Developing and testing remote sensing indices for explaining animal abundance in Russia

By

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Chapter 1: Introduction

Knowing factors that drive population dynamics over a large spatial and temporal scale is important for the sustainable use of natural resources and conservation of biodiversity. Population size of mammals is influenced by the availability of food, habitat conditions and the impact of human disturbance. The availability of forage in time and space is reflected through the home range size and shape of an individual species (Herfindal et al., 2005; Nilsen et al., 2005). A good indicators of the availability of forage and habitat for shelter are measures of vegetation productivity or the availability of biomass. Climate is influencing favorable habitat conditions for the species to live. For example, the degree to which animals are adapted to severe winter condition is a factor limiting their northern distributions (Formozov, 2010; Williams et al., 2015). Even though Russia has vast territories with no human influence, human disturbance through development, habitat degradation or poaching needs to be considered while evaluation factors influencing population dynamics.

Remote sensing provides a set of tools that are able to estimate ecosystem functions over wide areas such as vegetation or primary productivity, information characterizing snow cover and pattern of freeze and thaw, and human disturbance (Coops et al., 2008; Kerr and Ostrovsky, 2003; Turner, 2014; Turner et al., 2003). Here we captured both food availability and winter conditions with newly developed remote sensing indices. We analyzed the Dynamic Habitat Indices (DHIs) as a proxy of availability of energy, environmental stress and environmental stability (Radeloff et al., n.d.). The DHIs were calculated from MODIS products of vegetation productivity including NDVI, EVI, fPAR, LAI, GPP with a spatial resolution of 1 km for the period of 2003-2014 (Hobi et al., 2017). The DHIs consist of three components: (1) overall, cumulative productivity over the course of the year (sites with high cumulative component have more available food); (2) minimum productivity throughout the year (sites with high minimum productivity are more biodiverse); and (3) the coefficient of variation (CV) in productivity over the course of the year (sites with high CV values represent high seasonality) (Hobi et al., 2017). To capture winter conditions, we analyzed a new global dataset characterizing winter related variables including the duration of frozen ground with and without snow cover, and the timing (start date, length, and end date) of the frozen season with a 500 m spatial resolution for the period of 2000-2012 (Zhu et al., 2017). To capture human influence on wildlife, we analyzed human footprint index with a 1-km spatial resolution (Sanderson et al., 2002).

The DHIs have been successfully used to explain patterns of bird species richness in Canada, United States, and Thailand (Coops et al., 2009a, 2009b; Hobi et al., 2017; Suttidate, 2016), the butterfly richness in Canada (Andrew et al., 2012), and the DHIs were even tested as predictors for moose occurrence and abundance in Canada (Michaud et al., 2014). However, the DHIs have not been evaluated in Russia, and it is not clear if the DHIs can be used in models for explaining animal abundance for species with a variety of life history traits. Indices characterizing winter conditions have not previously been used in models of animal abundance, to my knowledge.

The overall goal of this work was to evaluate the utility of remotely sensed indices including the Dynamic Habitat Indices and winter-related indices for explaining animal density of species varying in life history, within Russian territory.

The main objective of the second chapter was to explain moose abundance using the Dynamic Habitat Indices in combination with environmental variables in Russia. More specifically, two main goals were: (1) to evaluate how much variation in moose density can be explained by the DHIs in combination with other environmental variables and (2) to understand the impact of collapse of Soviet Union in 1991 on the development of the moose population size.

We used multiple linear regression, in which the dependent variable was log-transformed moose density, and the explanatory variables included the three components of the DHIs, human footprint, road density, elevation, temperature, precipitation, and rural human population. We used best subset regression to find the “good” models. Each model was tested by variance inflation factor (VIF) to detect multicollinearity. To assess the importance of each variable included in the model, we used hierarchical partitioning. For the second part of our analysis, we analyzed moose density during the three separate time periods, namely 1981 – 1990, 1991 – 2000, and 2001 – 2010. We run an additional sum of squares test to evaluate if there are significant differences between the three time periods.

Our results showed that the individual components of the DHIs along had low explanatory power. Models with a combination of the DHIs and the environmental variables such as temperature and precipitation explained up to 79% of variation in moose density. While evaluating the three periods separately we found a decrease in the explanatory power of the models through time, indicating an influence of other factors not included in our model. In summary, our results showed that combination of using remote sensing data including land cover classification, the DHIs with environmental variables is a promising approach for explaining animal abundance over vast territories.

In the third chapter, we extended our analysis to eight species with different life history characteristics, and explored the utility of using two sets of remote sensing indices (Dynamic Habitat Indices and the winter related variables) in explaining animal density. Our eight species represented animals at different trophic levels and included omnivores, herbivores, carnivores: brown bear (*Ursus arctos*), wild boar (*Suc scrofa*), European hare (*Lepus europaeus*), moose (*Alces alces*), roe deer (*Capreolus pygargus Pallas, Capreolus capreolus Linnaeus*), lynx (*Felis lynx*), red fox (*Vulpes vulpes*), and wolf (*Canis lupus*). We analyzed population trends of the mammal species and tested if these trends are significant. In order to do that, for each species in turn we summed up the result of winter track count (population totals) for all regions for a given year, and fitted a linear regression of the population totals as a function of time from 1981 to 2010. We found that brown bear, roe deer, wild boar and wolf population trends significantly increased while European hare, lynx, and moose significantly decreased, and red fox increased but not significantly.

To relate species population densities to our predictor variables, we applied multivariable linear regression and made a selection of the variables using best subset selection. Our dependent variable for each species was population density, which we calculated by dividing regional population totals by the area of suitable habitat in each region, as defined independently for each species. Our explanatory variables were the Dynamic Habitat Indices, road density, human footprint, elevation, temperature, precipitation, duration with snow-free frozen ground, duration of snow-covered ground, the timing and the length of the frozen season and of snow cover. We found that both the DHIs and the winter-related variables contributed greatly to our multivariate models and provided complementary information to climate and human disturbance related variables. Together, our suite of variables explained the variation in species density well, with R^2_{adj} ranging from 0.61 to 0.94. Which subset of predictors was most useful in explaining species density was greatly dependent on the focus species. In general, the pattern of animal density was found to be similar to the pattern of primary productivity, indicating how plant productivity is shaping animal density at multiple trophic levels. Our results also highlight the high importance of variables related to human disturbance for carnivores and herbivores for explaining their declining trends.

Significance

The main results of this work add deeper understanding of utility of remote sensing indices for explaining animal abundance over vast territories of Russia. This master work contributes greatly in **management and conservation science** of wildlife, and has direct management applications. For example, we suggested that wildlife officials may want to consider reducing hunting quotas in years following harsh winter and low plant productivity, to increase anti-poaching activity in regions with low animal density and perhaps to provide supplementary feeding during winter for regions with limited food resources. Our research highlights the requirement of establishing a monitoring program for lynx for deeper understanding of the decline of the lynx population.

In summary, we suggest that using remote sensing indices including the DHIs and winter-related variables can be an effective tool for explaining animal density for wildlife species from different trophic levels. In this study we showed that a combination of remote sensing indices and land cover together with climate and human-related variables has high explanatory power. The DHIs provided valuable information about primary productivity while winter-related variables provide important information about the effect of winter on species survival. Moreover, both remote sensing datasets are available globally free of charge.

Reference

Andrew, M.E., Wulder, M.A., Coops, N.C., Baillargeon, G., 2012. Beta-diversity gradients of butterflies. Glob. Ecol. Biogeogr. 21, 352–364. doi:10.1111/j.1466-8238.2011.00676.x

Coops, N.C., Waring, R.H., Wulder, M.A., Pidgeon, A.M., Radeloff, V.C., 2009a. Bird diversity: A predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. J. Biogeogr. 36, 905–918. doi:10.1111/j.1365-2699.2008.02053.x

Coops, N.C., Wulder, M.A., Duro, D.C., Han, T., Berry, S., 2008. The development of a Canadian dynamic habitat index using multi-temporal satellite estimates of canopy light absorbance. Ecol. Indic. 8, 754–766. doi:10.1016/j.ecolind.2008.01.007

Coops, N.C., Wulder, M.A., Iwanicka, D., 2009b. Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. Remote Sens. Environ. 113, 668–679. doi:10.1016/j.rse.2008.11.012

Formozov, A.N., 2010. Snow cover in the ecology of mammals and birds, 3rd ed. LKI, Moscow (In Russian).

Herfindal, I., Nilsen, E.B., Andersen, R., Linnell, J.D.C., Odden, J., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J. Zool. 265, 63–71. doi:10.1017/S0952836904006053

Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M., Radeloff, V.C., 2017. A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. Remote Sens. Environ. 195, 142–152. doi:10.1016/j.rse.2017.04.018

Kerr, J.T., Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. Trends Ecol. Evol. 18, 299–305. doi:10.1016/S0169-5347(03)00071-5

Michaud, J.S., Coops, N.C., Andrew, M.E., Wulder, M.A., Brown, G.S., Rickbeil, G.J.M., 2014. Estimating moose (Alces alces) occurrence and abundance from remotely derived environmental indicators. Remote Sens. Environ. 152, 190–201. doi:10.1016/j.rse.2014.06.005

Nilsen, E.B., Herfindal, I., Linnell, J.D.C., 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? Ecoscience 12, 68–75. doi:10.2980/i1195-6860-12-1-68.1

Radeloff, V.C., Dubinin, M., Coops, N.C., Allen, A., Brooks, T.M., Clayton, M., Costa, G., Graham, C., Ives, A.R., Kolesov, D., Kuemmerle, T., Pidgeon, A.M., Rapacciuolo, G., Razenkova, E., Rondinini, C., Suttidate, N., Young, B., Zhu, L., M. Hobi, n.d. The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity. Prep.

Sanderson, E.W., Jaiten, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The Human Footprint and the Last of the Wild. Bioscience 52, 891. doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Suttidate, N., 2016. Spatial patterns of primary productivity derived from the Dynamic Habitat Indices predict patterns of species richness and distributions in the tropics. Doctoral thesis submitted at the University of Wisconsin - Madison.

Turner, W., 2014. Sensing biodiversity. Science. 346, 301–302. doi:10.1126/science.1256014

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. Trends Ecol. Evol. 18, 306–314. doi:10.1016/S0169-5347(03)00070-3

Williams, C.M., Henry, H.A.L., Sinclair, B.J., 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol. Rev. 90, 214–235. doi:10.1111/brv.12105

Zhu, L., Radeloff, V.C., Ives, A.R., 2017. Characterizing global patterns of frozen ground with and without snow cover using microwave and MODIS satellite data products. Remote Sens. Environ. 191, 168–178. doi:10.1016/j.rse.2017.01.020

Chapter 2: Explaining moose abundance with the Dynamic Habitat Indices and environmental variables in Russia

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Abstract

Knowing factors that drive wildlife population dynamics over broad spatial and temporal scales is important for their conservation. Ecosystem productivity is an important factor to determine habitat suitability, especially for large mammals. In this study we use the Dynamic Habitat Indices (DHIs) which are remote sensing based measures of vegetation productivity and available globally. The DHIs summarize three measures of vegetation productivity: cumulative productivity (DHI Cum), minimum productivity (DHI Min), and seasonality (DHI Var). We evaluated the utility of the DHIs to explain the spatial distribution of moose (*Alces alces*) abundance in Russia using multiple regression. Our two main goals are: (1) to test how well the DHIs, together with other environmental variables, explain variation in moose abundance and (2) to understand the impact of political upheaval on the moose population over three specific time periods. Overall we found that the individual components of the DHIs had low predictive power, suggesting that moose populations were mainly driven by other factors. However, in combination with environment variables, the DHIs could explain up to 79% of variation in moose abundance. Predictive power of our model for the three periods decreased through time. We assume other factors influenced moose abundance, for example, increased poaching. Overall, combining the DHIs with climate data may be a promising approach for explaining moose abundance.

Keywords

Moose abundance, game mammals, dynamic habitat indices, winter track count, Russia.

Introduction

Human activity causes significant changes in ecosystems and leads to climate change, accelerates biodiversity loss (Butchart et al., 2010; Rockström et al., 2009; Turner, 2014) and forest degradation (Hansen et al., 2014). How biodiversity responds and adapts to new environmental conditions is an important question for management and conservation. It is crucial to understand the species ecology and what the main driver for the current pattern of biodiversity is. Remote sensing is a very effective tool for this assessment, because data are collected systematically at broad scales and for long time periods (Turner et al., 2003). Habitat and land cover maps based on remotely sensed data provide valuable information about the condition of an ecosystem and can explain species distribution over vast territories (Kerr and Ostrovsky, 2003; Nagendra, 2001; Turner et al., 2003).

The Moderate Resolution Imaging Spectroradiometer (MODIS) is an instrument aboard NASA's Terra and Aqua satellites developed to monitor the condition of the Earth, understand global dynamics, and predict future changes. MODIS data are collected daily in 36 high spectral resolution bands with spatial resolutions of 250 m, 500 m, and 1000 m (Savtchenko et al., 2004). MODIS data products including land cover and Fraction of absorbed Photosynthetically Active Radiation (FPAR) are available since 2003, providing a unique opportunity to design relevant, meaningful indices for biodiversity studies. We explored Dynamic Habitat Indices (DHI) which summarize three important measures of vegetative productivity: cumulative productivity (DHI Cum), minimum productivity (DHI Min), and seasonality (DHI Var) based on MODIS FPAR product with 8-day temporal and 1 km spatial resolution.

The species-energy hypothesis predicts a relationship between energy availability and the number of species, and hypothesizes that areas with high productivity are able to support a greater number of species (Gaston, 2000; Hawkins et al., 2003a, 2003b; Wright, 1983). Furthermore, the DHIs were successfully used to support this theory, and were tested as a predictor of bird species richness in Canada and US (Coops et al., 2009a, 2009b; Hobi et al., 2017) and in Thailand (Suttidate, 2016). While the species-energy hypothesis predicts responses in species richness, energy, as represented by DHIs, may also be useful in predicting abundance within a given species. This is suggested by the fact that in areas with higher vegetation productivity, animal home ranges are smaller (Bjørneraas et al., 2012; Herfindal et al., 2005), and reproductive and survival rates are higher (Massei et al., 1996). In fact, the prediction of animals' abundance is a complex problem because it involves many factors, variously, availability of forage in space and time, necessary climate conditions for survival and animal growth, predation, harvest.

Wildlife abundance data collected in Russia provides an ideal opportunity to explore the relationship between species-abundance and vegetative productivity given the broad spatial and temporal coverage of wildlife surveys and the large variability in climate and consequent vegetative productivity. Russia has collected data of game species for a long period of time using the winter track count method (WTC) (Lomanov, 2000; Stephens et al., 2006), aerial surveys, and surveys of local hunters (Lomanov et al., 1996). Data for moose (*Alces alces*) abundance for the whole territory of Russia are available from 1981 to 2010. During these years Russia underwent radical political and economic changes as it moved from government centralization to an open market economy. Lax government control and a decline in the economy after the collapse of the Soviet Union in 1991 affected human livelihoods and increased poverty (United Nations Statistics Division, 2016), and resulted in agricultural land abandonment (Prishchepov et al., 2012) and a decline in forest cover (Baumann et al., 2012). The economic downturn also affected the wildlife population primarily due to overexploitation of natural resources, as people relied more heavily on wildlife for food (Bragina et al., 2015; Wittemyer, 2011).

We analyzed population trends for moose from 1981 to 2010 over the Russian territory. During this period, the moose population experienced dramatic changes after the collapse of socialism (Figure 1). We hypothesized that if we divide the whole study period into three decades, our model would provide different results for each of the three periods. The first period is before the collapse from 1981 to 1990; the second period, from 1991 to 2000, includes the transition from a government based to an open market economy and the third period is after the collapse from 2001 to 2010.

The main goal of this study was to evaluate the utility of the Dynamic Habitat Indices (DHI) to explain moose abundance for the Russian territory. We expected a higher moose abundance in regions with high vegetation productivity (DHI Cum), high minimum productivity (DHI Min), and relatively low variation in productivity over the course of a year (DHI Var). Specifically, we were interested (1) to know which of the DHI components are most relevant for predicting moose abundance and (2) to understand the impact of the political upheaval on the moose population.

Methods

Study area

The study area covers most of the territory of Russia and includes 69 administrative regions (13.64 million km2). Some regions of Russia have changed their borders and were split during the study period of 1981-2010. In our analysis we consider 62 regions with their original borders before splitting. This vast area is ideal to test DHI predictions because it covers multiple landscape zones, and includes a diversity of topographic and vegetation types, resulting in substantial diversity of habitats and DHI value. The topography of Russia can be divided into two parts: the East European Plain, which is mainly a plain with hills located in the west, and the West Siberian Plain-Central Siberian Plateau where mountains and large, well-draining plains span the east of the country. The dominant climate of both parts is continental with two main seasons, winter and summer, and two short transitional seasons, spring and fall. The average annual temperature is -5.5°C, the coldest month is January (the range of mean temperature from -38.6 °C in Yakutsk to -6.3°C in Volgograd), and the warmest month is July (the range of mean temperature from 19.5 °C in Yakutsk to 23.6 °C in Volgograd). The area includes tundra, taiga (boreal forest), temperate broadleaf forest, and steppe. The vegetation of tundra is composed of polar willow (*Salix polaris*), Betula nana, lichens, mosses, and shrubs. The dominant species of boreal forest are Scots pine (*Pinus sylvestris L.*), Siberian fir (*Abies sibirica*), spruce (*Picea obovata*), Siberian pine (*Pinus sibirica*), and larch (*Larix decidua*). The temperate broadleaf forest is dominated by European beech (*Fagus sylvatica L.*), oak (Quercus robur), ash (*Fraxinus excelsior*), maple (*Acer platanoides*), and Silver birch (*Betula pendula*) (Alehin, 1951).

Winter track count data, and range map

Moose abundance data were provided by the database of the Russian Federal Agency of Game Animals for 1981-2010 using the winter track count (WTC) (Lomanov, 2000) for 62 regions of Russia (Borisov et al., 1992; Gubar et al., 2007; Lomanov et al., 2004, 2000, 1996; Lomanova et al., 2011). The WTC involves counting tracks on the snow that intersect fixed transects and measuring daily travel distance of surveyed species (Kuzyakin, 1983). WTCs were first proposed in 1934 by A.N. Formozov, who showed how the occurrence of tracks on snow, length of travel distance, and population density were related (Kuzyakin, 1983). Later on his formula was refined and verified by several other techniques (Chelintsev, 2000; Lomanov, 2000; Stephens et al., 2006). The WTC was increasingly applied in parts of Russia from 1964, and from 1981 the WTC method became the main method for monitoring game animals (14-33 species depending on the year) in all territories of Russia, including the Asian part of Russia. Approximately 30,500 transects were monitored in 1981 and the length of an individual transect ranged from 8 to 12 km (Kuzyakin, 1983). The monitoring results were used to obtain seasonal hunting quotas. The WTC method was only applied in regions with stable snow cover.

Moose is the most valuable game species living in almost all territories of Russia, except for arctic tundra and semi-desert (Figure 1). Several methods have been applied to estimate moose abundance including aerial surveys and surveys of local hunters. For this reason, the moose data are considered more reliable compared to other species surveyed (Lomanov et al., 1996). In some regions or parts of regions, e.g. Amur Oblast, data were collected by aerial survey (Lomanov et al., 1996). We used the map for the moose range from the game animal’s analytical materials (Lomanov et al., 1996).

In the first part of our analysis, we calculated the average moose density over the whole study period. For the second part, we divided the study period into three decades: 1981-1990, 1991-2000, and 2001-2010, and calculated the average moose density for each time period. In our analysis we included all regions even though we did not have data for the year 1996 and there were 25 missing values in individual years throughout the whole study period.

Dynamic Habitat Indices and land cover

We calculated the Dynamic Habitat Indices (DHIs) based on the Fraction of Absorbed Photosynthetically Active Radiation (FPAR) collected by the Moderate Resolution Imaging

Spectroradiometer (MODIS) instrument aboard the Terra and Aqua satellite with 1-km spatial resolution and 8-day temporal resolution from 2003-2014. The DHIs contain three measures of vegetation productivity: annual cumulative productivity (DHI Cum), annual minimum productivity (DHI Min), and seasonality (DHI Var). We calculated DHI Cum by summing FPAR values over a year; DHI Min is the lowest FPAR value during a year and DHI Var is the coefficient of variation (standard deviation divided by mean) (Figure 2). For all analyses we used the composite product which is based on the median FPAR values between 2003 and 2014 (Hobi et al., 2017).

We used the MODIS International Geosphere-Biosphere Programme Classification (IGBP) product which includes 17 land cover classes with 500 m spatial resolution to produce a stable land cover data set for 2003-2012 (Friedl et al., 2010). For the stable land cover product, we separated each pixel of the MODIS land cover into binary masks for every year, then for every land cover class we summed up the values. We applied a majority threshold of 50%, which only allows changes in the land cover class for half of the considered time period. Based on this stable land cover data we defined regions that correspond to suitable habitat for moose. It includes the following classes: 1-evergreen needle leaf forest, 2-evergreen broadleaf forest, 3-deciduous needle leaf forest, 4-deciduous broadleaf forest, 5-mixed forest, 7-open shrub lands, 8-woody savannas, and 11-permanent wetland (Figure 1a) (Danilkin, 1999; Timmermann and McNicol, 1988). Accordingly, the total area of suitable habitat within the moose range map was 10.6 million km^2. We projected our data to an Albers equal area conic projection (Datum D European 1950), to calculate the suitable habitat area for each individual region.

Environmental variables and elevation

We obtained nineteen BIOCLIM variables (Hijmans et al., 2005) (Table 1) and elevation data with 1 km resolution from WorldClim (http://worldclim.com). Our data set therefore included 11 variables characterizing temperature and 8 variables for precipitation. The elevation data used in the WorldClim project is based on the Shuttle Radar Topography Mission (SRTM). We calculated mean values for all variables within suitable moose habitat for the 62 regions in our study.

Human footprint

Human footprint index (HFI) data were downloaded from http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic with 1-km resolution. The HFI was created from nine data layers including human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers) (Sanderson et al., 2002).

Road density

We obtained road data for the Russian Federation from DIVA-GIS (http://www.diva-gis.org). The data were projected onto an Albers equal area conic projection to calculate the length of roads. Then the length of roads was normalized by area of the regions to obtain road density.

Rural human population

Rural human population data were provided by Russian Federal service of state statistics for 1991-2010. Rural populations include all those situated outside of cities and towns as approved by legislative acts. It is an estimation of the population based on results of a periodic population census by adding the number of newborns and subtracting the number of deaths within each territory (Rosstat, 2010). We divided the rural population data into two time periods: 1991-2000 and 2001-2010, and then we calculated the average over each time period.

Statistical analysis

Variation in moose abundance (1981 – 2010)

For the statistical analysis of WTC data, we used a multiple linear regression approach and selected the “best” model based on a set of criteria. The response variable was log-transformed moose density, which was estimated by dividing the results of the WTC with suitable moose habitat (Figure 1b). Moose density was log-transformed to normalize the data and based on residual plots there was no evidence of outliers. The explanatory variables in the multiple regression included the DHIs, the BIOCLIM variables (11 temperature variables, 9 precipitation variables), elevation, road density, HFI and rural population. We calculated correlation coefficients for all explanatory variables to check for multicollinearity and we ran a hierarchical cluster analysis for environmental variables using squared Spearman correlation to determine their similarity (Supplementary Material Figure S1). We used best subset regression to find the “good” models, based on the different criteria. The best subset approach fits all possible models and identifies the best model from the list (Draper and Smith, 1998). The Bayesian Information Criteria (BIC) was used for model selection of competing models (Burnham and Anderson, 2002) and the adjusted coefficient of determination (R^2_{adj}) to estimate how much of the variation in the response variable is explained by the model. After selecting several “good” models, multicollinearity was assessed by examining the variance inflation factor (VIF) for each variable, applying a threshold of VIF <10 (Dormann et al., 2013). We measured spatial autocorrelation with semivariograms and we used the hierarchical partitioning approach to assess the importance of each variable included in the model (Chevan and Sutherland, 1991; MacNally, 1996).

Variation in moose abundance by time period

For the second part of our analysis, we analyzed moose density during the three separate time periods, namely 1981 – 1990, 1991 – 2000 and 2001 – 2010. Our aim was to determine whether the relationship between moose density and the explanatory variables differed among the three periods. We selected the most parsimonious model from the first part of the analysis and refit the model for each time period. We compared the intercepts and slopes across the time periods using an additional sum of squares test. In addition, for the second and the third periods, we fitted an additional model that included rural population to determine whether changes in rural populations over time affected moose density.

We performed our analysis in R version 3.3.1 (R Core Team, 2016). We used the following R packages: Hmisc (Harrell and Dupon, 2016) to run cluster analysis, leaps (Lumley, 2009) to perform best model selection, geoR (Ribeiro and Diggle, 2016) for semivariograms, and hier.part (Walsh, C., Mac Nally, 2013) for hierarchical partitioning.

Results

Moose population dynamics

Moose populations experienced large changes during the study period. From 1981 to 1991 the moose population fluctuates with an overall growth trend, and reaches a maximum at the end of this period with 900,000 individuals over the Russian territory. After the collapse of the Soviet Union in 1991, the moose population rapidly declines and reaches a minimum in 2002 with 520,000 individuals, signalizing a decline of 42%. To illustrate this decline, we created a map showing the percent of decline in each regions from 1981 to 2010. In some regions the moose population decline is up to 98% during the whole study period (Figure 1d). After reaching the minimum in 2002, the moose population increased and in 2010 it numbered 645,000 individuals.

Based on MODIS stable land cover information we created a map with suitable habitat for moose, where the total area within the range map was 10.6 million km^2 (Figure 1a). In some regions, for example, Volgograd and Orenburg, there is hardly any forest, and we identified only small areas with suitable habitat based on the eight selected land cover classes. That is why the moose density in these regions is extraordinary high. However, both regions are located on large rivers and moose can live in the floodplain. In general, moose density is higher in the European part of Russia then in the Asian part.

DHI and moose density

The DHIs capture the pattern of vegetation productivity over the Russian territory; values for DHI Cum were highest for areas with mixed and deciduous needle leaf forests. DHI Min had low values in the northern and northeastern parts of Russia, which are areas that are mainly covered by snow, and high values in the southeast of the Asian part of Russia (south of Far East) and the south of Russia (Caucasus region) characterized by a mild climate. In contrast to DHI Cum, DHI Var showed high values for the north, north-east of Russia, for areas covered by shrub lands, woody savannas, and deciduous needle leaf forests (Figure 2).

Our first step in exploring the DHIs was an evaluation of each component separately in order to see how much of the variation in moose density was explained. DHI Cum had a positive correlation with moose density (R^2_{adj} =0.23, P<0.01). As we expected, DHI Var showed the opposite trend, and moose density decreased for areas with high DHI Var (R^2_{adj} =0.23, P<0.01). DHI Cum and DHI Var showed very similar results in explaining variability for moose density, but DHI Min did not have a notable trend (R^2_{adj} =-0.02, P=0.8) (Figure 3).

DHI Cum, DHI Var, human footprint, road density, and some BIOCLIM variables were included in the “best” models. We selected the top three performing models and two of them included the DHIs (Table 2). In order to determine the relationship between moose density and each variable, we fitted univariate models with these variables. The R^2_{adj} varied from 0.23-0.68 for positively correlated variables and from 0.27-0.3 for negatively correlated variables (Figure 4). We found a positive correlation between human footprint and moose density. Due to some interaction between human footprint and road density in the multivariate model, road density was selected only in combination with human footprint. However, we did not consider those models due to high correlation between human footprint and road density showing a Pearson correlation coefficient r=0.95. When we included road density without human footprint in the models, road density was not significant.

The “best” model based on BIC included cumulative productivity (DHI Cum), annual mean temperature (BIO1), temperature annual range (BIO7), and human footprint (Table 2), however, the VIF of BIO7 was 16 due to high collinearity between BIO1 and human footprint (r=0.89), and between BIO1 and BIO7 (r=-0.85). Therefore, the “best” models excluded those with high collinearity and BIOCLIM variables that were clustered (Supplementary materials S1). The most parsimonious model included cumulative productivity (DHI Cum), annual mean temperature (BIO1), and temperature seasonality (BIO4). The next “best” model included only two explanatory variables: BIO5 and BIO9. To evaluate other components of the DHIs, we used this model and fitted the models with DHI Min and DHI Var instead of DHI Cum. DHI Cum in combination with other variables performed better than DHI Var and DHI Min, as measured by BIC, but the R^2_{adj} was similar between all three models (Table 2). The variation in the most important explanatory variables over the Russian territories can be viewed in Figure 4.

Difference between the three periods

The most parsimonious model used to evaluate moose densities from the three time periods included the variables cumulative productivity (DHI Cum), annual mean temperature (BIO1), and temperature seasonality (BIO4). Moose density increased with increasing values of DHI Cum and BIO1, while it decreased for increasing values for BIO4 (Figure 3). The slopes of the regression lines for the univariate models of the three periods are only slightly different based on the scatter plots (Figure 5). However, we found that the lines of the multivariate models are significantly different between the first and the third period (P=0.005), and between the second and the third period (P=0.013); however, there is no difference between the first and the second period (P=0.89). The correlation between moose density and DHI Cum, BIO1, and BIO4 was stronger (R^2_{adj} =0.81) for the first period compared with the second period (R^2_{adj} =0.73) and third period (R^2_{adj} =0.67) (Table 3). Rural population was not significant in the models based on these three time periods.

Discussion

In this study, we evaluated the utility of the DHIs as predictors for moose abundance in Russia. Our results show that models with the individual DHIs had low predictive power. However, models combining the DHIs and environmental variables with or without an anthropogenic predictor (e.g., human footprint) were able to explain up to 79% of variation in moose density. The relationship between the moose density and the DHIs and environmental variables changed significantly over the three study periods, suggesting the impact of human activities on moose density. The predictive power of our model based on R^2_{adj} was highest for the first time period and lowest for the third time period, suggesting the decline in moose density depends on factors unaccounted for in the model (e.g., poaching). Our results when using only the DHIs are similar to Michaud et al (2014), a study based in Canada that uses different data sources for moose abundance, but nonetheless indicating that moose abundance is driven by a more complex combination of environmental factors (Michaud et al., 2014).

Variation in moose density was best explained by vegetative productivity and temperature-related variables, and for example these explained 81% of variation in moose densities during the time period 1981 – 1990. Previous studies of ungulates have also shown that abundance of roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) were positively correlated with vegetative productivity (Melis et al., 2009, 2006). Reproductive performance of moose is also positively related to vegetative productivity, with higher twinning rates by females with good body condition (Allen et al., 2017; Testa and Adams, 1998), thus providing support to our findings. Interestingly, Michaud et al. (2014) found that the minimum levels of productivity (DHI Min) during winter were more important for explaining abundance of moose. DHI Min may indicate levels of forage availability during winter, an important determinant of moose space uses during the lean winter months (van Beest et al., 2010), and forage availability during winter may also have carryover effects to calf survival the following spring thus affecting population recruitment (Allen et al., 2017; Milner et al., 2013). In our analyses, DHI Min tended to perform poorly and explained very little variation in moose density. An explanation may be due to missing values arising from periods of darkness or snow cover in the northern parts of our study region, with a number of steps and data checking required to identify the last correct minimum reading of FPAR (Beck et al., 2006; Bischof et al., 2012; Hird and McDermid, 2009).

We hypothesized that increasing human presence would have a negative effect on moose density. We did not find a strong relationship between moose density and road density or rural populations, however, the human footprint index was positively correlated with moose density. Although human effects on biodiversity may often be negative, for example how ungulates may alter their activity patterns in response to human disturbance (Ciuti et al., 2012; Ensing et al., 2014), improved hunter access (Brown, 2011) and the barrier effects that human developments cause (Bartzke et al., 2015), human presence may also positively influence wildlife populations. Predators often avoid human-dominated areas thus providing a safe-haven for prey species (Hebblewhite and Merrill, 2009), humans may increase forage availability through fertilizers and thus increase vegetative productivity (Polis, 1999) and logging practices by forestry may open up habitats and thus improve habitat suitability for moose (Lavsund et al., 2003), which may contribute to the positive correlation between moose density and the HFI in our results. Human effects on the environment are an important consideration given how the bottom-up and top-down effects in the food web become less certain with increasing human densities (Muhly et al., 2013). An important consideration is that human population density is often positively correlated with vegetative productivity, as shown by Evans and Gaston (2005), and we also found that human footprint had a positive relationship with DHI Cum and DHI Min, and a negative relationship with DHI Var.

In addition, rapid changes in political and economic activity lead to changes in land use and forest cover. Immediately after the collapse of socialism, agricultural abandonment was common across the country and widespread in the European part of Russia (Prishchepov et al., 2013). As a consequence, forested area increased (Baumann et al., 2012), and potentially expanded the habitat area for wildlife. However, the moose population experienced high hunting pressure immediately after 1991, because of government instability and a lack of wildlife protection, resulting in poor people overharvesting natural resources (Bragina et al., 2015; Danilkin, 2008; Wittemyer, 2011). In the second part of our analysis, we found that the predictive power of our model decreased through time, suggesting that vegetation productivity was more important in the first period, while human pressure was more important in the second and third periods. We conclude that moose density depends on vegetation productivity and suitable climatic conditions; however, human pressure has the most significant role in moose population dynamics.

However, there are limitations of WTC data. Aggregated WTC data were processed by the Russian Federal Agency of Game Species in Moscow, Russia. We are aware of data errors due to human errors made at different stages of collection, processing, and reporting of WTC data. Moreover, data were collected over a very long period of time including a politically unstable period. We expect that the WTC data quality had decreased after the collapse of the Soviet Union.

In summary, the Dynamic Habitat Indices provided valuable information about productivity of ecosystems and are very suitable for biodiversity studies. In this study, we calculated the DHIs based on the MODIS FPAR and showed that the combination of remote sensing based products incorporated in the DHIs and land cover together with climate variables are very promising for the prediction of animal abundance.

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References

Alehin, A.A., 1951. Vegetation of Soviet Union in major zones. Sovetskaya nauka, Moscow (In Russian).

Allen, A.M., Dorey, A., Malmsten, J., Edenius, L., Ericsson, G., Singh, N.J., 2017. Habitat-performance relationships of a large mammal on a predator-free island dominated by humans. Ecol. Evol. 7, 305–319. doi:10.1002/ece3.2594

Bartzke, G.S., May, R., Solberg, E.J., Rolandsen, C.M., Røskaft, E., 2015. Differential barrier and corridor effects of power lines, roads and rivers on moose (*Alces alces*) movements. Ecosphere 6, art67. doi:10.1890/ES14-00278.1

Baumann, M., Ozdogan, M., Kuemmerle, T., Wendland, K.J., Esipova, E., Radeloff, V.C., 2012. Using the Landsat record to detect forest-cover changes during and after the collapse of the Soviet Union in the temperate zone of European Russia. Remote Sens. Environ. 124, 174–184. doi:10.1016/j.rse.2012.05.001

Beck, P.S.A., Atzberger, C., Høgda, K.A., Johansen, B., Skidmore, A.K., 2006. Improved monitoring of vegetation dynamics at very high latitudes: A new method using MODIS NDVI. Remote Sens. Environ. 100, 321–334. doi:10.1016/j.rse.2005.10.021

Bischof, R., Loe, L.E., Meisingset, E.L., Zimmermann, B., Van Moorter, B., Mysterud, A., 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? Am. Nat. 180, 407–424. doi:10.1086/667590

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.E., van Moorter, B., Rolandsen, C.M., 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia 168, 231–243. doi:10.1007/s00442-011-2072-3

Borisov, B.P., Gibet, L.A., Gubar, Y.P., Kukushkin, M.A., Mosheva, T.S., Nazarov, A.A., Naumov, A.A., Novikov, B.V., Petrashov, V.V., Paponov, V.A., Tomilova, T.P., 1992. Fond of hunting grounds and number of main wild species in Russian Soviet Federative Socialist Republic. Moscow (In Russian).

Bragina, E. V., Ives, A.R., Pidgeon, A.M., Kuemmerle, T., Baskin, L.M., Gubar, Y.P., Piquer-Rodriguez, M., Keuler, N.S., Petrosyan, V.G., Radeloff, V.C., 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. Conserv. Biol. 29, 844–853. doi:10.1111/cobi.12450

Brown, G.S., 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. J. Anim. Ecol. 80, 1288–1298. doi:10.1111/j.1365-2656.2011.01875.x

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed), Ecological Modelling. doi:10.1016/j.ecolmodel.2003.11.004

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.C., Watson, R., 2010. Global Biodiversity: Indicators of Recent Declines. Science. 328, 1164–1168. doi:10.1126/science.1187512

Chelintsev, N.G., 2000. The mathematical basis of animal censuses. Moscow: Centrokhotcontrol (In Russian).

Chevan, A., Sutherland, M., 1991. Hierarchical Partitioning. Am. Stat. 45, 90–96. doi:10.2307/2684366

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. PLoS One 7. doi:10.1371/journal.pone.0050611

Coops, N.C., Waring, R.H., Wulder, M.A., Pidgeon, A.M., Radeloff, V.C., 2009a. Bird diversity: A predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. J. Biogeogr. 36, 905–918. doi:10.1111/j.1365-2699.2008.02053.x

Coops, N.C., Wulder, M.A., Iwanicka, D., 2009b. Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. Remote Sens. Environ. 113, 668–679. doi:10.1016/j.rse.2008.11.012

Danilkin, A.A., 2008. Climate and efficiency of vegetation as factors of number dynamics and areas wild ungulates in Russia. Vestn. ohotovedeniya 5, 251–260 (In Russian).

Danilkin, A.A., 1999. Mammals in Russia and adjacent regions. Deer (Cervidae). Moscow: GEOS, Moscow (In Russian).

Division, U.N.S., 2016. National accounts main aggregates database [WWW Document]. https://unstats.un.org/unsd/snaama/selbasicFast.asp.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). 36, 027–046. doi:10.1111/j.1600-0587.2012.07348.x

Draper, N.R., Smith, H., 1998. Applied regression analysis, third edit. ed. John Willey & Sons, Inc, New York.

Draper, N.R., Smith, H., 1966. Applied regression analysis. John Willey & Sons, Inc, New York.

Ensing, E.P., Ciuti, S., De Wijs, F.A.L.M., Lentferink, D.H., Hoedt, A., Boyce, M.S., Hut, R.A., 2014. GPS based daily activity patterns in european red deer and North American elk (Cervus elaphus): Indication for a weak circadian clock in ungulates. PLoS One 9, 1–11. doi:10.1371/journal.pone.0106997

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., Huang, X., 2010. MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets. Remote Sens. Environ. 114, 168–182. doi:10.1016/j.rse.2009.08.016

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–7. doi:10.1038/35012228

Gubar, Y.P., Borisov, B.P., Volodina, O.A., Lomanov, I.K., Lomanova, N.V., Mezhnev, A.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., Tcarev, S.A., 2007. Status of resources game animals in Russian Federation 2003-2007. Information & analytical materials. Moscow (In Russian).

Hansen, M.C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L., Justice, C.O., Townshend, J.R.G., 2014. High-Resolution Global Maps of 850, 850–854. doi:10.1126/science.1244693

Harrell, F.E., Dupon, C., 2016. Harrell Miscellaneous. R package version 4.0-0.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G., 2003a. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84, 3105–3117. doi:10.1890/03-8024

Hawkins, B.A., Porter, E.E., Diniz, J.A.F., 2003b. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. Ecology 84, 1608–1623.

Hebblewhite, M., Merrill, E.H., 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90, 3445–3454. doi:10.1890/08-2090.1

Herfindal, I., Nilsen, E.B., Andersen, R., Linnell, J.D.C., Odden, J., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). J. Zool. 265, 63–71. doi:10.1017/S0952836904006053

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. doi:10.1002/joc.1276

Hird, J.N., McDermid, G.J., 2009. Noise reduction of NDVI time series: An empirical comparison of selected techniques. Remote Sens. Environ. 113, 248–258. doi:10.1016/j.rse.2008.09.003

Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M., Radeloff, V.C., 2017. A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. Remote Sens. Environ. 195, 142–152. doi:10.1016/j.rse.2017.04.018

Kerr, J.T., Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. Trends Ecol. Evol. 18, 299–305. doi:10.1016/S0169-5347(03)00071-5

Kuzyakin, V.A., 1983. Winter track count in the government system for counting the game resources of Russian Soviet Federative Socialist Republic, in: Winter Track Counts of Game Animals (in Russian). pp. 3–18.

Lavsund, S., Nygrén, T., Solberg, E.J., 2003. Status of Moose Populations and Challenges to Moose Management in Fennoscandia. Alces 39, 109–130.

Lomanov, I.K., 2000. Winter transect count of game animals for large territories: Results and prospects. Zool. Zhurnal 79, 430–436 (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mezhnev, A.P., Mezhneva, O.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., 2004. Status of resources game animals in Russian Federation 2000-2003. Information & analytical materials. Moscow (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mezhnev, A.P., Mezhneva, O.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., 2000. Status of resources game animals in Russian Federation. Information & analytical materials. Moscow (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Novikov, G.V., Ovsyukova, N.Y., 1996. Resources of main game species and hunting grounds in Russia (1991-1995 years). Moscow (In Russian).

Lomanova, N.V., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lyapina, M.G., Komissarov, M.A., Mosheva, T.S., Naumova, A.A., Sidorov, S.V., Tcarev, S.A., Yudina, T.V., Fokin, S.Y., Blohin, Y.Y., Zverev, P.A., Kozlova, M.V., Mezhnev, A.P., Romanov, Y.M., 2011. Status of resources game animals in Russian Federation 2008-2010. Information and analytical materials. Moscow (In Russian).

Lumley, T., 2009. Regression subset selection. R package version 2.9.

MacNally, R., 1996. Hierarchical partitioning as an interpretative tool in multivariate inference. Austral Ecol. 21, 224–228. doi:10.1111/j.1442-9993.1996.tb00602.x

Massei, G., Genov, P. V, Staines, B.W., 1996. Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriol. (Warsz). 41, 307–320. doi:10.4098/AT.arch.96-29

Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V.E., Zawadzka, B., Zhyla, S., 2009. Predation has a greater impact in less productive environments: Variation in roe deer, *Capreolus capreolus*, population density across Europe. Glob. Ecol. Biogeogr. 18, 724–734. doi:10.1111/j.1466-8238.2009.00480.x

Melis, C., Szafrańska, P.A., Jędrzejewska, B., Bartoń, K., 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia 803–811. doi:10.1111/j.1365-2699.2006.01434.x

Michaud, J.S., Coops, N.C., Andrew, M.E., Wulder, M.A., Brown, G.S., Rickbeil, G.J.M., 2014. Estimating moose (*Alces alces*) occurrence and abundance from remotely derived environmental indicators. Remote Sens. Environ. 152, 190–201. doi:10.1016/j.rse.2014.06.005

Milner, J.M., van Beest, F.M., Solberg, E.J., Storaas, T., 2013. Reproductive success and failure: The role of winter body mass in reproductive allocation in Norwegian moose. Oecologia 172, 995–1005. doi:10.1007/s00442-012-2547-x

Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S., Musiani, M., 2013. Humans Strengthen Bottom-Up Effects and Weaken Trophic Cascades in a Terrestrial Food Web. PLoS One 8. doi:10.1371/journal.pone.0064311

Nagendra, H., 2001. Using remote sensing to assess biodiversity, review article. Int. J. Remote Sens. 22, 2377–2400. doi:10.1080/0143116001

Polis, G.A., 1999. Why Are Parts of the World Green? Multiple Factors Control Productivity and the Distribution of Biomass. Oikos 86, 3–15.

Prishchepov, A. V, Müller, D., Dubinin, M., Baumann, M., Radeloff, V.C., 2013. Determinants of agricultural land abandonment in post-Soviet European Russia. Land use policy 30, 873–884. doi:10.1016/j.landusepol.2012.06.011

Prishchepov, A. V, Radeloff, V.C., Baumann, M., Kuemmerle, T., Daniel, M., 2012. Effects of institutional changes on land use: agricultural land abandonment during the transition from state-command to market-driven economies in post-Soviet Eastern Europe. Environ. Res. Lett. 7. doi:10.1088/1748-9326/7/2/024021

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ribeiro, R.J., Diggle, P.J., 2016. Analysis of Geostatistical Data. R package version 1.7-5.2.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., Lambin, E., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J., 2009. Planetary boundaries: Exploring the safe operating space for humanity. Ecol. Soc. 14. doi:10.1038/461472a

Rosstat, 2010. Regions of Russia. Socio-Economic Indicators. Moscow: Russian Federal Service of State Statistics.

Sanderson, E.W., Jaiten, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The Human Footprint and the Last of the Wild. Bioscience 52, 891. doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Savtchenko, A., Ouzounov, D., Ahmad, S., Acker, J., Leptoukh, G., Koziana, J., Nickless, D., 2004. Terra and Aqua MODIS products available from NASA GES DAAC. Adv. Sp. Res. 34, 710–714. doi:10.1016/j.asr.2004.03.012

Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G., Myslenkov, A.I., Hayward, G.D., 2006. Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereleshin formula. Anim. Conserv. 9, 339–348. doi:10.1111/j.1469-1795.2006.00044.x

Suttidate, N., 2016. Spatial patterns of primary productivity derived from the Dynamic Habitat Indices predict patterns of species richness and distributions in the tropics. Doctoral thesis submitted at the University of Wisconsin - Madison.

Testa, J.W., Adams, G.P., 1998. Body Condition and Adjustments to Reproductive Effort in Female Moose (*Alces alces*). J. Mammal. 99518, 1345–1354. doi:10.2307/1383026

Timmermann, H.R., McNicol, J.G., 1988. Moose Habitat Needs. For. Chron. 64, 238–245. doi:10.5558/tfc64238-3

Turner, W., 2014. Sensing biodiversity. Science. 346, 301–302. doi:10.1126/science.1256014

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. Trends Ecol. Evol. 18, 306–314. doi:10.1016/S0169-5347(03)00070-3 van Beest, F.M., Mysterud, A., Loe, L.E., Milner, J.M., 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J. Anim. Ecol. 79, 910–922. doi:10.1111/j.1365-2656.2010.01701.x

Walsh, C., Mac Nally, R., 2013. Hierarchical Partitioning. R package version 1.0-4.

Wittemyer, G., 2011. Effects of Economic Downturns on Mortality of Wild African Elephants. Conserv. Biol. 25, 1002–1009. doi:10.1111/j.1523-1739.2011.01713.x

Wright, D.H., 1983. Species-energy theory: an extension of species–area theory. Oikos 41, 496–506.

Table 1: Environmental variables from WorldClim.

Variables	**Description**
BIO1	annual mean temperature (^{o}C*10),
BIO2	mean diurnal range (mean of monthly(max-min) (^{o}C*10))
BIO3	isothermally (mean diurnal range/ temperature annual range)
BIO4	temperature seasonality (standard deviation*100)
BIO5	maximum temperature of the warmest month (^{o}C*10)
BIO6	minimum temperature of the coldest month (^{o}C*10)
BIO7	temperature annual range (maximum temperature of warmest month minimum temperature of coldest month (^{o}C*10))
BIO8	mean temperature of wettest quarter (^{o}C*10)
BIO9	mean temperature of driest quarter (^{o}C*10)
BIO10	mean temperature of warmest quarter (^{o}C*10)
BIO11	mean temperature of coldest quarter (^{o}C*10),
BIO12	annual precipitation (mm)
BIO13	precipitation of wettest month (mm)
BIO14	precipitation of driest months (mm)
BIO15	precipitation seasonality (coefficient of variation)
BIO16	precipitation of wettest quarter (mm)
BIO17	precipitation of driest quarter (mm),
BIO18	precipitation of warmest quarter (mm)
BIO19	precipitation of coldest quarter (mm)

Table 2: Bayesian Information Criteria (BIC), adjusted coefficient of determination (R^2_{adj}), and the root mean square error (RMSE) for top performing models with the DHIs covering the whole time period 1981-2010.

Model	**BIC**	**∆BIC**	**R^2_{adj}**	**RMSE [ind./km^2]**
DHI Cum+ BIO1+BIO7+ human footprint	23.59	0	0.79	0.24
DHI Cum+ BIO1+BIO4	24.97	1.38	0.77	0.25
BIO5+BIO9	33.18	9.59	0.73	0.28
DHI Var+ BIO1+BIO4	33.21	9.62	0.74	0.27
DHI Min+ BIO1+BIO4	36.23	12.64	0.73	0.27

Table 3: Bayesian Information Criteria (BIC), adjusted coefficient of determination (R^2_{adj}), and the root mean square error (RMSE) for the three time periods.

Period (years)	**Model**	**BIC**	**R^2_{adj}**	**RMSE [ind./km^2]**
First (1981-1990)	DHI Cum+ BIO1+BIO4	23.49	0.81	0.25
Second (1991-2000)	DHI Cum+ BIO1+BIO4	35.05	0.73	0.27
Third (2001-2010)	DHI Cum+ BIO1+BIO4	42.25	0.67	0.29

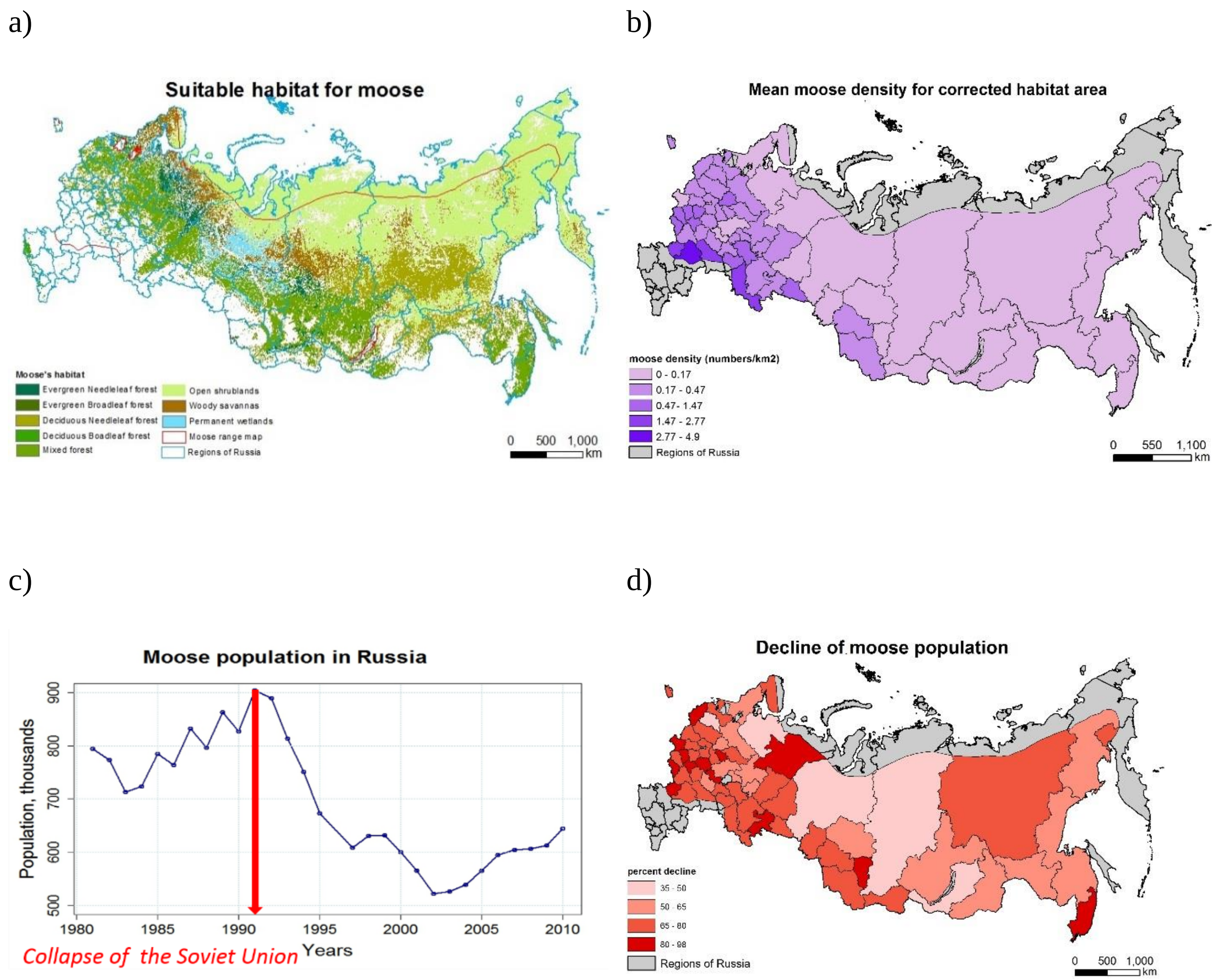


Figure 1: a) Suitable habitat for moose based on MODIS stable land cover data from 2003 to 2012, moose range map are shown in red, b) moose density (individuals per 1 km^2) based on suitable habitat within the moose range area, c) the trend of moose population for Russia from 1981 to 2010, d) the decline of moose population over Russia.

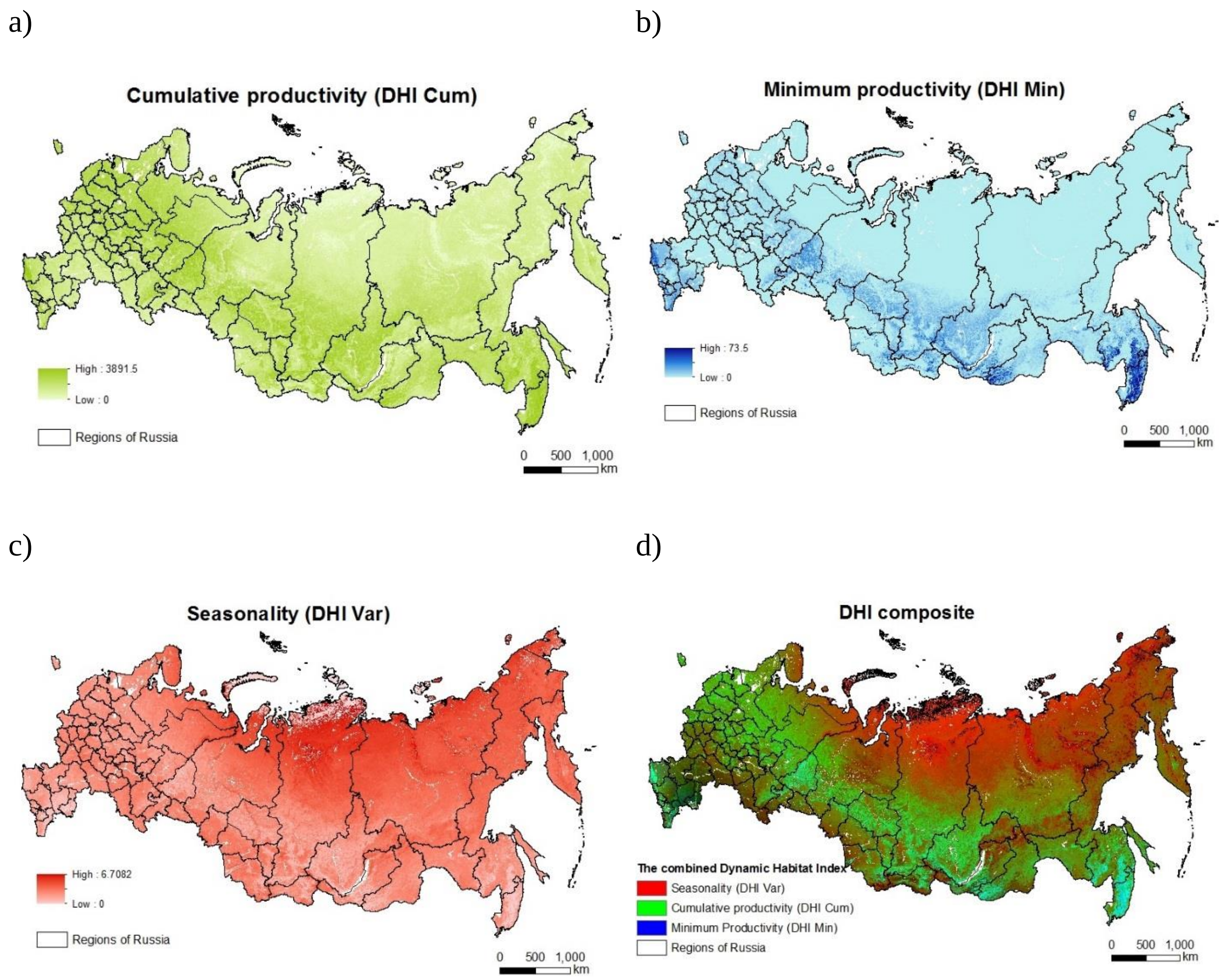


Figure 2: The Dynamic habitat indices based on FPAR with 8-day temporal resolution: a) Cumulative Productivity - DHI Cum, b) Minimum productivity - DHI Min, c) Seasonality - DHI Var and d) The three DHIs, cumulative productivity, minimum productivity, and seasonality, displayed in Green, Blue, Red. The boundaries of regions of Russia are shown in black. Areas with white color are no data.

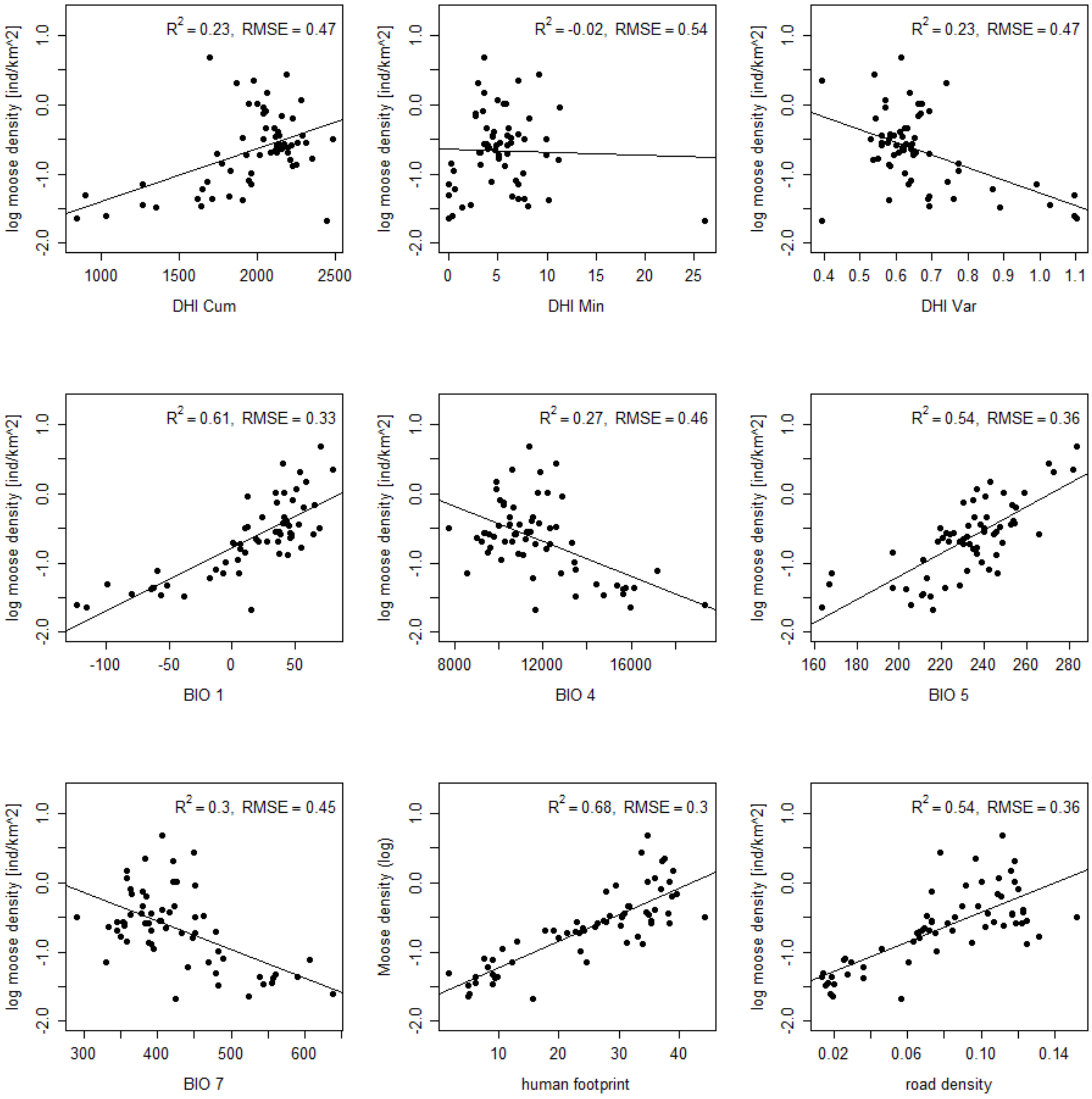
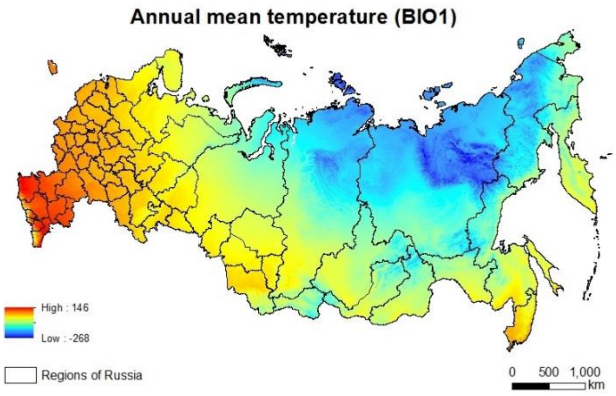
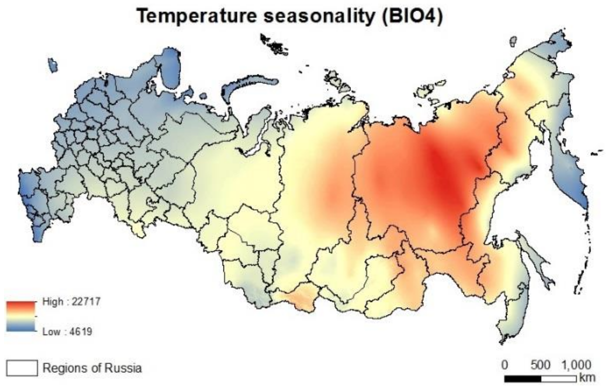


Figure 3: Relationship between log-transformed moose density (individuals per 1 km^2) from 1981 to 2010 and cumulative productivity (DHI Cum), minimum productivity (DHI Min), seasonality (DHI Var), annual mean temperature (BIO1), temperature seasonality (BIO4), maximum temperature of warmest month (BIO5), temperature annual range (BIO7), human footprint, and road density.

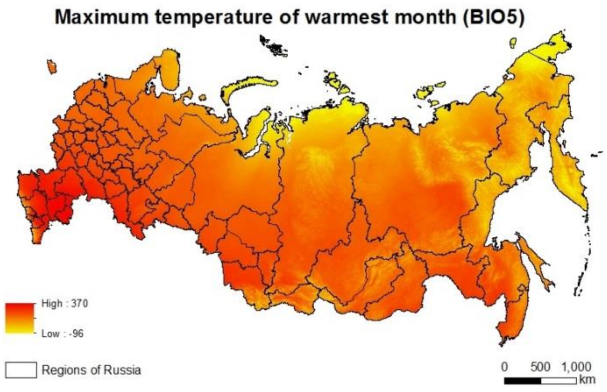
a)


Annual mean temperature (BIO1)
High : 146
Low : -268
Regions of Russia
0 500 1,000
km

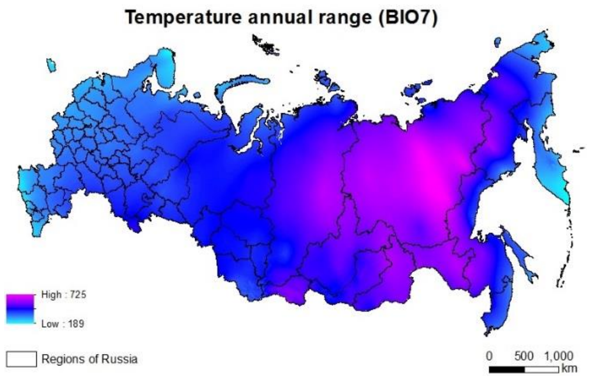
b)


Temperature seasonality (BIO4)
High : 22717
Low : 4619
Regions of Russia
0 500 1,000
km

c)


Maximum temperature of warmest month (BIO5)
High : 370
Low : -96
Regions of Russia
0 500 1,000
km

d)


Temperature annual range (BIO7)
High : 725
Low : 189
Regions of Russia
0 500 1,000
km

e)


Human footprint
High : 100
Low : 0
Regions of Russia
0 500 1,000
km

f)


Roads
Roads
Regions of Russia
0 500 1,000
km

Figure 4: Most important explanatory variables for moose density: a) annual mean temperature (BIO1), b) temperature seasonality (BIO4), c) maximum temperature of warmest month (BIO5), d) temperature annual range (BIO7), e) human footprint, f) roads are shown in white.

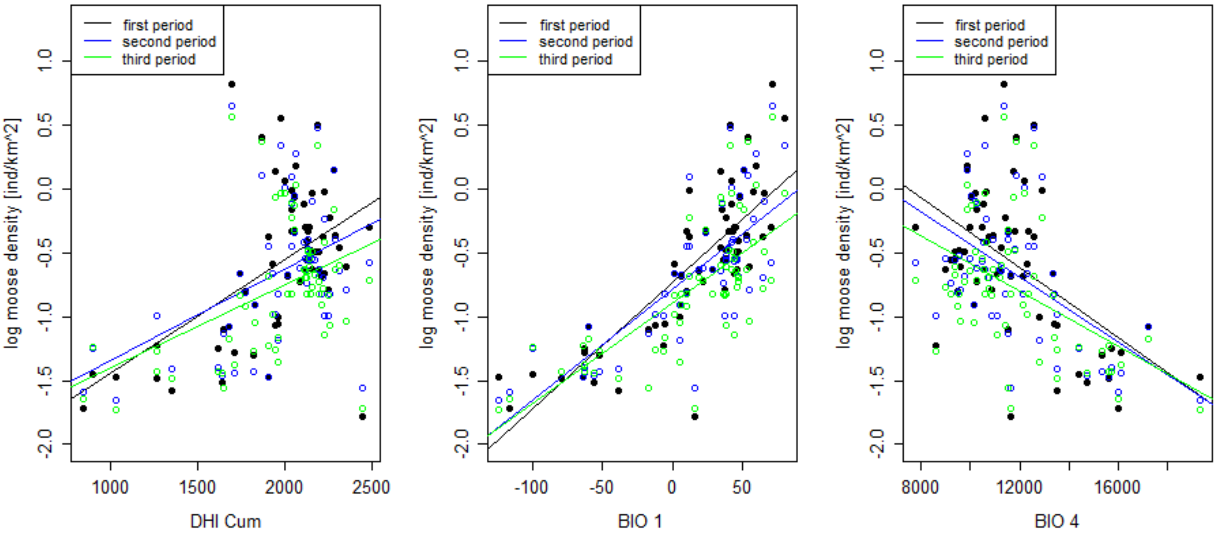


Figure 5: Relation between log-transformed moose density (individuals per 1 km^2) for the three periods and cumulative productivity (DHI Cum), annual mean temperature (BIO1), temperature seasonality (BIO4).

Supplementary materials

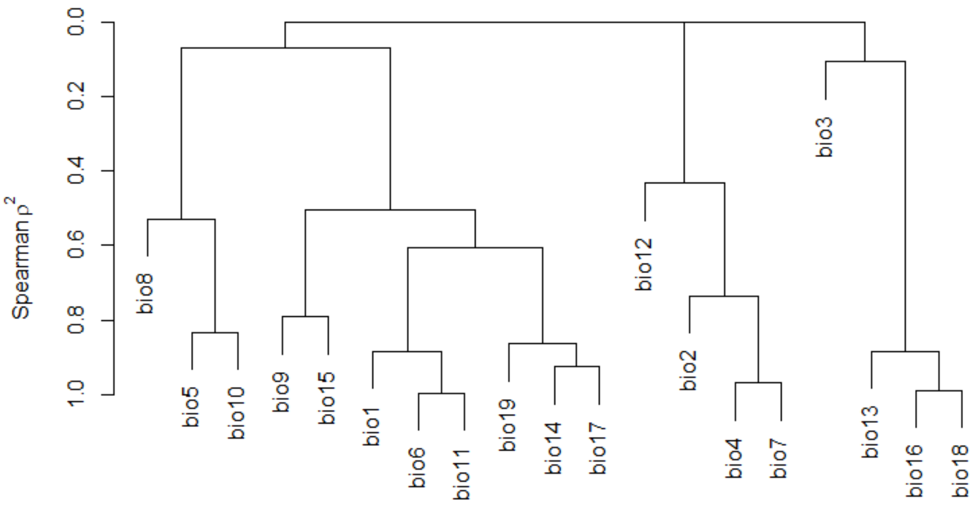


Figure S1: A hierarchical cluster analysis for the environmental variables from WorldClim using the squared Spearman's rank correlation coefficient.

Chapter 3: Difference in the relationships of the abundances of eight mammal species with remotely sensed indices in Russia

Abstract

The density of wildlife populations can vary greatly in space, mainly due to differences in both environmental conditions and human activities. Our main goal here was to examine the relationship of densities of eight large mammal species with different remotely sensed indices. We analyzed average densities, and population trends across Russia from 1981 to 2010 based on Winter Track Count censuses. Our eight species represented different trophic levels and included omnivores, herbivores, carnivores: brown bear (*Ursus arctos*), wild boar (*Suc scrofa*), European hare (*Lepus europaeus*), moose (*Alces alces*), roe deer (*Capreolus pygargus Pallas, Capreolus capreolus Linnaeus*), lynx (*Felis lynx*), red fox (*Vulpes vulpes*), and wolf (*Canis lupus*). Populations of brown bear, roe deer, wild boar, and wolf significantly increased, while populations of European hare, lynx, and moose significantly decreased within the studied time period. To determine the main factors shaping density patterns in Russia we used multiple linear regression and best subset model selection. We included as predictor variables the Dynamic Habitat Indices (DHIs), which capture food availability; the duration of snow-free and snow-covered ground, and the timing of the frozen season as a proxy for winter severity; elevation and BIOCLIM to reflect climate; and human footprint, and road density as proxies for human disturbance. For all species, model fit was high (R^2_{adj} ranged from 0.61 to 0.94), however which variables were selected for the top models varied greatly among the species. To our surprise we found that the DHIs were selected in the top models not only for herbivores and omnivores, but also for all carnivores, with the exception of lynx. Winter-related variables were included in the models for all species, except lynx. In general, the pattern of animal density was found to be similar to the pattern of primary productivity, indicating how plant productivity is shaping animal density at different trophic level. Our results highlight the high importance of variables related to human disturbance for carnivores and herbivores for explaining the declining trends. The remote sensing indices that we tested provided considerable explanatory power in our models of mammal density, especially when used in combination with climate data and measures of human disturbance. Our results have implications for management and conservation practices of game species over large territories, e.g. while making decision for hunting quotas at regional level.

Keywords

Animal abundance, Dynamic Habitat Indices, winter track count, Russia, carnivores, omnivore, herbivore, brown bear (*Ursus arctos*), European hare (*Lepus europaeus*), lynx (*Felis lynx*), moose (*Alces alces*), roe deer (*Capreolus pygargus Pallas, Capreolus capreolus Linnaeus*), red fox (*Vulpes vulpes*), wild boar (*Suc scrofa*), and wolf (*Canis lupus*).

Introduction

The density of wildlife species can vary greatly in space and time (Currie et al., 1993). In some areas animal density is high, as in tropical forest, other areas have a limited number of species such as tundra and Polar regions. Major factors for the variability of animal density are environmental conditions and human activities (Melis et al., 2009; Muhly et al., 2013). Understanding the relative importance of environmental conditions and human activities for the spatial patterns of wildlife density is thus key for proper management and the conservation of wildlife. Remote sensing is an ideal tool to conduct such an assessment because satellite data and derived data products provide valuable information about habitat conditions including land cover maps, measurements of primary productivity, information characterizing snow cover and patterns of freeze and thaw, and human disturbances across large areas (Kerr and Ostrovsky, 2003; Turner, 2014; Turner et al., 2003).

What controls animal density is a central question in ecology, and different factors matter in different areas and for different species. One group of mechanisms is related to food availability resulting in bottom-up effects, in which plant productivity controls the density of herbivores, and herbivore density controls carnivore density (Scherber et al., 2010). Closely related to food availability (Currie et al., 1993) is home range size for those species that are territorial. With more available food home range size tends to be smaller, leading to higher animal density (Desy et al., 1990; Herfindal et al., 2005; McLoughlin and Ferguson, 2000; Morellet et al., 2013; Tufto et al., 1996). There are many factors influencing home range sizes of species such as the species diet, their habitat location and their position within the food chain. The relationship between home-range size and body size depends for example on the different trophic levels (McLoughlin and Ferguson, 2000), so that carnivores tend to have larger home ranges, and hence lower densities than their prey. Also larger-bodied species have to consume more food to meet their metabolic requirements than smaller species (McLoughlin and Ferguson, 2000) A species home range size depends on the location of the habitat the species is living in too, because home ranges of species living in high latitudes tend to be larger than of those closer to the equator (McLoughlin and Ferguson, 2000; McNab, 1963; Morellet et al., 2013; Peters and Wassenberg, 1983; Ripple and Beschta, 2012). And last but not least, there are also top-down effects when predators control population of herbivores and thereby vegetation patterns (Hairston et al., 1960; Ripple and Beschta, 2012).

Animal densities are also strongly affect by survivorship during the most challenging seasons of the year, and for mammal species living in northern climates this is typically winter time. For example, whether or not the ground is covered with snow when temperatures drop below freezing makes a big difference, because snow cover maintains more stable temperatures for both soils and plants, due to its low thermal conductivity (Formozov, 2010; Pomeroy and Brun, 2001). Furthermore, depth and density of snow cover have an influence on animal movements, ability to reach food under layers of snow, and the ability of small mammals to tunnel under the snow. Indeed, for some animal snow cover is necessary for reproduction and survival, for example, the Arctic lemmings (Gilg et al., 2012), and often snow is the only source of available moisture for animals when surface water is frozen. Thus, the role of snow and snow cover is important but also rather complex. Unfortunately, climate change has rapidly changed winter conditions (Gilg et al., 2012; Safronov, 2016; Williams et al., 2015). Due to global warming there is an increase in precipitations especially during winter, and an increase in frequency and magnitude of extreme events (Safronov, 2016).

We captured both food availability and winter conditions with newly developed remote sensing indices. To capture food availability, we analyzed the Dynamic Habitat Indices (DHIs) as a proxy of availability of energy, environmental stress and environmental stability (Radeloff et al., n.d.). This DHIs summarize three measures of vegetation productivity over a course of the year: cumulative productivity (DHI Cum), minimum productivity (DHI Min), and seasonality or variation (DHI Var). The DHIs have proven to be good predictors of avian species richness in Ontario, Canada (Coops et al., 2009b), the USA (Coops et al., 2009a; Hobi et al., 2017), and Thailand (Suttidate, 2016), as well as for butterfly species diversity in Canada (Andrew et al., 2012), and for moose occurrence and abundance in Ontario, Canada (Michaud et al., 2014). To capture winter conditions, we analyzed a new global dataset characterizing winter related variables derived from satellite observations including the duration of frozen ground with and without snow cover, and the timing (start date, length, and end date) of the frozen season with 500 m spatial resolution (Zhu et al., 2017). These new winter-related remote sensing indices have not yet been related to wildlife populations, and while the DHIs have been tested, most of the tests have been for species richness, not wildlife densities.

Our main goal was to evaluate the utility of remote sensing indices in models of animal density across Russia. We focused on eight mammals with different life history representing herbivores, omnivore, and predators. We hypothesized that among the three DHIs cumulative productivity would be the most important. We expected higher densities of European hare, roe deer, moose for regions with higher DHI Cum. Also, we hypothesized that the DHIs would be important in models for herbivores but not for carnivores because of herbivore's dependence on vegetation as food. For wild boar we expected to see a strong negative correlation with the duration of snow-covered ground and the length of the frozen season because boar frequently root in the ground to forage. For lynx, red fox, and wolf we expected that snow cover, i.e., the duration of snow-covered ground, to be a strong positive correlate, because of their ability to travel on top of snow, while their prey cannot.

Methods

Study area

The vast territories of Russia provide a great opportunity to answer our research questions because they harbor broad ranges of vegetation, and climate conditions, and because of the availability of long-term data for game species. Moreover, Russia had experienced economic, political, and social changes during our study period, which affected human population and wildlife as well. This matters for wildlife populations because it is common that people overexploit natural resources during economic downturn and institutional changes (Bragina et al., 2015; Wittemyer, 2011).

Wildlife species' densities, and range maps

We focused on eight species with different life history including brown bear (*Ursus arctos*), European hare (*Lepus europaeus*), lynx (*Felis lynx*), moose (*Alces alces*), red fox (*Vulpes vulpes*), roe deer (*Capreolus pygargus Pallas, Capreolus capreolus Linnaeus*), wild boar (*Suc scrofa*), and wolf (*Canis lupus*). Wildlife population totals for each year and region were provided by the Russian Federal Agency of Game animals from 1981 to 2010 (Borisov et al., 1992; Gubar et al., 2007; Lomanov et al., 2004, 2000, 1996; Lomanova et al., 2011). Data are collected mainly using winter track counts (Kuzyakin, 1983; Lomanov, 2000). For remote or hard-to-reach areas airplane and hunter's surveys were conducted (Lomanov et al., 1996). Unlike other species, brown bear hibernates during winter, which means that other methods were employed to estimate the bear population, in particular mapping of home ranges and aerial survey (Gubar, 1990).

After the collapse of the Soviet Union in 1991 some regions of Russia were subdivided. In order to be consistent and analyze all data for the thirty years of our study, we merged those separated regions to make them comparable to the pre-1991 administrative boundaries. In total, we included 39 regions in our analysis for brown bear, 50 regions for European hare, 53 for lynx, 62 for moose, 71 for red fox, 48 for roe deer, 64 for wild boar and 69 for wolf (Table 4). We excluded regions with only a few years of available data.

Some of Russia's regions are large, and may only partly be within the range of a given wildlife species. We thus needed to restrict the area for which the predictor variables were summarized, and the area that was used to convert the population totals into densities. In order to do so, we compared several sources of range maps including those from the IUCN Red List, and others published in the Soviet and Russian literature, and by the Russian Academy of Science. Ultimately, for brown bear and European hare we used range maps from the Russian Academy of Science (Pavlov et al., 2002), for lynx and wolf from IUCN (IUCN, 2001), red fox range maps came from Soviet literature (Geptner et al., 1967), for wild boar and roe deer our source was Russian literature (Danilkin, 2002, 1999), and for moose it was the Game animal's analytical material (Lomanov et al., 1996). Data for roe deer represented two species *Capreolus pygargus Pallas* and *Capreolus capreolus Linnaeus*, which are not separated in the game surveys, and therefore we combined their range maps.

Dynamic Habitat Indices

The Dynamic Habitat Indices contain three components of different measurement of vegetative productivity: annual cumulative productivity (DHI Cum), annual minimum productivity (DHI Min), and seasonal variation (DHI Var). To calculate the DHIs we used MODIS Fraction of Absorbed Photosynthetically Active Radiation (FPAR) provided by the MCD15A2 data product with 1-km spatial and 8-day temporal resolution for 2003-2014. We summed up all FPAR values for annual cumulative productivity (DHI Cum); selected the minimum value for annual minimum productivity (DHI Min); and calculated coefficient of variation for seasonality (DHI Var). Missing values of DHI Min due to polar nights are set to zero. For all analyses we used the composite product which is based on median FPAR values between 2003 and 2014 (For further information of the calculation see Hobi et al., 2017).

Land cover

We used MODIS land cover with 17 classes based on the International Geosphere-Biosphere Programme Classification with 500 m spatial resolution. We derived a map of stable land cover for the period 2003-2012, for which we set the change threshold to 50%, that is to say we allowed changes in land cover classes for up to half of the time period (Figure 6). Based on this land cover information we defined the suitable habitat for each species (Table 5) and calculated the areal extent of suitable habitat within the range map (Table 4).

Winter's variables

The severity of winter conditions varies greatly across Russia. In some regions animals spend half of the year overwintering. To characterize winter, we used a recently completed dataset with 500 m spatial resolution that provided data on the duration of snow-covered ground (dws), the duration of snow-free frozen ground (dwos), the timing (start and end date) and the length of the frozen season from 2000-2012 (Zhu et al., 2017). There are no data for dwos and dws above 62^0N due to polar night. We calculated mean values for all winter-related variables within suitable habitat for each animal species.

Human disturbance

We included two variables in our analysis as proxies of human disturbance: human footprint and road density. Human footprint index (HFI) was downloaded from http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic and has a 1 km spatial resolution (Sanderson et al., 2002). The HFI was created from nine data layers including human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers) (Sanderson et al., 2002). We calculated mean values for HFI within range map for each species. Vectorized road data were downloaded from DIVA-GIS (http://www.diva-gis.org). The road density by region was calculated by normalizing the length of roads by the area of the regions. The density of roads in a region is a good indicator of how developed a region is. We performed all calculations in Albers equal area conic projection (Datum D European 1950).

Elevation, climatic variables

Elevation and climate data, i.e., the nineteen BIOCLIM variables, were downloaded from WorldClim with 1-km spatial resolution (Hijmans et al., 2005). Eleven of the BIOCLIM variables were related to temperature, and eight to precipitation (Table 6). The elevation data used in the WorldClim is based on Shuttle Radar Topography Mission (SRTM). We calculated mean values per region for all variables within suitable habitat for each species.

Statistical analyses

To analyze population trends of the mammal species and test if these trends are significant, we summed up the results of winter track count (population total) for all regions for a given year. Then we fitted a liner regression of the population totals as a function of time from 1981 to 2010, and tested if the slope was significantly different from zero.

To relate species population densities to our predictor variables, we applied multivariable linear regression and best subset model selection. Our dependent variable was the species population density, which we calculated by dividing the regional population total by the area of suitable habitat in that region and for that species. Our explanatory variables were the DHIs, road density, human footprint, elevation, temperature, precipitation, duration with snow-free frozen ground, duration of snow-covered ground, the timing and the length of the frozen season and of snow cover. To meet the assumptions of multiple linear regression we applied log-transformation for brown bear, lynx, moose, red fox, roe deer, wolf. We ran Bonferroni outlier tests (Cook and Weisberg, 1982) to detect outliers in the models, which we then excluded. Specifically, we detected the following outliers: Kabardino-Balkaria for brown bear, Tyumen region for European hare and Orenburg for lynx. Also, we removed 5 regions from the analysis for European hare where the species was introduced. In order to detect multicollinearity, we calculated Pearson's correlation coefficients among all explanatory variables. Some of our explanatory variables were highly correlated, especially BIOCLIM variables. After fitting a model with all the explanatory variables, we used best subset regression for each species to identify those variables that were most commonly included in the top models. We ranked models based on the Bayesian Information Criteria (BIC), and calculated the adjusted coefficient of determination (R^2_{adj}) for the top model to estimate how much of the variation in density of a given species our variables were able to explain (Burnham and Anderson, 2002). However, the top model based on BIC criterion does not always result in the highest R^2_{adj}. Also, we calculated variance inflation factor (VIF) for the top model in order to see how much collinearity we have.

We performed all analyses in R version 3.3.1 (R Core Team, 2016), specifically the psych package (Revelle, 2017) to calculate correlation matrices, the leaps package (Lumley, 2009) to perform best subset selection and the car package (Fox and Weisberg, 2016) to run Bonferroni outlier test to identify outliers and calculate variance inflation factor (VIF) for explanatory variables included into the top model.

Results

Spatial pattern of the explanatory variables

The DHIs captured the broad patterns of primary productivity across Russia well. Mixed forest, deciduous needle leaf forest, and deciduous broad leaf forest in the Caucasus and in the southern Primorsky Krai had the highest DHI Cum. DHI Min had the highest values in southern Russia, especially in southern part of Krasnodar Krai, in Primorsky Krai, Zabaykalskiy Krai, Sverdlovskaya Oblast where climate is mild. Mixed forest were the most common land cover type where DHI Min was high. DHI Var had the highest values in the tundra of northern Siberia and Chukotka (Figure 7a).

Duration of snow-free frozen ground (dwos) had the highest values in south part of Russia (Caucasus region) and south east of the Asian part of Russia. Duration of snow-covered ground (dws) showed the highest value toward the north, north east part of Russia, also at higher elevation (Figure 7b). Highest values for start of frozen season were located in European part of Russia and in areas close to the sea. Both length and the end of frozen season were inversely related to start of the frozen season, and had the highest values in East Siberia.

Areas with high elevation are located in the south of Russia (Caucasus), between European part and Asian part of Russia (Ural Mountains), East Siberia (Altai Mountains, Verkhoyansk Range, Sayan Mountains, Chersky Range), Far East (Sikhote-Alin) (Figure 7c). Annual mean temperature (BIO1) increases from north-east to south of Russia, the coldest places are located in Yakutia (Figure 7d). Annual mean precipitation also increases from north-east to south of Russia, the highest amount of precipitation can be found in the Caucasus region, Primosky Krai, Khabarovsk Krai, and Kamchatka Krai (Figure 7e). Human footprint index (HFI) has the highest values in European part of Russia, where most of human population of Russia live.

Wildlife population trends

To understand the nature and the significance of species population trends, we fitted the data with a simple linear regression and checked the p-value for the coefficient for the slope. We found that brown bear, roe deer, wild boar and wolf populations significantly increased (p-value<<0.05) while European hare, lynx, and moose significantly decreased, and red fox increased but not significantly so (p-value = 0.157) (Figure 8). However, population trend fluctuated greatly for all the species over time, and most species had population drops after the collapse of Soviet Union in 1991, with the exception of wolf, which increased in the post-collapse period. The largest population declines occurred for European hare and lynx, whose populations declined by 62% and 61.7% from 1980 levels, respectively.

Using MODIS stable land cover map, we calculated the areal extent of suitable habitat within range map for all the species, and total area of the regions included in the analysis (Table 4). Based on our calculations wolf, red fox, and moose have the greatest amount of suitable habitat among the studied species of 16.0 million km^2, 15.9 million km^2, and 10.6 million km^2, respectively. For most species the total area within range and area of suitable habitat were fairly similar. For example, the total range area for European hare was 3 million km^2 while suitable habitat was 2.8 million km^2 (96%). However, lynx and brown bear habitat was only 52% and 59% of their total range.

Variation in animal density

The density of the studied species varied greatly over the territory of Russia. In general, the pattern of animal density was similar to pattern of primary productivity, which increased from north or north-east toward the south. Generally, the species density was much higher in the European part of Russia compared to the Asian part. The density for lynx, roe deer, and wild boar was higher in regions with higher values of DHI Min. In some regions, for example in the Kamchatka Krai and Magadan oblast we identified only a relatively small areas of suitable habitat for brown bear and lynx. That is why the density for brown bear and lynx in these regions was very high. European hare density increased from its northern boundary of the range map toward its southern boundary.

We used best subset selection to identify which explanatory variables were the most significant ones and could explain great portions of variation in species density. Our models performed very well, and all of our explanatory variables were important at least for some species. The adjusted coefficient of variation (R^2_{adj}) was high for all the models, ranging from 0.61 to 0.94. However, there was a considerable variability in which variables were selected in the top models of different species (Figure 9). For all carnivores HFI and temperature related variables were included in the models for most species, and the DHIs and winter related variables were important for red fox and wolf, but not for lynx. Altitude, temperature related variables, and winter related variables were included in top models for omnivores (wild boar and brown bear), and the DHIs were included for wild boar. For herbivores some temperature and precipitation related variables were included in top models, and HFI and winter related variables were included in the models of the declining herbivore populations (European hare and moose), and DHI Min in model for moose.

Discussion

Our main goal of this study was to assess the value of several new remotely sensed indices in models of species density for a range of mammals capturing different trophic levels, i.e., omnivores, carnivores, and herbivores. We found that both the DHIs and the winter-related variables contributed greatly to our multivariate models and provided complementary information to climate and human disturbance related variables. Together, our suite of variables explained the variation in species density well, with R^2_{adj} ranging from 0.61 to 0.94. Which subset of predictors was most useful in explaining species density was greatly dependent on the focus species.

Vegetation productivity was one of the main explanatory variables of animal density. Across Russia animal density was higher in regions with higher DHI Cum, mostly in the European part of Russia where the climate is relatively mild, and growing seasons are longer. Interestingly, the densities for brown bear and lynx were high for Magadan Oblast and Kamchatka Krai. It seems that particularly for these regions more land cover classes should be included in the definition of suitable habitat; both regions have mountains, probably, a combination of complex landscape elements with open shrub lands is preferably used by brown bear and lynx. Unexpectedly, the DHIs could explain parts of the species density not only for herbivores and omnivores, but also for all carnivores except lynx. This suggests that primary productivity can also be a limiting factor for predators, and that the effects of productivity propagate through the food chain. Such bottom-up effects are more pronounced when a population reaches carrying capacity, and are weak when population levels are very low (Currie et al., 1993; Lawton, 1990). Our result that primary productivity was not significant for lynx makes good sense given the strong declines in lynx populations, which occurred despite the concomitant increases of roe deer populations, one of lynx' main prey species (Odden et al., 2006; Okarma et al., 1997). However, we note that another important prey species, i.e., hare, also declined. Lynx population dynamics are often cyclical depending on the cycles of its prey (Matyushkin and Vaisfeld, 2003), and the reproductive rate of lynx responds strongly to prey decline (Okarma et al., 1997).

We were also surprised to see that the DHIs were not included in models of roe deer and brown bear, even though a previous study showed that roe deer abundance was positively correlated with vegetation productivity (Melis et al., 2009). Our explanation for this is that roe deer prefers forest edges (Danilkin, 1999), and we were not able to determine this preferable habitat with the MODIS land cover data due to their relatively coarse resolution (500 m). Furthermore, we could only analyze roe deer as one species, but in reality there are two species which are different in size and habitat preferences. In case of brown bear other factors influence brown bear population (in our model, altitude, temperature related variables, and winter related variables), and the bear's great dietary flexibility may reduce the importance of primary productivity even though the bulk of their diet is typically plant-based.

Wildlife population density highly depends on the quality and quantity of available food. However, winter is often a time of high mortality, and both snow cover and frozen ground can be important limiting factors (Danilkin, 2008). We found that for all species except for lynx winter related variables were contributing to explain their density. Our results indicate that how tolerant or adapted a given species is to winter conditions can be an important driver of contemporary patterns of wildlife densities in Russia. Indeed, the northern limit of roe deer range is determined by snow depth of 50 cm and 60 cm for European and Siberian roe deer, respectively (Danilkin, 1999; Grøtan et al., 2005).

Climate is a well-known driver of animal density (Michaud et al., 2014; Skidmore et al., 2003). Indeed, temperature and precipitation were included in all models for all species. We will not discuss why a particular variable is important for species, however, we will discuss the effect of climate change on animals. Climate change has already had major influence on wildlife population (Baskin, 1996; Gilg et al., 2012; Rempel, 2011; Safronov, 2016; Stepanova and Ohlopkov, 2010). We speculate that there may be a link between the increase in brown bear, roe deer, and wild boar population and climate change. For example, the population of red deer is increasing in Yakutia and extending its range toward northeast due to climate change (Safronov, 2016).

Human activities, can also greatly affect densities, both by bottom-up mechanisms when food availability is altered due to land use change (Foley et al., 2005; Kehoe et al., 2015) or by top-down effects through overharvesting or poaching (Muhly et al., 2013; Okarma et al., 1997). In our analysis we found that HFI was included in top models for those herbivore species that are declining, i.e., European hare and moose; and for all carnivores, i.e., lynx, red fox, and wolf irrespective of their population trends. The other indication for strong top-down effects of humans on wildlife populations is what happened in the politically unstable period after the collapse of the Soviet Union in 1991, when animal population rapidly dropped for all species except for wolf (Bragina et al., 2015). However, while most species recovered since, the population of lynx continues to decline rapidly, and the European hare population is consistently low. In general, lynx is a vulnerable animal; it’s population can decrease rapidly under unfavorable conditions (Matyushkin and Vaisfeld, 2003), and there are probably many factors which have had negative effect on lynx population, including anthropogenic and natural, such as the effects of increasing wolf populations.

We see some limitations of our study and want to elaborate on them here. In our analysis we used an animal density averaged over 30 years, but the density was changing over time and mean values are not meaningful in this case. There are several limitations of WTC data: data cannot be collected in regions without snow cover or dense snow (Mirutenko et al., 2009); possible data errors made by humans during collection, processing and reporting; changing quality of WTC over time due to political and economic changes in Russia.

Knowing the factors influencing animal density is important when it comes to making recommendations for management of wildlife despite limitation of our analysis and WTC data. While making a decision about hunting quotas, it is important to take into account losses of animals due to illegal hunting or poaching; recommended hunting quotas should be lowered in years with low plant productivity and harsh winter. To stabilize a declining mammal population our suggestions would be to reduce hunting quotas, particularly, at the northern border of the species range. Other recommendations are to increase anti-poaching activity in regions with low animal density and provide supplementary feeding during winter for regions with limited food resources (where DHI Min has the lowest values). A monitoring program for lynx should be established to get more information related to the interaction between wolf and lynx. In case of a continuing decline in the lynx population, temporary or complete prohibition of hunting for this species should be implemented in regions where suitable habitat areas are limited.

In summary, we suggest that using remote sensing indices including the DHIs and winter-related variables can be an effective tool for explaining animal density for species at different trophic level. In this study we showed that a combination of remote sensing indices and land cover together with climate and human-related variables has high explanatory power. The DHIs provided valuable information about primary productivity while winter-related variables provide important information about the effect of winter on species survival. Moreover, both remote sensing datasets are available globally free of charge.

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References

Andrew, M.E., Wulder, M.A., Coops, N.C., Baillargeon, G., 2012. Beta-diversity gradients of butterflies. Glob. Ecol. Biogeogr. 21, 352–364. doi:10.1111/j.1466-8238.2011.00676.x

Baskin, L.M., 1996. Brown bear in Russia: has it the future? Bulleten' Mosk. Obs. Ispit. Prir. Otd. Biol. 101, 18–29.

Borisov, B.P., Gibet, L.A., Gubar, Y.P., Kukushkin, M.A., Mosheva, T.S., Nazarov, A.A., Naumov, A.A., Novikov, B.V., Petrashov, V.V., Paponov, V.A., Tomilova, T.P., 1992. Fond of hunting grounds and number of main wild species in Russian Soviet Federative Socialist Republic. Moscow (In Russian).

Bragina, E. V., Ives, A.R., Pidgeon, A.M., Kuemmerle, T., Baskin, L.M., Gubar, Y.P., Piquer-Rodriguez, M., Keuler, N.S., Petrosyan, V.G., Radeloff, V.C., 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. Conserv. Biol. 29, 844–853. doi:10.1111/cobi.12450

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed), Ecological Modelling. doi:10.1016/j.ecolmodel.2003.11.004

Cook, R.D., Weisberg, S., 1982. Residuals and Influence in Regression, Monographs on Statistics and Applied Probability. Charman and Hall. doi:10.2307/1269506

Coops, N.C., Waring, R.H., Wulder, M.A., Pidgeon, A.M., Radeloff, V.C., 2009a. Bird diversity: A predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. J. Biogeogr. 36, 905–918. doi:10.1111/j.1365-2699.2008.02053.x

Coops, N.C., Wulder, M.A., Iwanicka, D., 2009b. Exploring the relative importance of satellite-derived descriptors of production, topography and land cover for predicting breeding bird species richness over Ontario, Canada. Remote Sens. Environ. 113, 668–679. doi:10.1016/j.rse.2008.11.012

Currie, D.J., Fritz, J.T., Currie, D.J., Fritz, J.T., Global, J.T., 1993. Global Patterns of Animal Abundance and Species Energy Use. Nord. Soc. Oikos 67, 56–68.

Danilkin, A.A., 2008. Climate and efficiency of vegetation as factors of number dynamics and areas wild ungulates in Russia 5, 251–260.

Danilkin, A.A., 2002. Mammals in Russia and adjacent regions. Pigs (Suidae). Moscow: GEOS, Moscow (In Russian).

Danilkin, A.A., 1999. Mammals in Russia and adjacent regions. Deer (Cervidae). Moscow: GEOS, Moscow (In Russian).

Desy, E.A., Batzli, G., Liu, J., 1990. Effects of Food and Predation on Behaviour of Prairie Voles: A Field Experiment. Nord. Soc. Oikos 58, 159–168.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global Consequences of Land Use. Science. 309, 570–575.

Formozov, A.N., 2010. Snow cover in the ecology of mammals and birds, 3rd ed. LKI, Moscow (In Russian).

Fox, J., Weisberg, S., 2016. Companion to Applied Regression.

Geptner, V.G., Naumov, N.P., Yurgenson, P.B., Sludskiy, A.A., Chirkova, A.F., Bannikov, A.G., 1967. Mammals of the Soviet Union. Sea cows and predators, Volume 2. ed. Vysshaya shkola, Moscow (In Russian).

Gilg, O., Kovacs, K.M., Aars, J., Gauthier, G., Gr, D., Ims, R.A., Meltofte, H., Post, E., Schmidt, N.M., 2012. Climate change and the ecology and evolution of Arctic. Ann. N. Y. Acad. Sci. 1249, 166–190. doi:10.1111/j.1749-6632.2011.06412.x

Grøtan, V., Sæther, B.-E., Engen, S., Solberg, E.J., Linnell, J.D.C., Andersen, R., Brøseth, H., Lund, E., 2005. Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. Ecology 86, 1472–1482.

Gubar, Y.P., 1990. Guidelines for brown bear population assessment. Moscow (In Russian).

Gubar, Y.P., Borisov, B.P., Volodina, O.A., Lomanov, I.K., Lomanova, N.V., Mezhnev, A.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., Tcarev, S.A., 2007. Status of resources game animals in Russian Federation 2003-2007. Information & analytical materials. Moscow (In Russian).

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community Structure, Population Control, and Competition. Am. Nat. 94, 421–425.

Herfindal, I., Nilsen, E.B., Andersen, R., Linnell, J.D.C., Odden, J., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J. Zool. 265, 63–71. doi:10.1017/S0952836904006053

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. doi:10.1002/joc.1276

Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M., Radeloff, V.C., 2017. A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. Remote Sens. Environ. 195, 142–152. doi:10.1016/j.rse.2017.04.018

IUCN, 2001. The IUCN red list of threatened species [WWW Document]. URL http://www.iucnredlist.org/ (accessed 1.5.17).

Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Vaclavik, T., Kreft, H., 2015. Global pattern of argicultural land-use intensity and vertebrate diversity. Divers. Distrib. 21, 1308–1318. doi:10.1111/ddi.12359

Kerr, J.T., Ostrovsky, M., 2003. From space to species: ecological applications for remote sensing. Trends Ecol. Evol. 18, 299–305. doi:10.1016/S0169-5347(03)00071-5

Kuzyakin, V.A., 1983. Winter track count in the government system for counting the game resources of Russian Soviet Federative Socialist Republic, in: Winter Track Counts of Game Animals (in Russian). pp. 3–18.

Lawton, J.H., 1990. Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space. Philos. Trans. Biol. Sci. 330, 283–291.

Lomanov, I.K., 2000. Winter transect count of game animals for large territories: Results and prospects. Zool. Zhurnal 79, 430–436 (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mezhnev, A.P., Mezhneva, O.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., 2004. Status of resources game animals in Russian Federation 2000-2003. Information & analytical materials. Moscow (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mezhnev, A.P., Mezhneva, O.P., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Paponov, V.A., Sigolaeva, E.A., Sidorov, S.V., 2000. Status of resources game animals in Russian Federation. Information & analytical materials. Moscow (In Russian).

Lomanov, I.K., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lomanova, N.V., Mirutenko, V.S., Molochaev, A.V., Mosheva, T.S., Naumova, A.A., Novikov, G.V., Ovsyukova, N.Y., 1996. Resources of main game species and hunting grounds in Russia (1991-1995 years). Moscow (In Russian).

Lomanova, N.V., Borisov, B.P., Volodina, O.A., Gubar, Y.P., Lyapina, M.G., Komissarov, M.A., Mosheva, T.S., Naumova, A.A., Sidorov, S.V., Tcarev, S.A., Yudina, T.V., Fokin, S.Y., Blohin, Y.Y., Zverev, P.A., Kozlova, M.V., Mezhnev, A.P., Romanov, Y.M., 2011. Status of resources game animals in Russian Federation 2008-2010. Information and analytical materials. Moscow (In Russian).

Lumley, T., 2009. Regression subset selection. R package version 2.9.

Matyushkin, Y.N., Vaisfeld, M.., 2003. The Lynx. Moscow Nauka, Moscow.

McLoughlin, P.D., Ferguson, S.H., 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience.Sainte-Foy 7, 123–130. doi:10.2307/42902482

McNab, B.K., 1963. Bioenergetics and the Determination of Home Range Size. Am. Nat. 894, 133–140.

Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V.E., Zawadzka, B., Zhyla, S., 2009. Predation has a greater impact in less productive environments: Variation in roe deer, Capreolus capreolus, population density across Europe. Glob. Ecol. Biogeogr. 18, 724–734. doi:10.1111/j.1466-8238.2009.00480.x

Michaud, J.S., Coops, N.C., Andrew, M.E., Wulder, M.A., Brown, G.S., Rickbeil, G.J.M., 2014. Estimating moose (Alces alces) occurrence and abundance from remotely derived environmental indicators. Remote Sens. Environ. 152, 190–201. doi:10.1016/j.rse.2014.06.005

Mirutenko, V.S., Lomanova, N.V., Bersenev, A.E., Morgunov, N.A., Volodina, O.A., Kuzyakin, V.A., Chelintsev, N.G., 2009. Guidelines for organization, conducting, and processing winter track count data for game species. Moscow (In Russian).

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J.D.C., Nicoloso, S., Sustr, P., Urbano, F., Mysterud, A., 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. J. Anim. Ecol. 82, 1326–1339. doi:10.1111/1365-2656.12105

Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S., Musiani, M., 2013. Humans Strengthen Bottom-Up Effects and Weaken Trophic Cascades in a Terrestrial Food Web. PLoS One 8. doi: 10.1371/journal.pone.0064311

Odden, J., Linnell, J.D.C., Andersen, R., 2006. Diet of Eurasian lynx, Lynx lynx , in the boreal forest of southeastern Norway : the relative importance of livestock and hares at low roe deer density. Eur J Wildl Res 52, 237–244. doi:10.1007/s10344-006-0052-4

Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R., Jędrzejewska, B., 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. Acta Theriol. (Warsz). 42, 203–224.

Pavlov, D.S., Petrosyan, V.G., Dgebuadze, U.U., Reshetnikov, U.S., Kuzmin, S.L., Varshavskiy, A.A., Korneeva, T.M., Pavlov, A.V., Bessonov, S.A., Veprintseva, O.D., Omelchenko, A.V., Pavlinov, I.J., Orlova, V.F., Loskot, V.M., Dorofeeva, E.A., Sideleeva, V.., 2002. Biodiversity of vertebrates in Russia [WWW Document]. URL http://www.sevin.ru/vertebrates/ (accessed 2.20.17).

Peters, R.H., Wassenberg, K., 1983. The effect of body size on animal abundance. Oecologia 60, 89–96.

Pomeroy, J.W., Brun, E., 2001. Physical Properties of Snow, in: Jones H.G., Pomeroy J.W., Walker D.A., H.R.W. (Ed.), Snow Ecology. An Interdisciplinary Examination of Snow-Covered Ecosystems. Cambridge University Press, Cambridge, UK, pp. 45–126.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Radeloff, V.C., Dubinin, M., Coops, N.C., Allen, A., Brooks, T.M., Clayton, M., Costa, G., Graham, C., Ives, A.R., Kolesov, D., Kuemmerle, T., Pidgeon, A.M., Rapacciuolo, G., Razenkova, E., Rondinini, C., Suttidate, N., Young, B., Zhu, L., M. Hobi, n.d. The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity. Prep.

Rempel, R.S., 2011. Effects of climate change on moose populations: Exploring the response horizon through biometric and systems models. Ecol. Modell. 222, 3355–3365. doi:10.1016/j.ecolmodel.2011.07.012

Revelle, W., 2017. Procedures for Psychological, Psychometric, and Personality Research.

Ripple, W.J., Beschta, R.L., 2012. Large predators limit herbivore densities in northern forest ecosystems. Eur J Wildl Res 58, 733–742. doi:10.1007/s10344-012-0623-5

Safronov, V.M., 2016. Climate Change and Mammals of Yakutia. Biol. Bull. 43, 1256–1270. doi:10.1134/S1062359016110121

Sanderson, E.W., Jaiten, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The Human Footprint and the Last of the Wild. Bioscience 52, 891. doi:10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., Konig, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Muller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M., Tscharntke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556. doi:10.1038/nature09492

Skidmore, A.K., Oindo, B.O., Said, M.Y., 2003. Biodiversity Assessment by Remote Sensing. Proc. 30th Int. Symp. Remote Sens. Environ. Inf. risk Manag. Sustain. Dev. 1–4.

Stepanova, V.., Ohlopkov, I.M., 2010. Range and abundance of red deer in Yakutia. Geogr. Nat. Resour. 4, 95–100.

Suttidate, N., 2016. Spatial patterns of primary productivity derived from the Dynamic Habitat Indices predict patterns of species richness and distributions in the tropics. Doctoral thesis submitted at the University of Wisconsin - Madison.

Tufto, J., Andersen, R., Linnell, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J. Anim. Ecol. 65, 715–724.

Turner, W., 2014. Sensing biodiversity. Science. 346, 301–302. doi:10.1126/science.1256014

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. Trends Ecol. Evol. 18, 306–314. doi:10.1016/S0169-5347(03)00070-3

Williams, C.M., Henry, H.A.L., Sinclair, B.J., 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biol. Rev. 90, 214–235. doi:10.1111/brv.12105

Wittemyer, G., 2011. Effects of Economic Downturns on Mortality of Wild African Elephants. Conserv. Biol. 25, 1002–1009. doi:10.1111/j.1523-1739.2011.01713.x

Zhu, L., Radeloff, V.C., Ives, A.R., 2017. Characterizing global patterns of frozen ground with and without snow cover using microwave and MODIS satellite data products. Remote Sens. Environ. 191, 168–178. doi:10.1016/j.rse.2017.01.020

Table 4: Overview of the number of regions used for different parts of the analysis. Area of suitable habitat within the regions and total area.

Species	**Number of regions included in analysis**	**Number of regions included in range map**	**Number of regions excluded from analysis (outliers)**	**Number of regions with no data or few available years**	**Area of suitable habitat (million km^2)**	**Total area without outliers (million km^2)**
Brown bear	39	50	1	10	7.03	11.88
European hare	50	59	1+5(introduced)	3	2.80	2.92
Lynx	53	65	1	11	6.97	13.26
Moose	62	62	0	0	10.62	13.64
Red fox	71	71	0	0	15.86	16.15
Roe deer	48	59	0	11	3.98	4.89
Wild boar	64	65	0	1	4.95	5.77
Wolf	69	70	0	1	16.18	16.46

Table 5: Suitable habitat based on the MODIS IGBP land cover classification for brown bear, European hare, lynx, moose, red fox, Roe deer, wild boar, and wolf. 0- class was not considered suitable habitat; 1- class was included as suitable habitat.

Land cover classes	**Brown bear**	**European hare**	**Lynx**	**Moose**	**Red fox**	**Roe deer, wild boar**	**Wolf**
0-water	0	0	0	0	0	0	0
1 -evergreen needle leaf forest	1	1	1	1	1	1	1
2-evergreen broadleaf forest	1	1	1	1	1	1	1
3- deciduous needle leaf forest	1	0	1	1	1	1	1
4-deciduous broadleaf forest	1	1	1	1	1	1	1
5-mixed forest	1	1	1	1	1	1	1
6-closed shrub lands	0	0	0	0	0	0	1
7-open shrub lands	0	0	0	1	1	0	1
8-woody savannas	1	0	1	1	1	1	1
9-savannas	1	0	1	0	1	1	1
10-grassland	0	1	0	0	1	0	1
11-permanent wetland	1	0	1	1	1	1	1
12-cropland	0	1	0	0	1	1	1
13-urban and built-up	0	0	0	0	0	0	0
14-cropland/natural vegetation mosaic	1	1	0	0	1	1	1
15-snow and ice	0	0	0	0	0	0	0
16-barren or sparsely vegetated	0	0	0	0	0	0	1

Table 6: Summary of explanatory variables indicating their spatial resolution and the sources from which they were downloaded.

Data	**Resolution**	**Source**
Dynamic Habitat Indices (DHIs)	1-km	http://silvis.forest.wisc.edu/data/DHIs
Duration of snow-free frozen ground (dwos), duration of snow-covered frozen ground (dws), start, length, and end of frozen season	500 m	http://silvis.forest.wisc.edu
Temperature and Precipitation from BIOCLIM	1-km	http://www.worldclim.org
Elevation	1-km	http://www.worldclim.org
Human footprint index (HFI)	1-km	http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic
Roads	-	http://www.diva-gis.org

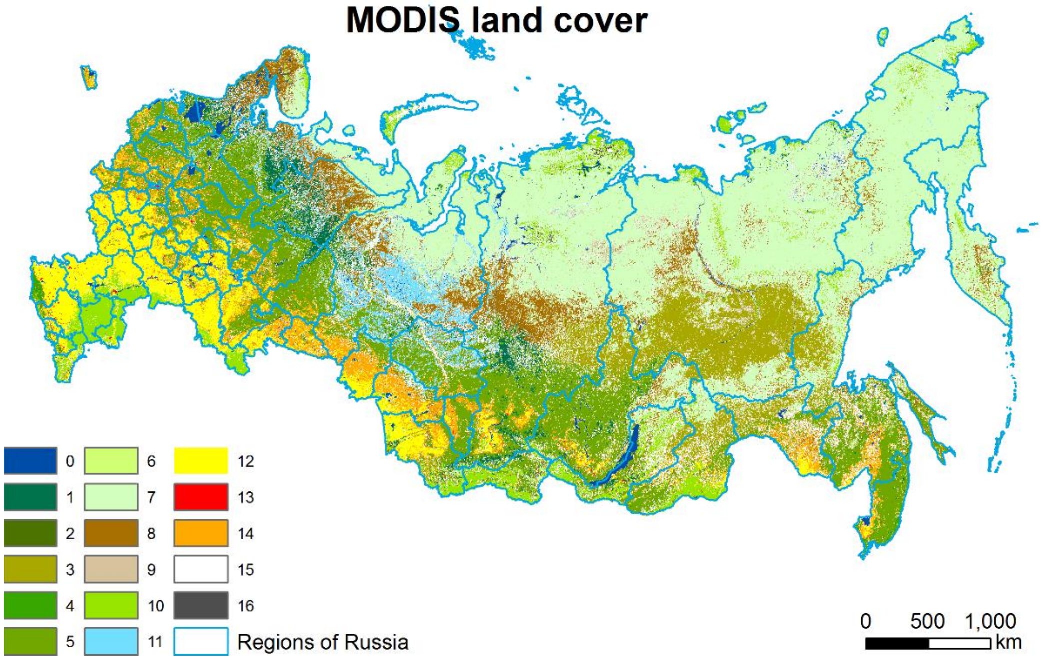


Figure 6: MODIS land cover based on IGBP classification for the regions of Russia: 0-water, 1-evergreen needle leaf forest, 2-evergreen broadleaf forest, 3-deciduous needle leaf forest, 4-deciduous broadleaf forest, 5-mixed forest, 6-closed shrub lands, 7-open shrub lands, 8-woody savannas, 9-savannas, 10-grassland, 11-permanent wetland ,12-cropland, 13-urban and built-up, 14-cropland/natural vegetation mosaic, 15-snow and ice, 16-barren or sparsely vegetated.

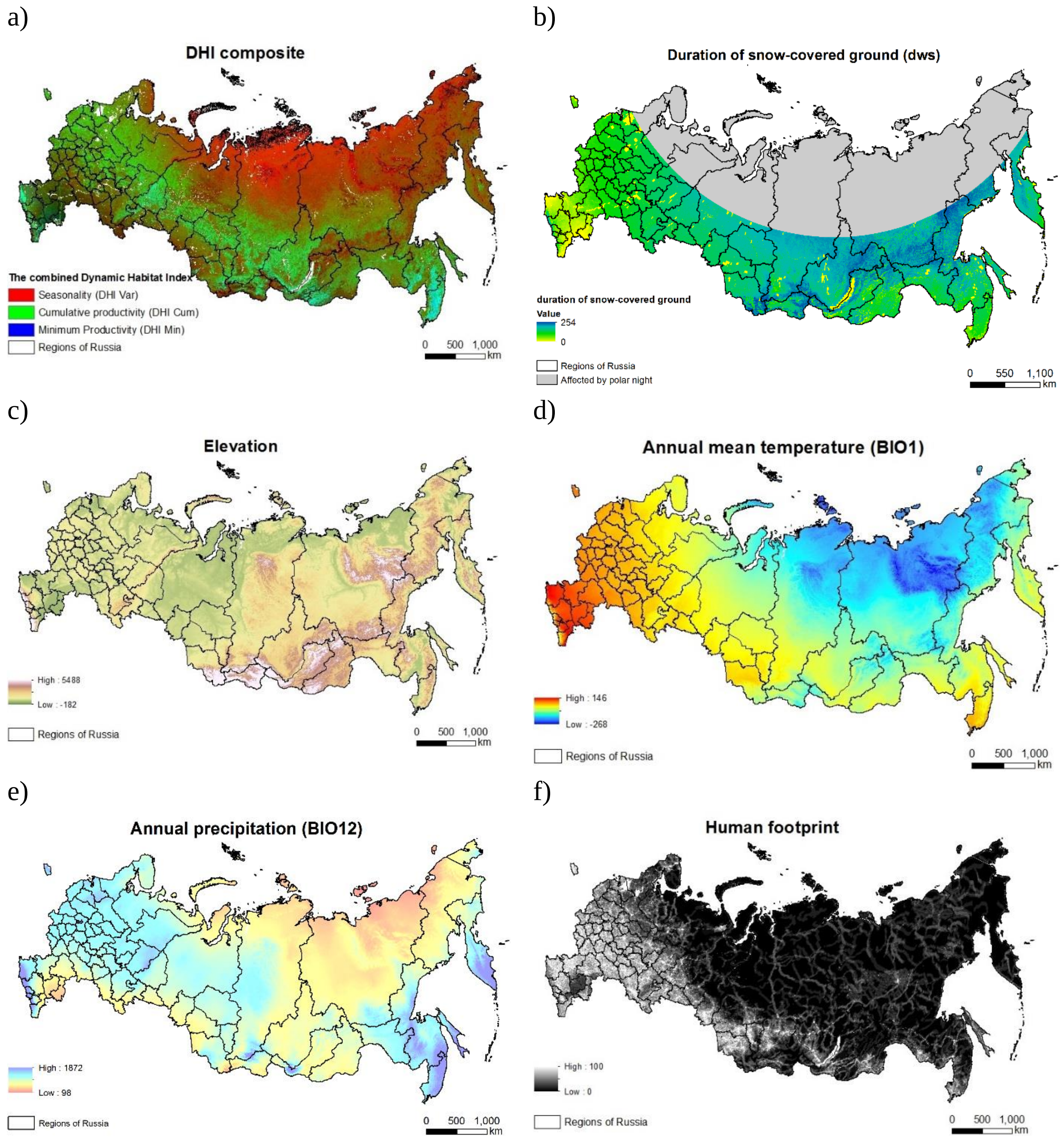
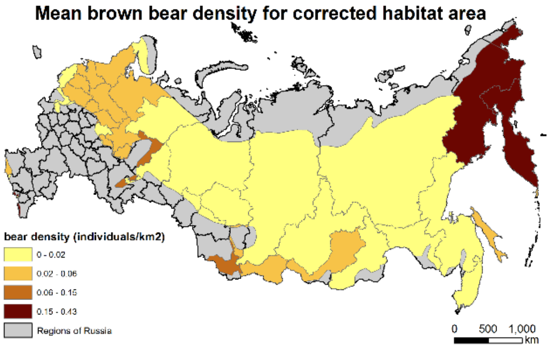
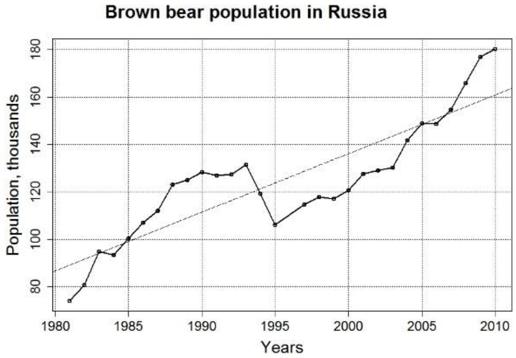
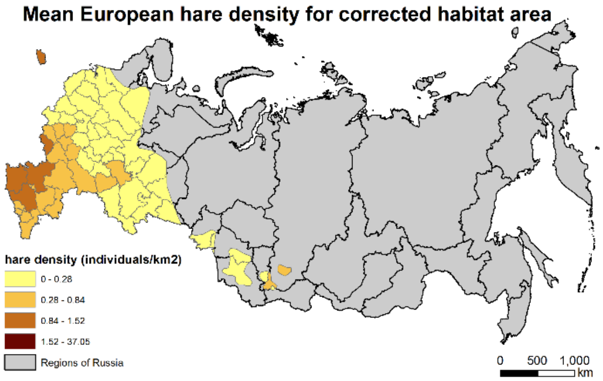
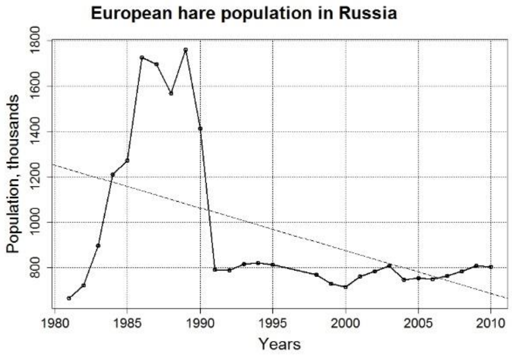


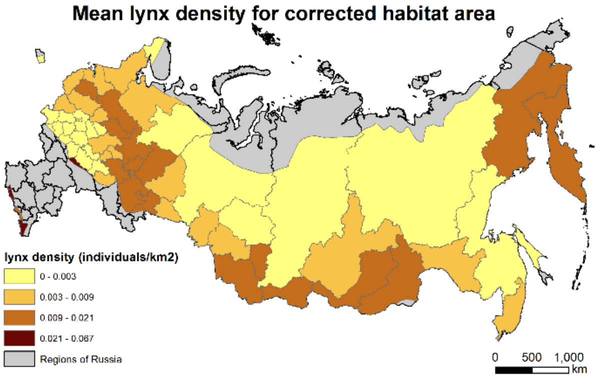
Figure 7: Some explanatory variables: a) the Dynamic Habitat Indices are shown in RGB where DHI Var was assigned to red, DHI Cum to green, DHI Min to blue; b) duration of snow-covered ground; c) elevation above sea level (m) from SRTM; d) annual mean temperature (BIO1) (°C*10); e) annual precipitation (BIO12) (mm); f) human footprint index (HFI).

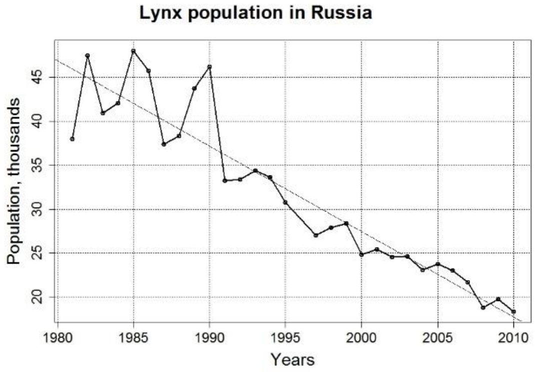

Mean brown bear density for corrected habitat area

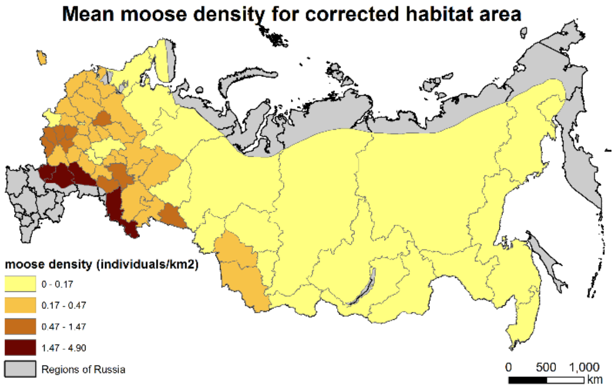

Brown bear population in Russia

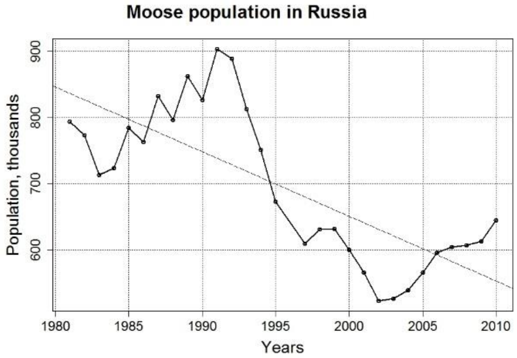

Mean European hare density for corrected habitat area


European hare population in Russia


Mean lynx density for corrected habitat area


Lynx population in Russia


Mean moose density for corrected habitat area


Moose population in Russia

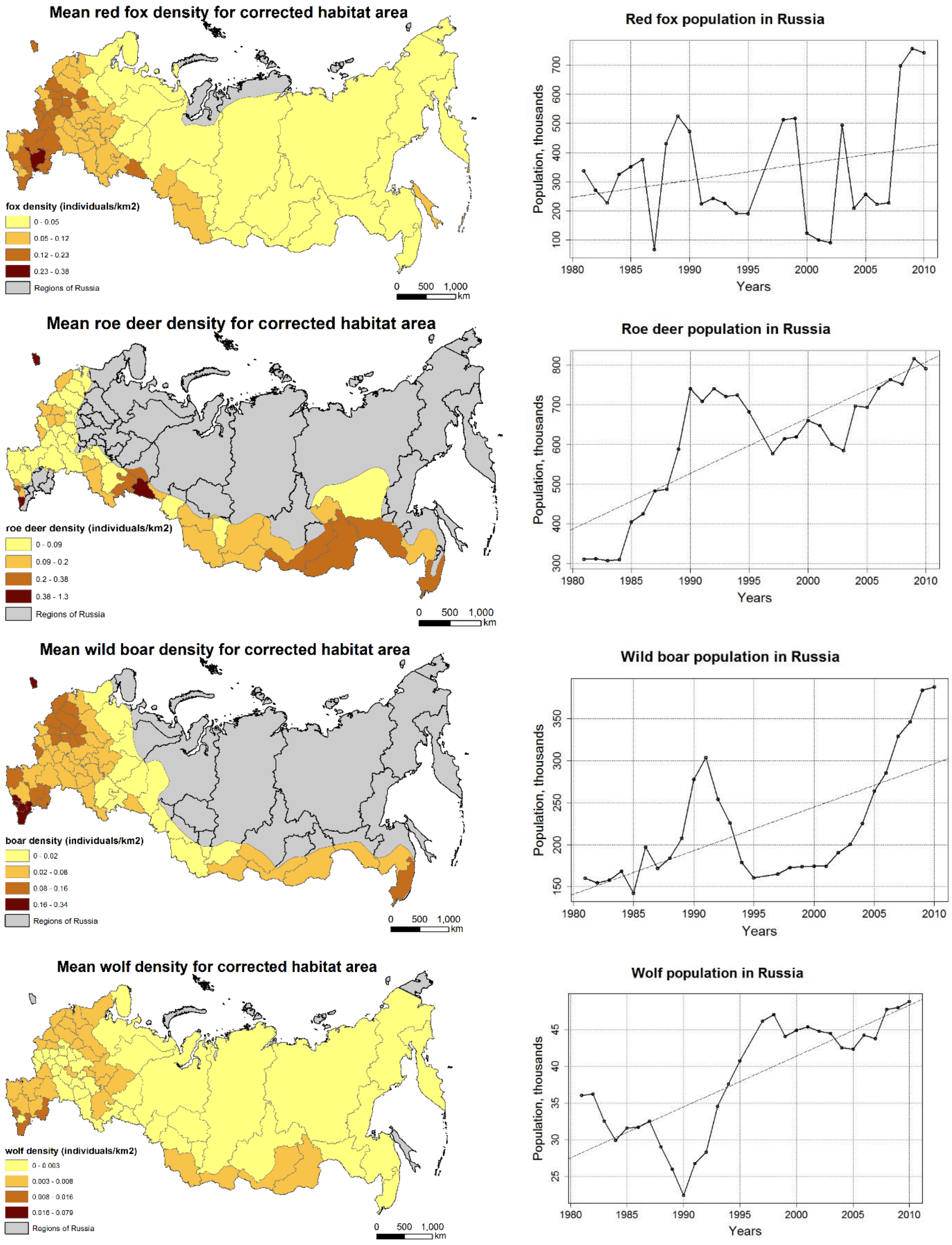
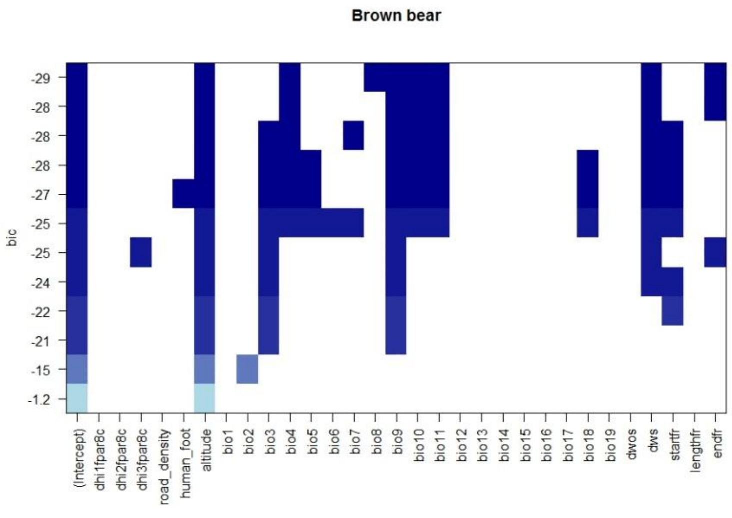
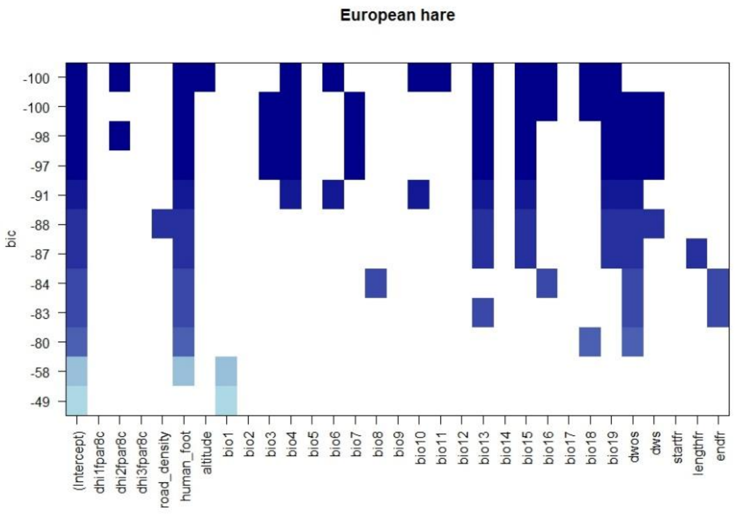


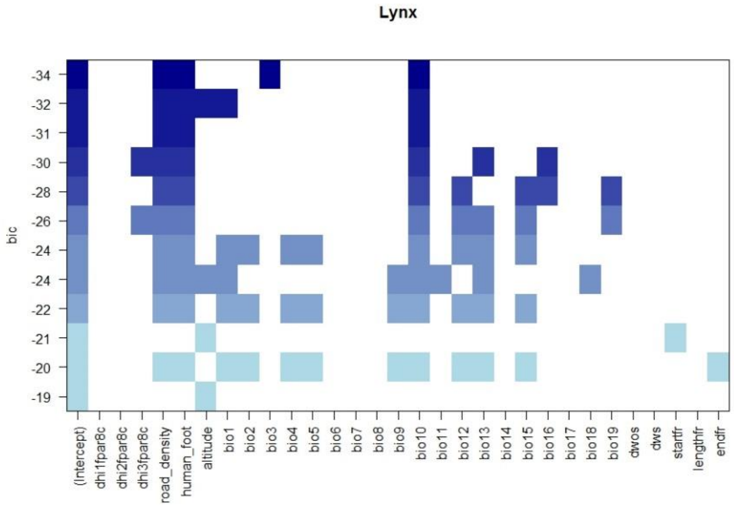
Figure 8: Animal species density corrected by its suitable habitat and population trends from 1981 to 2010.



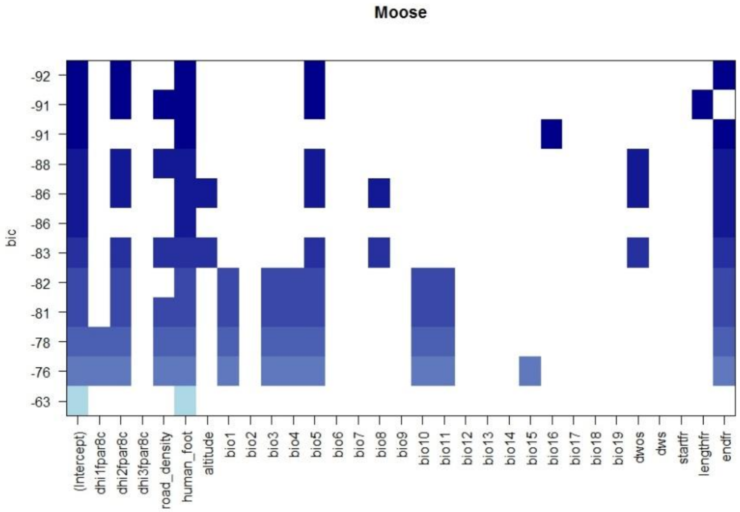
R^2_{adj}=0.74 for first top model



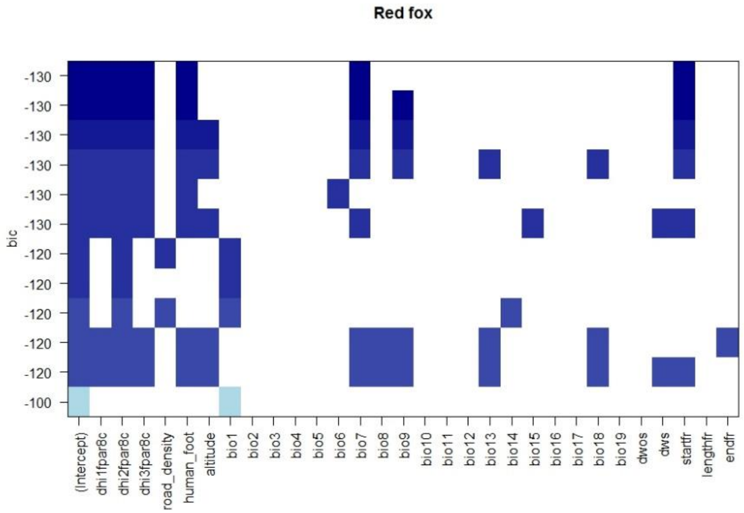
R^2_{adj}=0.94 for first top model



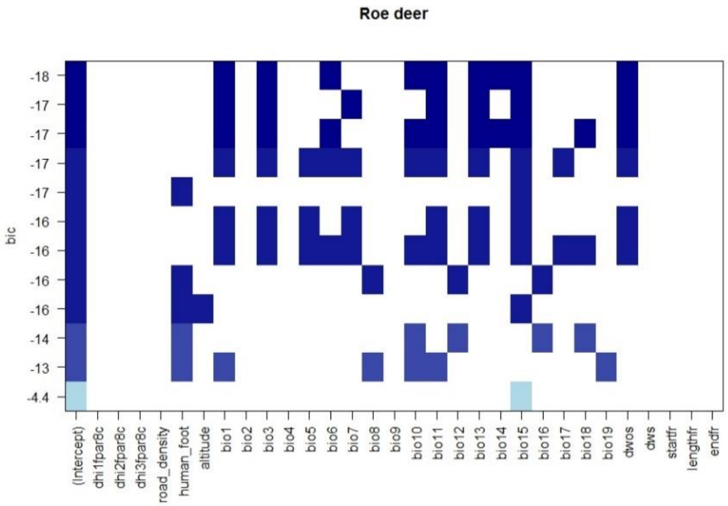
R^2_{adj}=0.61 for first top model



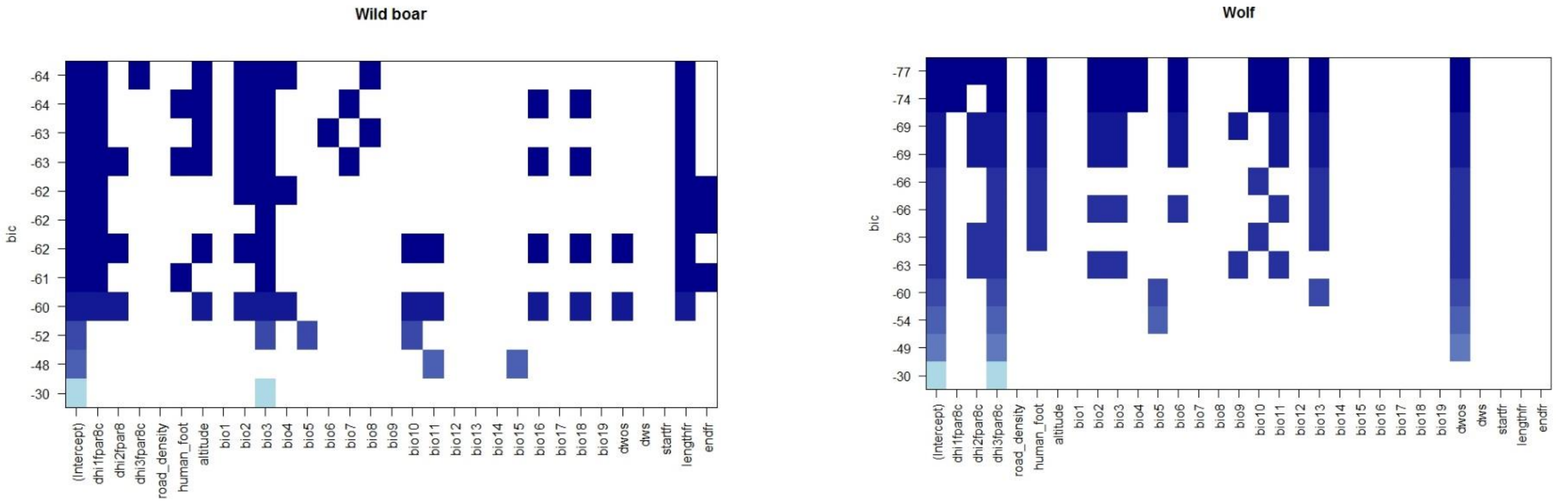
R^2_{adj}=0.81 for first top model



R^2_{adj}=0.89 for first top model



R^2_{adj}=0.62 for first top model



R^2_{adj}=0.77 for first top model

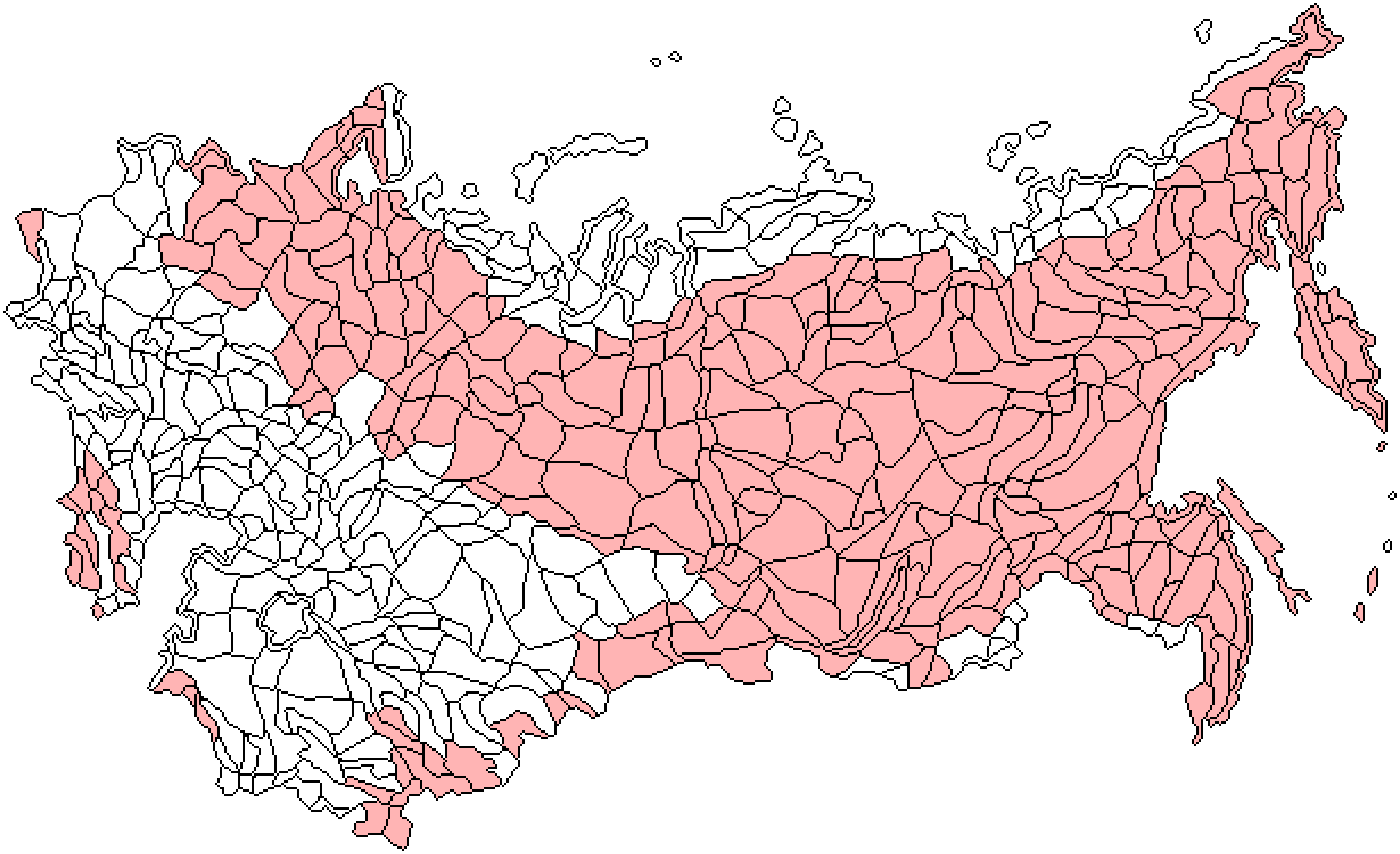
R^2_{adj}=0.82 for first top model

Figure 9: Main results of best model selection for all animal based on BIC criterion. R^2_{adj} is indicating the overall variance explained by the first top model.

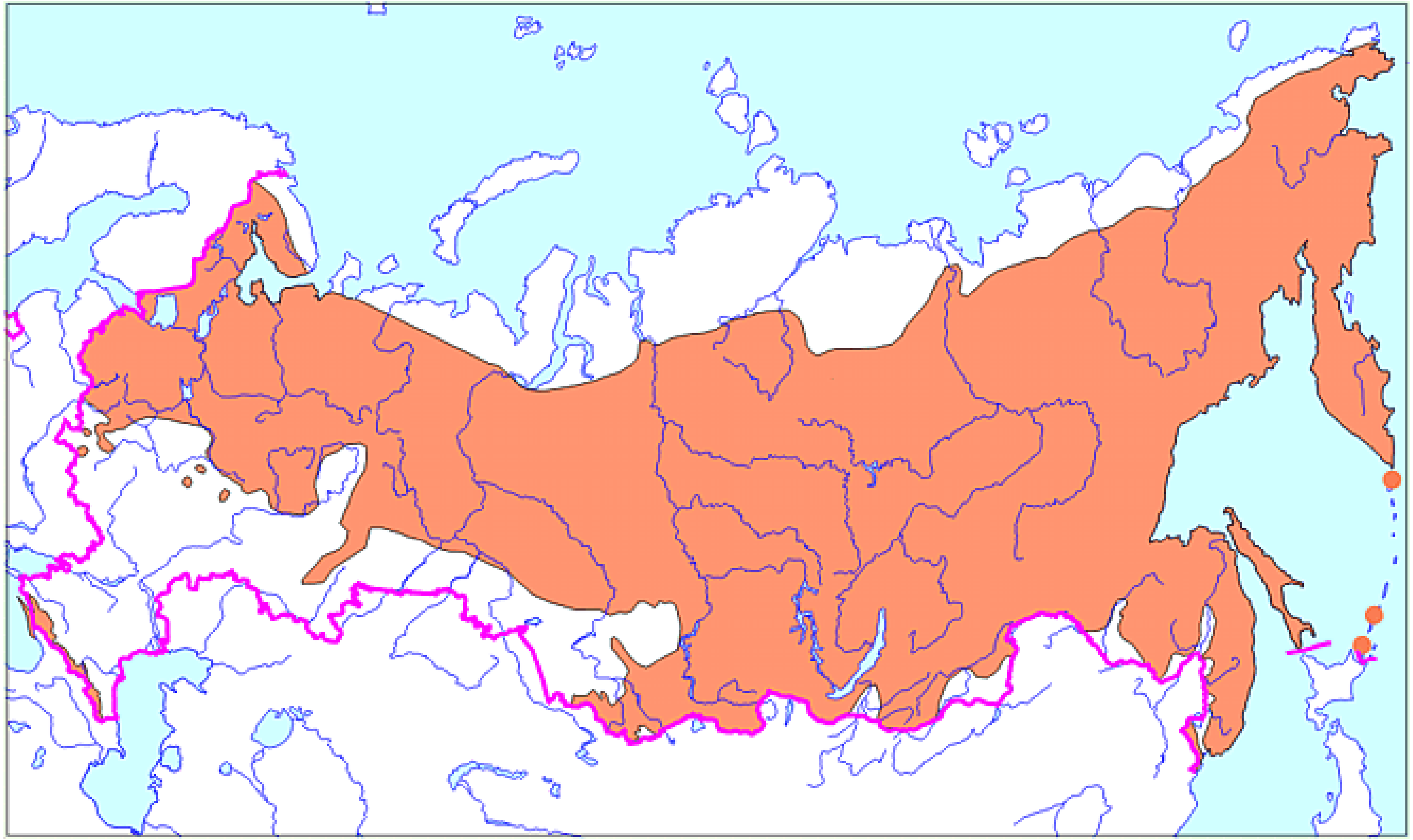
Appendices

It is very important to have quality range maps for our analysis. For Russian territory IUCN range maps lack accuracy. That is why we analyzed several resources to find accurate range maps including IUCN, Soviet and Russian literature, and Russian Academy of Science. Also, we included a map showing the distribution of European hare, including some regions with artificially developed populations. Another map shows the home range size for wolf. Our choice of range maps was described in chapter 3.

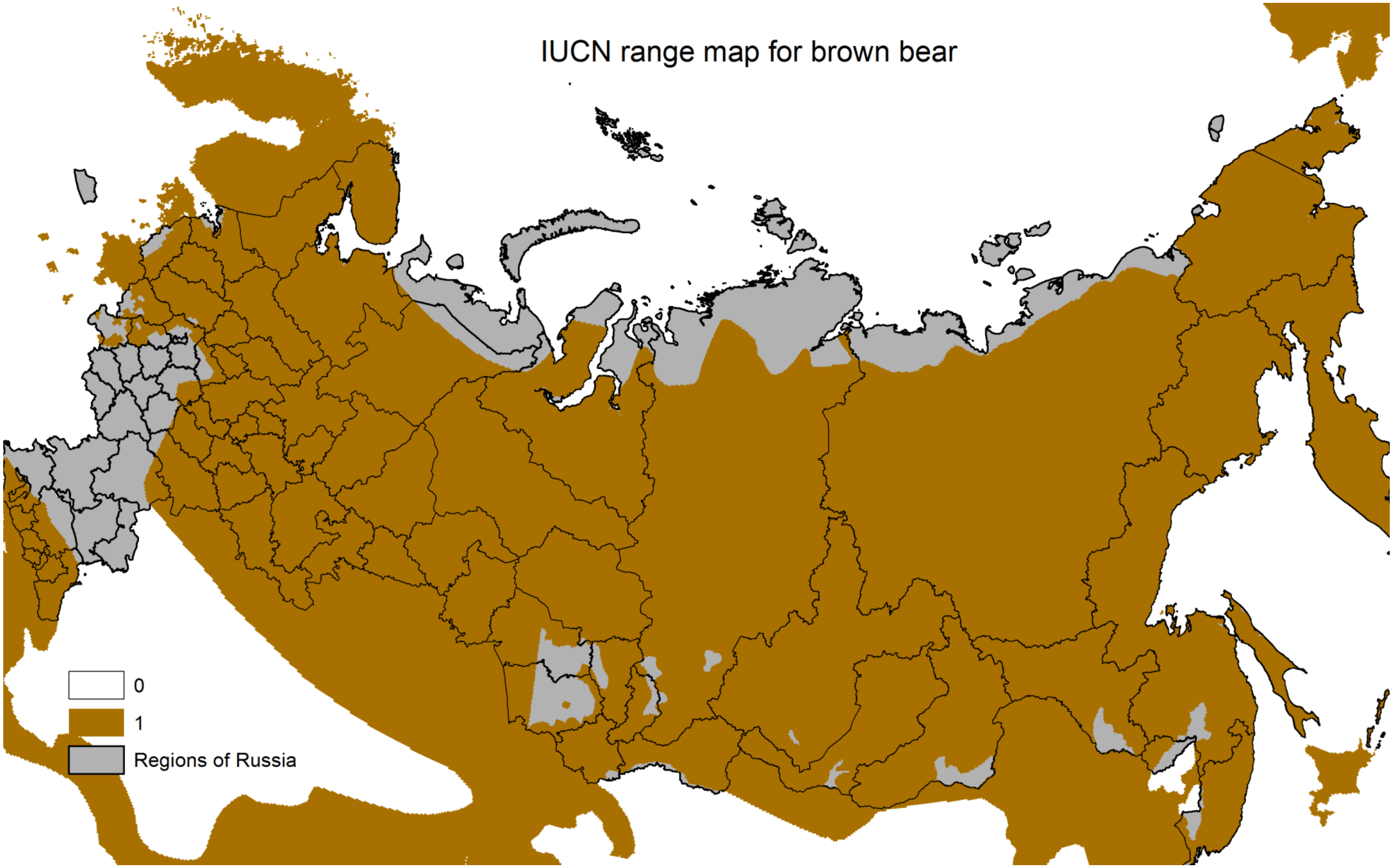
Appendix 1: Brown bear *(Ursus arctos)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017).



Appendix 2: Brown bear *(Ursus arctos)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in pink (Pavlov et al., 2002).



Appendix 3: Brown bear *(Ursus arctos)* IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001).



Appendix 4: Brown bear (*Ursus arctos*) range map in Soviet Union by Geptner V. G. (1967)
Legend: 1 – boundaries of the reconstructed range, 2 – southern boundary of brown bear distribution in western Siberia and in European part of Soviet Union in late 1950s and in 1960s, 3 – north boundary of regular occurrence into taiga of Western Siberia, 4 – isolated points of habitat in Białowieża Forest. Arrows at the north indicate the limit of the farthest visits in tundra, and in the south arrows indicate isolated habitats in Carpathian Mountains, Talysh, and Kopet Dag (Geptner et al., 1967, p.415).

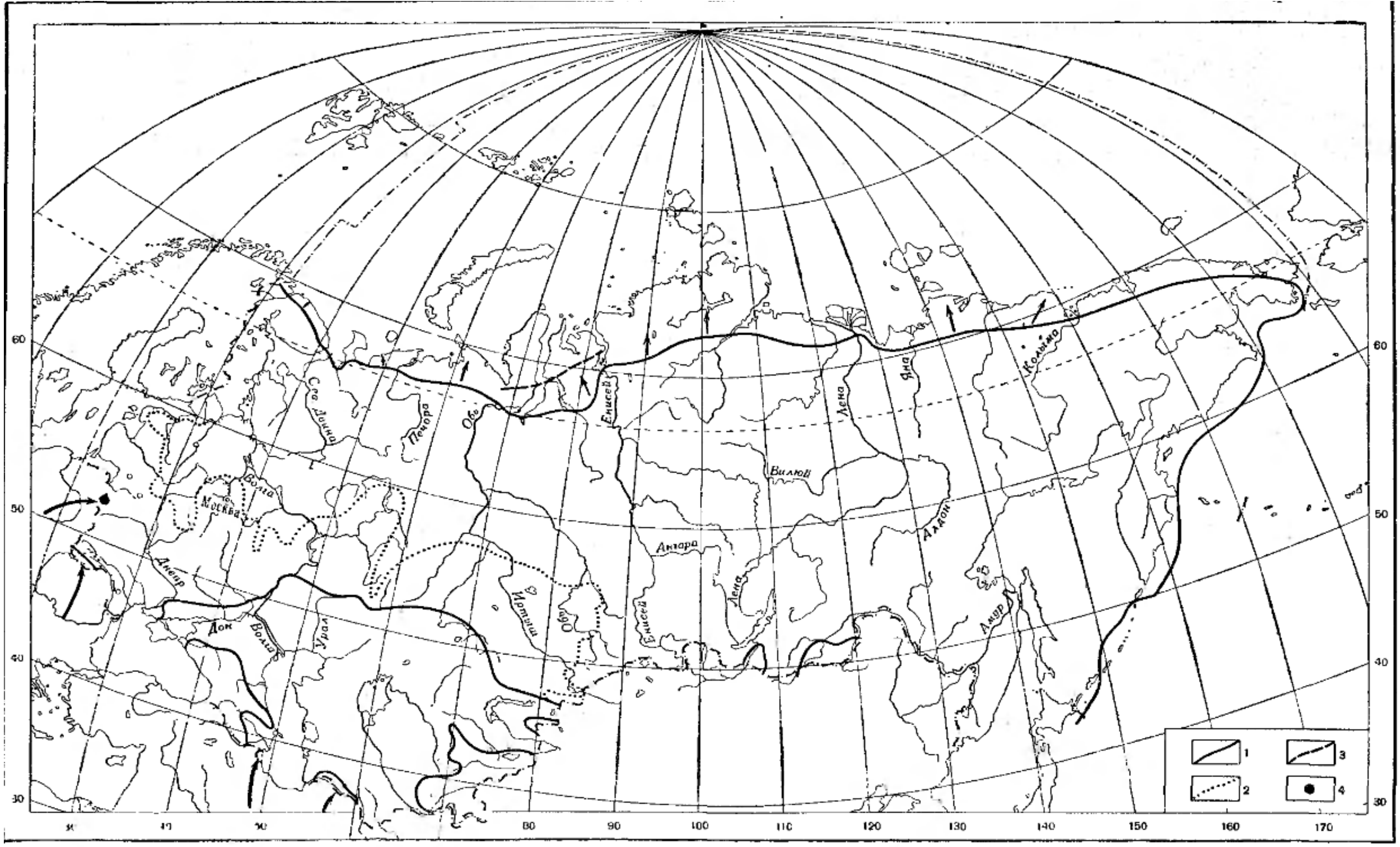
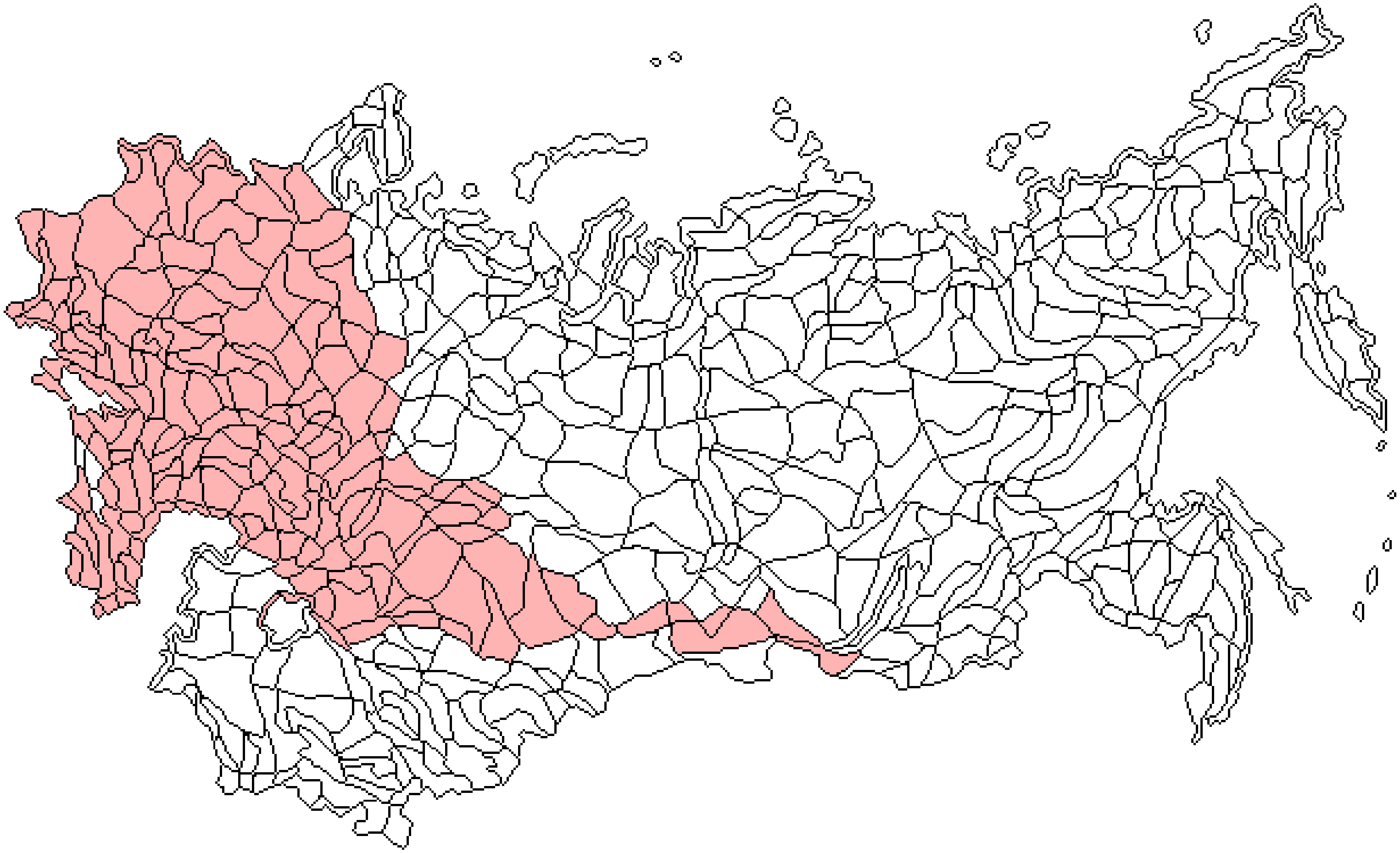


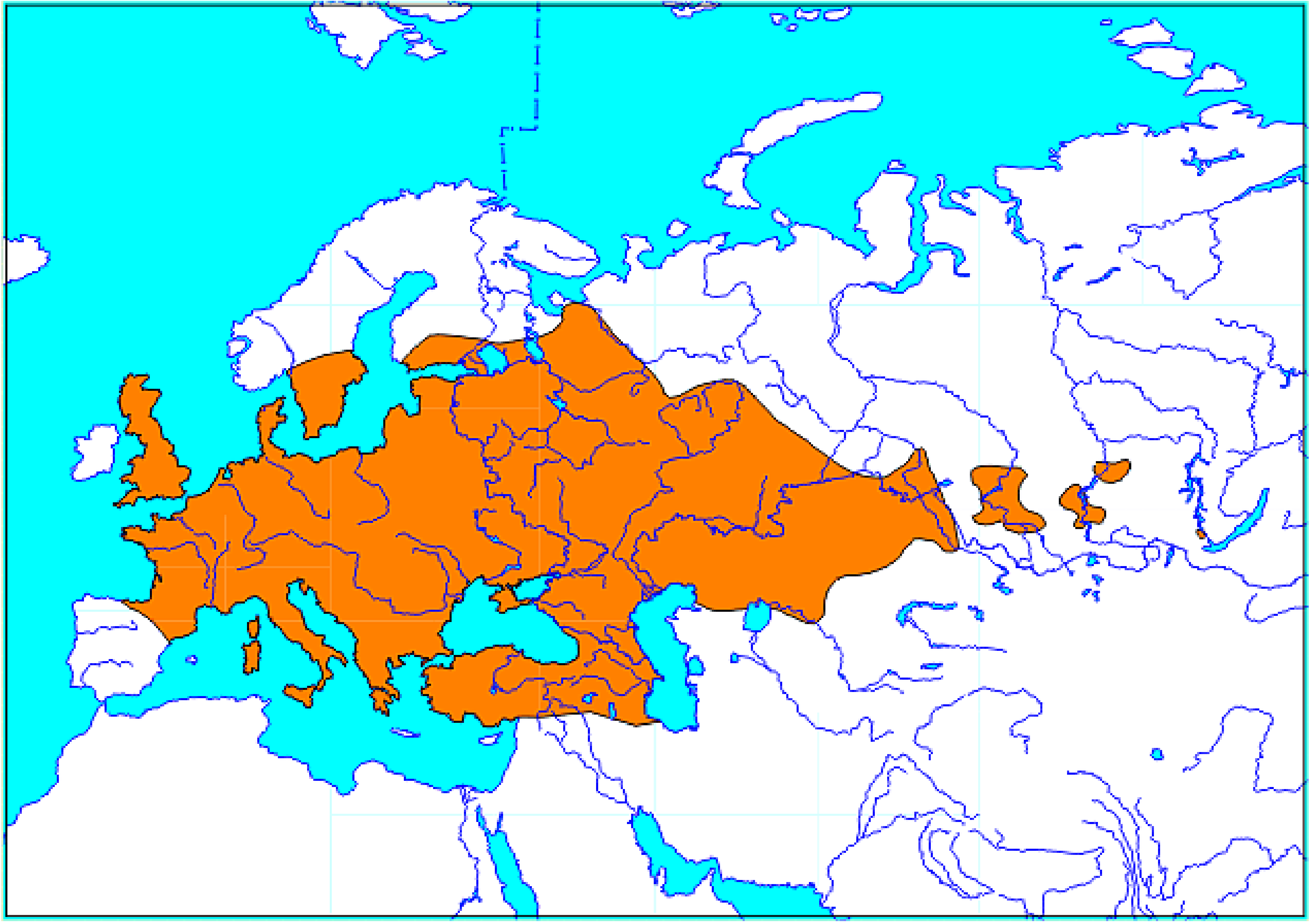
Рис. 152. Ареал бурого медведя, *Ursus* (*Ursus*) *arctos* L., в СССР (В. Г. Гептнер):

1 — границы восстановленного ареала, *2* — южная граница распространения в Западной Сибири и в европейской части СССР на конец 50-х годов XX в. и на 1960 г., *3* — северная граница регулярных заходов в тундры Западной Сибири, *4* — изолированная точка обитания в Беловежской Пуще. Стрелки на севере указывают на пределы дальних заходов в тундру, на юге — оторванные области обитания в Карпатах, Талыше и Копет-Даге

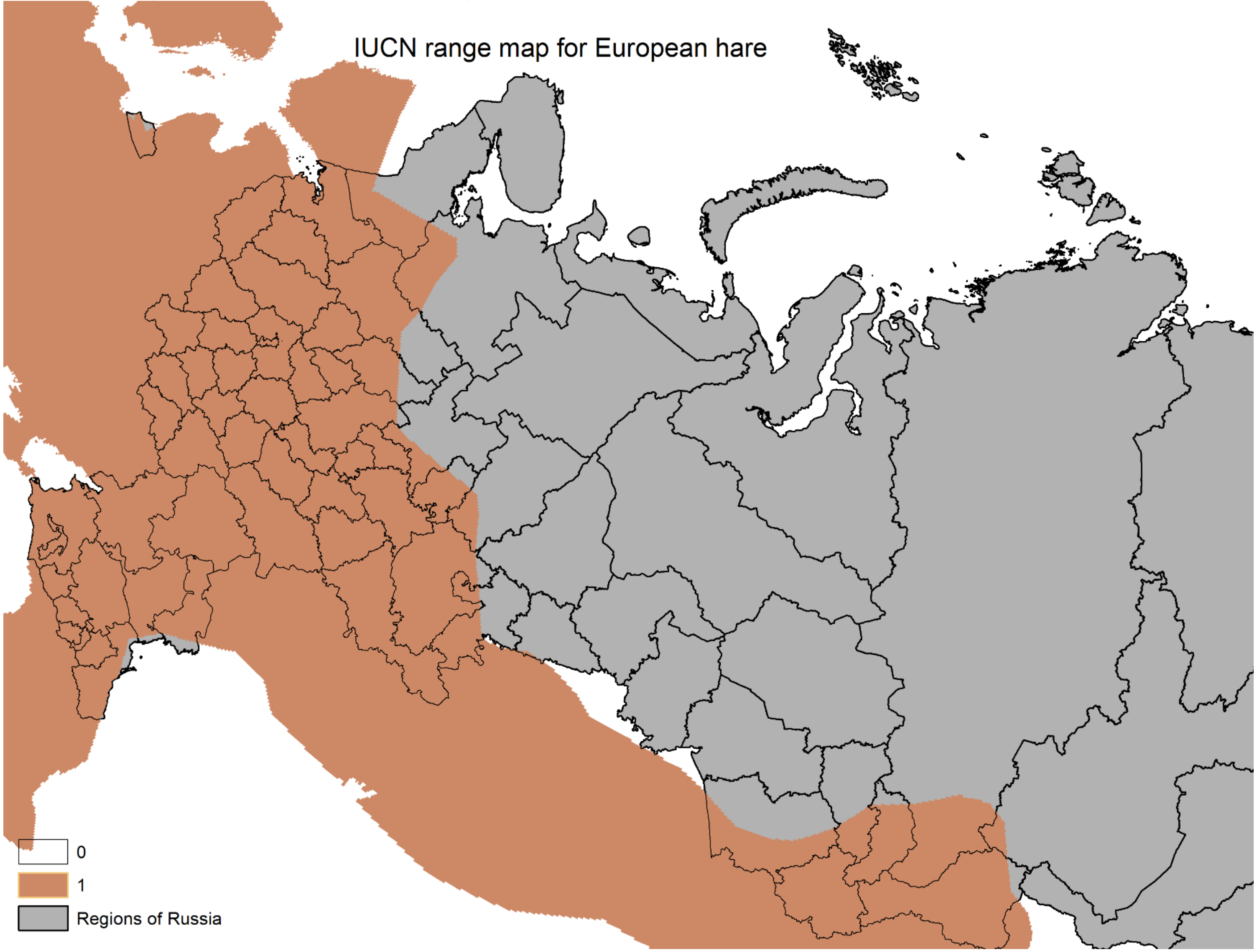
Appendix 5: European hare *(Lepus europaeus*) range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017).



Appendix 6: European hare *(Lepus europaeus*) range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue (Pavlov et al., 2002).



Appendix 7: European hare (*Lepus europaeus*) IUCN range map is shown in brown: 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001).



Appendix 8: European hare (*Lepus europaeus*) range map
Legend: 1- European hare occurrence according to museum collections, 2-places of introduction, 3-points of presence of newly developed populations of European hare, 4-regions with artificially developed populations, 5-northern boundary of European hare range based on data from 1964, 6-northern boundary of presence of European hare based on literature (by Gruzdev, 1974) (reported in Sokolov et al., 1994, p.211)

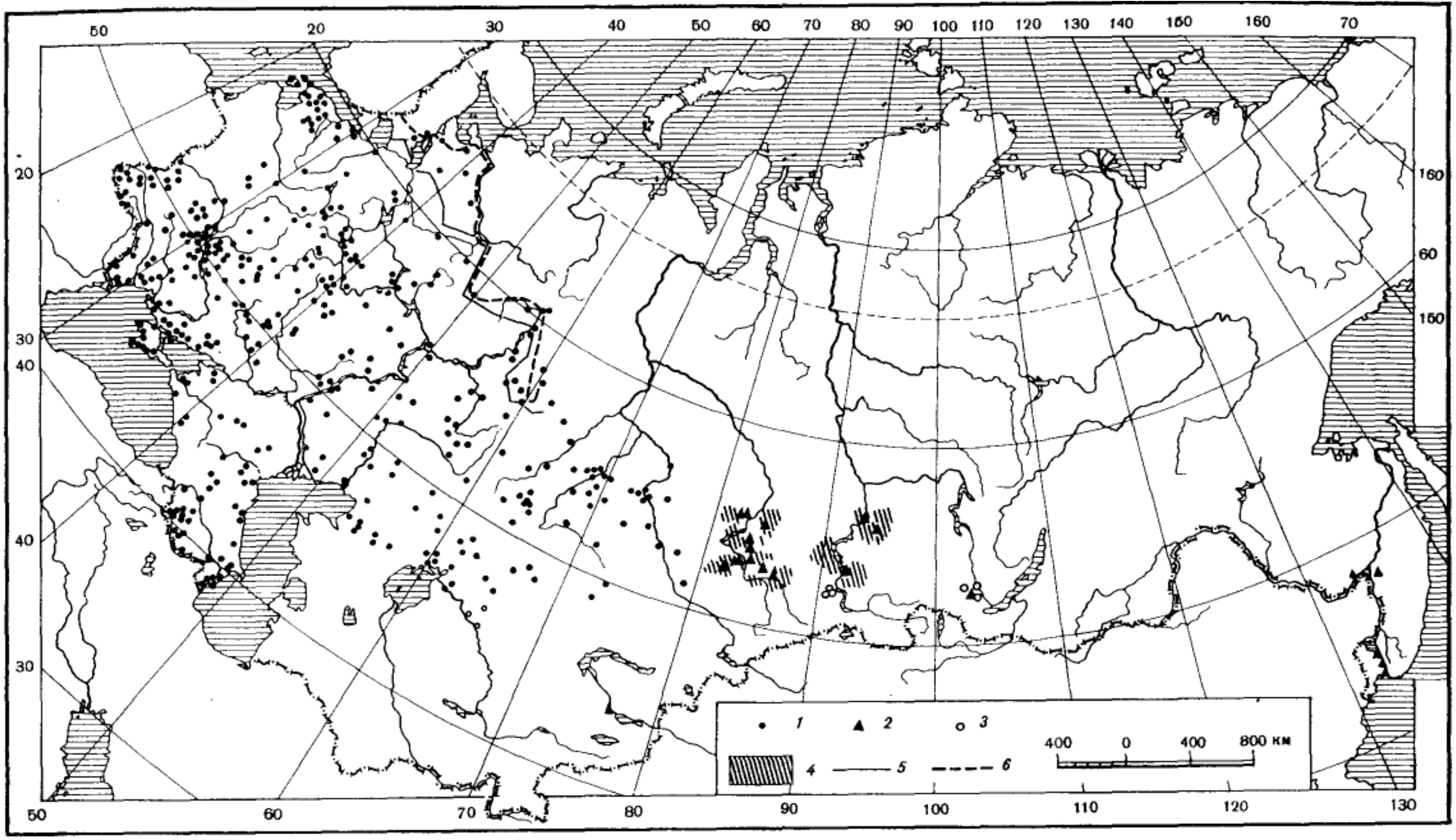
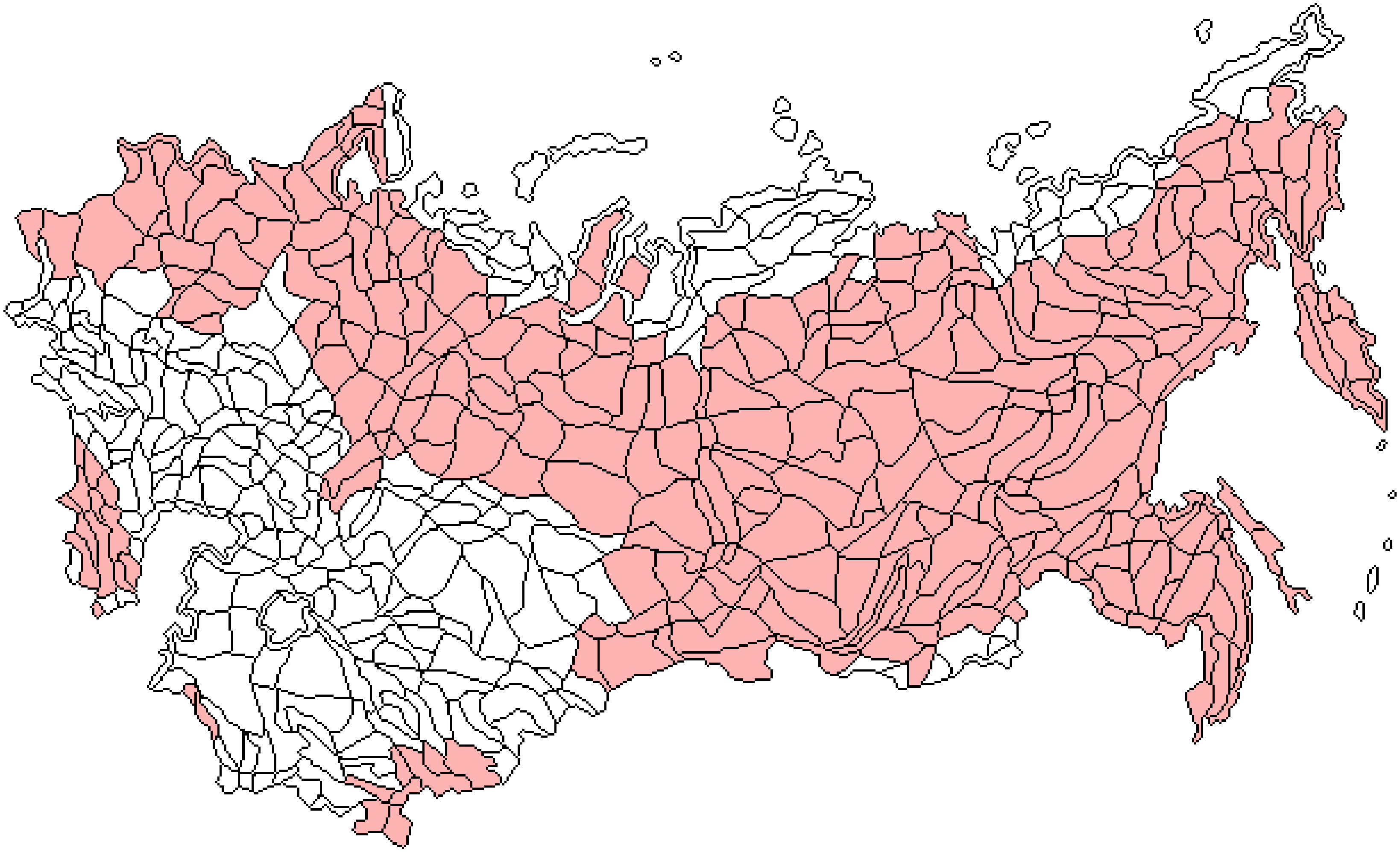


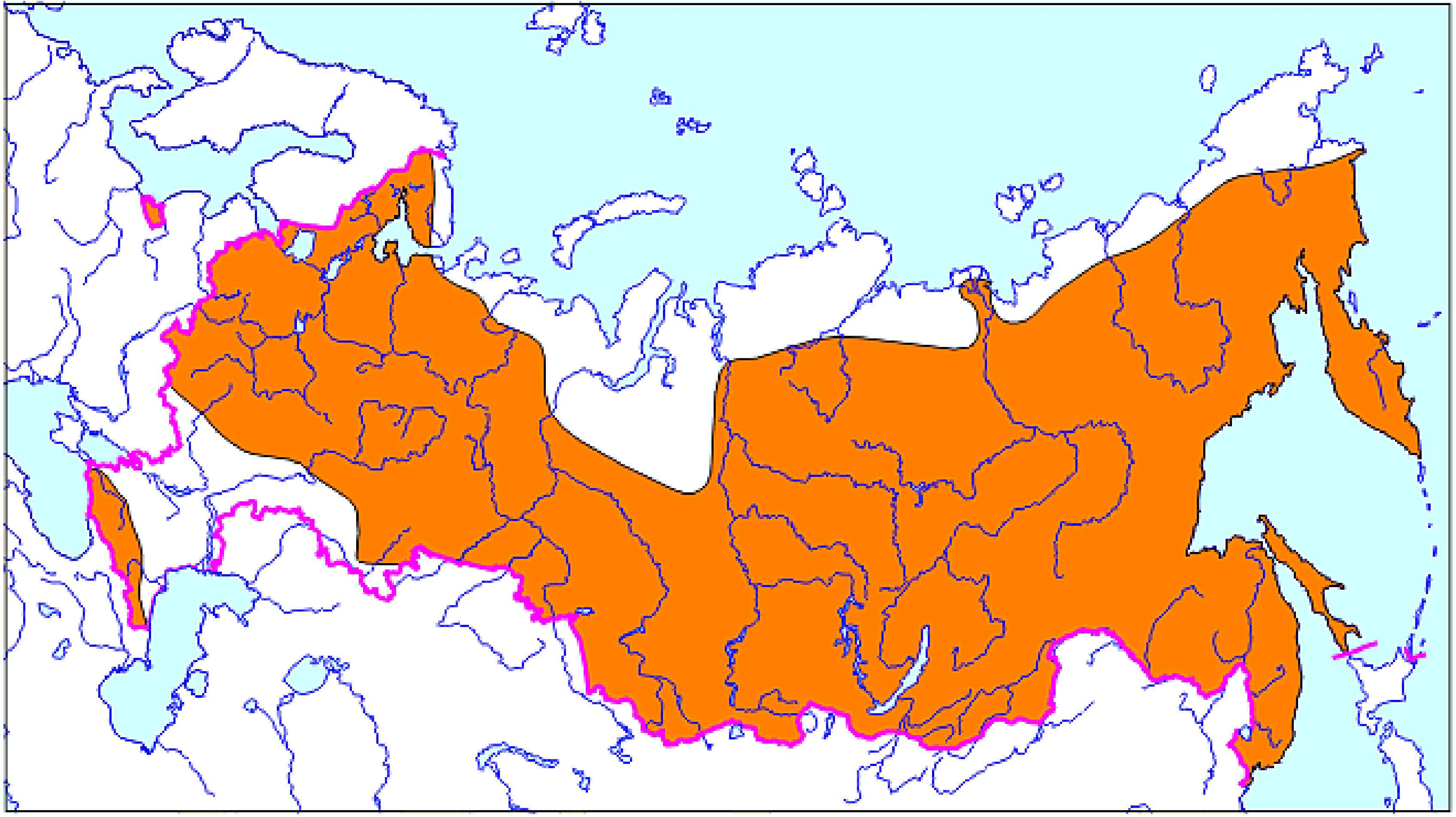
Рис. 48. Распространение зайцев-русаков

1 — точки находок русаков (в основном по данным коллекционных сборов); *2* — места акклиматизации; *3* — точки находок русаков во вновь созданных популяциях; *4* — область распространения искусственно созданных популяций (Груздев, 1969); *5* — северная граница ареала русака по данным 1964 г. (Груздев, 1974); *6* — северная граница находок русаков по данным литературы (Груздев, 1974)

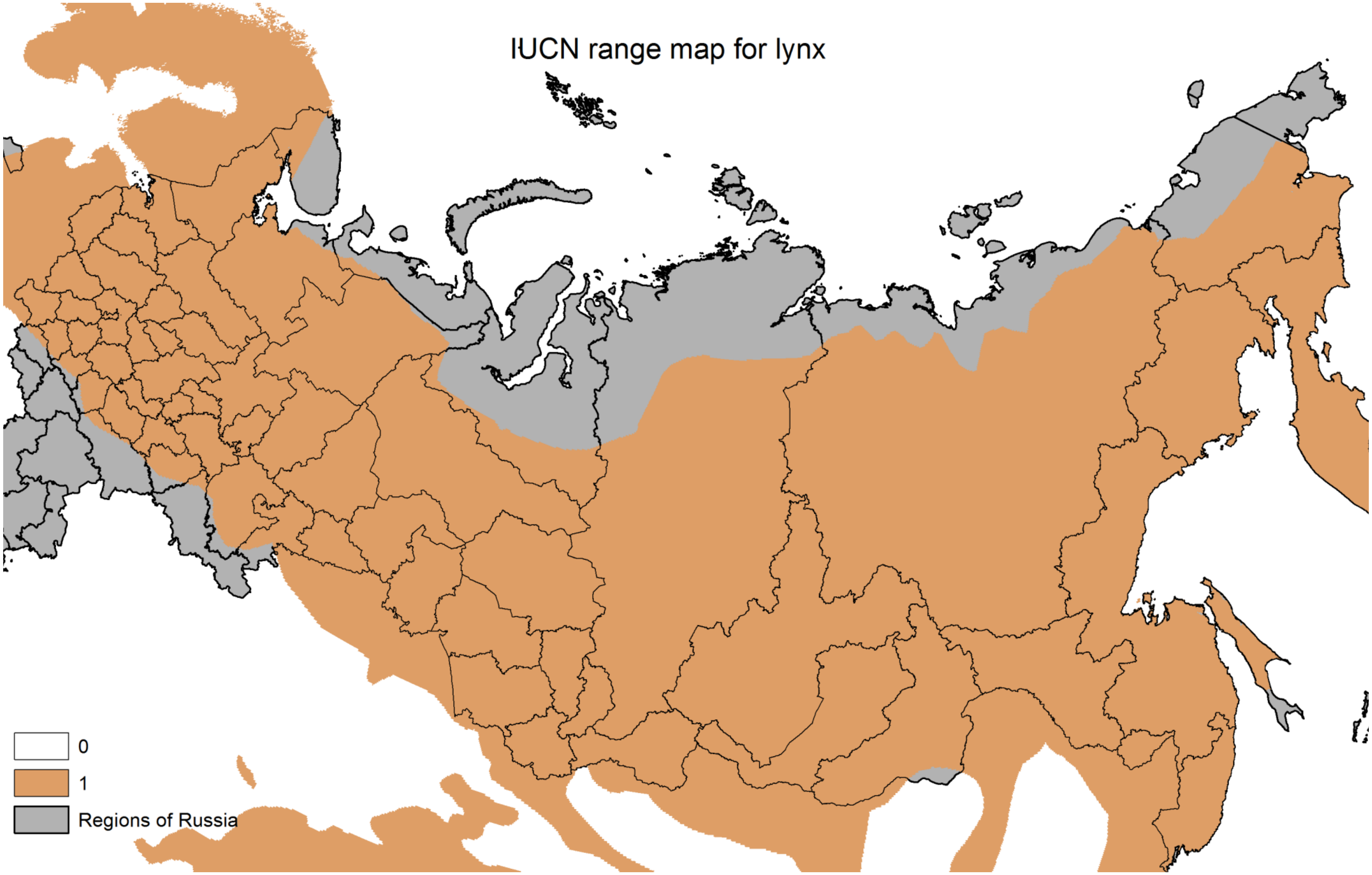
Appendix 9: Lynx *(Felis lynx)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)



Appendix 10: Lynx *(Felis lynx)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in pink (Pavlov et al., 2002).



Appendix 11: Lynx *(Felis lynx)* IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)



Appendix 12: Range for lynx, *Felis (lynx) lynx L.* in Soviet Union.
Solid line shows historical and current range in the north and east. Dashed line shows the current boundary of permanent habitat in European part of the Soviet Union and in Caucasus. In West Siberia dashed line shows the southern boundary of permanent habitat in the period of maximum reduction of range in late 1930's. By the end of 1960's, there was only few local populations or occurrences at the south of historical range in Kazakhstan. Some of these places are marked with points. It is likely that there are no lynx in Karatau (Geptner and Sludskiy, 1972, p.396)

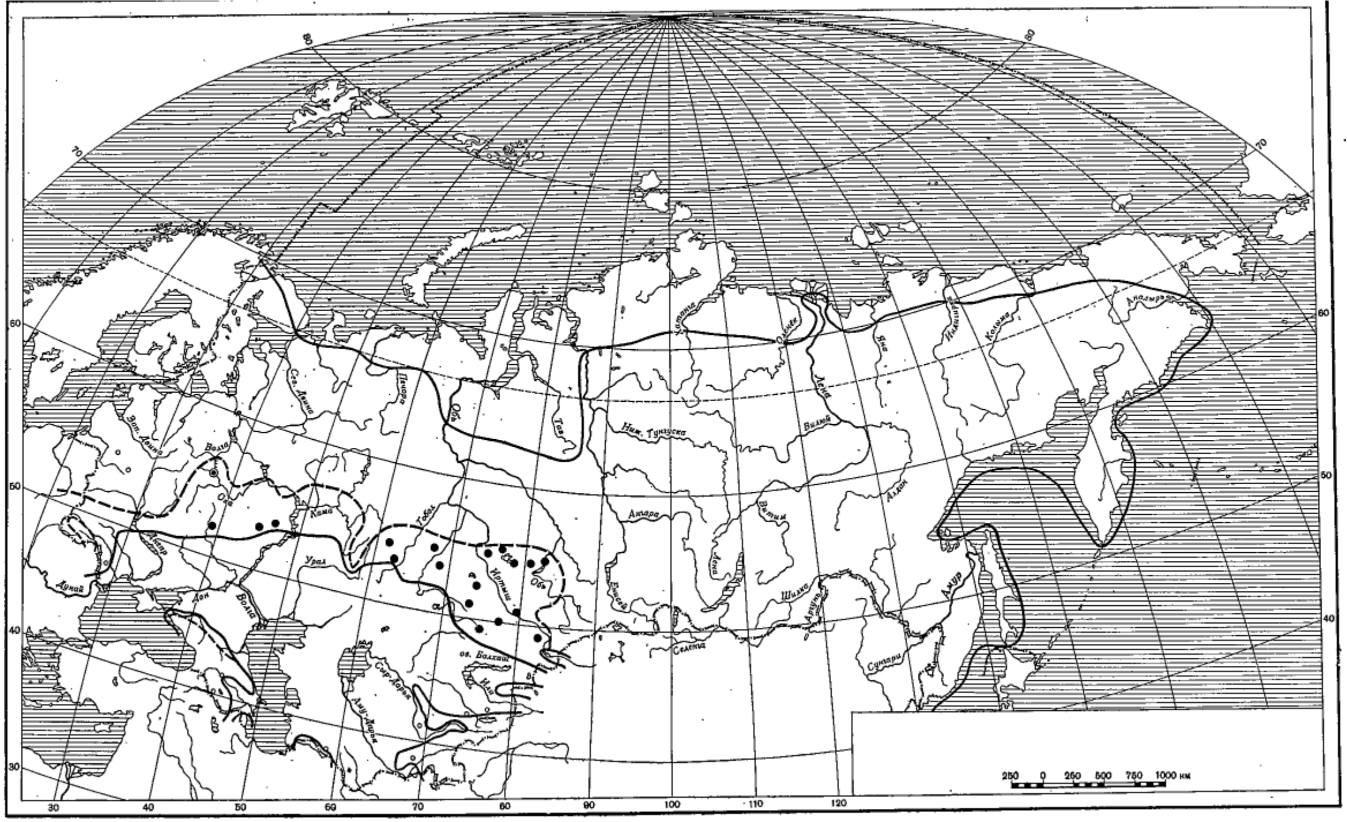
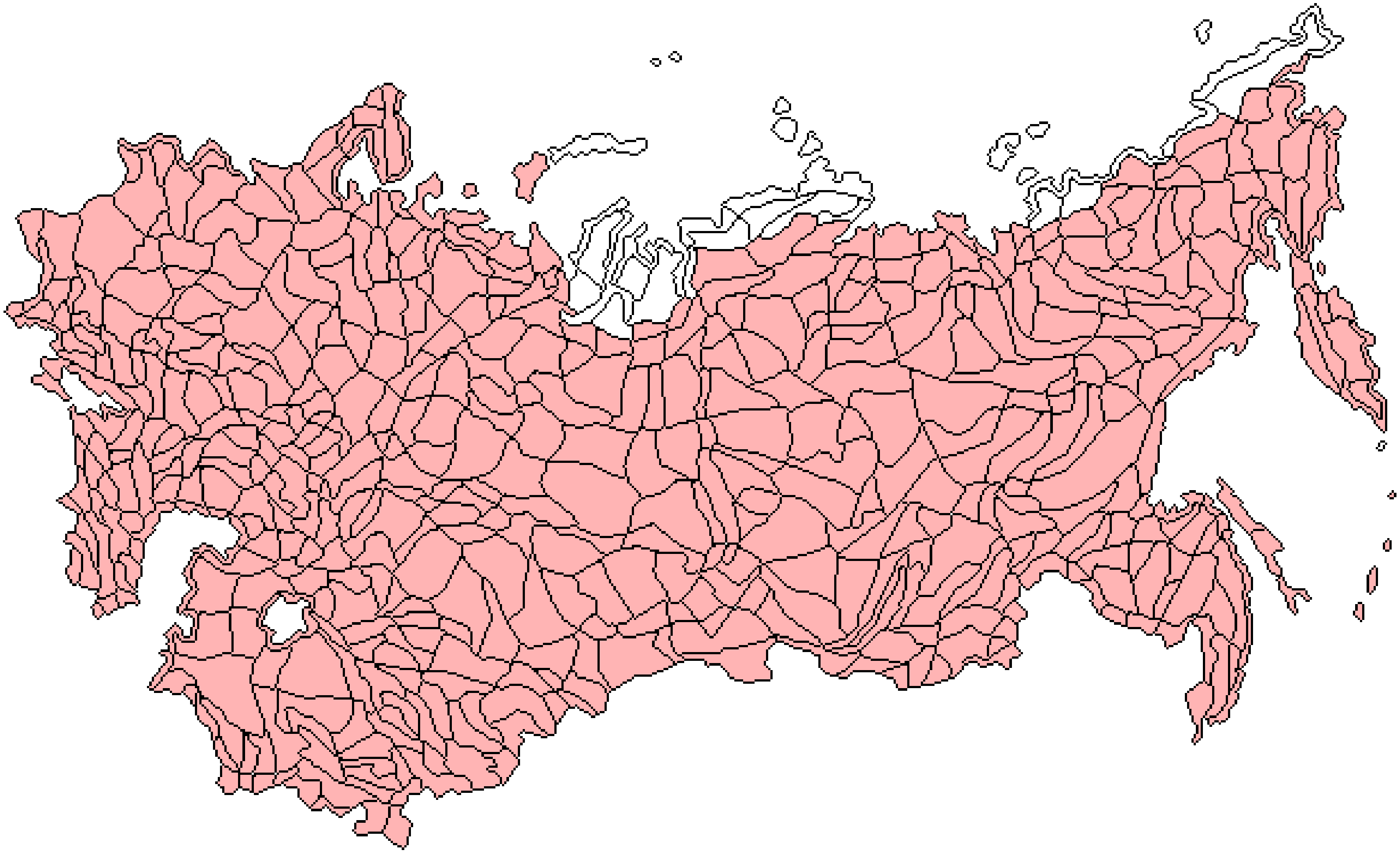
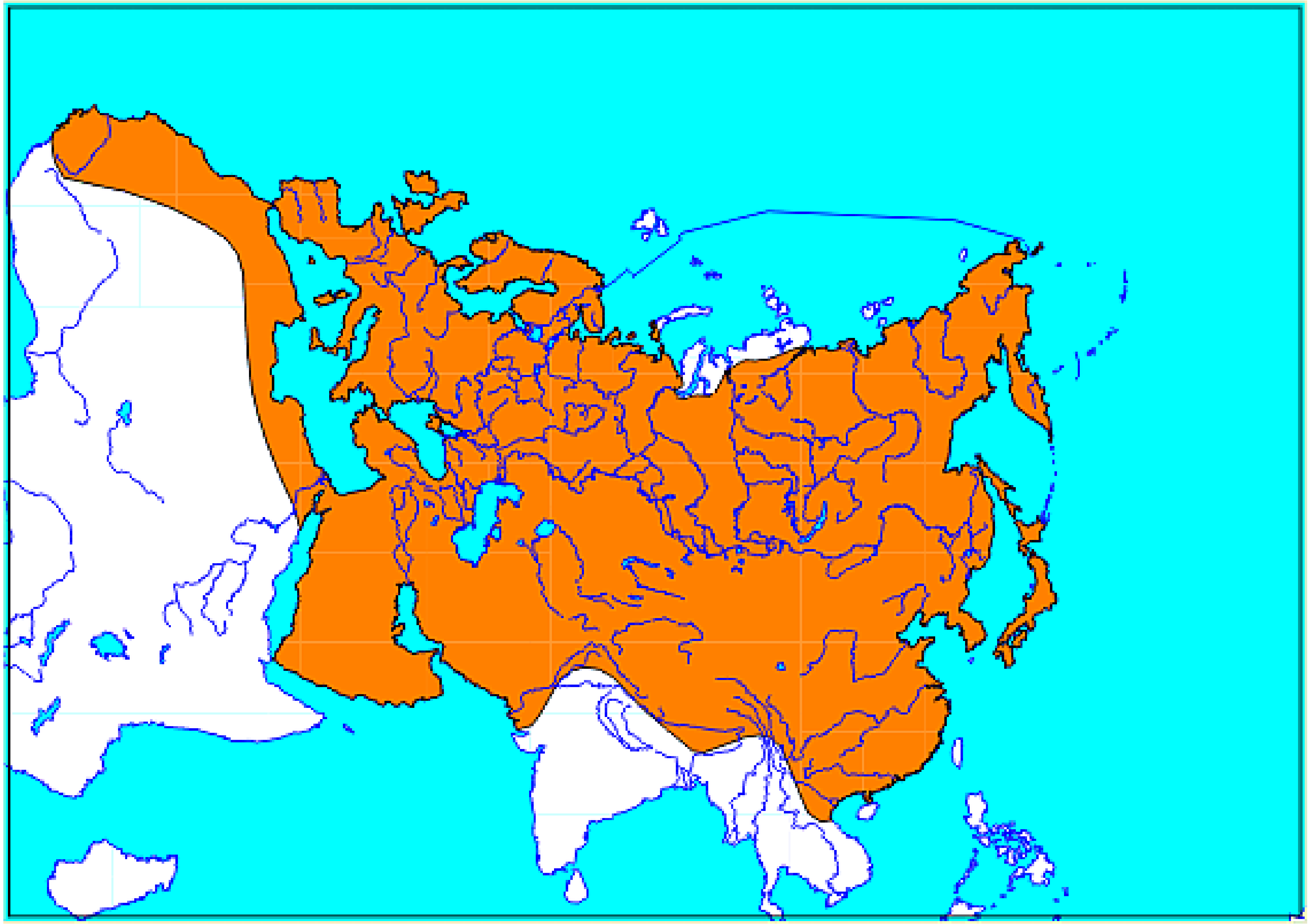


Рис. 222. Ареал рыси, *Felis* (*Lynx*) *lynx L.* в СССР. Сплошная линия — ареал в историческое время на севере и востоке, также современный. Пунктирная линия — современные границы постоянного обитания в европейской части страны и на Кавказе. В Западной Сибири пунктирная линия обозначает южную границу постоянного обитания в период наибольшего отступания границы к концу 30-х годов XX в. К концу 60-х годов пространство до исторической границы на юг в Казахстане представляет собой область заходов, местами отдельные участки постоянного обитания. Некоторые из этих мест отмечены точками, как и отдельные заходы в европейской части. В Каратау в настоящее время рыси, по-видимому, нет. В. Г. Гептнер

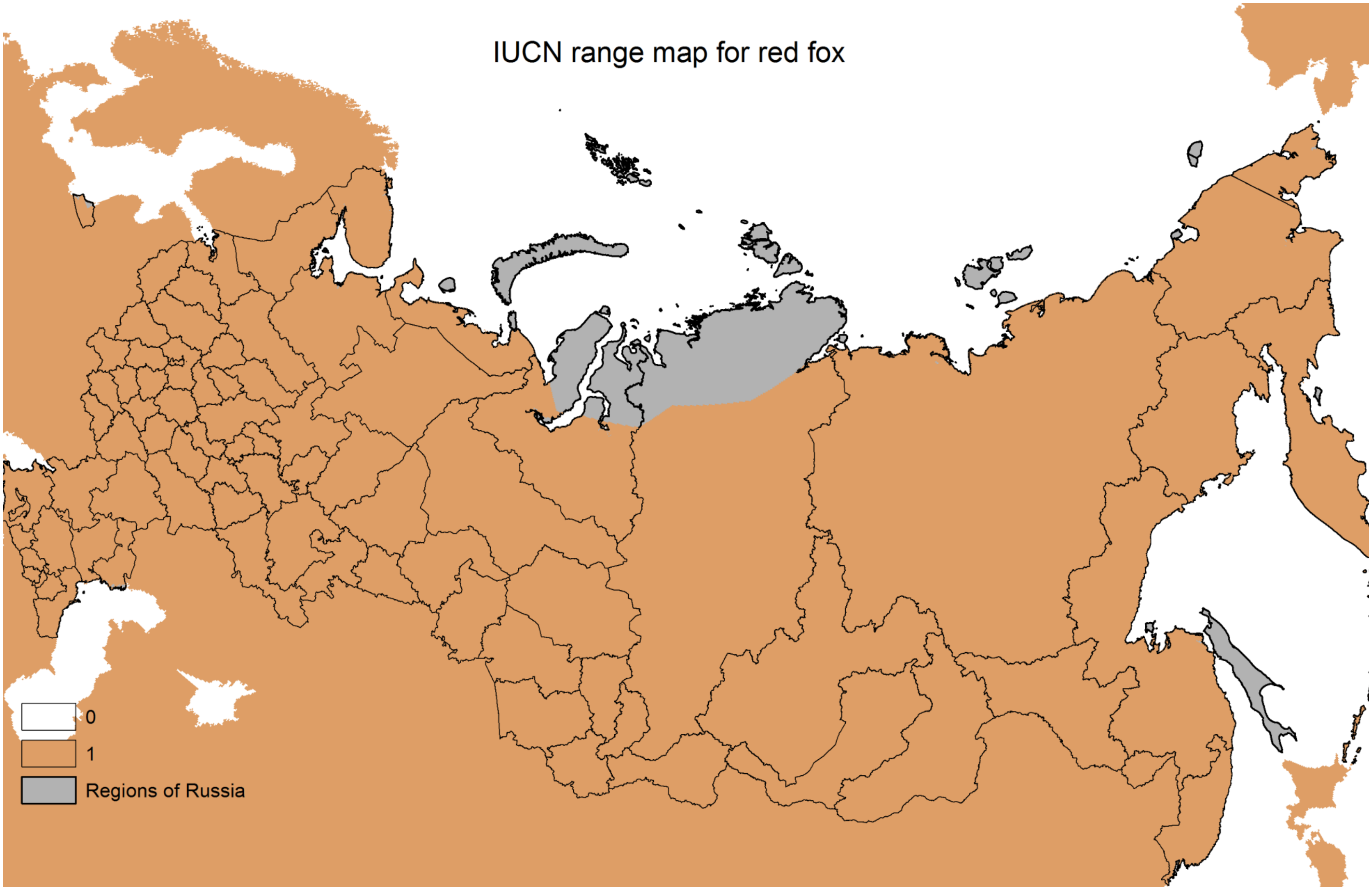
Appendix 13: Red fox *(Vulpes vulpes)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)



Appendix 14: Red fox *(Vulpes vulpes)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue (Pavlov et al., 2002).



Appendix 15: Red fox *(Vulpes vulpes)* IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)



Appendix 16: North and east boundaries of fox habitat, *Vulpes vulpes L.*, in Soviet Union.
Arrows show direction and places for far occurrences to the north (V.P.Geptner) (Geptner et al., 1967, p.330)

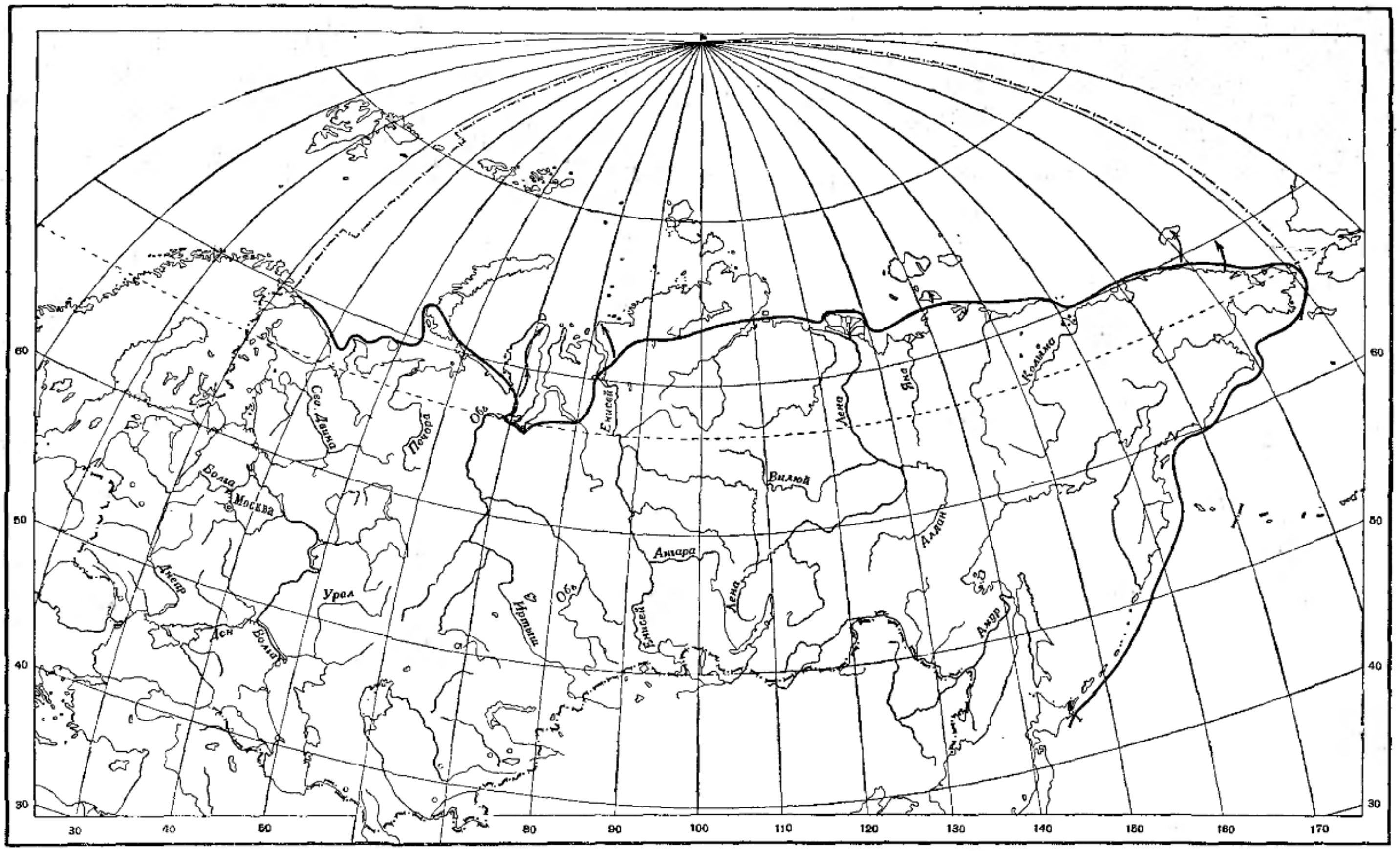
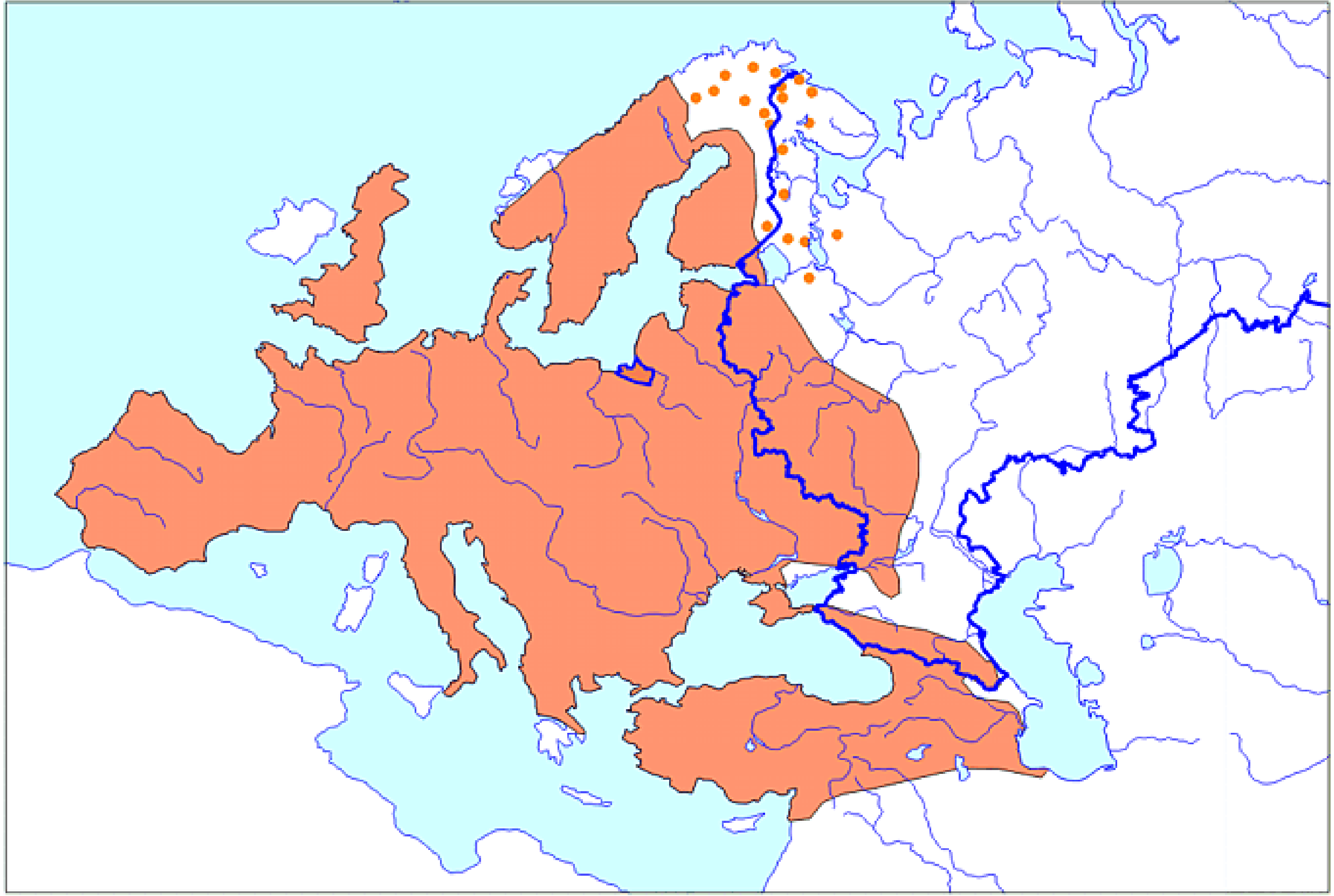


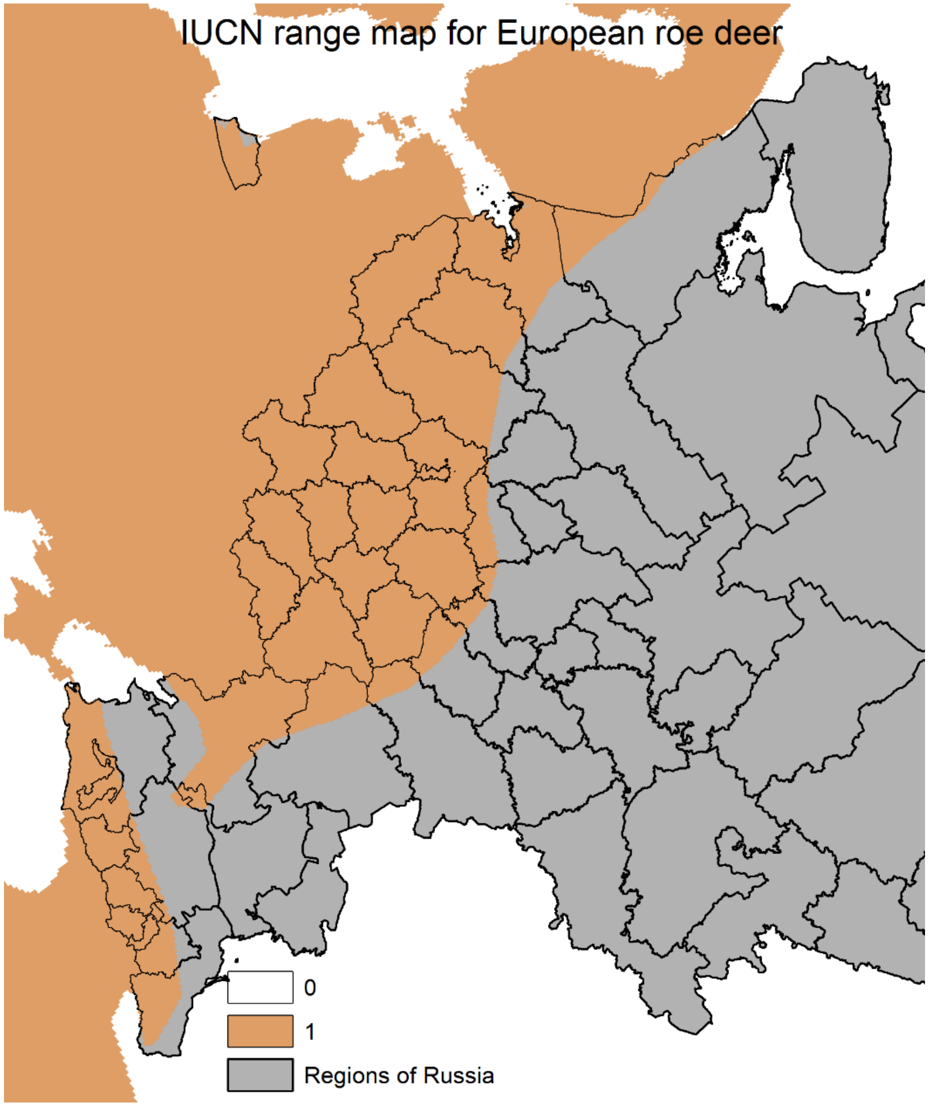
Рис. 119. Северная и восточная границы области распространения лисицы, *Vulpes vulpes* L., в СССР. Стрелки указывают направления и места особенно далеких заходов на север (В. Г. Гептнер)

Appendix 17: European roe deer *(Capreolus capreolus Linnaeus)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)

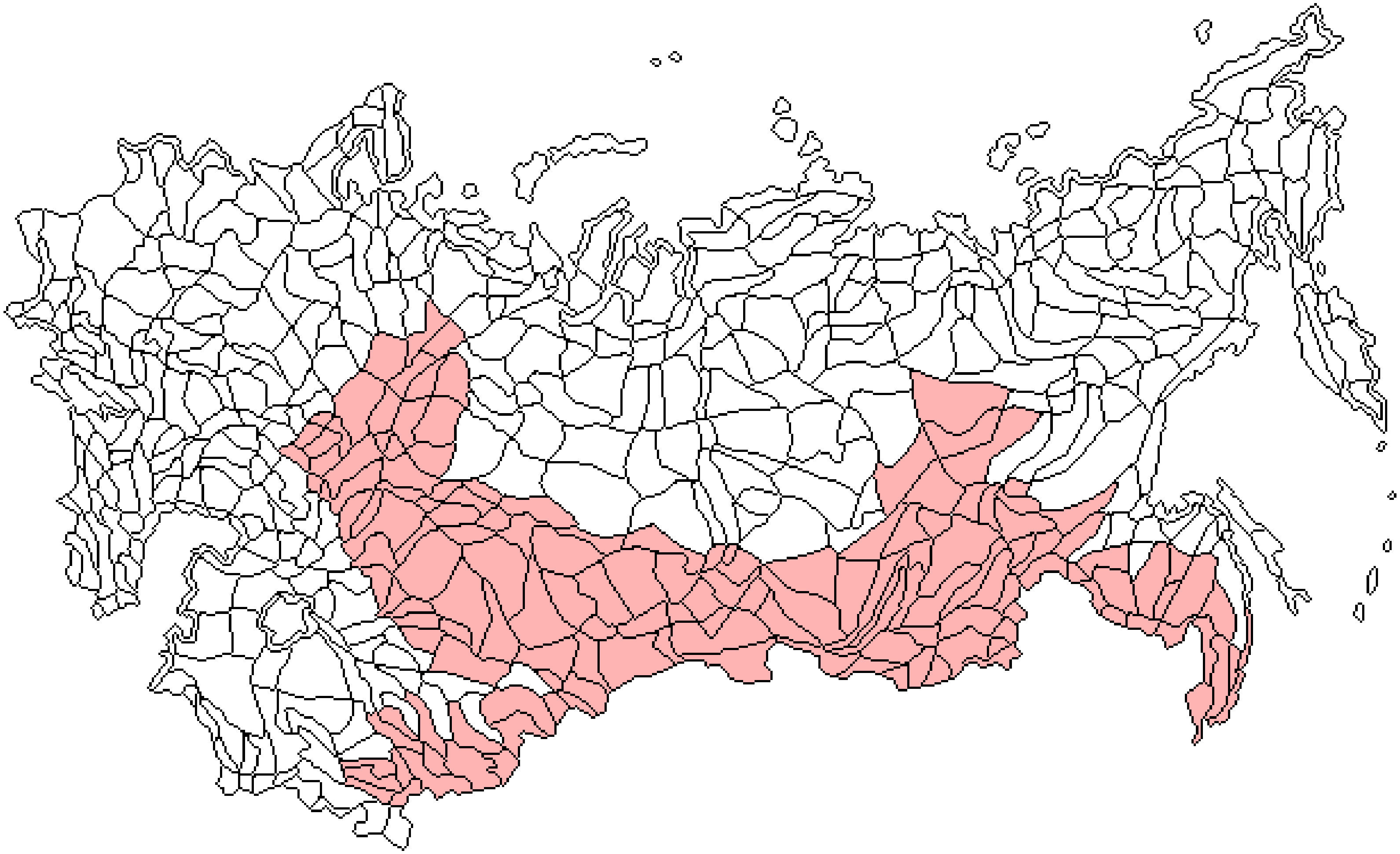
Appendix 18: European roe deer (*Capreolus capreolus Linnaeus*) range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in dark blue. Circles show occurrence outside the range boundary (Pavlov et al., 2002).



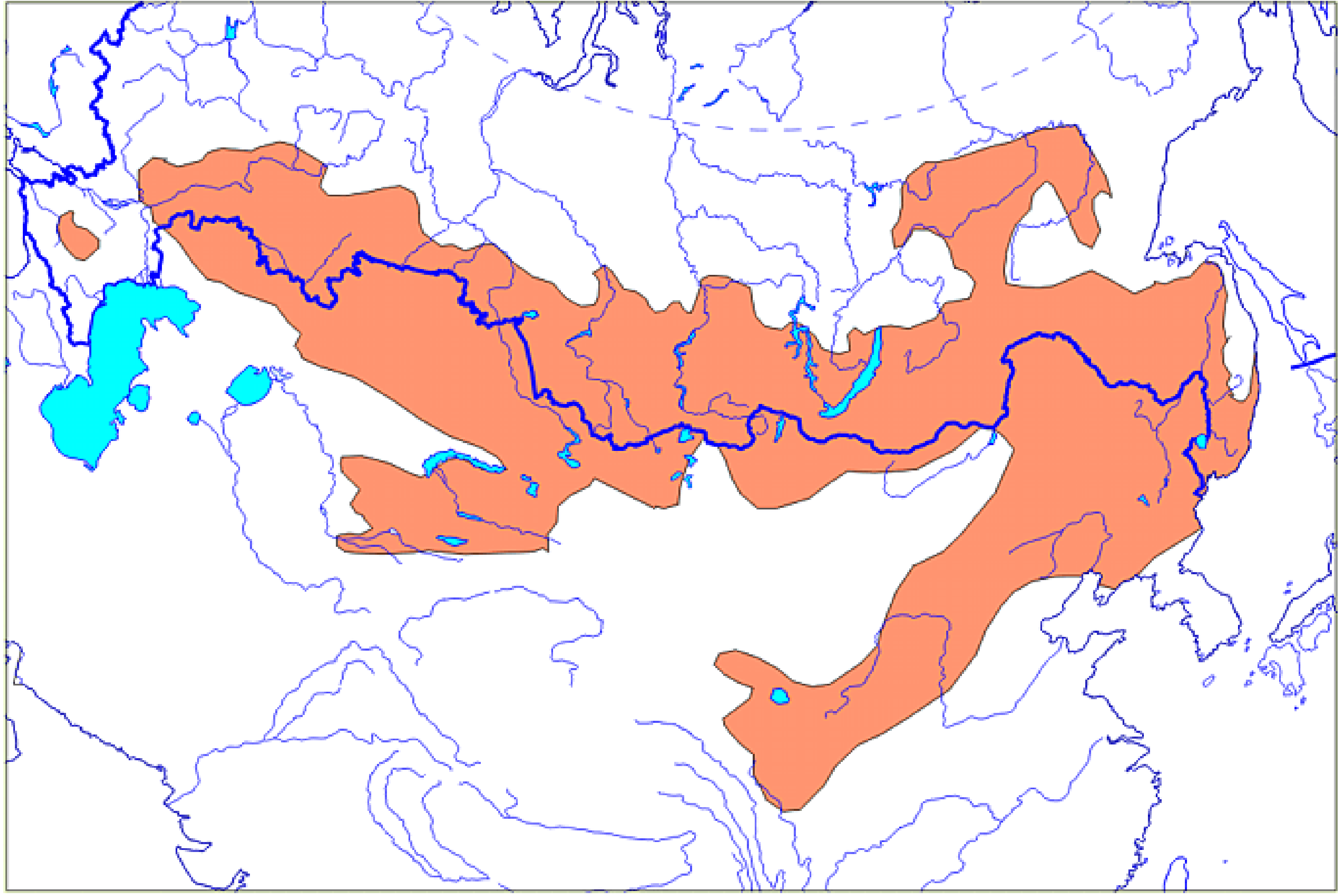
Appendix 19: European roe deer ***(Capreolus capreolus)*** IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)



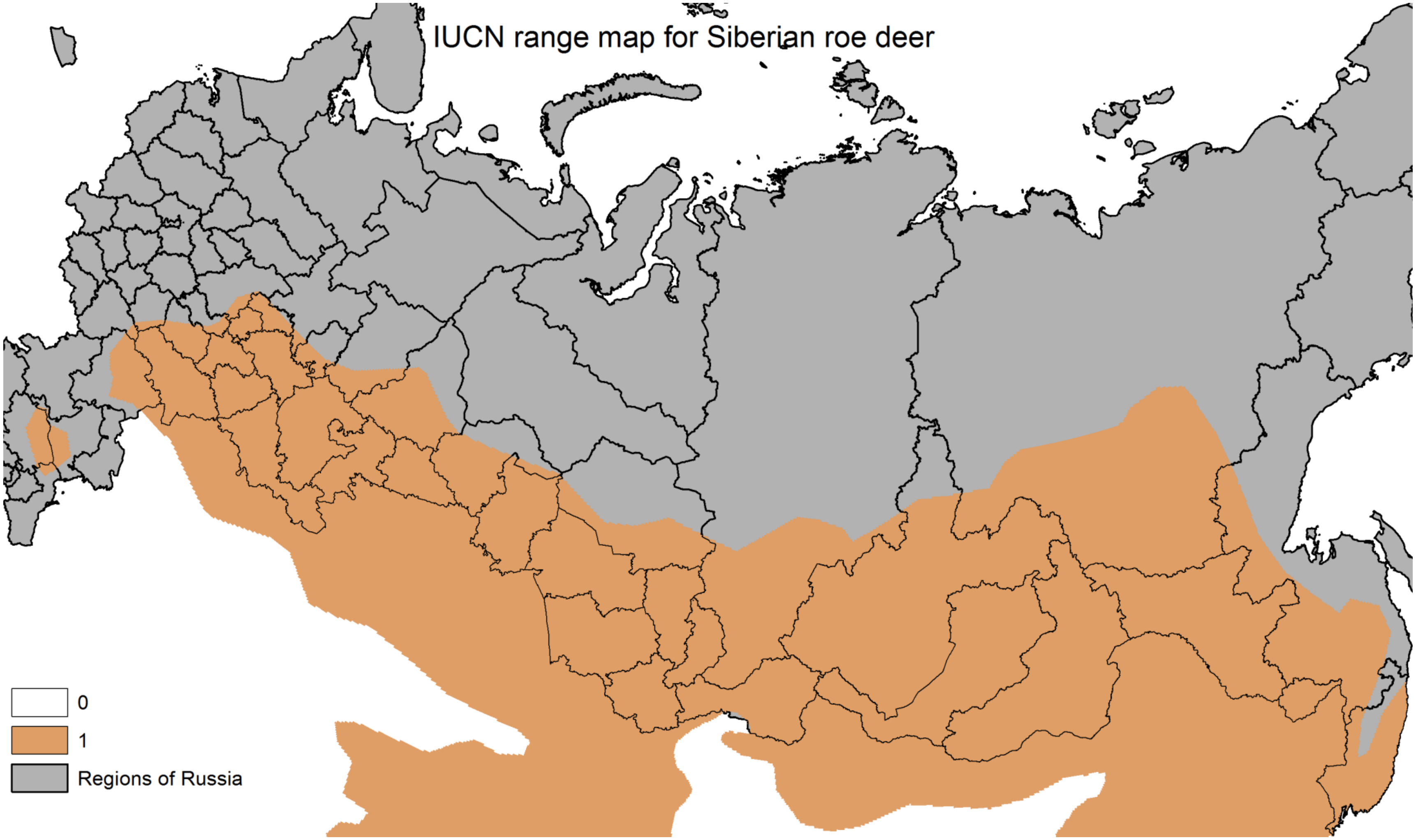
Appendix 20: Siberian roe deer *(Capreolus pygargus Pallas)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)



Appendix 21: Siberian roe deer *(Capreolus pygargus Pallas)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in dark blue (Pavlov et al., 2002).



Appendix 22: Siberian roe deer (*Capreolus pygargus*) IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)



Appendix 23: Current range of European and Siberian roe deer.
Legend: 1-*Capreolus capreolus,* 2-*C. pygargus pygargus Pall*, 3-*C. pygargus tianschanicus Satunin*. Circles show occurrence outside the range boundary (Danilkin, 1999, p.59)

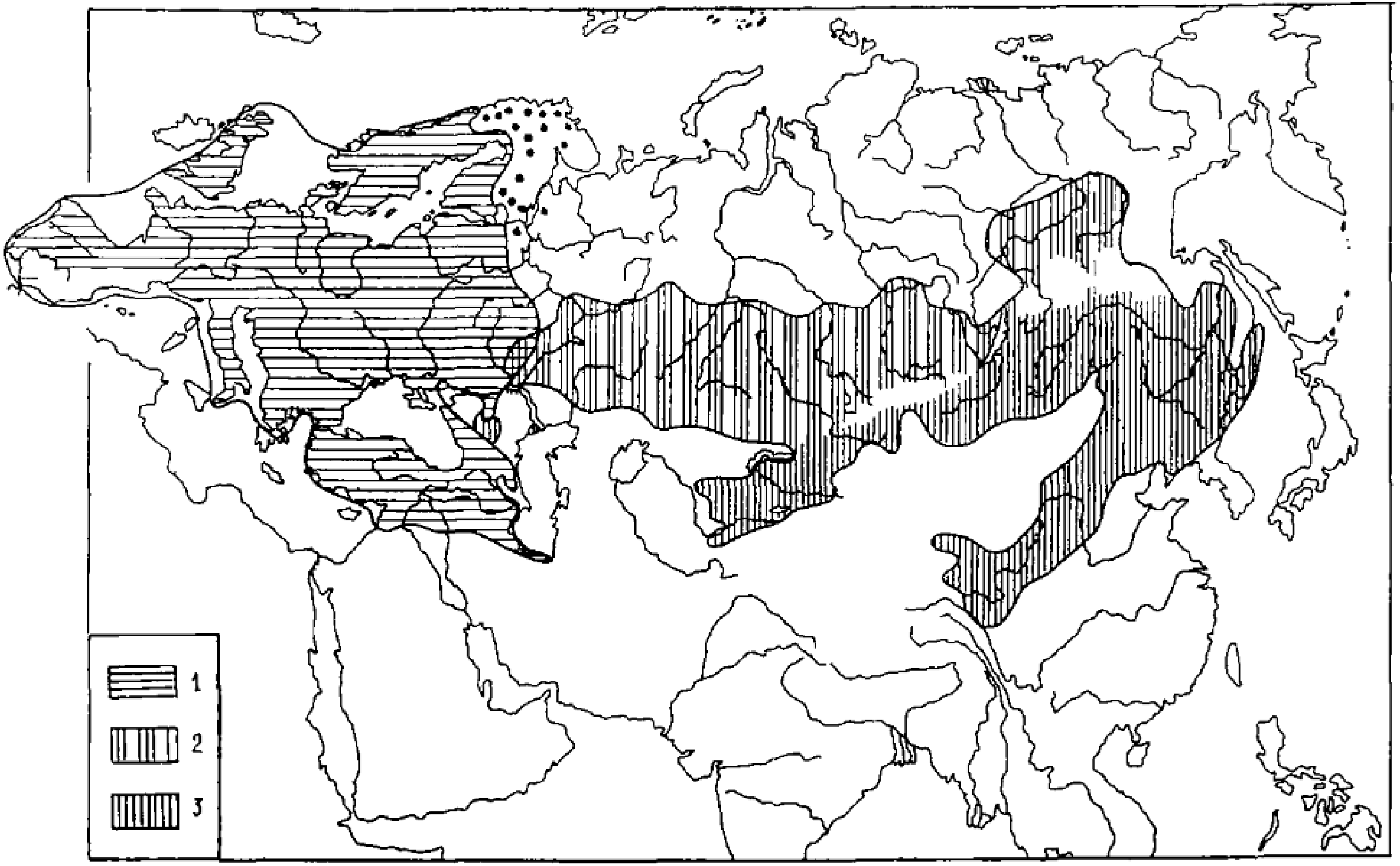
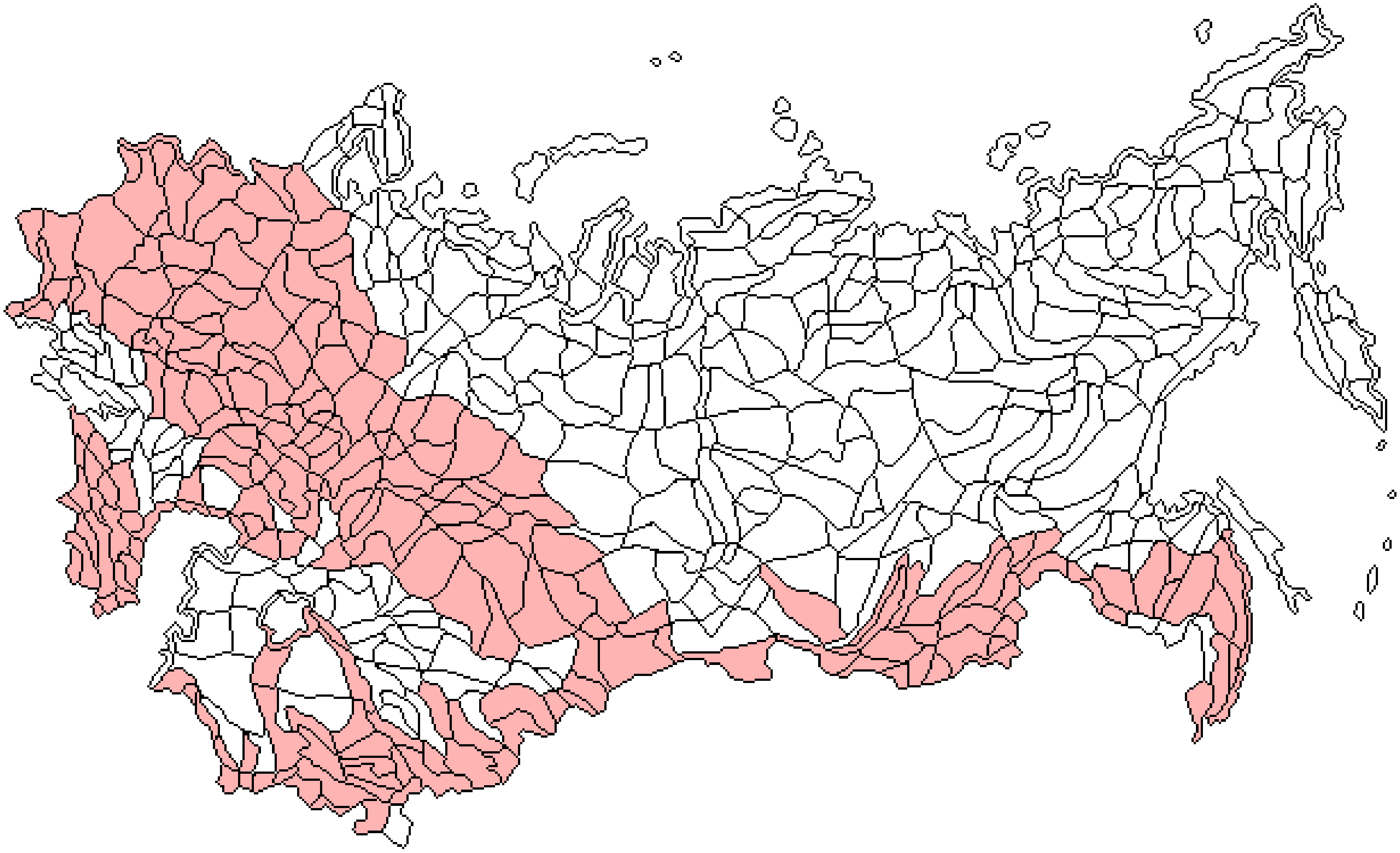


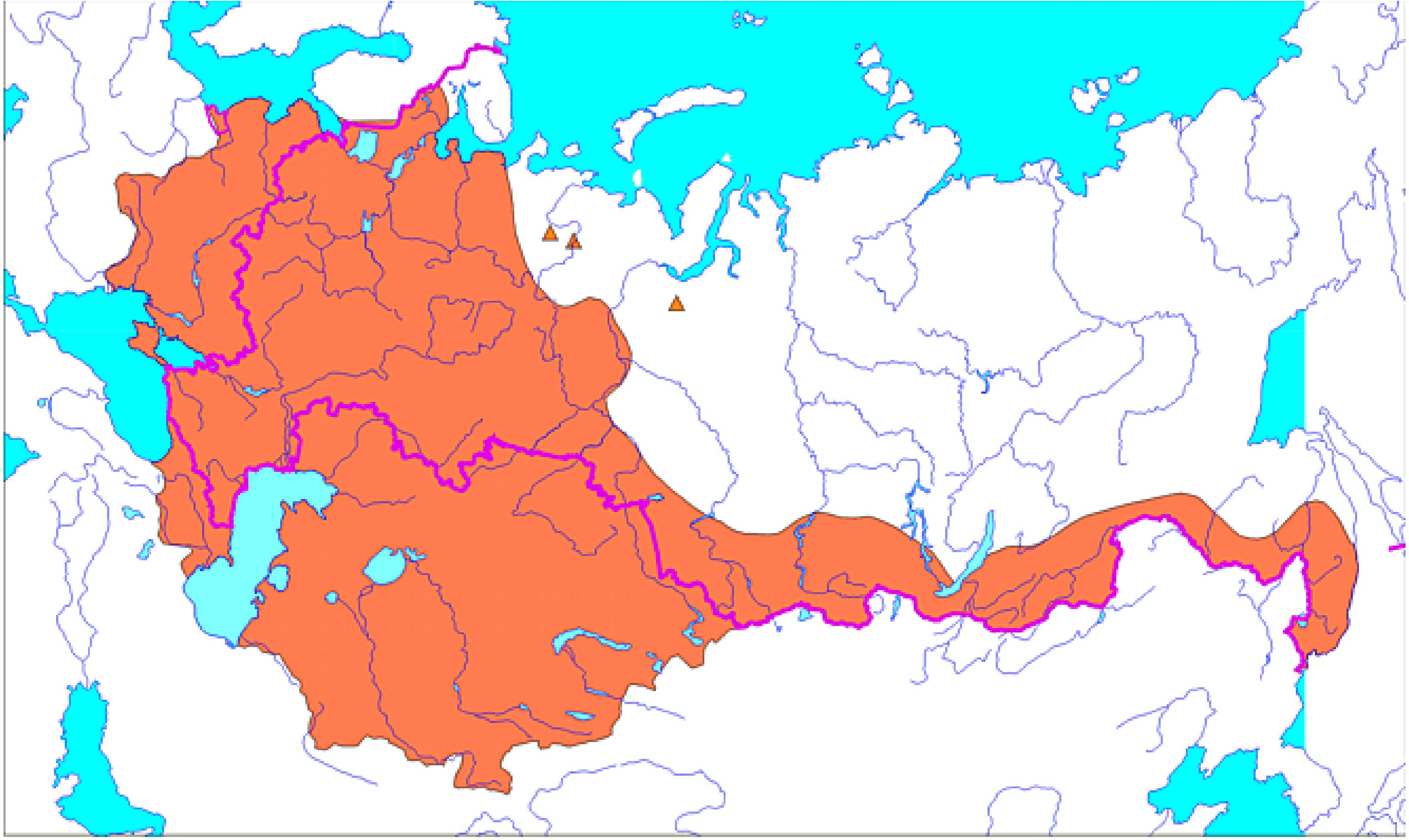
Рис. 24. Современные ареалы европейской и сибирской косуль

1 – *Capreolus capreolus* L.; 2 – *C. pygargus pygargus* Pall.; 3 – *C. pygargus tianschanicus* Satunin. Кружками обозначены заходы за границы ареала

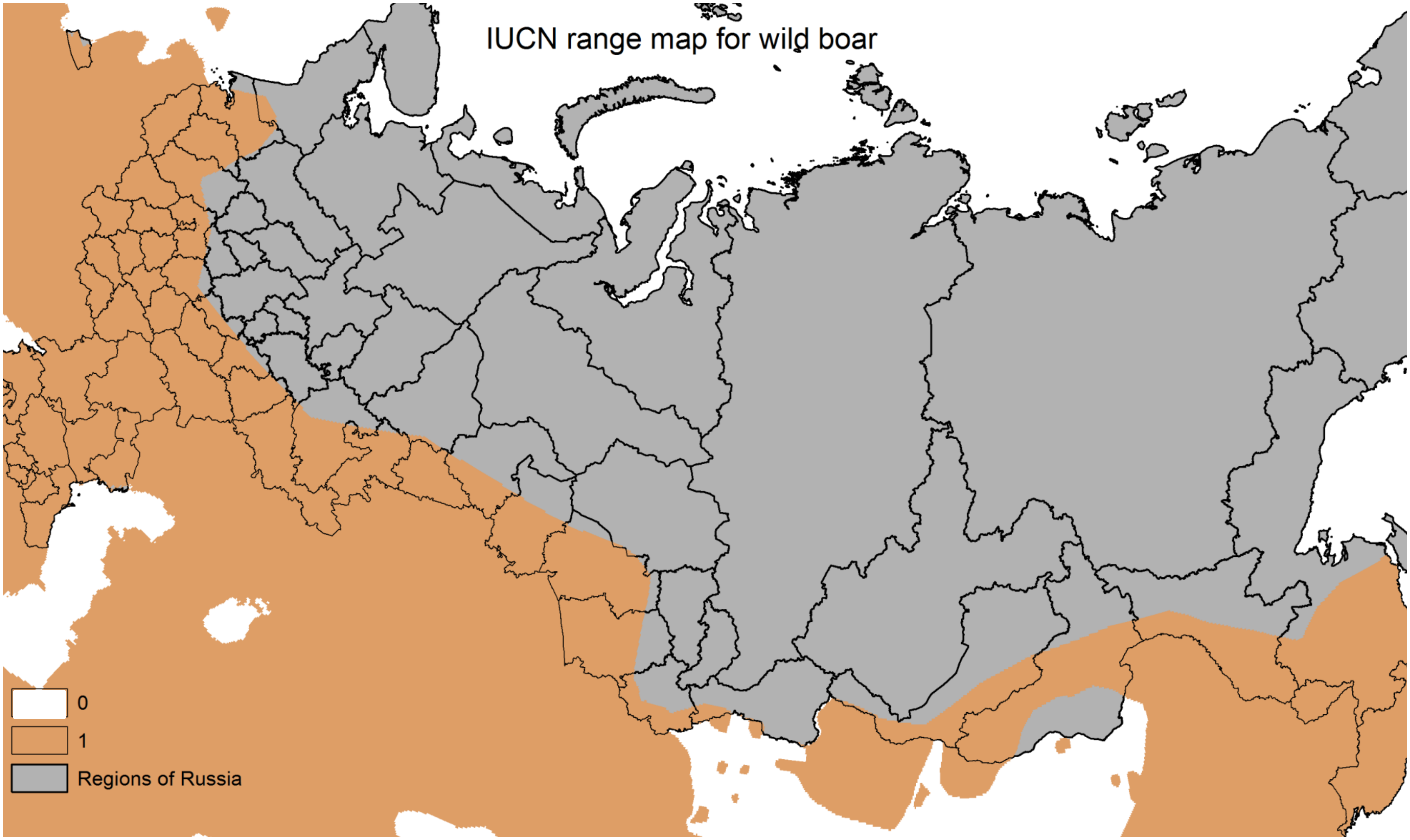
Appendix 24:Wild boar *(Sus scrofa)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)



Appendix 25: Wild boar *(Sus scrofa)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in pink. Triangles show the northern occurrence (Pavlov et al., 2002).



Appendix 26: Wild boar (*Suc scrofa*) IUCN range map is shown in brown: 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)



Appendix 27: Wild boar range map in Russia and adjacent regions (in boundaries of former Soviet Union)
Legend: 1-northern boundary of reconstructed range (where the boundary is different from the current boundary), 2-minimal range at the beginning of XX century (by Geptner, 1961) with changes, 3-maximal range in the end of XX century (including irregular occurrence),4-points of the northern occurrence (Danilkin, 2002,p.56)

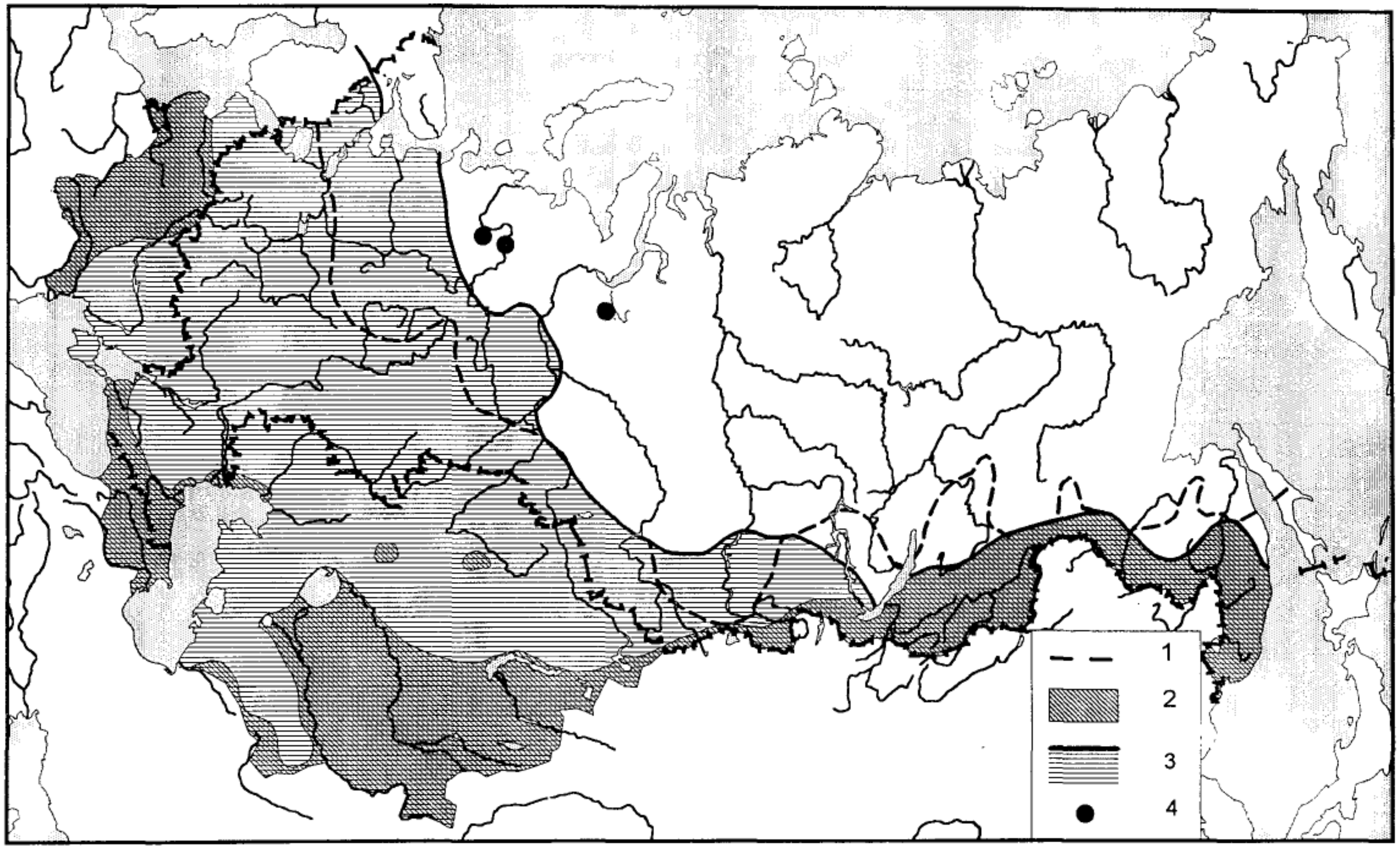
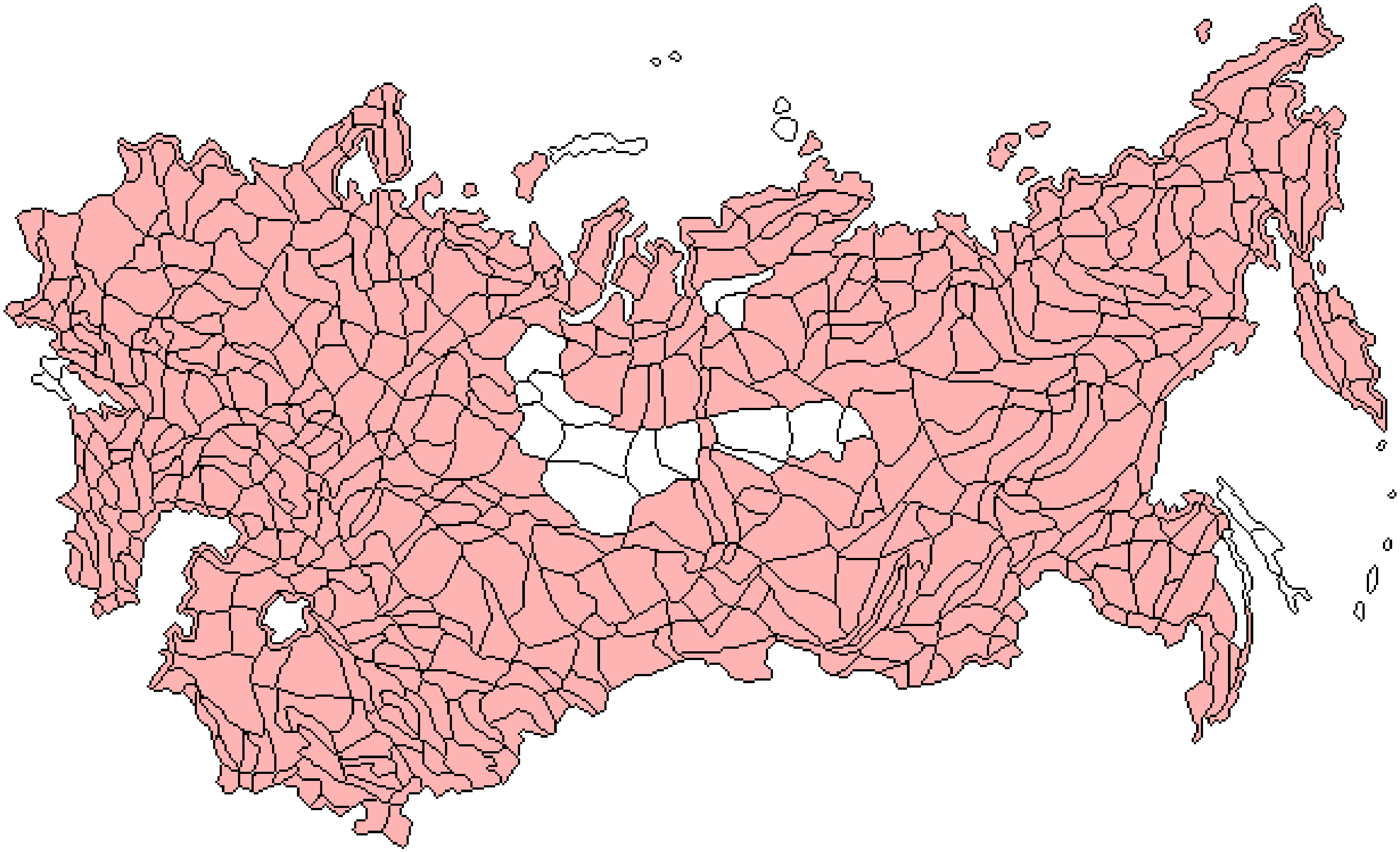


Рис. 19. Распространение кабана в России и сопредельных регионах (в границах бывшего СССР)
1 – северная граница восстановленного ареала (там, где она не совпадает с современной границей); 2 – минимальная область обитания в начале XX в. (по [Гептнер и др., 1961], с изменениями); 3 – максимальный ареал в конце XX в. (включая периодические заходы); 4 – крайние северные пункты заходов

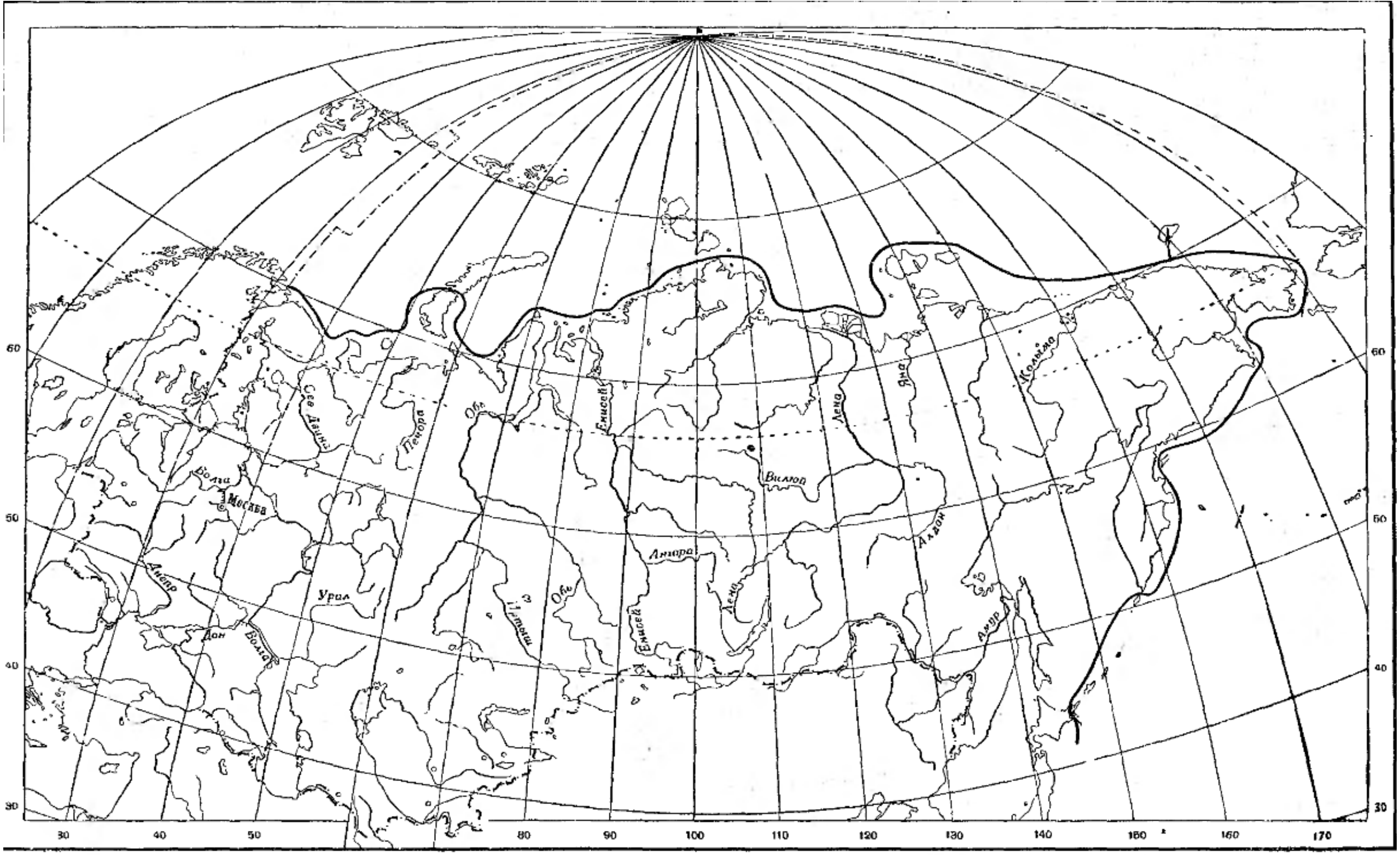
Appendix 28: Wolf *(Canis lupus)* range map by Puzachenko A. Yu. is shown in red color. Sub regions are the regions of natural zoning (Puzachenko, 2017)



Appendix 29: Wolf *(Canis lupus)* range map by Russian Academy of Sciences is shown in orange. Rivers, lakes, seas are shown in blue; the border of Russia is shown in pink (Pavlov et al., 2002)

Appendix 30: Wolf (*Canis lupus*) IUCN range map is shown in brown**:** 0-not included in range; 1-included in range. The administrative regions of Russia are shown in gray (IUCN, 2001)

Appendix 31: Northern and eastern boundary of wolf’s range, *Canis lupus L.*, in Soviet Union (V.G.Geptner) (Geptner et al., 1967, p.133)



ис. 49. Северная и восточная границы распространения волка, *Canis lupus* L., в СССР (В. Г. Гептнер)

Appendix 32: Home-range size of family packs in different climatic zones in Soviet Union

Legend: 1- area of home-range in summer, 2-area of home-range in winter: 1cm^2=154km^2, numbers represent an average size of packs (Bibikov, 1985, p.417)

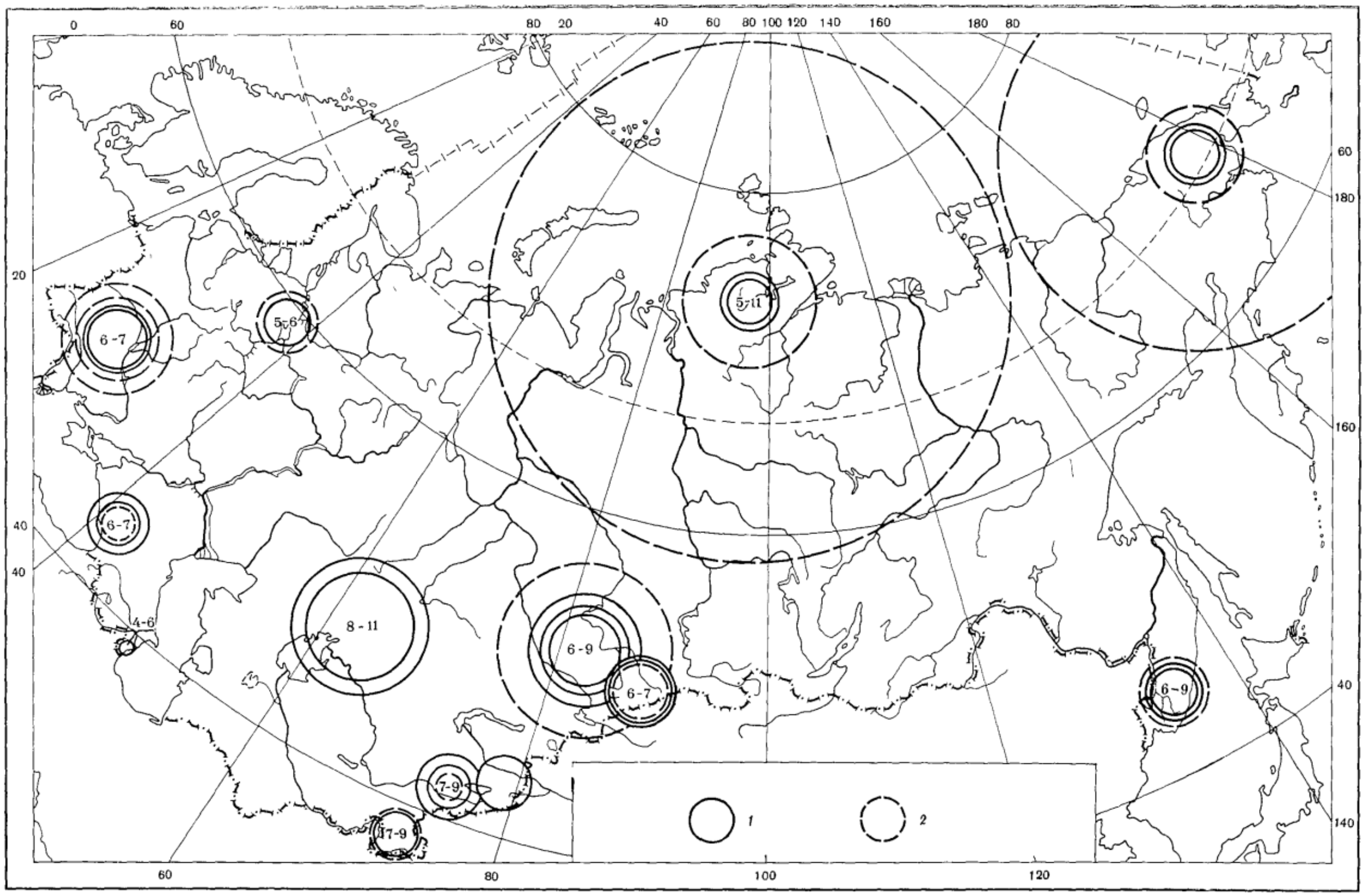


Рис. 151. Величина семейных участков волка в различных природных зонах СССР

1 — площадь летнего участка; 2 — площадь зимнего участка: 1 см^2 = 154 км^2; цифры — средний размер стаи

Reference

Bibikov, D.I., 1985. The wolf. Nauka Publishers, Moscow (In Russian).

Danilkin, A.A., 2002. Mammals in Russia and adjacent regions. Pigs (Suidae). Moscow: GEOS, Moscow (In Russian).

Danilkin, A.A., 1999. Mammals in Russia and adjacent regions. Deer (Cervidae). Moscow: GEOS, Moscow (In Russian).

Geptner, V.G., Naumov, N.P., Yurgenson, P.B., Sludskiy, A.A., Chirkova, A.F., Bannikov, A.G., 1967. Mammals of the Soviet Union. Sea cows and predators, Volume 2. ed. Vysshaya shkola, Moscow (In Russian).

Geptner, V.G., Sludskiy, A.A., 1972. Mammals of the Soviet Union. Predator (hyena and cats), Volume 2. ed. Vysshaya shkola, Moscow (In Russian).

IUCN, 2001. The IUCN red list of threatened species [WWW Document]. URL http://www.iucnredlist.org/ (accessed 1.5.17).

Pavlov, D.S., Petrosyan, V.G., Dgebuadze, U.U., Reshetnikov, U.S., Kuzmin, S.L., Varshavskiy, A.A., Korneeva, T.M., Pavlov, A.V., Bessonov, S.A., Veprintseva, O.D., Omelchenko, A.V., Pavlinov, I.J., Orlova, V.F., Loskot, V.M., Dorofeeva, E.A., Sideleeva, V.., 2002. Biodiversity of vertebrates in Russia [WWW Document]. URL http://www.sevin.ru/vertebrates/ (accessed 2.20.17).

Puzachenko, A.Y., 2017. Areal for mammals [WWW Document]. URL http://biodat.ru/db/areal/ (accessed 2.23.17).

Sokolov, V.E., Ivanitskaya, E.Y., Gruzdev, V.., Geptner, V.G., 1994. Mammals of Russia and adjacent regions: lagomorphs, Nauka. ed. Moscow (In Russian).