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USE OF SPACE INFORMATION ABOUT THE EARTH
ENVIRONMENTAL STUDIES BASED ON SPACE DATA

MaxEnt Modeling for Predicting Suitable Habitats in the North Caucasus (Russian Part) for Persian Leopard (*P. p. ciscaucasica*) Based on GPS Data from Collared and Released Animals

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Abstract—The first leopards were released into the wild in the Russian Caucasus in 2016 and 2018 as the first step of the Federal leopard restoration program. Leopards were tagged with GPS-Iridium collars. The obtained GPS-coordinates were used to create and verify a mathematical model of the potential habitats of this species and evaluate the possibility of the way choice made by leopards on the move. The modeling was performed by the maximum entropy method using the MaxEnt program based on the data from six leopards (four males and two females). A variety of basic habitat factors and characteristics are reflected in WorldClim bioclimatic indicators, including the data on surface radar imagery, and indices calculated on the basis of Landsat8 satellite image mosaic. To describe and verify biotopes, the field data collected in the Republics of North Ossetia-Alania, South Ossetia and Kabardino-Balkaria were used. The obtained results confirmed a high) accuracy in determining the predicted points. The largest contribution to the common model of potential leopard habitats is made by 10 main factors from the whole set. That list includes the slope steepness, altitude, several climatic characteristics, bioclimatic indices, and the vegetation index. According to the modeling results, the most preferred habitats for the leopard in the Caucasus are not very steep (up to 30°) slopes with grassy vegetation at altitudes of about 800–1500 m above sea level, independent of exposure, but with the average value of snow indices.

Keywords: leopards, habitats modeling, GPS-Telemetry, reintroduction to the wild, MaxEnt

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INTRODUCTION

The conservation and restoration of flag rare species of animals is a complex task of both fundamental and applied importance, which allows, inter alia, to ensure the preservation of ecosystems as a whole. Animal reintroduction is one of the most important conservation and restoration methods for endangered species (Sarrazin and Barbault, 1996; Hayward and Somers, 2009). It is a generally accepted practice to create special centers for breeding and preparing anuimals to be further released into the wild (into their natural range). The basic requirements for places of release are: (a) location within the species' historical area; (b) good feeding grounds; and (c) far away (remote location from*) from human settlements (Hayward and Somers, 2009).

The Persian leopard (*Panthera pardus ciscaucasica*), historically inhabiting the Caucasus, is the largest subspecies of leopard in the world and is currently listed in the Red Book of the Russian Federation (*Krasnaya*..., 2001) and Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In 2007 wildlife biologists of Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (IEE RAS) supported by WWF-Russia developed a program to restore the population of the Persian leopard in the Caucasus. They applied the best practices for breeding in captivity breeding and a subsequent reintroduction of big cats corresponding to the norms of behavior that characterizes wild individuals and their physiological status (Rozhnov and Lukarevskiy, 2008). In 2016 and 2018 in the Western and Central Caucasus the first leopards prepared for living in the wild were released. These animals were bred and grown at the Caucasian Leopard Recovery Center of Sochi

National Park (Semenov, 2016). Prior to release, the animals were tagged with GPS-Iridium-collars (Lotek, Canada). GPS fixes received from the collars allowed us to track how the animsals used space after release in detail and in dynamics.

Currently, non-invasive techniques are becoming increasingly relevant when working with endangered species (Rozhnov et al., 2019). These methods include mathematical modeling of developmental variations for each population (Kanagaraj et al., 2013; Carter et al., 2015; Goltsman et al., 2016, 2018; Rodionova et al., 2018), distribution and habitat options based on environmental characteristics (Safford, 2004; Hebblewhite et al., 2014; Dobrynin et al., 2017; Zhu et al., 2019; Rozhnov et al., 2019). There are numerous modeling algorithms for predicting the spatial distribution of species and the areas of their habitats (Stockwell and Peters, 1999; Guisan and Zimmermann, 2000; Austin, 2002; Guisan et al., 2007; Guo and Liu, 2010; Hijmans et al., 2005; Stigall, 2012). The mathematical maximum entropy algorithm (Phillips et al., 2006; Phillips and Dudik, 2008; Elith et al., 2010) built into the MaxEnt software is currently the most frequently used one. MaxEnt uses only the data of the reliable presence of the species, and the approximation satisfies all the restrictions known to the researcher, while the resulting distribution has maximum entropy (Phillips et al., 2006). The result of the calculation of the algorithm is presented in the form of a map with a probability prediction of the species' presence in each cell/pixel grid.

The inaccessibility of numerous sites for direct assessment by researchers seriously limits animal ecology surveys in mountainous areas. Applying the non-invasive methods—remote sensing—and interpolating the results obtained for a limited territory to the area of the entire region may help overcome this difficulty. Spatial modeling is useful in the first place for planning both land development (Safford, 2004) and environmental conservation (Rondinini et al., 2005); for a retrospective analysis of evolutionary processes within the territories of population settlement; managing invasive species—controlling their populations' density. Last but not least, it is useful for other purposes, including determining the suitability of the species habitat (Jiang et al., 2016), predicting trends in species distribution at regional level (Giovannelli et al., 2010), as well as identifying potential areas of high risk, areas of likely imminent humanwildlife conflict (Naqibzadeh et al., 2019).

This work aims to estimate leopards' habitat preferences in the Western and Central Caucasus through mathematical modeling based on GPS-collar data of the released leopards, remote sensing and in situ habitat verification in one of the modelled regions (the Republic of North Ossetia-Alania, Republic of South Ossetia and the Kabardino-Balkar Republic). Hence, the first task is to assess the probability of using habitats with different characteristics in the most extensive area of the Western and Central Caucasus. The second one is to test the predictive ability of the model in three stages (before animals' release, six months after release, one year after release), taking into account population density and in situ habitat verification. As an object for testing the predictive ability of the model, we selected the female leopard named Volna and the territories of the Kabardino-Balkar Republic and the Republic of North Ossetia-Alania.

MATERIAL AND METHODS

Research Area

Potentially suitable habitats of Persian leopard were modeled and the results were interpolated for the territory covering the Caucasian mountain country in the following physical and geographical boundaries: in the east—the Caspian Sea, in the north—from the Caspian Sea to the Kumo-Manych depression and further along the border of the Krasnodar Region to the Black Sea, in the west—along the coast of the Black Sea, in the south—along the Kura-Araksk lowland and the southern borders of Azerbaijan, Armenia, and Georgia (Fig. 1).

GPS-Fixes

GPS locations from six released Persian leopards: two females (Victoria and Volna) and four males (Akhun, Killi, Artek, and Elbrus) were used to design the model. In the Western Caucasus at the Caucasus Nature State Reserve (within the boundaries of Krasnodar Region, Republics of Karachay-Cherkessia and Adygea) female Victoria and two males, Killi and Akhun, were released in 2016, and male Artek was released in 2018. Female Volna and male Elbrus were released in 2018 in the Central Caucasus, into the Alania National Park (Republic of North Ossetia-Alania). We used Lotek GPS Iridiumtrack M collars (LOTEK Engineering Ltd., Newmarket, ON, Canada) able to upload GPS-fixes through the Iridium satellite network. Collars deployed in 2016 were scheduled for 12 fixes per day and transmitting collected data once a day (12 fixes per iridium message). Collars deployed in 2018 were scheduled for 24 fixes per day and data upload twice a day (also 12 fixes per iridium message). The downloaded GPS data for the operational period of each collar after release is provided in Table 1. A total of 14620 fixes were used for modeling. In assessing the possible spatial distribution of the leopard throughout the Caucasus, we analyzed potentially suitable habitats for the species as a whole. Furthermore, we analyzed animal space use by sex and individually for each individual.

Modeling Parameters

To construct the interpolation models environmental features—115 variables were grouped into three blocks.

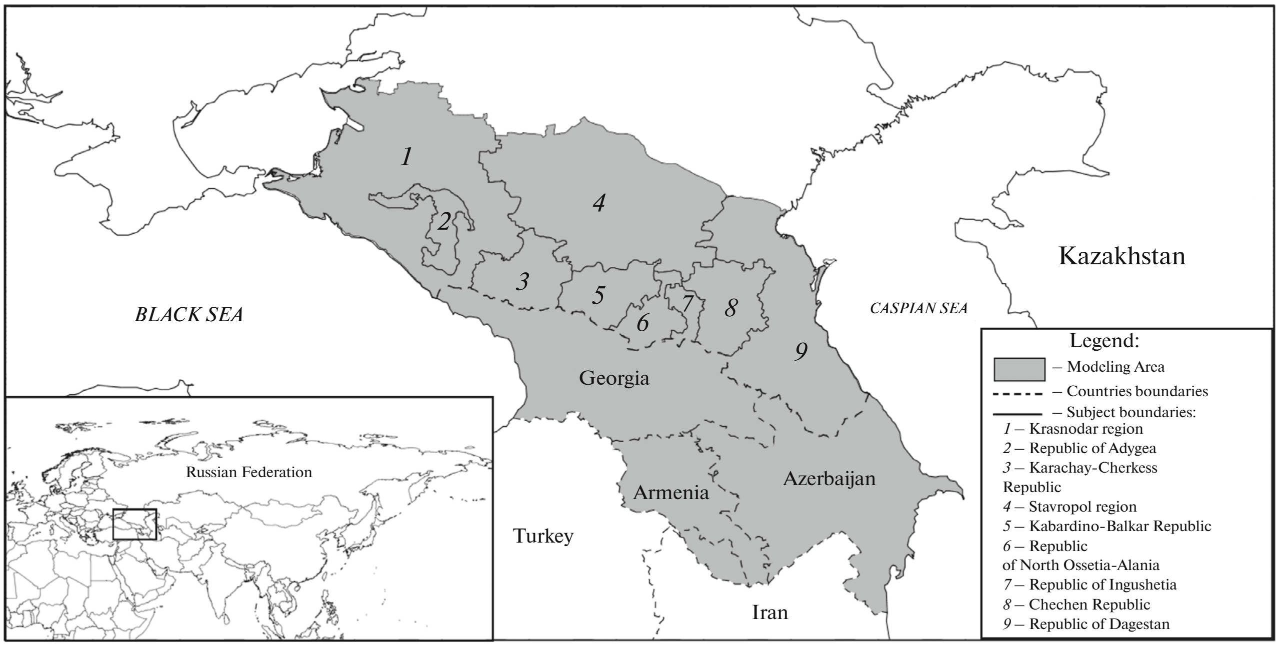

Fig. 1. Research area.

(1) WorldClim bioclimatic indicators, including monthly data on average, minimum and maximum temperature, precipitation, solar radiation, water vapor pressure, wind speed—7 environmental variables for 12 months (84 in total) and their bioclimatic characteristics—19 bioclimatic parameters (Hijmans et al., 2005), indicated in the work as follows: t_{min} (1–12)—minimum values of the average monthly temperature, °C; t_{max} (1–12)—maximum values of the average monthly temperature, °C; t_{avg} (1–12)—average monthly temperature, °C; prec (1–12)—amount of precipitation, mm; srad (1–12)—solar radiation, kJ/m^2 per day; wind (1–12)—wind speed, m/s; vapr (1-12)—water vapor pressure, kPa; bio1—average annual temperature, °C; bio2—daily average temperature amplitude, °C; bio3—isothermal ratio of the average daily and annual average temperatures,%; bio4—temperature seasonality, standard deviation of temperature,%; bio5—maximum temperature of the warmest month, °C; bio6—minimum temperature of the coldest month, °C; bio7—annual temperature amplitude, °C; bio8—average temperature of the wettest quarter, °C; bio9—average temperature of the driest quarter, °C; bio10—average temperature of the warmest quarter, °C; bio11—average temperature of the coldest quarter, °C; bio12—annual precipitation, mm; bio13—rainfall in the wettest month, mm; bio14—rainfall in the driest month, mm; bio15—seasonality of precipitation, coefficient of variation; bio16—rainfall in the wettest quarter, mm; bio17—rainfall in the driest quarter, mm; bio18—amount of precipitation in the warmest quarter, mm; bio19—

Table 1. General characteristics of the modeling of potentially suitable habitats: amount of locations used in the model, model accuracy, estimated area

Persian leopards (ID)	N (Locations used in the model)	AUC ± SD_{auc}	Area, km^2
Overall	14620	0.935 ± 0.003	4508.13
Females ♀♀	6416	0.977 ± 0.002	705.64
Males ♂♂	8204	0.944 ± 0.002	2365.04
Akhun ♂	214	0.988 ± 0.001	82.50
Artek ♂	2989	0.969 ± 0.001	983.96
Elbrus ♂	1709	0.981 ± 0.002	808.15
Killi ♂	3292	0.970 ± 0.002	1190.76
Viktoria ♀	3048	0.986 ± 0.001	610.49
Volna ♀	3368	0.9981 ± 0.000	738.09

rainfall in the coldest quarter, mm. The variables characterizing the snow cover were also used—snowcover (kg/m^2), snow depth—snowdepth (m), based on the Worldclim2 and FLDAS Noah Land Surface Model global climate databases (McNally et al., 2017)—only 2 snow cover indicators.

(2) Data of radar survey of the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) relief with a resolution of 250 m. Based on them, altitude and morphometric characteristics of the relief were calculated: slope—slope, exposure—aspect, various types of curvature (general—curv, planned—plcurv, longitudinal—longcurv and transverse—cscurv), slope illumination indicators from the east (sh_r_e) and south (sh_r_s) and the Laplacian index (lap): 10 morphometric characteristics of the relief (Zevenbergen and Thorne, 1987; Moore et al., 1991; Buckley, 2010), which in the mountains can directly affect the distribution of species.

(3) The vegetation indices of the NDVI summer (ndvi_s) and winter (ndvi_w) periods, calculated based on measurements of the reflected solar radiation of the study area mosaic from the Landsat 8OLI / TRS satellite—2 vegetation indices.

The issues of using the correlated factors in models, the problem of collinearity, and increasing uncertainty of parameters, were extensively considered in the literature on modeling using the MaxEnt method, yet still remain debatable (Dormann et al., 2008; Araujo and Peterson, 2012; De Marco, Nobrega, 2018). In our work, we present the results of modeling using all the information available—115 variables listed above. All variables used in the work are reduced to a resolution of 250 m/pixel by a software method of cubic interpolation through splines (Studley and Weber, 2011).

Modeling Methods

Potentially suitable habitats were determined by the method of maximum entropy (Maxent software for species habitat modeling). This method is relatively new, but it has become popular in recent years in studying the distribution of animals (Baldwin, 2009; Elith et al., 2006, 2010; Ogurtsov, 2019). Is demonstrated heuristic potential in studying and predicting the spatial distribution of various components of the Caucasian mountain ecosystems: lichens and liverworts (Pshegusov and Khanov, 2015; Zhashuev and Pshegusov, 2016), grass communities (Tsepkova et al., 2015), birds of prey and large mammals (Przegusov, 2014; Bleyhl et al., 2015). The logical and mathematical basis of MaxEnt methods using information only on the species presence allows distinguishing the most optimal habitats. In this case, repeated assessment and verification of the model is possible. To obtain the most objective final model, we performed 15 replications (repeated calculations) of 500 iterations in each pixel of the entire analyzed area, 25% of discrete points in each analysis were randomly determined previously as verification ones.

The results were represented with an estimate of the species presence probability ranged from 0 to 1. Regions with a species probability of occurrence of 0.8 or higher were considered as optimal (those where individuals of a species can be detected with a probability of 80% or higher). Areas with a probability of 0.5 to 0.8 were characterized as potentially suitable, i.e. those that the species can inhabit/use under certain conditions or use to move, resettle, during migratory transitions.

Model Verification. A Model Predicting the Potentially Suitable Habitats Should Be Verified

Typically, this procedure is performed by comparing the potential suitability of habitats modeled in MaxEnt with the actual data collected in field studies, including the results of modeling (West et al., 2016). In this work, verification was carried out using GPS locations obtained from the collars of the released leopards. We analyzed the occurrence probability at the location pointsusing the Extract Multi Values To Points geoprocessing tool in the ArcGIS Spatial Analyst extension. Our approach was tested on the movements of a female leopard Volna as an example. The verification took place in three stages.

At the first, preliminary stage (before release into the wild), the model was calculated and the habitat that a leopard can choose after the release was assessed. This simulation was based on the information about two locations—real observations of wild leopard in North Ossetia – encounters in the territory of Zaramagskaya (2015 and 2017) and Gizeldonskaya (2012) hydropower plants. Since the research object was rather specific and the predicted points were defined with a high degree of randomness, the initial model is not characterized by high reliability (AUC = 0.892 ± 0.003). However, we considered it expedient to carry out its calculation, since the reintroduction of this large cat has no analogs in the world, and free-ranging individuals are so rare in the wild in Russia that each encounter can be considered unique. In this regard, calculating a model of this nature can still provide valuable information for planning future/ further work on animal release.

At the second stage, the model was based directly on the collar locations obtained during the first six months of the female's use of space after release (Volna 2018; AUC = 0.932 ± 0.001).

At the third stage, we built a model for the complete data set for the entire period of the collar's operation (Volna 2019; AUC = 0.998 ± 0.000). The results of the calculation of the complete model for all leopards (see above) and the model calculated separately for females were also used. During the analysis, a complete set of locations for the female Volna was superimposed on

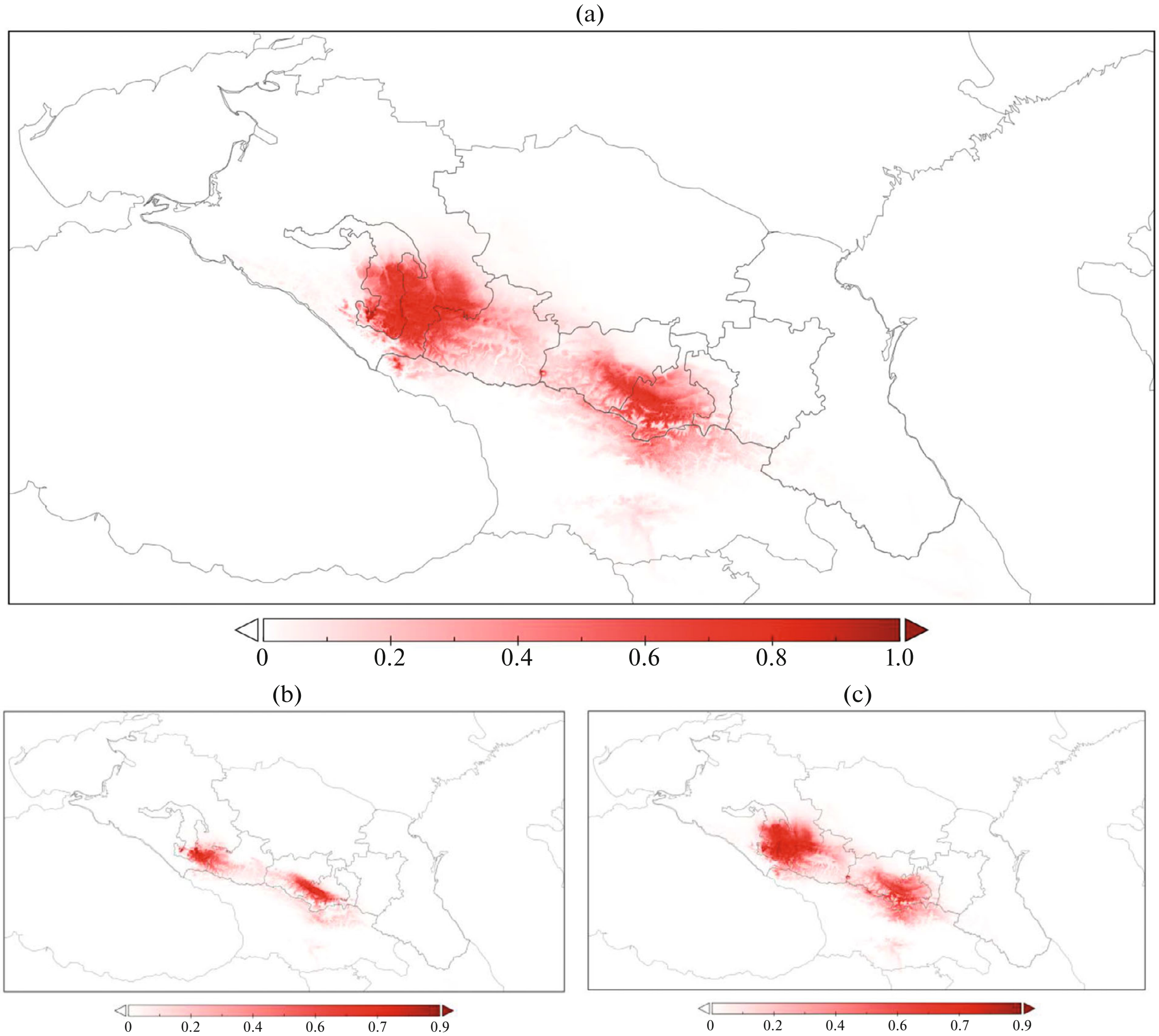

Fig. 2. Model of potentially suitable habitats for leopard in the Western and Central Caucasus. based on GPS telemetry data: (a) all individuals; (b) females; (c) males. Graduation: from 0 (white, unsuitable habitats) to 1 (red, optimal habitats).

the other models, and as a result of extracting the values of cells from one or more rasters into the class of point objects, the probability values for each point were obtained.

RESULTS AND DISCUSSION

General Characteristics of the Model

For the studied species, modeling showed high accuracy (nonrandomness) in determining the predicted points. The indicator representing the area under the curve, used to evaluate the resulting model, is characterized by high values (the average AUC for 15 repetitive models for the species as a whole is 0.935, and the standard deviation is 0.003). Values for other calculations are given in Table 1.

We calculated the optimal habitat area for the leopards using the results of our mathematical modeling and taking into account the individual differences in space using (according to GPS telemetry data) (Table 1). Therefore, the range which the leopards are most likely to inhabit is about 4500 km^2 (450000 ha) (Fig. 2). Since home range area of studied species varies from 15 to 45000 ha (Chistopolova et al., 2018; Fahradinia et al., 2018) depending on the leopard population density, the density and spatial distribution of the prey populations, and external conditions, the analyzed range may be suitable for 5–7 leopard individuals (e.g. two breeding females, one male, and 3–4 different-aged immature individuals). Given that leopard home ranges (Swanepoel and Van Hoven, 2008; Chistopolova et al., 2018), including those of the Near East one (Farhadinia et al., 2018), tend to overlap each other, the provided range

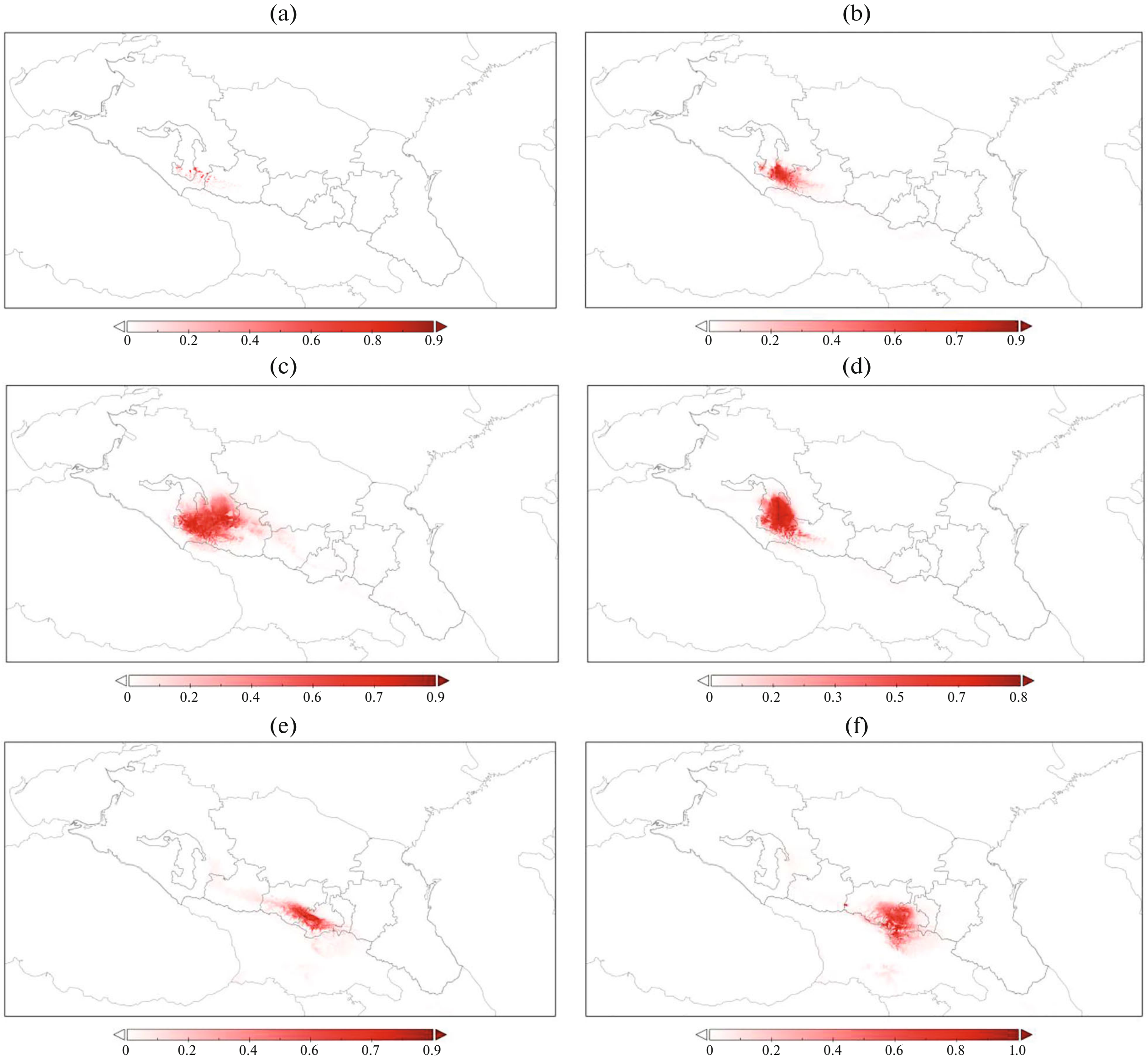

Fig. 3. Model of potentially suitable habitats for leopard in the Western and Central Caucasus. based on GPS telemetry data. Individuals released in the Western Caucasus: (a) male Akhun; (b) female Victoria; (c) male Killi; (d) male Artek. Individuals released in the Central Caucasus: (e) female Volna; (f) male Elbrus.

can accommodate at least 10 (up to 30) individuals, i.e. 5 (up to 15) pairs of leopards.

Our results (Figs. 2, 3). also suggest a possible direction for expanding the area used by leopards including the corridors ranging from the West Caucasus region to habitats in the Central Caucasus. The model allows us to highlight two corridors. One of them, more alpine, involves a part of the southern macro slope of the Greater Caucasus Mountain Range and also covers the upper border of the forest belt with the subalpine and alpine landscapes adjacent above. The other is located in the foothill zone, closer to the border of forest habitats and foothill open areas including the landscapes transformed by humans. These directions are characteristic of the transition from the Western Caucasus to the Central (Kabardino-Balkar Republic) via Karachay-Cherkessia. There is only one transition from the Central Caucasus (from the territory of Ossetia) to the Western Caucasus. it is the most extensive and is localized mainly in the broad-leaved forest belt. Since in the foothill strip the human and settlements density is the highest, the upper border of broad-leaved forests seems to be the most likely corridor to be used by leopards.

Analysis of the Leopard Spatial Distribution Based on Modeling Results

Figures 2 and 3 show that the obtained model also affects the southern slopes of the Greater Caucasus as

Table 2. Some habitat characteristics with a probability of leopards' occurrence equal or above 0.8

Model	Value	Habitat characteristics			
		height a.s.l., m	slope exposure, deg	slope steepness, deg	vegetation index
Overall	Mean	1374.34	169.61	8.51	0.75
	Min	571.00	2.68	0.87	0.13
	Max	2814.00	355.05	27.01	0.83
	SD	573.61	97.27	4.84	0.11
	CV	41.74	57.35	56.89	14.96
Males	Mean	1189.54	197.58	7.21	0.76
	Min	337.00	4.68	0.66	0.14
	Max	4810.00	353.05	27.01	0.84
	SD	607.39	92.79	4.74	0.14
	CV	51.06	46.96	65.61	17.41
Females	Mean	1582.34	181.49	0.74	10.58
	Min	623.00	5.71	0.36	1.98
	Max	3022.00	350.69	0.83	30.45
	SD	456.61	99.82	0.08	5.43
	CV	28.85	55.01	11.11	51.30

well as possible transitions from the Greater Caucasus to the Lesser one corresponding to the region of the Likh (Suram) ridge. This natural bridge was used by leopards for dispersing in the past (prior population extinction due to humans) as evidenced by several historical data sources (Vereshchagin, 1959; Geptner and Sludsky, 1972). The correspondence of our prognosis regarding the expansion of the range in Transcaucasia with the historical registration sites of this species indicates, in our opinion, a high level of accuracy of the provided model.

Our data (Table 1, Fig. 2) also indicate that males are less demanding of space conditions than females as their behavior seems to be more exploratory. Therefore, they master larger areas with a larger spectrum and a variety of conditions than females do. This assumption is based on the results given in Tables 2 and 3a, 3b: the group of factors (characteristics of space) the most significant for the model suitable for males is much narrower than the group of factors determining the choice of a geographical area by a female. Moreover, in this model we did not take into account the data on density of prey populations, as well as the degree of human pressure on the region which is obviously uneven. It also correlates with the results of assessing the path chosen by animals following the relief guides (Rozhnov et al., 2019). Large felines often prefer to move along the slopes focusing on the natural guides of the relief (Koshkarev, 1984). According to our preliminary data, females of big cat species including the Persian leopard prefer the least energy-consuming strategy of moving along the slopes, while the movement of males is characterized by a large range of altitude and relief preferences and height difference (Rozhnov et al., 2019).

If we consider the ranges most preferred by leopard as the release place, for animals released in the Caucasus State Nature Reserve, the set of factors determining the habitat is somewhat different from that of the animals released in North Ossetia. This, probably, can be connected both with a higher variability and comparative softness of climatic conditions in the northwestern part of the Caucasus relative to its central part and with a lesser human population density. In each new situation, the choice of the location by the animal is affected by a different set of factors in each part of the range. So, in the western part of the Caucasus, lands with a more favorable relief for leopard and ungulates are more extensive, the heights are not as large as in the Central Caucasus, the forested area is larger, the subalpine area is also wider, the climate is milder (Gvozdetsky, 1963; Gerasimov et al., 1980). All this combined with the vast extension of protected areas (*Osobo okhranyaemie*..., 2009), determines, among other things, the high diversity of the potential leopard food supply in the Western Caucasus. In the Central Caucasus, the conditions are more severe: the range of critical values of external factors (climate and relief) is greater than in the Western Caucasus. Accordingly, a limited number of factors (both quantitative and qualitative) that determine the leopard's choice of range in the Central Caucasus, differs from that in the Western Caucasus. Besides, the area of undisturbed territories in the Central Caucasus is smaller, and their mosaicity, on the contrary, is higher (Krever et al., 2001).

According to human population estimates in the regions (*Chislennost'*..., 2019), the population density in the Central Caucasus (Ingushetia, North Ossetia-

Table 3

a. Contribution of environmental factors to the prognostic model of occurrence for the species, and separately for females and males

Overall			Females			Males		
variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient
prec8	36.4	0.1	**prec1**	25.9	13.8	prec8	50.2	0
alt	13.1	3	**alt**	25.4	2	**wind3**	11.5	16.7
bio18	10.5	1.2	**bio18**	3.9	0.3	**alt**	8.7	4.1
wind3	9.8	13.7	**srad9**	4.7	11.7	**prec1**	7	0
prec1	9.7	0.5	**wind3**	4.2	0.9	bio9	3.2	2.2
srad9	3.6	11	srad3	3.7	25.9	ndvi_s	2.6	0.5
bio9	3.5	3.8	bio17	3.7	0.3	prec3	2.5	2.4
prec10	3.2	4.4	srad12	2	2.7	**bio18**	2.4	1.2
ndvi_s	1.5	1.2	wind7	2	4	**srad9**	2.2	8.2
prec5	1.1	30	ndvi_w	1.4	0	prec10	1.5	2.1
			ndvi_s	1.4	1.7			
			bio15	1.2	5.2			
			slope	1.1	2.7			
			prec10	1.1	3.8			

For the description of variables, see Materials and methods.

Table 3 (Contd.)

b. Contribution of environmental factors to the prognostic model of occurrence for each individual

Females ♂♂												Males ♀♀					
Akhun			Artek			Elbrus			Killi			Viktoria			Volna		
variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient	variable	variable contribution, %	permutation coefficient
prec4	15.2	0	**prec11**	43.1	1.4	**prec1**	15.7	2.5	prec8	36.7	0	**prec11**	47.3	4.9	**prec1**	25.5	16.4
srad4	12.2	6	**srad4**	12.1	42.9	**alt**	14.8	2.1	**srad4**	22.1	35.8	**alt**	15.5	2.6	**alt**	22.2	2.6
tavg5	9.3	0	**alt**	11.9	5.6	**bio18**	12.2	13.8	**alt**	14.9	7.7	**srad4**	10.5	36.6	**bio15**	14.8	12.4
tavg4	7.6	26.7	prec1	10.1	4.3	srad4	11.4	41.1	wind2	7.6	1.7	tmin4	6.9	0	**bio18**	11.3	3
sh_r_s	7.1	0	wind2	7.2	0	wind3	8.6	0.5	prec3	2.3	1.5	bio17	4.5	4.1	srad8	7.7	0.3
bio15	6.4	44.3	bio9	4.9	0.3	**bio15**	6.8	11.2	ndvi_s	2.1	0.3	prec10	2.3	0.9	prec11	3.3	2.7
tmin5	5.3	2.4	prec3	4.6	2.6	prec7	5.3	0.7	bio2	2	0.6	tmin5	2.2	0.1	srad4	2.3	23.2
bio14	3.4	1.8	ndvi_s	1.3	0.6	prec11	4.8	0.2	srad9	1.9	3.6	tavg4	1.3	0	bio8	1.7	4.2
sh_r_e	2.9	0				prec5	3.7	0.4				bio1	1.1	0	prec5	1.6	2.3
srad6	2.9	0				bio4	3.4	2.3				ndvi_w	1	0	slope	1.1	5.8
bio1	2.6	0				bio8	2.5	0.9				tmax4	1	0			
tmax4	1.6	0				srad10	1.7	0.3									
bio13	1.5	6.3				wind6	1.5	2.3									
bio17	1.5	0															
ndvi_s	1.3	0															
prec11	1.2	4															
aspect	1	0															

For the description of variables, see Materials and methods.

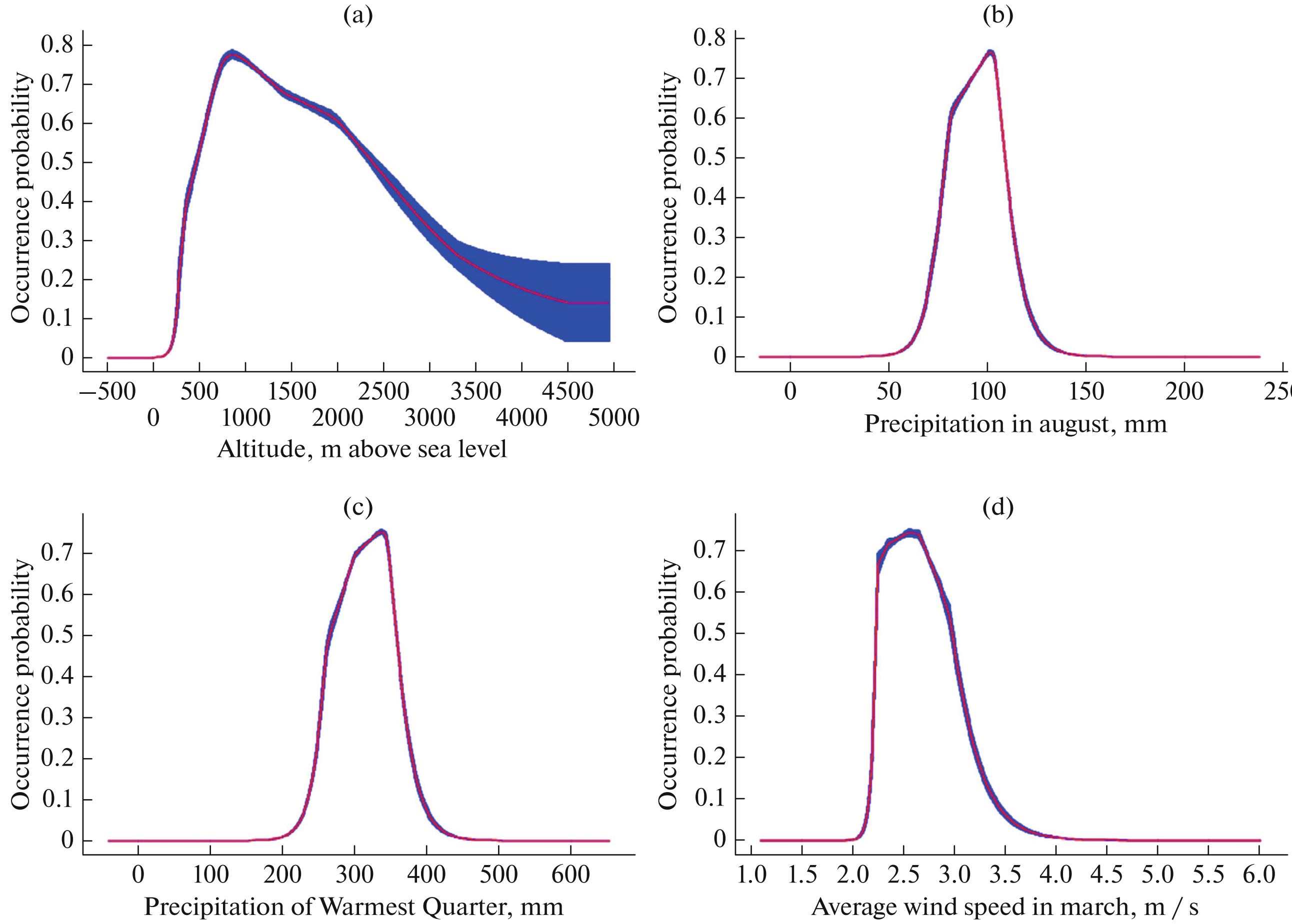

Fig. 4. The values of various factors that make the greatest contribution to the formation of potentially suitable habitats of the Persian leopard in the Caucasus: (a) height (m above sea level); (b) rainfall in August; (c) amount of precipitation in the warmest quarter; (d) average wind speed in March.

Alania, Kabardino-Balkaria, Karachay-Cherkessia) is 81.7 people/km^2, and in the Western Caucasus (Krasnodar Territory, Adygea) 66.5 people/km^2. These data are comparable with those for the provinces of Iran, where the leopard is present (Sanei and Zakaria, 2011): the average density per province is 85.2 people/km, and the medial density is 62 people/km^2 (Provinces..., 2019). Thus, the difference in population density in the Western and Central Caucasus will probably not play a paramount role when leopards choose their future home range.

The results based only on GPS telemetry data reveal that out of 115 factors of the interpolation model common for all individuals, only 10 contribute more than 1% to the construction of an objective model of potentially suitable habitats. Separately, the number of determining factors for females is greater—14 (Table 3a). For male Akhun, their number is even greater, but this may be due to a small number of points obtained from his collar (Table 3b), and the interpretation of these data cannot be objective for this individual. Among the main factors in the complex contributing to the model of potential leopard habitats the most, the amount of precipitation in the warmest quarter (on average about 300 mm) and in August (about 100 mm), and altitude (from 500 to 2000 mN m), as well as the wind speed in March (Fig. 4) should be specially noted.

The combined contribution of these four factors to the model is more than 60%. The snow depth index does not make a significant overall contribution to the model, but it has a high permutation coefficient. If we compare the General model and the model calculated for females and males separately, then the 5 factors with the greatest contribution are common determinants, along with height, precipitation during the warmest period and wind speed, as well as the level of solar radiation in September and the amount of precipitation in January (Table 2).

When comparing the factors that determine the models for each leopard individual released in the Central Caucasus, the amount of rainfall in January and the seasonality of precipitation generally take the

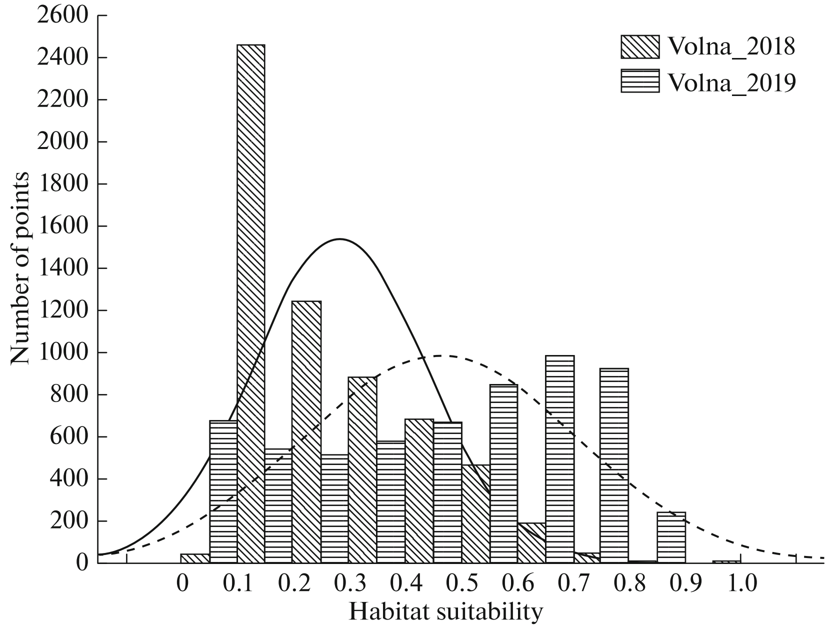

Fig. 5. Comparative histogram of frequency of probability of occurrence (habitat suitability index) for the 2018 and 2019 Volna models.

leading places, and for the West Caucasian individuals, the influence of precipitation in November and the level of solar radiation in April are high.

Significant influence of the factors characterizing the relief was not revealed. In general, the most significant, in various combinations, were climatic factors and, for some individuals, the vegetation index as well. The territories with the highest probability of occurrence were localized in the foothills and midlands with grassy vegetation, where, with a low degree of exposure, the average values of the snow cover in winter (up to 30 cm) prevail.

Verification of the Model

According to the results of verification based on GPS telemetry locations, the probability of occurrence of a female leopard at the points predicted for the species is on average 0.65, with a median value of 0.66. For models constructed for all females, these values are comparable (average 0.65, median 0.69) (Table 4). Directly for the female Volna, the indicators of 2019 (a model with a full set of points) are characterized by higher values of the probability of occurrence in comparison with the preliminary model.

These diverging values of probability of habitat suitability for different models, and the lack of probability values of habitat suitability close to 1, even at the maximum, can be explained by the individual characteristics of Volna movements (although bearing traits of the species as a whole but with individual characteristics), and the small amount of time that passed after the release. This may also be because the Volna home range has not yet been formed. We can find one more argument in favor of the latter in the comparative histogram of the distribution of occurrence probability (habitat suitability) values for the 2018 and 2019 models (Fig. 5). The figure shows that the distribution of 2019 is characterized as more uniform, with an increased proportion of optimal habitats, it is close to normal. Thus, this means progress in the home range formation (Hernandez-Blanco et al., 2020).

Table 4. Cumulative verification of models using GPS locations of the female Volna

	N (number of locations from Volna used for the analysis)	Values for the probability of habitat suitability						
		mean value	median	min	max	SD	CV	SE
All leopards	3368	0.65	0.66	0.20	0.86	0.11	16.5	0.002
All females	3368	0.65	0.69	0.03	0.86	0.15	22.2	0.002
Volna 2018	3368	0.47	0.54	0.02	0.69	0.19	39.7	0.003
Volna 2019	3368	0.51	0.60	0.03	0.80	0.20	40.78	0.005

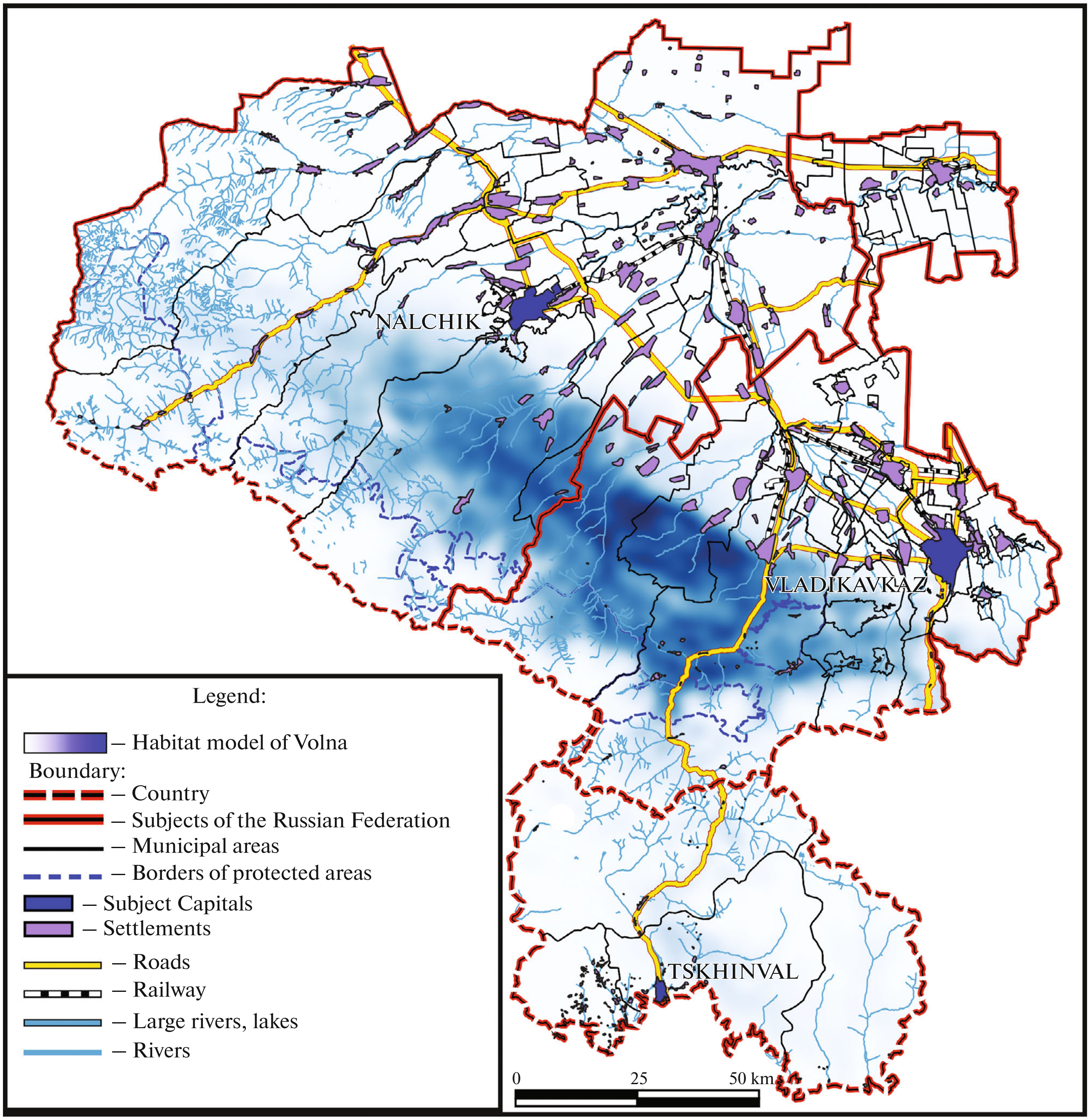

Fig. 6. Potentially suitable habitat model for female leopard Volna superimposed on the administrative-territorial map of the Kabardino-Balkar Republic, and Republics of North and South Ossetia.

The model verification approach described above for one individual needs to be further developed on other individuals, but it shows, in our opinion, the possibility of its preliminary application for predicting the use of space by individuals after release, which facilitates rapid response in the event of spontaneous situations of potential predator-human conflict.

Models similar to those devised in this paper can be used to assess sites that are potentially suitable for the species, as well as to correct the geographical localization of release sites in the future, to conduct bioengineering measures, to optimize environmental measures and resource use, etc. They can also be useful to predict possible routes of animals' movement and, accordingly, the risks associated with the possible oncoming of animals to settlements and the emergence of conflict situations. To illustrate such possibilities, the result of analyzing the model for the full track of Volna with the overlay of the simulated range on the administrative map of the Central Caucasus is shown (Fig. 6).

Table 5. Population size, population density, and amount of large cattle (LC) and small cattle (SC) by administrative units with a high probability of encountering the female Volna according to the model (*Pogolov'ye*..., 2019; *Chislennost'*..., 2019)

Population size, People	Population size, people	Population density, people/km^2	Livestock number, ×1000 units	
			LC	SC
Kabardino-Balkar Republic	**866219**	**69.5**	**265.1**	**375.9**
Leskenskiy district	29612	56.6	15.9	8.6
Cherekskiy district	28081	12.7	32.5	119.8
Chegemskiy district	69149	46.0	29.5	32.0
Rep. North Ossetia-Alania	**699253**	**87.55**	**91.2**	**74.8**
Alagirskiy district	36598	18.2	No Data	No Data
Irafskiy district	15107	11.2	No Data	No Data
Digorskiy district	18283	31.9	No Data	No Data

Table 6. Population size and probability values of leopard occurrence according to the primary model and female Volna models in the human settlements of the analyzed area (*Chislennost'*...., 2019)

No.	Human settlement	Population size, people	Occurrence probability		
			primary model	Volna models	
				2018	2019
	Kabardino-Balkar Republic				
1	Verkhniy Lesken	146	0.28	0.52	0.61
2	Tashly-Tala	646	0.16	0.77	0.71
3	Verkhnyaya Balkaria	4272	0.21	0.52	0.51
4	Verkhnyaya Zhemtala	1638	0.21	0.55	0.61
5	Karasu	517	0.15	0.59	0.71
	Republic of North Ossetia-Alania				
6	Dzivgis	15	0.45	0.52	0.53
7	Verkhniy Fiagdon	1483	0.36	0.54	0.62
8	Gorniy Kartsa	46	0.47	0.54	0.37
9	Verkhniy Biragzang	860	0.52	0.56	0.53
10	Khidikus	117	0.46	0.57	0.74
11	Verkhniy Zgid	204	0.55	0.58	0.60
12	Sadon	492	0.52	0.58	0.59
13	Mizur	3166	0.61	0.65	0.68
14	Buron	548	0.73	0.69	0.57
15	Akhzarisar	350	0.38	0.74	0.78

According to this model, the main areas of potentially suitable habitats in the Central Caucasus are located in the foothills of North Ossetia, partially including the area of the North Jurassic depression of the Central Caucasus (the southern and South-Western spurs of the Rocky Ridge). Administratively, these areas cover the territory of Alagirskiy, Digorsky, and Irafskiy districts of Republic North Ossetia-Alania and Leskenskiy, partially Cherekskiy and Chegemskiy districts of Kabardino-Balkar Republic. Administrative regions and localities that have a high probability of being visited by a leopard according to the model (from 0.7) are characterized by common features, such as a low number and density of population, a lower level of breeding of large and small cattle grazed on summer pastures in the mountainous part (Table 5), according to data on agricultural production (Balaeva, 2005; Khapachev and Bogotov, 2008).

A comparative analysis of the primary model with prognoses for 2018 and 2019 showed an increase in the probability of encounters of female Volna in the vicinity of the localities in North Ossetia and Kabardino-Balkaria, and a shift of the potentially selected habitats to the Northwest from the release site (Table 6, Fig. 7). Subsequently, during a spatial assimilation, leopard came close to many human settlements following the

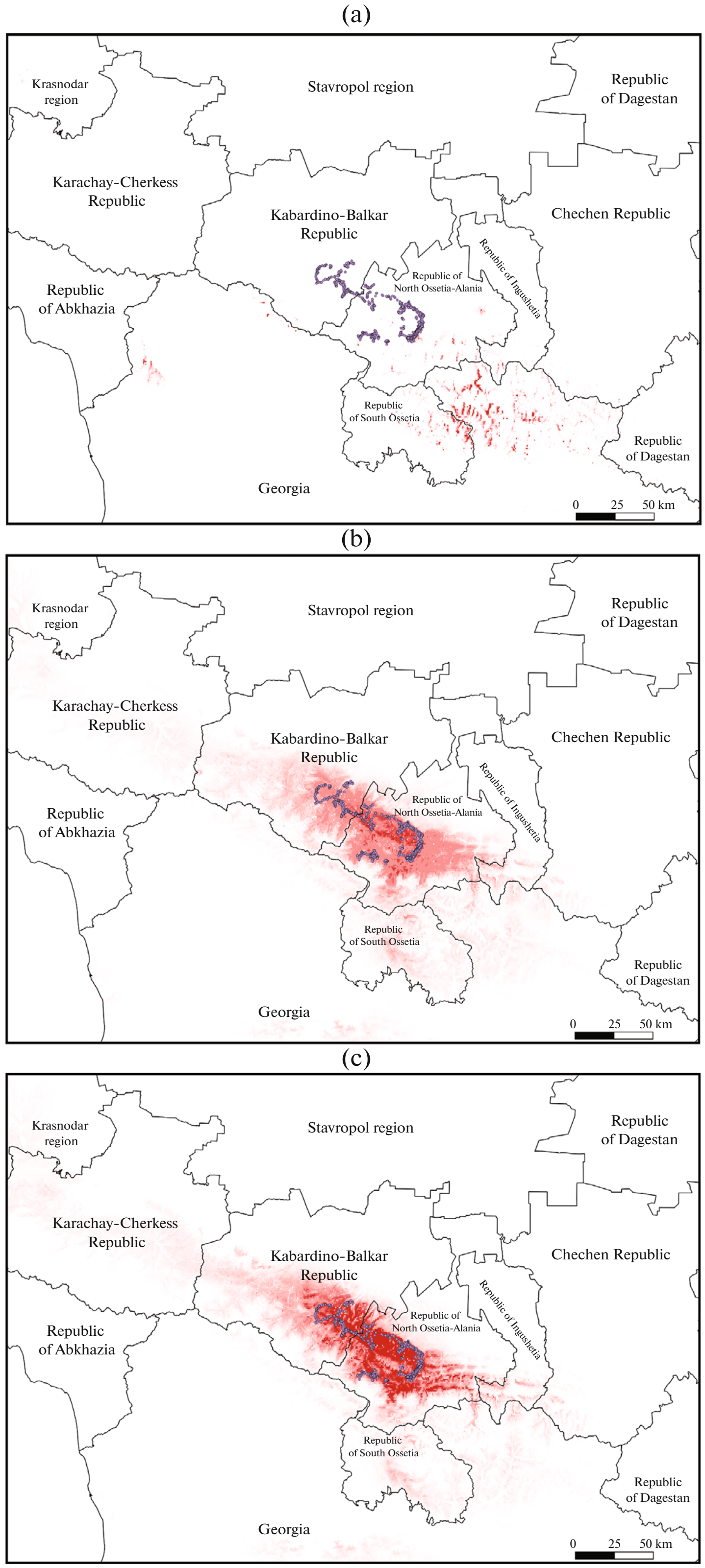

Fig. 7. Model of habitat verification for female Volna with leopard full track: (a) primary model for two locations of wild leopards in the area of hydropower stations Zaramag and Gizeldon; (b) model according to the data from the GPS collar during 2018; (c) model according to the data from the GPS collar during 2019.

prognosis. For the 2018 model, this type of information is particularly important for identifying priority areas for public environmental education, as well as for locally increasing conservation and security measures. However, during the period we analyzed, no real conflict situation was recorded (created by a leopard concerning a person or livestock), which indicates the people avoidance tactics by the released animal.

CONCLUSIONS

The area of optimal habitats for Persian leopard in the study regions is about 4500 km^2 and may be suitable for 10 to 30 individuals, even though males can master even larger ranges, with more diverse climatic conditions, than females. The main factors determining home range choice are the amount of precipitation in the warmest quarter, altitude (up to 2000 m above sea level), the steepness of the slope (up to 30°), and the vegetation index characterizing grassy slopes. The variation in the depth of snow cover on the slopes also plays a significant role.

Although the territory of the Western Caucasus provides a wider range of conditions optimal for the species (more favorable landscape-climatic and socioeconomic conditions), it is farthest from the main dispersion routes of leopards, which were also identified as a result of this work.

Verifying the model revealed the applicability of spatial analysis and modeling methods to identify and evaluate potentially suitable habitats and transition sites for individuals of the species, to assess the risk of potential conflicts and can be used to develop the evidence-based conservation measures, as well as to identify the priority areas when planning environmental education projects. Also, the model can be applied to locally enhance practical conservation measures.

In the future, the model can be improved, taking into account the influence of human factors (the presence of human facilities) on leopards' home range formations, as well as biotic factors such as the spatial distribution and density of competitors and potential prey populations.

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