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Abundance of Eurasian lynx in the mountain taiga of the Southern Urals

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Abstract. The study aims to analyze the dynamics of the Eurasian lynx in the mountain taiga, and to search for the factors affecting the numbers of this predator. The study was conducted in the Southern Urals (Russia) from 2008 to 2019. The dynamics of lynx and its main prey numbers *Capreolus pygargus*, *Lepus timidus* and *L. europaeus*, *Tetrao urogallus* and *Bonasa bonasia* is based on the data obtained during the complex winter census (CWC). Annual CWCs were performed in Chelyabinsk Oblast with total area of 23.445.5 km². The hypotheses on the influence of snow depth on the number of lynx and the relationship between the dynamics of the predator and prey abundances were tested using regression method. The relationship between the number of lynx and snow depth were obtained using Spearman's coefficient. The number of lynxes varied from 51 to 281 individuals, population density - from 0.09 lynx/100 km^2 to 0.48 lynx/100 km^2. The lowest abundances were recorded in 2013 and 2016. In the winters of 2013 and 2016, the snow depth was 2.0-2.5 times greater than on average for long-term observations. However, no significant decrease in the number of the Siberian roe deer was observed in these years, while the number of lynxes decreased by 2 times compared to the previous years. No significant correlation was found between the abundance of lynxes and the Siberian roe deer, $r = 0.25 \pm 0.3$. A negative relationship was found between the amount of precipitation and the winter number of lynxes ($r = -0.717 \pm 0.22$; $p < 0.05$). The amount of snow cover in the Southern Ural Mountains is an important factor affecting the distribution of ungulates. The snow depth may determine the lynx presence both directly and through the changes in the number of its main prey.

Keywords: *Lynx lynx*, population dynamics, snow depth, predator-prey relationship, Southern Urals

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Численность евразийской рыси в горной тайге Южного Урала

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Аннотация. Целью исследования является анализ динамики численности рыси в горной тайге и поиск факторов, влияющих на численность этого хищника. Исследование проводилось на Южном Урале (Россия) в 2008–2019 гг. Динамика численности рыси и ее основных жертв – *Capreolus pygargus*, *Lepus timidus* и *L. europaeus*, *Tetrao urogallus* и *Bonasa bonasia* – основана на данных, полученных в ходе комплексного зимнего учета (КЗУ). Ежегодные КЗУ проводились в Челябинской области на общей площади 23 445,5 км^2. Гипотезы о влиянии глубины снега на численность рыси и взаимосвязи между динамикой численности хищника и жертв были проверены с использованием метода линейной регрессии. Взаимосвязь между численностью рыси и глубиной снега была выяснена с использованием коэффициента ранговой корреляции Спирмена. Численность рыси варьировала от 51 до 281 особи, плотность популяции – от 0,09 рыси/100 км^2 до 0,48 рыси/100 км^2. Наименьшая численность была зафиксирована в 2013 и 2016 гг. Зимой 2013 и 2016 годов толщина снежного покрова была в 2,0–2,5 раза больше, чем в среднем за многолетние наблюдения. Однако существенного снижения численности сибирской косули в эти годы не наблюдалось, в то время как численность рыси сократилась в 2 раза по сравнению с предыдущими годами. Не было обнаружено значимой корреляции между численностью рыси и сибирской косули, $r = 0,25 \pm 0,3$. Отрицательная зависимость была обнаружена между количеством осадков и зимней численностью рыси ($r = -0,717 \pm 0,22$; $p < 0,05$). Количество снежного покрова в горах Южного Урала является важным фактором, влияющим на распределение копытных животных. Глубина снега может определять присутствие рыси как непосредственно, так и по изменению численности ее основной добычи.

Ключевые слова: *Lynx lynx*, динамика численности, глубина снежного покрова, взаимоотношения хищника и жертвы, Южный Урал

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Introduction

Estimation of animal population density is a key step in providing sound conservation and management strategies for wildlife [1]. Eurasian lynx *Lynx lynx* (L 1758) (here in after: lynx and Eurasian lynx) is a widespread Palaearctic forest species inhabiting different natural zones. The abundance of lynx is believed to be closely related to that of its main prey [2-3].

The highest population density of the Eurasian lynx in Europe is due to a high proportion of roe deer in its diet, and its population density is lower if it feeds on hares and tetraonids [4]. The number of predators is often closely related to the abundance of their prey, therefore, in order to understand the peculiarities of lynx dynamics, it is necessary to consider features of spatial placement of prey and its abundance.

Eurasian lynx is versatile in prey selection [4]. Over 30 different species have been recorded as the prey of the Eurasian lynx [5]; its diet varies significantly in different regions [6, 4]. The European roe deer *Capreolus capreolus* (L 1758) is the preferred prey for lynx in Norway, Sweden, Estonia, Latvia, Poland, Switzerland [7-8], Slovenia, Croatia [9], the Czech Republic [10], and countries of the Balkan region [11]. In the northern and lowland taiga regions, lagomorphs and Tetraonids form the basis of the lynx diet [11, 12-15]. When the main prey is lacking, the Eurasian lynx hunts for rodents and birds. It has been reported that rodents make up < 1% of the biomass consumed by the lynx [5, 14]; the lynx hunts for rodents relatively rarely throughout its range [6]. However, in the northern Dinaric Mountains of Croatia and Slovenia, dormouse *Glis glis* (L 1766) is an alternative prey for lynx, which may constitute 7% of the total ration [9]. On the Putorana Plateau, the occurrence of the northern pika *Ochotona hyperborean* (Pallas 1811) in the feces of the lynx exceeds that of the mountain hare, while willow ptarmigan *Lagopus lagopus* (L 1758) is the most frequent part of the diet [15]. In the northern Far East, the average annual share of small mammals (lemmings, mice, voles, etc.) may reach 25% [3].

The diet of the lynx in the Ilmen State Nature Reserve is known from 343 samples of lynx feces collected in different types of mountain taiga. There, the main prey for the lynx are the hares and birds (mainly black grouse), ungulates (mainly the Siberian roe deer *Capreolus pygargus* (Pallas 1771), and small mammals. The other remains namely, squirrel, muskrat *Ondatra zibethicus* (L 1766), and European hamster *Cricetus cricetus* (L 1758), moose *Alces alces* (L 1758) were rarely found in the feces of the lynx [16]. In another area of the Southern Ural (the Bashkirsky Nature Reserve) in the feces (n = 64) of the lynx, the remains of hares accounted for 72% Tetraonids 12% ungulates 12% (including red deer) [17]. Therefore, the lynx's diet was similar in different areas of the Southern Urals, the most important prey for the lynx were hares, ungulates, birds (Tetraonids), and small mammals – an important feed for yearling Eurasian lynxes.

In recent decades, the abundance of lynx and its prey in Russia has been estimated based on direct counts of animals or their tracks [4]. There are few data obtained as a result of long-term tracking [15], radio telemetry techniques [18] or using camera traps, and they are fragmentary.

The purpose of our study is to analyze the abundance and dynamics of the lynx population in the mountain taiga of the Southern Urals and search for factors affecting the numbers of this predator, compare the dynamics of the lynx population and its main prey, and test the hypothesis about the effect of snow depth on the number of lynxes.

Material and methods

Study area. Chelyabinsk Oblast belongs to the Southern Urals; it is located in the center of the Eurasian continent, its area is 87.9 thousand km^2; the length from north to south is about 490 km (from 51°57′ N to 56°22′ N), from west to east, about 400 km (from 57°05′E to 63°25′E). The region borders the Republic of Bashkortostan and Sverdlovsk Oblast. Ilmen State Nature Reserve is located on the eastern macroslope of the southern Ural Mountains, its area is 303.8 km2. The southern border of the forest zone and the northern border of the steppe zone, both adjoined by the forest-steppe zone, pass through Chelyabinsk Oblast. More than three-quarters of Chelyabinsk Oblast is located in the forest-steppe and steppe zones of Trans-Urals, the rest of the territory is covered by mountain taiga (Fig. 1). The Southern Ural Mountains are a system of meridional ridges of various heights from 400-600 to 1000-1400 m above sea level, separated by wide intermontane depressions. Despite the low altitude, the Southern Ural is an important climatic boundary dividing the region into climatic zones of varying degrees of continentality. The climate is cool and humid; the temperature regime largely depends on the land relief. Permanent snow cover forms from October 25 to November 5 and lasts until the end of April, in some years, until mid-May. The snow depth is uneven; it reaches 1.5-2.0 m on the northern slopes, in the ravines and valleys, but only a few centimeters in the upper part of the southern slopes and on the ridges.

Deep snow is the main reason for pronounced seasonal migration of ungulates in mountainous areas. In autumn, the Siberian roe deer move from eastwards and northeastwards of the ridge to the Ilmen Mountains, some of them go further east and southeast into the forest-steppe, reaching Kazakhstan. A moose migration distance is about 250 km [19-21].

The diversity of the relief determines the great diversity of microclimatic parameters of the environment and significant meteorological differences even between the territories slightly distant from each other.

The dynamics of lynx and its main prey (Siberian roe deer, hares, and Tetraonids) numbers are based on the data obtained during the complex winter census (CWC) (which is called Winter Route Census in Russia). The latter consists of a registration of tracks on the snow cover (and following the daily track in order to obtain a conversion factor, so that the trace index can be then converted into the number of individuals using Formozov-Malyshev-Perelishin (FMP) formula [22]; the formula based on the Buffon's needle problem). For many decades in Russia, CWC in areas with stable snow cover in winter has been the main type of registration of game animals. These data are used to assess the population density of each species; when recalculated for the habitat of each species, the absolute number of most species of game animals in certain area is determined. The CWC is

held annually throughout Russia in accordance with the "Methodological Guidelines for the Implementation of State Monitoring of Hunting Resources and Their Habitat by the Method of Winter Route Census" [23]. On the territory of Chelyabinsk Oblast, accounting is carried out on 1100-1200 routes [24].

The CWC is held within two days. On the first day of counting, the tracks of animals are wiped out along the survey route, which allows determining the next day fresh tracks left within 20-28 hours after the wiping out. At the same time, the length of the daily trace of at least five lynx individuals is found on this territory and the average value is used to calculate population density according to the FMP formula [23]. As practice has shown, this coefficient varies little over the years in lynx. The regional conversion factor for lynx in Chelyabinsk Oblast is 1.0.

Counting of game birds during the CWC is carried out simultaneously with that of the mammals' tracks, but the seen birds are counted on a 50 m wide transect (25 m apart from the route left and right). Bird counting on the route is carried out twice, on the day of wiping out the tracks and on the day after. The average number of birds of each species per 10 km of the route is determined (the "counting rate"). The population density of birds of each species is determined (individuals per 1000 ha, or per 10 km^2). The snow depth is measured several times in each category of landscape.

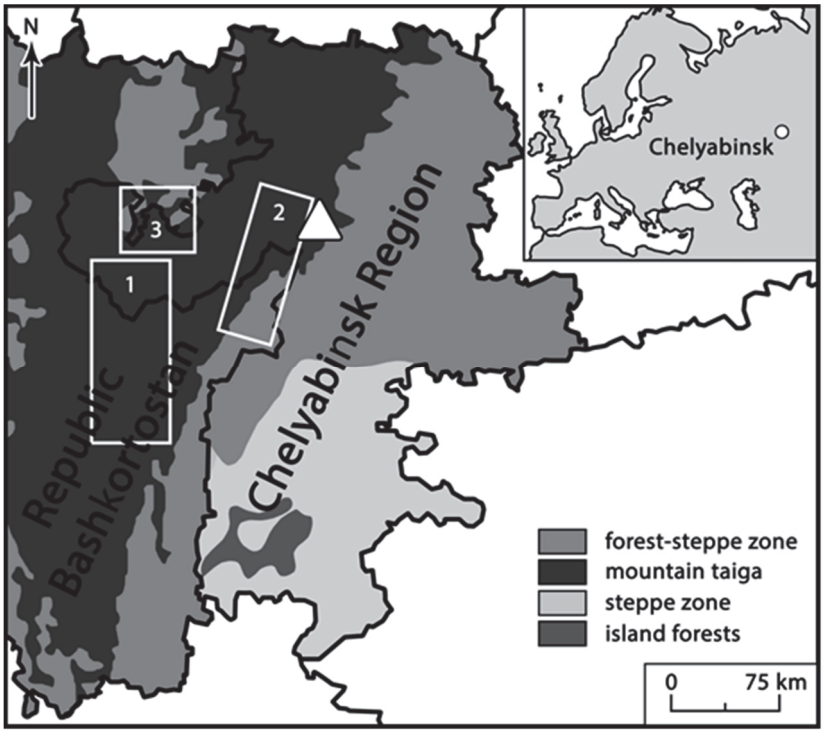

Fig. 1. Study area:
△ - The Ilmen State Nature Reserve; 1-3 - the number of a pair of neighboring game husbandries of Chelyabinsk Oblast and the Republic of Bashkortostan

In many regions, ungulates move to areas with a lower depth of snow during snowy winters and are followed by predators [3, 21]. Therefore, we have collected the CWC data on the number of lynx in Chelyabinsk Oblast and in the Republic of Bashkortostan (Table 1) and in the three districts of the Republic of Bashkortostan [25] adjacent to Chelyabinsk Oblast in 2014-2019 (Fig. 1; Table 2). We compared the data on the lynx population in these and neighboring game husbandries of Chelyabinsk Oblast: Beloretskoe and Katav-Ivanovskoe (53°44′-54°89′ N, 57°65′-59°93′ E), Uchalinskoe and Miasskoe (54°03′-55°38′ N, 59°09′-60°42′ E), Salavatskoe and Katavskoe (54°31′-55°24′ N, 58°64′-58°33′ E). Uchalinskoe and Salavatskoe game husbandries are located in the forest-steppe landscape, the rest in the taiga (Table 2). The territories of Beloretskoe and Katav-Ivanovskoe game husbandries are mountainous, with highly rugged terrain resulting in great landscape diversity and, thus, a very uneven distribution of snow cover in winter. The second pair of game husbandries, Uchalinskoe and Miasskoe, adjoin each other, but they are located in different natural zones. Uchalinskoe game husbandry is located in the forest-steppe zone, whereas Miasskoe in the mountain taiga. Salavatskoe and Katavskoe game husbandries are also united geographically, but there are few mountainous areas in the Salavat District, mainly the northern forest-steppe there; Katavskoe game husbandry is located in the remote mountain taiga.

In our study, we consider changes in the number of lynx and its main prey: two species of hares *Lepus timidus* and *L. europaeus* in total, hereinafter – hares (two species were combined as their tracks are not distinguishable with certainty according to the CWC; although it is known that *L. timidus* is common in the mountain taiga, while *L. europaeus* is rare), the Siberian roe deer, the western capercaillie *Tetrao urogallus* (L 1758), and hazel grouse *Bonasa bonasia* (L 1758). The numbers are based on the annual CWC in 13 game husbandries, five game reserves, two national parks, and one nature reserve in Chelyabinsk Oblast, which altogether covered an area of 23445.5 km² for the period from 2008 to 2019. Data on the lynx CWC counted in the Ilmen State Nature Reserve (54°48′ N, 58°53′ E) in 2017 and 2019, and expel (run) animals' method [16] in 1975, 1976, and 1983 are given based on the annual Reserve Chronicles of the Nature. The CWC-based data on the number of lynx in the Republic of Bashkortostan (Table 1) are provided by the Ministry of Nature Management and Ecology of the Republic of Bashkortostan [25, 26]. Freely available meteorological data are provided by the Chelyabinsk Center for Hydrometeorology and Environmental Monitoring [27].

The hypotheses on the influence of snow depth on the number of lynx and the relationship between the dynamics of the predator and prey abundances were tested using the linear regression method. The monthly average data on the amount of precipitation for December-March was set as a predictor. Statistical analyses were carried out using StatSoft Statistica 12.0 and Microsoft Excel 2016. Arithmetic means (m), standard deviation (SD), and minimum/maximum (limits) were calculated. Statistical significance was set at $p < 0.05$. The Mann-Whitney test was used to assess the differences between the number of lynx from different types of landscape and the relationship between the number of lynx and snow depth was established using Spearman's rank correlation coefficient.

Table 1

The abundance of Eurasian lynx *Lynx lynx* in Chelyabinsk Oblast and the Republic of Bashkortostan in 2008-2019

Year	Abundance of lynx, individuals			Snow depth (cm) in the mountain taiga, Chelyabinsk Oblast
	Mountain taiga, Chelyabinsk Oblast	Island forests in the forest-steppe and steppe zone, Chelyabinsk Oblast	The Republic of Bashkortostan (entire area)	
2008	159	22	no data	85
2009	104	44	no data	90
2010	165	16	no data	76
2011	152	46	145	85
2012	122	67	160	70
2013	51	31	235	157
2014	132	29	291	61
2015	153	23	no data	90
2016	84	23	232	137
2017	173	37	301	68
2018	264	37	419	93
2019	281	75	381	65

Table 2

The abundance of lynx in neighboring game husbandries of Chelyabinsk Oblast and the Republic of Bashkortostan

The number of a pair of neighboring game husbandries	Name of game husbandry	Landscape	Years					
			2014	2015	2016	2017	2018	2019
			Abundance of lynx, individuals					
1	**Beloretskoe***	Mountain taiga	31	9	43	33	54	34
	Katav-Ivanovskoe		5	16	14	30	34	30
2	Uchalinskoe	Forest-steppe	11	6	6	4	6	2
	Miasskoe	Mountain taiga	39	33	4	41	39	42
3	Salavatskoe	Forest-steppe	8	4	19	26	23	19
	Katavskoe	Mountain taiga	25	13	65	0	6	7

Note. * The game husbandries located on the territory of the Republic of Bashkortostan are highlighted in bold.

Results and discussion

In 2008-2019, the number of lynxes in Chelyabinsk Oblast varied from 51 to 281 individuals, population density: from 0.09 lynx/100 km^2 to 0.48 lynx/100 km^2, three minimums and three peaks of the abundance were noted. The lowest abundance was recorded in 2013 and 2016 (Fig. 2, *A*).

In the entire observation period, the largest amount of snow falls in December-March of 2013 and 2016 (Table 1). A negative significant relationship between precipitation and lynx abundance has been found ($r = -0.717 \pm 0.22$; $p < 0.05$) (Fig. 2, *B*). The depth of snow has a negative impact on the number of hares, but it is insignificant at the level of significance ($r = -0.19 \pm 0.3$; $p > 0.05$).

Since 2010, the number of hares in the mountain taiga declined gradually. In 2013 and 2016, the number of hares decreased by 1.4-1.5 times compared to 2012 and 2015 (Fig. 2, *C*). The strong decrease of 2009-2011 did not coincide with particularly snowy winters but winter temperatures were as low as -35°C and -40°C, and the summer was dry. When considering the relationship between the number of lynx and hares, data for 2013 and 2016 were excluded from the analysis, because in these years the winter seasons were characterized by an abnormally high level of snow cover which could have a significant impact on the number of both these species and their relationships. A negative, but insignificant relationship between the numbers of lynx and hares has been found (r = -0.587 ± 0.3) (Fig. 2, *D*).

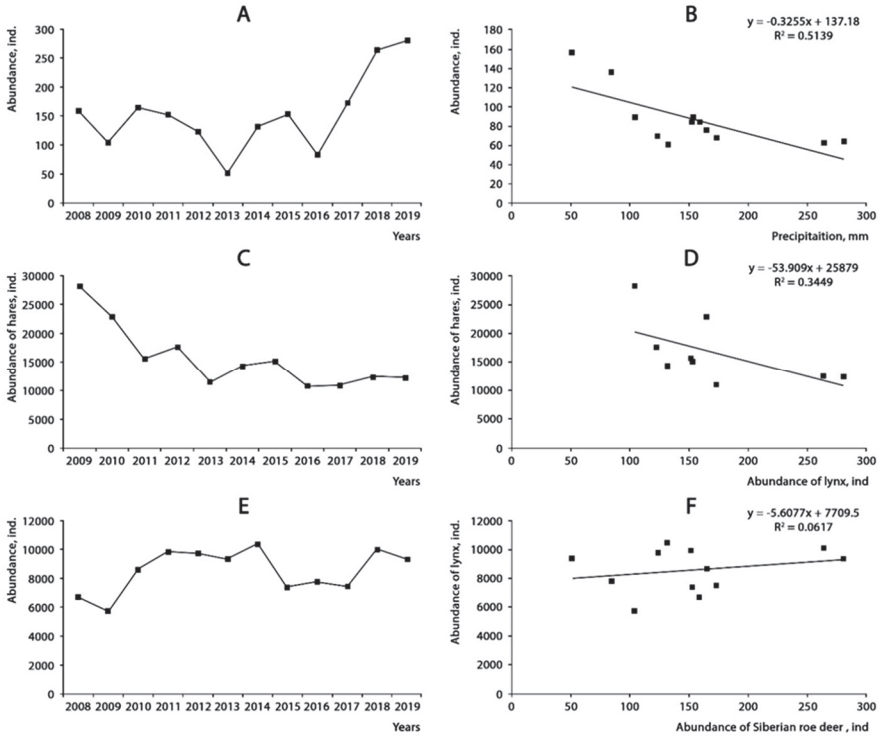

Fig. 2. The dynamics of abundances of lynx *Lynx lynx,* hare *Lepus timidus* and *L. europaeus*, and the Siberian roe deer *Capreolus pygargus* in Chelyabinsk Oblast mountain taiga in 2008-2019 and their interrelations: A - the lynx abundance dynamics; B - the dependence of lynx abundance on the amount of snowfall in December-March 2008-2019; C - the hare abundance dynamics; D - the dependence of lynx abundance on hare abundance (excluding the years of 2013 and 2016); E - the Siberian roe deer abundance dynamics; F - the dependence of lynx abundance on the Siberian roe deer abundance

The number of the Siberian roe deer was the lowest at the beginning of the study period; it slightly increased by 2010. In 2011-2013, the number of this species did not change significantly, but the maximum was observed in 2014. After a decline in 2015, the number remained at the same level for three years; in 2018,

it increased again. No significant correlation was found between the abundance of lynx and the Siberian roe deer, r = 0.25 ± 0.3 (Fig. 2, *E*).

In the snowy winter of 2013, the number of Western capercaillie decreased by 2.3 times compared to 2012 (Fig. 3, *A*), while the number of hazel grouse decreased by 1.8 times (Fig. 3, *B*).

We analyzed the CWC data for 2014-2019 on the depth of snow cover and the number of lynx in Chelyabinsk Oblast and the Republic of Bashkortostan (Table 1). To identify possible movements of predators, we conducted an analysis of the number of game husbandries located nearby, but differing in landscape features (Fig. 1; Table 2). Analysis of changes in the number of lynx on the territories of neighboring game husbandries with landscape differences over the period from 2014 to 2019 showed that in each of the neighboring husbandries there were interannual changes in the number lynx (Table 2). In some years, the number of lynx in certain game husbandries could decrease, in others it could increase in the same year; in some years it could remain constant. For example, 65 lynxes were registered in the Katavskoe game husbandry (mountain taiga) in 2016; the following year not a single individual was registered, but in the adjacent Salavatskoye game husbandry (forest-steppe), the number of lynxes increased (Table 2). In Miasskoe game husbandry (mountain taiga), the number of lynx is usually higher than in Uchalinskoe game husbandry (forest-steppe), but in 2016, the opposite phenomenon was observed (Table 2). In game husbandries located in different types of mountain taiga (Beloretskoe and Katav-Ivanovskoe), interannual changes in the number of lynx were also observed, the differences are statistically significant for game husbandries Uchalinskoe and Beloretskoe ($p = 0.02$), and Uchalinskoe and Miasskoe ($p = 0.03$).

The territories of Beloretskoe and Katav-Ivanovskoe game husbandries are mountainous, with highly rugged terrain. This results in landscape diversity and the mosaic of the environment parameters and, consequently, to a very uneven distribution of snow cover in winter and more places with suitable conditions for feeding ungulates and lynxes. We believe that the landscape features allow the lynx to move to areas with more suitable conditions in unfavorable seasons.

Undoubtedly, the predator movements take place not only between these game husbandries, as there are other areas nearby. Therefore, if we take into account the abundance of lynxes in administrative territories, then sharp "declines" and "rises" in numbers are obvious. In fact, they are most likely associated with predator movements, when lynxes either follow migrating ungulates or seek more optimal conditions, especially in snowy winters. Meteorological factors in 2013 and 2016 were characterized by sharp contrasts during the seasons. In the winter of 2013 and 2016 there were severe frosts down to -36°C and -45°C, the snow depth was 2.0-2.5 times greater than on average for a long-term observation period (Table 1). There was a sharp decline in the number of hares, western capercaillies, and hazel grouses. However, no significant decrease in the number of the Siberian roe deer was observed in these years, while the number of lynx decreased by 2 times compared to previous years.

Due to the weather features of the winter seasons of 2013 and 2016 and the large depth of snow, the predators seem to have left Chelyabinsk Oblast and migrated to the western slopes of the Ural Mountains, i.e. to the territory of the Republic of Bashkortostan, where the number of lynx increased significantly at that time (Table 1).

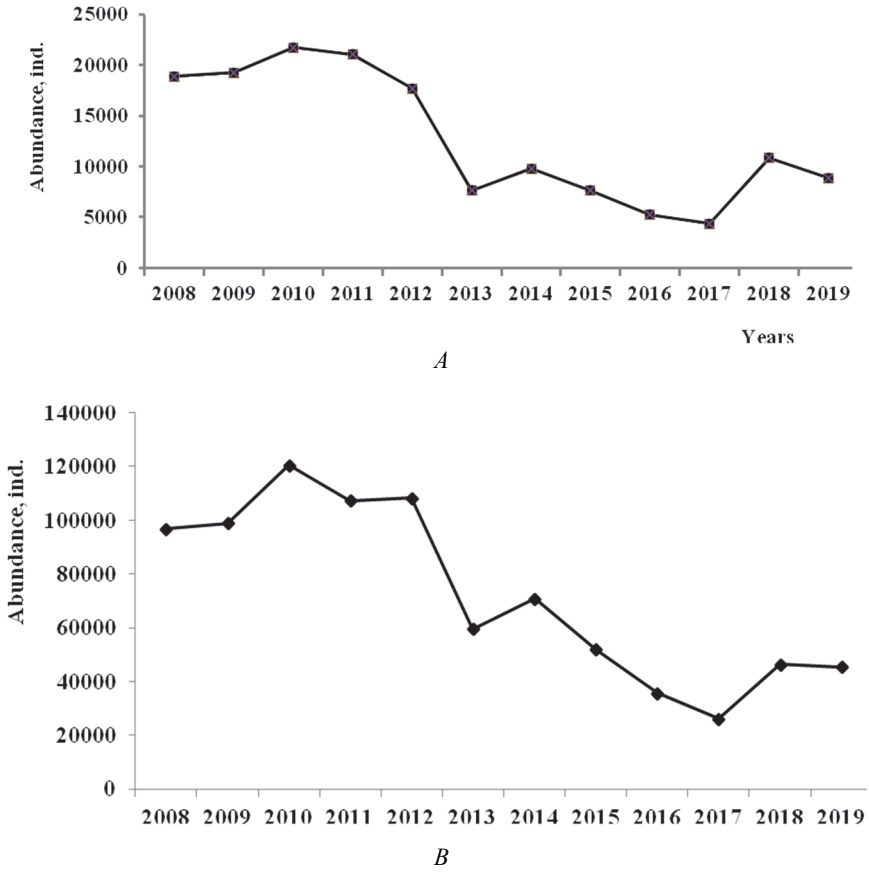

Fig. 3. The dynamics of abundance (ind. - individuals) of the western capercaillie *Tetrao urogallus* (A) and hazel grouse *Bonasa bonasia* (B) in the mountain taiga in 2008-2019

In Chelyabinsk Oblast, 75% of the lynx population inhabits the mountain taiga [24]. According to the survey results in the Ilmen Nature Reserve, the population density of lynx in the winter of 1973-1974 was 2.5 lynx/100 km^2, in the winter of 1974-1975 – 3.5 lynx/100 km^2, in February 1983 – 1.0 lynx/100 km^2 [26].

For 12 years (2008-2019), the population density of lynxes varied from 0.09 lynx/100 km^2 to 0.48 lynx/100 km^2. This is two and ten times lower than the population density obtained by the same method in the same area in 1983, and seven and thirty-five times lower than the population density obtained by the method of absolute population accounting (run method) in this area in 1974-1975. The population densities in Chelyabinsk Oblast are lower or approximately the same for those obtained for different areas in Western Europe: 0.58 ± 0.13 lynx/100 km^2 in the Štiavnica Mountains, and 0.81 ± 0.29 lynx/100 km^2 in Veľká Fatra National Park in Slovakia (by camera-trapping surveys) [28-29]; 0.4 individuals/100 km^2 from camera trapping data or 0.9 individuals/100 km^2 from telemetry data within

the Bavarian Forest National Park [30], and between 0.24 and 0.91 lynx/100 km^2 from camera trapping data in the French Jura and Vosges mountains [31].

In the Ilmen Nature Reserve, the population density of lynx in 1970s and 1983 was from 3.5 lynx/100 km^2 to 1.0 lynx/100 km^2 [26]. In nature reserves, the population number of predators is usually higher than in hunting areas [4, 32]. In addition, in the 1970s and 1980s, there was an increase in the population of lynx on the territory of former USSR after the abolition of its unlimited production as an animal harmful to hunting farms. At that time, lynx population densities ranged from 1-2 to 5-8 lynx/100 km^2 in Karelia, 3.2-4.0 in the Vyatka-Kama Region, 0.5-2.0 in the Yenisei Region of Siberia, 0.1-4.0 in the Sayan Mountains, 2.0-6.0 in the Tien Shan Mountains in Kazakhstan, 2.0-4.0/lynx/100 km^2 in the south of Amur Oblast [4].

The Russian Federation has large hunting territories and a service for protection and accounting of game animals. Experts of the service periodically publish reports on different species of animals. Therefore, in their opinion, over the past 30 years (since early 1990s), there has been a steady decline in the number of lynx in Russia [33].

In 2017, the number of lynx slightly increased from 30.1 to 30.9 thousand individuals [34]. It is impossible to assess the trends in dynamics unambiguously due to the vastness and diversity of the territory inhabited by the lynx. It is also difficult to identify the limiting ecological factors.

The Ural Mountains is inhabited by *L. lynx* (L 1758) [28]. In the Middle Urals bordering with Chelyabinsk Oblast and Bashkiria on the south, the mountain hare is the main food item for the lynx [34], its share in the lynx diet varies from 30% to 35.1%; however, in the southern part of this region, the share of the Siberian roe deer increases significantly, up to 21% of frequency of occurrence [13, 34]. For these flat areas, Malafeev, Mikheeva [35] found that the population cycles of the lynx and mountain hare are closely linked. In different parts of the Ural Mountains, populations of the Eurasian lynx and hare (*Lepus* sp.) may be closely related.

In recent decades, the number of the European (brown) hare and mountain hare has decreased significantly in different regions of Russia [36] as well as, for example, in Fennoscandia [37]. In 2015-2017, the total number of hares in the game husbandries of Chelyabinsk Oblast reached an absolute minimum over the past 30 years; the hunting of these animals in some game husbandries was banned for one to three years [24]. The population of mountain hare continues to decline in Chelyabinsk Oblast. The reasons for this decline in numbers have not been established. During this period of low hare numbers, a negative significant relationship between the number of lynx and hares was obtained ($r = -0.587 \pm 0.3$). Obviously, when the number of hares is very low, the lynx switches to preying on ungulates.

For any predator, the abundance of prey is one of the priority factors. A stable and high number of prey allows the predator to maintain a high level of its own numbers. In the Southern Urals, the number of roe deer is stable and quite high, and even with very low number of hares, the number of lynx is maintained at a high level. There is no significant correlation between the number of lynx and Siberian roe deer ($r = 0.25 \pm 0.3$), it is likely that the interannual fluctuations in the number of lynx are not due to nutritional factors.

One of these factors may be an increase in the number of wolves. It is known that the lynx disappeared in eastern Slovakia after the number of wolves increased after the Second World War [28]. Over the past ten years, the number of wolves in the entire territory of the Southern Urals has increased by three to four times [24]. With such a large number, wolves can influence the lynx population both directly and through competition for food, but there is no data on the number of wolves in the mountain taiga to assess this influence.

A deep and loose snow cover can significantly reduce the success of hunting. In snowy winters, lynxes often die of exhaustion, go hunting to poultry farms, and hunt domestic dogs and cats [4]. Snowy winters constrain the animals to find areas characterized by lesser snow depth and more food [38-39]. Snow forces ungulates to move to less snowy places and lynxes move behind them. A negative significant relationship between precipitation in December-March and lynx abundance ($r = -0.717 \pm 0.22$; $p < 0.05$) (Fig. 2, *B*) confirms the hypothesis on the influence of snow on the lynx population.

Weather events can cause reduction in the number of preys. A thick ice crust can cork grouse birds (Poddubnaya, unpublished data) in the snow and close the access of predators to forest rodents; an ice crust wounds ungulates and lynxes. The inclement weather, usual in the beginning of winter, a sharp change in air temperature, and alternation of heavy snowfalls and rain may completely suppress the activity of the lynx for up to three days [40]. The continuous repetition of such phenomena, up to several times during the winter, may be accompanied by a high mortality of young animals in different carnivorous species. Rainy cold spring and extremely dry hot summer can also reduce the number of prey and predator populations. The weather in 2013 and 2016 was characterized by sharp contrasts throughout all seasons. The summer of 2016 was extremely hot and dry, being the most extreme (since 1864) for the entire period of instrumental observations on the territory of Chelyabinsk Oblast. Most rivers had a reduced water level (20-60% of the norm), small rivers dried up completely [27]. The number of forest rodents, for example, in the Ilmen Nature Reserve, dropped to a multi-year minimum [41]. Summer heat and drought could have a negative impact on the lynx during the rearing period. First of all, due to the lack of important food for cubs – small mammals and birds, and possibly due to the lack of water to drink during the period when 2.5-3-month-old cubs left the family shelter and started moving around the territory with their mother.

Cold and wet weather can contribute to high mortality of cubs at their early age [7]. Cubs have not yet established homeostatic body functions, which leads to easy overcooling or overheating (dehydration), as is known for other mammals [32]. Small mammals are primarily exposed to direct adverse effects of meteorological factors and since small mammals absolutely dominate in the diet of young lynxes up to 1.5 years of age [3], their low availability may cause low survival of young predators. Thus, a rainy cold spring and extremely dry hot summer can have a negative effect on the number of lynx both directly and through prey.

The number of animals can be significantly affected by intensive hunting. In five different regions of Scandinavia, poaching accounted for 46% of adult lynx mortality, but legal hunting also significantly reduces population growth [42].

Could hunting have influenced the abundance of lynx in Chelyabinsk Oblast in 2008-2018 and interfere with the identification of natural population dynamics? Lynx hunting in Chelyabinsk Oblast is allowed, the size of the possible lynx catch varies as 3 to 10% of the population. The catch limit for specific game husbandries is set at no more than 10% of the species population in each of them. In 2014-2016, the annual limit of lynx catch in Chelyabinsk Oblast was set to 2.8-5.2% of the abundance, which were not fewer than 7 and not more than 25 individuals. In 2015, no more than 60% of the established limit was harvested; in 2016, it was 0% of the established lynx catch limit. No facts of illegal hunting (poaching) of lynx were revealed during the period under review [24]. Therefore, legal hunting and poaching could not be the reasons for the sharp drop in the number of lynx in Chelyabinsk Oblast in 2008-2018, and especially in 2016. The population declines of 2013 and 2016 were not caused by an anthropogenic factor.

Conclusions

Therefore, in the Southern Urals, the lynx has no shortage of fodder. Unlike other regions of Europe, where the number of lynx depends on the population of ungulates, the Siberian roe deer ensures the sustainability of the lynx population in the Southern Urals, and apparently reduces the amplitude of long-term population dynamics. Anthropogenic factors are insignificant; the number of lynx, in our opinion, is regulated by a complex of natural factors, among which the level of snow in winter in the mountains directly or indirectly affecting the placement of lynx during the population census in January-February.

References

1. Williams BK, Nichols JD, Conroy MJ. Analysis and Management of Animal Populations. San Diego: Academic Press.; 2002. 817 p.
2. Yan C, Stenseth NC, Krebs CJ, Zhang Z. Linking climate change to population cycles of hares and lynx. *Global Change Biology*. 2013;19:3263-3271.
3. Yudin VG, Yudina E. Rys' Dal'nego Vostoka Rossii [Lynx of the Russian Far East]. Vladivostok: TIG FEB RAS Publ.; 2019. 424 p. In Russian
4. Rys'. Regional'nye osobennosti ekologii, ispol'zovanija i ohrany [The Lynx. Regional Features of Ecology, Use and Protection]. Matyushkin YeN, Vaisfeld MA editors. Moscow: Nauka; 2003. 523 p. In Russian, English Summary
5. Odden J, Linnell JDC, Andersen R. 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. *European Journal of Wildlife Research*. 2006;52:237-244. doi:10.1007/s10344-006-0052-4
6. Nowicki P. Food habits and diet of the lynx (*Lynx lynx*) in Europe. *European Journal of Wildlife Research*. 1997;2:161-166.
7. Jedrzejewski WB, Jedrzejewska B, Okarma H, Schmidt K, Bunevich AN, Milkowski L. Population dynamics (1869-1994), demography, and home ranges of the lynx in Białowieża Primeval Forest (Poland and Belarus). *Ecography*. 1996;19:122-138.
8. Jobin A, Molinari P, Breitenmoser U. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. *Acta Theriologica*. 2000;45:243-252.
9. Krofel M, Huber D, Kos I. Diet of Eurasian lynx *Lynx lynx* in the northern Dinaric Mountains (Slovenia and Croatia). Importance of edible dormouse *Glis glis* as alternative prey. *Acta Theriologica*. 2011;56:315-322. doi:10.1007/s13364-011-0032-2

10. Belotti E, Červeny J, Šustr P, Kreisinger J, Gaibani G, Bufka L. Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence. *Wildlife Biology*. 2013;19:188-201.doi:10.2981/12-077
11. Breitenmoser U, Breitenmoser-Würsten C. Der Luchs: Ein Grossraubtier in der Kulturlandschaft. Band 2. Wohlen/Bern, Schweiz.: Salm Verlag; 2008. 584 p. In Deutsch
12. Pulliainen E. Winter diet of *Felis lynx* L. in SW Finland as compared with the nutrition of other northern lynxes. *Zeitschrift für Säugetierkunde*. 1981;46:249.
13. Malafeev YuM, Kryazhimskiy FV. Pitanie rysi i ee vzaimootnoshenija s kopytnymi na srednem Urale [Eurasian lynx *Lynx lynx* feeding and relationships with ungulates in the Central Urals, USSR]. *Bulletin of Moscow Society of Naturalists, Biological series.*1984;89(4):70-81. In Russian
14. Jędrzejewski W, Schmidt K, Milkowski L, Jędrzejewska B, Okarma H. Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. *Acta Theriologica*. 1993;38:385-403.
15. Krashevsky OR. On the lynx ecology of the Putoran Plateau. Resources, ecology and conservation of mammals and birds in the northern part of the Yenisei River. *Scientific and Technical Bulletin*. 1989;1-2:23-26. Novosibirsk. In Russian
16. Davydov VG. K pitaniyu rysi na Yuzhnom Urale [On the lynx feed in the Southern Urals]. In: *Ekologicheskie osnovy ratsional'nogo ispol'zovaniya khishchnykh mlekopitayushchikh* [*Ecological bases of rational using of predatory mammals*]. M.: Nauka Publ.; 1979;261-262. In Russian
17. Gordiyuk NM. Vzaimootnosheniya khishchnikov i kopytnykh v usloviyakh Bashkirskogo zapovednika [The relationship between predators and ungulates in the conditions of the Bashkir Nature Reserve]. In: *Ekologicheskie osnovy ratsional'nogo ispol'zovaniya khishchnykh mlekopitayushchikh* [*Ecological bases of rational using of predatory mammals*]. M.: Nauka Publ.; 1979:23-25. In Russian
18. Seryodkin IV. Primenenie radiotelemetrii i sputnikovogo slezheniya za ispol'zovaniem territorii dlya izucheniya dikikh zhivotnykh na Dal'nem Vostoke Rossii [Application of radio telemetry and satellite tracking for the territory use study of wild animals in the Russian Far East]. In: *Distribution, migration and other movements of wildlife*: proceedings of the International conf. (Vladivostok, 25-27 November 2014). Saveljev AP, Seryodkin IV, editors.Vladivostok: Reya Publ.; 2014:292-299. In Russian
19. Ushkov SL. Perehody kosuli na Juzhnom Urale [Roe deer crossings in the Southern Ural]. *Bulletin of Moscow Society of Naturalists, Biological series.* 1954;89(5):70-81. In Russian
20. Gordiyuk NM. Vzaimootnosheniya kopytnykh zhivotnykh i krupnykh khishchnikov Yuzhnogo Urala [The relationship of ungulates and large predators of the Southern Urals]. Miass: Geotur Publ.; 2002. 76 p. In Russian
21. Danilkin AA. Kosuli. Biologicheskie osnovy upravlenija resursami [Roe Deer. Biological Bases of Resource Management]. Moscow: KMK Association of Scientific Editions; 2014. 172 p. In Russian
22. Stephens PA, Zaumyslova OY, Miquelle DG, Myslenkov AI, Hayward GD. Estimating population density from indirect sign: Track counts and the Formozov-Malyshev-Pereleshin formula. *Animal Conservation.*2006;9:339-348. doi: 10.1111/j.1469-1795.2006.00044.x
23. Ministry of Natural Resources and Environment of the Russian Federation. [Electronic resource]. Available at: https://rg.ru/2012/09/04/zimniy-uchet-site-dok.html (accessed 20.12.2020). In Russian
24. Ministerstvo ekologii Chelyabinskoy oblasti. Gosudarstvennyy monitoring okhotnich'ikh resursov i sredy ikh obitaniya [Ministry of Ecology of the Chelyabinsk region. State monitoring of hunting resources and their habitat]. [Electronic resource]. Available at: http://mineco.gov74.ru (accessed 20.12.2020). In Russian
25. Ministerstvo prirodopol'zovaniya i ekologii respubliki Bashkortostan. Rezul'taty zimnego marshrutnogo ucheta dikikh zhivotnykh [Ministry of Nature Management and Ecology of the Republic of Bashkortostan. The results of the winter route accounting of wild animals].

[Electronic resource]. Available at: https://ecology.bashkortostan.ru/documents/active/22128 (accessed 15.03.2021). In Russian
26. *Letopis' prirody Il'menskogo zapovednika [The nature chronicle of the Ilmen Nature Reserve*]. Miass: 1975, 1976, 1983, 2017, 2019. In Russian
27. Chelyabinskiy Tsentr po Gidrometeorologii i monitoringu okruzhayushchey sredy [Chelyabinsk Center for Hydrometeorology and Environmental Monitoring]. [Electronic resource]. Available at: http://www.chelpogoda.ru (accessed 15.12.2020). In Russian
28. Sunquist M, Sunquist F. Wild Cats of the World. Chicago: University of Chicago Press; 2002. 452 p.
29. Kubala J, Smolko P, Zimmermann F, Rigg R, Tám B, Il'ko T, Foresti D, Breitenmoser-Würsten Ch, Kropil R, Breitenmoser U. Robust monitoring of the Eurasian lynx *Lynx lynx* in the Slovak Carpathians reveals lower numbers than officially reported. *Oryx*. 2019;53(3):548-556. doi: 10.1017/S003060531700076X
30. Weingarth K, Heibl C, Knauer F, Zimmermann F, Bufka L, Heurich M. First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture-recapture techniques in a German national park. *Animal Biodiversity and Conservation.* 2012;35(2):197-207.
31. Gimenez O, Gatti S, Duchamp Ch, Germain E, Laurent A, Zimmermann F, Marboutin E. Spatial density estimates of Eurasian lynx (*Lynx lynx*) in the French Jura and Vosges Mountains. *Ecology and Evolution*. 2019;9(20):11707-11715. doi: 10.1002/ece3.5668
32. Poddubnaya NYa, Kolomiytsev N. Rol' mlekopitajushhih v lesnyh jekosistemah jugo-vostochnogo Sihotje-Alinja [The Role of Mammals in the Forest Ecosystems of the Southeastern Sikhote-Alin Mountains]. ChSU, Cherepovets: Cherepovets State University Publ.; 2016. 253 p. In Russian
33. Obzor sostoyaniya populyatsiy osnovnykh vidov pushnykh zverey na territorii Rossiyskoy Federatsii (po sostoyaniyu s 2005 g. po 2015 g.) [An overview of the number of the main fur-bearing animal species in the territory of the Russian Federation (from 2005 to 2015)]. Moscow: NO "Rossijskij pushno-mehovoj sojuz" Publ.; 2016. 104 p. In Russian
34. Bol'shakov VN, Korytin NS. The status of mammal populations in the middle Urals and factors determining their distribution and density. *Journal of Ecology*. 2014;45(6):456-462. doi:10.1134/S1067413614060058 In Russian
35. Malafeev YuM., Mikheeva KV. Rys' i sopryazhennye s ney vidy na Srednem Urale [Lynx and related species in the Middle Urals]. Mlekopitayushchie Ural'skikh gor [Mammals of the Ural Mountains]. Sverdlovsk: UNTs AN SSSR Publ., 1979;41–42. In Russian
36. Nauchno-obosnovannye predlozheniya dlya gosudarstvennoy sistemy monitoringa resursov osnovnykh vidov okhotnich'ikh zhivotnykh v Rossiyskoy Federatsii. Kirov: FGBNU VNIIOZ Publ.; 2017. 55-56. [Electronic resource]. Available at: http://vniioz-kirov.ru/publikatsii/knigi/nauchno-obosnovannye-predlozheniya-dlya-gosudarstvennoy-sistemy-monitoringa-resursov-osnovnykh-vidov (access 11.10.2020). In Russian
37. Newey S, Willebrand T, Haydon DT, Dahl F, Aebischer NJ, Smith AA, Thirgood S. Do mountain hare populations cycle? *Oikos.* 2007;116:1547-1557.
38. Stenseth NC, Shabbar A, Chan K-S, Boutin S, Rueness EK, Ehrich D, Hurrell JW, Lingjærde OC, Jakobsen KS. Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences USA*. 2004;101(29):10632-10634.
39. Guo K, Liu H, Bao H, Hu J, Wang S, Zhang W, Zhao Y, Jiang G. Habitat selection and their interspecific interactions for mammal assemblage in the Greater Khingan Mountains, northeastern China. *Wildlife Biology*. 2017;1:1-8. doi:10.2981/wlb.00261
40. Zheltukhin AS. O sutochnoj aktivnosti i razmerah uchastkov obitanija rysi v juzhnoj tajge Verhnevolzh'ja [Daily activity and sizes of home ranges of the European lynx in the southern taiga of the Upper Volga region]. *Bulletin of Moscow Society of Naturalists, Biological series*. 1984; 89(1):54-62. In Russian
41. Kiseleva NV. Long-Term Monitoring of the Numbers of Forest Rodents in Ilmen Reserve. *Biology Bulletin*. 2021;48(10):1839-1842.

42. Andrén H, Linnell JDC, Liberg O, Andersen R, Danell A, Karlsson J, Odden J, Moa PF, Ahlqvist P, Kvam T, Franzén R, Segerström P. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biological Conservation*. 2006;31:23-32.

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