly likely to be related to the different structure of the source data, as the maximum values of long-term series of figures were used in both cases. Perhaps this bias is caused by differences in the sizes of the studied territories, which result in different proportions of edge pixels (which then distort the total habitat suitability of the territorial unit in question to varying degrees) or by another calculation specificity.

To further improve the VNIOZ forecast system, we need to understand the reasons for notable deviations in the wild boar resource assessment in some regions (Karelia, the Khabarovsk Territory, etc., see *Results*). It is impossible to know this accurately without additional research; however, as a working hypothesis, we can assume that the bias in numbers is due to underestimation (in Karelia, the Arkhan-

gelsk Region, the Perm Territory and the Vologda Region) or overestimation (in the Amur Region, the Khabarovsk Region and the Transbaikal Territory) of the area inhabited by wild boar in the regions where the 'species distribution boundary' takes place. In this case, there may have been an initial error in calculating the correction coefficients for these regions (see *Methods*). An alternative hypothesis suggests local distortions of our model. In any case, every hypothesis should be validated by additional field studies.

In summary, it should be noted that the VNIOZ forecast data on the regional abundance match well the distribution of suitable wild boar habitats, with some individual exceptions. To improve the abundance forecast by VNIOZ, we recommend increasing the collection of data in Siberia and the Amur River region. In addition, it is desirable to consider habitat suitability when recalculating scores from regional respondents.

Acknowledgments

We are thankful to two anonymous reviewers, whose valuable comments allowed us to improve the manuscript notably. This study was supported by the Russian Science Foundation; Grant number: 18-14-00093.

References

- Acevedo, P., Croft, S., Graham, C., Smith, G., Blanco-Aguilar, A., Fernandez-Lopez, J., Scandura, M., Apollonio, M., Ferroglio, E., Keuling, O., Sange, M., Zanet, F., Brivio, F., Podgórski, T., Petrović, K., Soriguer, R. and Vicente, J. 2020. Validation and inference of high-resolution information (downscaling) of ENETwild abundance model for wild boar. *EFSA supporting publications* 17(1): EN-1787, 23 pp. (ENETWILD consortium). <https://doi.org/10.2903/sp.efsa.2020.EN-1787>.
- Acevedo, P., Croft, S., Smith, G.C., Blanco-Aguilar, J.A., Fernandez-Lopez, J., Scandura, M., Apollonio, M., Ferroglio, E., Keuling, O., Sange, M., Zanet, S., Brivio, F., Podgórski, T., Petrović, K., Body, G., Cohen, A., Soriguer, R. and Vicente, J. 2019. ENETwild modelling of wild boar distribution and abundance: update of occurrence and hunting data-based models. *EFSA Supporting Publications* 16(8): 1674E, 29 pp. (ENETWILD consortium). <https://doi.org/10.2903/sp.efsa.2019.EN-1674>.
- Belda, A., Zaragoza, B., Martínez-Pérez, J.E., Peiró, V., Ramón, A., Seva, E. and Arques, J. 2012. Use of GIS to predict potential distribution areas for wild boar (*Sus scrofa* Linnaeus 1758) in Mediterranean regions (SE Spain). *Italian Journal of Zoology* 79(2): 252–265. <https://doi.org/10.1080/11250003.2011.631944>.
- Bosch, J., Mardones, F., Pérez, A., de la Torre, A. and Muñoz, M.J. 2014a. A maximum entropy model for predicting wild boar distribution in Spain. *Spanish Journal of Agricultural Research* 4: 984–999.
- Bosch, J., Peris, S., Fonseca, C., Martínez, M., de la Torre, A., Iglesias, I. and Muñoz, M.J. 2012. Distribution, abundance and density of the wild boar on the Iberian Peninsula, based on the CORINE program and hunting statistics. *Journal of Vertebrate Biology* 61(2): 138–151.
- Bosch, J., Torre, A.D.L., Alexandrov, T., Iglesias, I., Miteva, A. and Muñoz, M.J. 2014b. Can habitat suitability

- predict the presence of wild boar? Suitable land uses vs. georeferenced data in Bulgaria. *Journal of Vertebrate Biology* 63(3): 194–205. <https://doi.org/10.25225/fozo.v63.i3.a7.2014>.
- Brown, R.D. and Brasnett, B.** 2010 (updated annually). Canadian Meteorological Centre (CMC) daily snow depth analysis data. Version 1. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. Data accessed: January 18, 2020. <https://doi.org/10.5067/W9FOYWH0EQZ3>.
- Danilkin, A.A.** (Данилкин, А.А.) 2002. Mlekopitaiuschie Rossii i sopredelnykh regionov. Svinnye (Suidae) [Mammals of Russia and adjacent regions. Pigs (Suidae)]. GEOS Scientific Publishing, Moscow, 309 pp. (in Russian with English abstract). Available online at: https://zoomet.ru/metod_zveri.html?start=18.
- Danilov, P.I.** (Данилов, П.Е.) 2017. Okhotnich'i zveri Karelii: ekologiya, resursy, upravlenie, okhrana [Game mammals of Karelia: ecology, resources, management, conservation]. 2nd ed., revised. The Institute for Biology. Karelskii Nauchnyi Tsentr RAN, Petrozavodsk, 388 pp. (in Russian with English abstract). Available online at: <http://elibrary.krc.karelia.ru/568/>.
- Dell. 2015. STATISTICA, advanced analytics software package, version 13.0. Dell, Inc., Round Rock, Texas, USA. URL: <http://software.dell.com/products/statistica/>.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. and Yates, C.J.** 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17(1): 43–57.
- FGBU Tsentr Okhot Kontrol. 2013–2017. Chislennost okhotnich'ikh resursov [The number of hunting resources]. ФГБУ «Федеральный центр развития охотничьего хозяйства» [FGBU “Federal Centre of Hunting Industry Development”] (in Russian). Available online at: <http://www.ohotcontrol.ru/resource/number/>.
- Glushkov, V.M., Grakov, N.N., Grevtsev, V.I., Zarubin, B.E., Karpukhin, V.I., Kozlovsky, I.S., Kulpin, A.A., Larionova, M.A., Makarov, V.A., Mashkin, V.I., Pankratov, A.P., Piminov, V.N., Sinitsyn, A.A., Shilyaeva, L.M. and Chesnokov, A.D.** (Глушков, В.М. и др.) 2007. Uchioty i resursy okhotnich'ikh zhyvotnykh Rossii. 2-e izd., dop. [Censuses and resources of game animals in Russia. 2nd ed., enlarged]. VNIIOZ, RASHN, VGSHA, Kirov, 248 pp. (in Russian).
- Gubar, Yu.P., Borisov, B.P., Volodina, O.A., Lomanov, I.K., Lomanova, N.V., Megnev, A.P., Myrutenko, V.S. Molochaev, A.V., Mocheva, T.S., Naumova, A.A., Raponov, V.A., Sygolaeva, E.A., Sydorov, S.V. and Tsarev, S.A.** (Губарь, Ю.П. и др.) 2008. Sostoianie resursov okhotnich'ikh zhyvotnykh v Rossiiskoi Federatsii v 2003–2007 gg. Informatsionno-analiticheskie materialy [The state of resources of game animals in the Russian Federation during 2003–2007. Information and analytical materials], Izdatelstvo FGU Tsentr Okhot Kontrol, Moscow, 163 pp. (in Russian).
- Guillera-Aroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R. and Wintle, B.A.** 2015. Is my species distribution model fit for purpose? Matching data and models to applications: Matching distribution models to applications. *Global Ecology and Biogeography* 24(3): 276–292.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. and Jarvis, A.** 2005. Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15): 1965–1978.
- Keuling, O., Podgórski, T., Monaco, A., Melletti, M., Merata, D., Albricht, M., Genov, P.V., Gethöffer, F., Vetter, S.G., Jori, F., Scalera, R. and Gongora, J.** 2018a. Eurasian Wild Boar *Sus scrofa* (Linnaeus, 1758). In: Melletti, M. and Meijaard, E. (Eds.) Ecology, Conservation and Management of Wild Pigs and Peccaries. Cambridge University Press, Cambridge, p. 202–233.
- Keuling, O., Sange, M., Acevedo, P., Podgórski, T., Smith, G., Scandura, M., Apollonio, M., Ferroglio, E., Vicente, J. and Enetwild Consortium.** 2018b. Guidance on estimation of wild boar population abundance and density: methods, challenges, possibilities. *EFSA Supporting Publications* 15(7): 1449E. <https://doi.org/10.2903/sp.efsa.2018.EN-1449>.
- Kulpin, A.A.** (Кульпин, А.А.) 2008. Osobennosti biologii kabana (*Sus scrofa* L., 1758) i ego ispolzovanie na severe evropeiskoi chasti Rossii [Peculiarities of biology of the wild boar (*Sus scrofa* L., 1758) and its use in the North of the European part of Russia]. Extended synopsis of Cand. Sci. (Biology) dissertation. All-Russian Research Institute for Game Management and Fur Farming (VNIIOZ), Dept. of Biology of Game Mammals and Birds, Viatka Agricultural Academy. Kirov, 22 pp. (in Russian with English abstract). Available online at: <https://www.dissercat.com/content/osobennosti-biologii-kabana-sus-scrofa-l-1758-i-ego-ispolzovanie-na-severe-evropeiskoi-chast/read>.
- Lisovsky, A.A., Sheftel, B.I., Stakheev, V.V., Ermakov, O.A., Smirnov, D.G., Glazov, D.M., Strelnikov, D.P., Ekonomov, A.V., Titov, S.V., Obolenskaya, E.V., Kozlov, Y.A. and Saveljev, A.P.** 2018. Creating an integrated information system for the analysis of mammalian fauna in the Russian Federation and the preliminary results of this information system. *Russian Journal of Theriology* 17(2): 85–90.
- Liu, C., White, M. and Newell, G.** 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* 40(4): 778–789.
- Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Yu.P., and Lomanova, N.V.** (Ломанов, И.К. и др.) 2004. Sostoianie resursov okhotnich'ikh zhyvotnykh v Rossiiskoi Federatsii v 2000–2003 gg. Informatsionno-analiticheskie materialy [The state of the resources of game animals in the Russian Federation during 2000–2003. Information and analytical materials]. Izdatelstvo GU Tsentr Okhot Kontrol, Moscow, 213 pp. (in Russian).
- Lomanov, I.K., Naumova, A.A., Lomanova, N.V., Novikov, G.V., Ovsyukova, N.E. and Myrutenko, V.S.** (Ломанов, И.К. и др.) 1996. Resursy osnovnykh vidov okhotnich'ikh zhyvotnykh i okhotnichii ugodia Rossii (1991–1995 gg.) [Resources of the main game animals and hunting grounds of Russia (1991–1995)]. Izdatelstvo TsNII, Moscow, 225 pp. (in Russian).
- Mammals of Russia. 2017–2020. Portal and Database. URL: <http://www.rusmam.ru>.
- Markov, N., Pankova, N. and Filippov, I.** 2019. Wild boar (*Sus scrofa* L.) in the North of Western Siberia: history of expansion and modern distribution. *Mammal Research* 64: 99–107.
- MinPrirody Rossii. 2003–2018. Gosudarstvennye doklady (ГД) «O sostoianii i ob okhrane okruzhaiuschei sredy Rossiiskoi Federatsii» [State Reports (GD) «On the State of the Environment and Environmental Protection of the Russian Federation»]. Ministry of Natural Resources and Environment of the Russian Federation; NPP «Kadastr», Moscow (in Russian). Available online at: https://www.mnr.gov.ru/docs/gosudarstvennye_doklady/o_sostoyanii_i_ob_okhrane_okruzhayushchey_sredy_rossiyskoy_federatsii/.
- MinPrirody Rossii. 2010. Prikaz ob utverzhenii poriadka osushchestvleniya gosudarstvennogo monitoringa okhotnich'ikh zhyvotnykh i sredy ikh obitaniia i primeneniia ego dannykh

ot 06.09.2010 N 344 [The order on the approval of the procedure for the state monitoring of game species and their habitats and the application of its data dated 06.09.2010 No. 344]. Ministry of Natural Resources and Environment of the Russian Federation (in Russian). Available online at: <http://docs.entd.ru/document/902235917>.

MinPrirody Rossii. 2011. Prikaz ob utverzhdenii poriadka vedeniia gosudarstvennogo uchiota, gosudarstvennogo kadastra i gosudarstvennogo monitoringa objektov zhivotnogo mira ot 22.12.2011 N 963 [The order on the approval of the procedure of keeping state records, state cadastre and state monitoring of wildlife items dated 22.11.2011 No. 963]. Ministry of Natural Resources and Environment of the Russian Federation. (in Russian). Available online at: <https://rg.ru/2012/03/15/jiv-mir-site-dok.html>.

MinPrirody Rossii. 2012. Prikaz ob utverzhdenii metodicheskikh ukazanii po osushchestvleniiu organami ispolnitelnoi vlasti sub'ektov Rossiiskoi Federatsii peredannogo polnomochiia Rossiiskoi Federatsii po osushchestvleniiu gosudarstvennogo monitoringa okhotnich'ikh resursov i sredy ikh obitaniia metodom zimnego marshrutnogo uchiota ot 11.01.2012 N 1 [The order on the approval of the guidelines for the implementation by the executive authorities of the federation members of the Russian Federation of the transferred authority of the Russian Federation to carry out state monitoring of game resources and game species habitats by winter route census dated 11.01.2012 No. 1]. Ministry of Natural Resources and Environment of the Russian Federation (in Russian). Available online at: <https://rg.ru/2012/09/04/zimniy-uchet-site-dok.html>.

Pavlov, M.P. (Павлов, М.П.) 1999. Akklimatizatsiia okhotnich'ie-promyslovykh zverei i ptits v SSSR. Chast 3. Kopytnye [Acclimatization of game animals and birds in the USSR. Part 3. Ungulates]. Kirov, 666 pp. (in Russian).

Phillips, S.J., Dudík, M. and Schapire, R.E. 2018. MaxEnt software for modeling species niches and distributions (Version 3.4.1). Available online at: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed: January 12, 2020.

Razenkova, E., Radeloff, V.C., Dubinin, M., Bragina, E.V., Allen, A.M., Clayton, M.K., Pidgeon, A.M., Baskin, L.M., Coops, N.C. and Hobi, M.L. 2020. Vegetation productivity summarized by the Dynamic Habitat Indices explains broad-scale patterns of moose abundance across Russia. *Scientific Reports* 10(1): article number 836, 1–12. <https://doi.org/10.1038/s41598-019-57308-8>.

Rosvold, J. and Andersen, R. 2008. Wild boar in Norway – is climate a limiting factor? *Norges teknisk-naturvitenskapelige universitet Vitenskapsmuseet Rapport zoologisk serie* 1: 1–23.

Sluzhba urozhaiia VNIIOZ, Lisovsky, A.A., Darensky, A.A., Piminov, V.N. et al. (Служба урожая ВНИИОЗ, Лисовский, А.А., Даренский, А.А., Пимин, В.Н. и др.) 2020. Sample_s_2_a061ae01e3. SluzhbaDataset: http://rusmam.ru/sample/records?id=s_2_a061ae01e3. Mammals of Russia. Created: A. Lisovsky, 17.03.2020.

Smirnov, M.N. (Смирнов, М.Н.) 2014. Los i kaban v tsentralnoi Sibiri [Moose and wild boar in Central Siberia]. Izdatelstvo Sibirskogo Federalnogo Universiteta, Krasnoyarsk, 298 pp. (in Russian with English abstract).

UMIACS. 2020. University of Maryland Institute for Advanced Computer Studies. URL: <http://glcf.umiacs.umd.edu/data>.

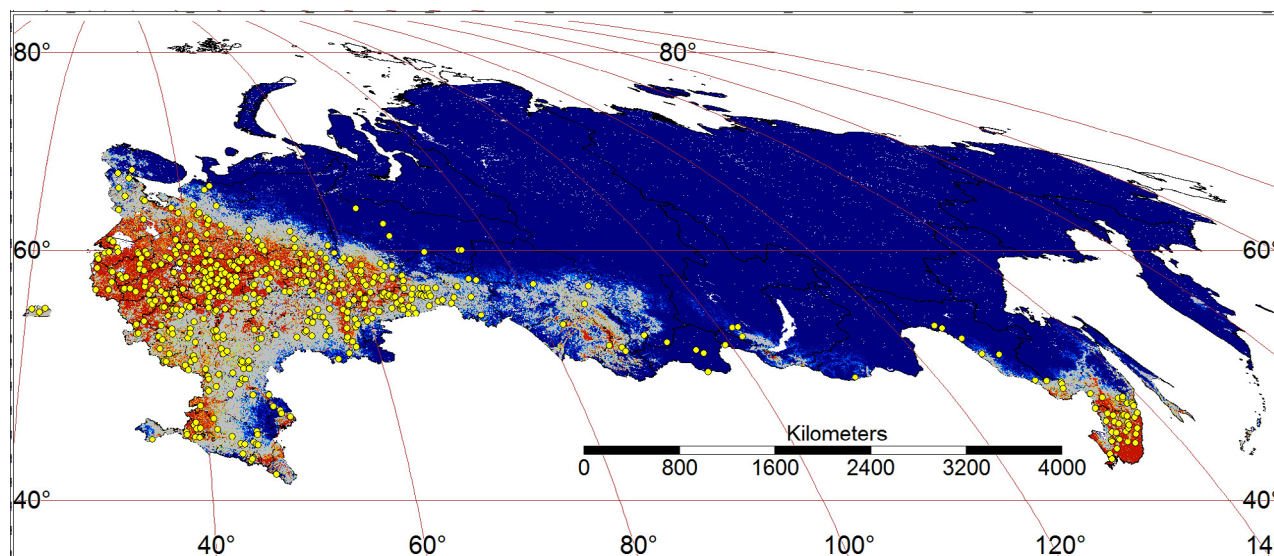
Vargas Amado, M.E., Grütter, R., Fischer, C., Suter, S., and Bernstein, A. 2020. Free-ranging wild boar (*Sus scrofa*) in Switzerland: Casual observations and model-based projections during open and closed season for hunting. *Schweizer Archiv für Tierheilkunde* 162(6): 365–376. <https://doi.org/10.17236/sat00262>.

WorldClim. 2020. Global climate and weather data. URL: <http://www.worldclim.org>.

Zarubin, B.E., Kolesnikov, V.V., Makarov, V.A., Safonov, V.G., Shevnina, M.S. and Utrobina, V.V. (Зарубин, Б.Е. и др.) 2012. Znachenie okhoty i eio produktsii glazami okhotnikov Rossii [The value of hunting and its products through the eyes of Russian hunters]. VNIIOZ, Kirov, 76 pp. (in Russian).

Supplements

Figure 1s. Spatial distribution of wild boar observation localities (yellow dots) used in this study



Note: Species distribution model (see *Methods* and *Results*) is used as a basic map layer.

