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Relationship between prey availability and population dynamics of the Eurasian lynx and its diet in northern Belarus

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The diet and population dynamics of the Eurasian lynx *Lynx lynx* Linnaeus, 1758 as well as an index of its main prey abundance were studied in transitional mixed forests of northern Belarus in 1985–2004. Monitoring of the lynx population and its main potential prey (the mountain hare *Lepus timidus*, and the roe deer *Capreolus capreolus*) was done by snow-tracking. Also, abundance of tetraonids (*Tetraonidae*) was monitored by sight count. Hare numbers were fairly stable during the study period, whereas density of the roe deer population markedly increased, and tetraonids decreased. Composition of the lynx diet was stable seasonally. Lynx fed mostly on hares, roe deer and birds (usually tetraonids) year-round. However, the share of roe deer in lynx diet increased significantly during the period of its higher abundance and the share of tetraonids decreased with their decreasing numbers. There was also a remarkable increase of lynx population, which followed that of the roe deer, despite the pronounced decline of tetraonids. The results of the study emphasised the importance of roe deer as a prey of the Eurasian lynx.

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Introduction

The Eurasian lynx *Lynx lynx* Linnaeus, 1758 is considered an endangered species in Belarus (Darapheev *et al*. 1981). In contrast to other European regions where intensive research was done (Jędrzejewska and Jędrzejewski 1998, Jobin *et al*. 2000, Sunde *et al*. 2000, Matyushkin and Vaisfeld 2003, and references therein), the ecology of this predator in Belarus is still poorly known. There are only a few publications on lynx distribution, hunting harvest, and ecology in the region; these are based either solely on hunting statistics or outdated records from local field research in the Belarusian part of the Białowieża Forest in 1960's and the Berezinsky Reserve in 1970's (Nikitenko and Kozlo 1965, Kozlo 1993, 2003). Therefore, there is a clear need for detailed research on the lynx ecology in this area. The goal of my study was to provide basic ecological data on the relative abundance and dynamics of the lynx population, and its diet and availability of its main prey in northern Belarus.

Study area

The study was carried out in northern Belarus. The area is characterized by mostly hilly relief that originated from the last glaciation (Matveev 1990). The region lies in the extended transitional zone between more southern deciduous (mostly broad-leaved) forests and the boreal coniferous forests. Spruce *Picea abies* and pine *Pinus sylvestris* are dominant coniferous species. Black alder *Alnus glutinosa* and grey alder *A. incana*, birches *Betula pendula*, and *B. pubescens*, and aspen *Populus tremula* are the most common deciduous species.

I established two study areas in Vitebsk region, northern Belarus, where forest habitats prevail and rural areas (agricultural fields, villages etc.) constitute only a small part of the landscapes. One study area, measuring approximately 800 km^2 was located at the source of the Lovat River in Gorodok District (55°45'N, 30°20'E). The second study area measured about 2400 km^2 and was located between three medium-sized rivers: Drissa, Nischa, and Svolna Rivers in Rossony District (56°00'N, 28°30'E).

Nearly all forest types in both study areas are logged, and heavily managed. Tree stands on dry lands predominate in woodland compositions; however, raised bogs with suppressed pine stands are also quite common. Patches of black alder swamps and open grassy marshes are widespread, but their total area covers only few percents of the study areas and is situated primarily in valleys of rivers and glacial lakes.

The climate of northern Belarus is moderately continental. The cold season is characterized by snow cover with average air temperature below 0°C, lasting from early November until early April. According to the data obtained by the hydrometeorological service in northern Belarus (Appendix I), severity of winters fluctuate from year to year, but there is no clear trend in winters becoming milder in recent years. In forest habitats there was no significant negative correlation between year and duration of snow cover (r_s = –0.06, p = 0.81), mean snow depth (r_s = –0.03, p = 0.91), mean night air temperature during snow period (r_s = –0.003, p = 0.99).

Among the prey species available to lynx are hares (mainly mountain hares *Lepus timidus*), roe deer *Capreolus capreolus* and tetraonids (capercaillie *Tetrao urogallus*, black grouse *Tetrao tetrix*, and hazel grouse *Tetrastes bonasia*). Red deer *Cervus elaphus*, which is locally distributed in northern Belarus, does not occur in the study areas. The range of brown bears *Ursus arctos* and wolves *Canis lupus* overlaps with lynx in much of northern Belarus.

Material and methods

A total of 399 scats were collected and analysed in 1985–2004. The data obtained were divided into the cold season (November–March) (n = 250 scats) and the warm season (April–October) (n = 149 scats). I also analysed diets separately in two periods: 1985–1996 – with a high density of tetraonids and very low density of roe deer (n = 219 scats), and 1997–2004 with markedly lower density of tetraonids, and a very high density of roe deer (n = 180 scats). The majority of scats collected (n = 320) were taken at lynx tracks in both the warm and cold seasons. Also in the warm season, periodically part of lynx scats (n = 79) were taken in eleven well-known latrine sites visited by lynxes for territorial marking, where the species tracks and marking behaviour (defecating, urinating and scratching) were frequently found.

To identify mammalian prey consumed by lynxes, I microscopically examined ten randomly taken hairs from washed scats (Debrot *et al*. 1982, Teerink 1991). I attributed all hairs of the family *Cervidae* to roe deer as there is no red deer in the study areas, while moose, which occurs there is not a prey species for lynx. I divided avian prey into three groups: (1) tetraonids, (2) other big and medium-sized birds, and (3) small passerine birds. To distinguish the bird groups, I used published reference (März 1987), bird specimens in the zoological museum of the state university in Minsk, augmented by my own reference material. The relative amounts of various prey items in lynx diet were given as percentage of occurrence in the total number of analysed scats (%OC) and percentage of biomass consumed (%BC). To obtain %BC, I followed the approach recommended by Jędrzejewska and Jędrzejewski (1998) based on coefficients of digestibility, ie the ratio of fresh weight of a given food item to the dry weight of its remains in scats. To compare the overall dietary diversity (food niche breadth) in different feeding conditions, I used Levin's index B (Levins 1968). The calculation was done for 19 food categories, so, B index varies from 1 (the narrowest niche) to 19, i.e. the maximum number of food categories used for calculations (the broadest niche possible). Pianka's index α (Pianka 1973) was used to compare diet between seasons and years.

Within the study areas I established two transects to record information on abundance of lynx and prey species: one 36 km-long transect located in Gorodok District, and another 44 km-long transect in Rossony District. The routes of transects were planned in a way that included a diversity of habitat types, such as different types of forest, river valley, glacial lake shore, reed and sedge marshes, and pine bogs. I inspected the transects, once every winter (late November-early January) between 1985–2004, 3–5 days after a snowfall. While walking the transects the occurrence of lynx, roe deer and hare tracks as well as sightings of grouse were noted. I calculated the abundance index for lynx, roe deer and hare as the number of tracks of the species crossing the transect divided by the number of kilometres inspected and the number of days since the last snowfall. This technique yielded the average number of tracks/km/day. In the case of tetraonids, I calculated the mean number of grouse seen/10 km of the transect as their abundance index.

To compare my results on lynx track counts with other data available in the literature, I converted it into density estimation using the Priklonsky's formula (Priklonsky 1965, see Jędrzejewska and Jędrzejewski 1998 for details). In the formula, I used an average daily movement distance of lynx that I assessed by means of snowtracking as the distance between two resting sites used by lynx for a sufficiently long time. The mean daily movement distance was equal to 9.8 km based on nine measures. Statistical analyses were done using the Spearman correlation – r_s, Mann-Whitney U-test**,** and G-test for homogeneity of percentages (Sokal and Rohlf 1995).

Results

Dynamics of the prey population

Hare numbers were generally stable on a multiannual scale (Fig. 1). The variation of abundance index between years was rather low (ν =20.9%) and there was no trend of its dynamic with time (r_s = –0.18, p = 0.44).

The index of the roe deer population abundance increased markedly during the course of the study (Fig. 1, r_s = 0.94, p < 0.001). Mean abundance of roe deer between the periods of 1985–1996 and 1997–2004 increased about 12 fold (0.93 versus 12.0 tracks/km/day; U = 96.0, p < 0.001).

The opposite trend in tetraonids was found (Fig. 2): data was pooled for all species – r_s = –0.89, p < 0.001; black grouse – r_s = –0.96, p < 0.001; capercaillie – r_s = –0.91, p < 0.001; hazel grouse – r_s = –0.67, p = 0.001. When the two periods were compared (1985–1996 vs. 1997–2004) the decrease of abundance was more pronounced for black grouse – about 2.8 fold (on average 20.2 versus 7.3 individuals seen/10 km; U = 96.0, p < 0.001) and for capercaillie – about 2.6 fold (3.1 versus 1.2; U = 94.5, p < 0.001), whereas it was not significant for hazel grouse – about 1.4 fold (11.2 versus 7.9; U = 68.0, p = 0.07).

Composition of lynx diet in the warm and cold seasons

Using Pianka's index of structural similarity, the lynx diet appeared to be very similar in the warm (April–October) and cold (November–March) seasons (Table 1): α = 0.96, for %OC; α = 0.98 for %BC. Nevertheless, the percentages of prey occurrences were significantly different when compared with G-test (G = 45.1, p = 0.001). Lynx fed primarily on hares – 39.1–45.7%BC, roe deer – 18.8–21.4%BC, and birds (mostly tetraonids) – 14.3–25.7%BC in both seasons. Other prey species were less important for the predator. The food niche was slightly wider during the warm season (Table 1).

Changes in the lynx diet in relation to population dynamics of prey

I compared the lynx diet between periods 1985–1996 and 1997–2004 as they were characterized by different prey supply (Figs 1 and 2).

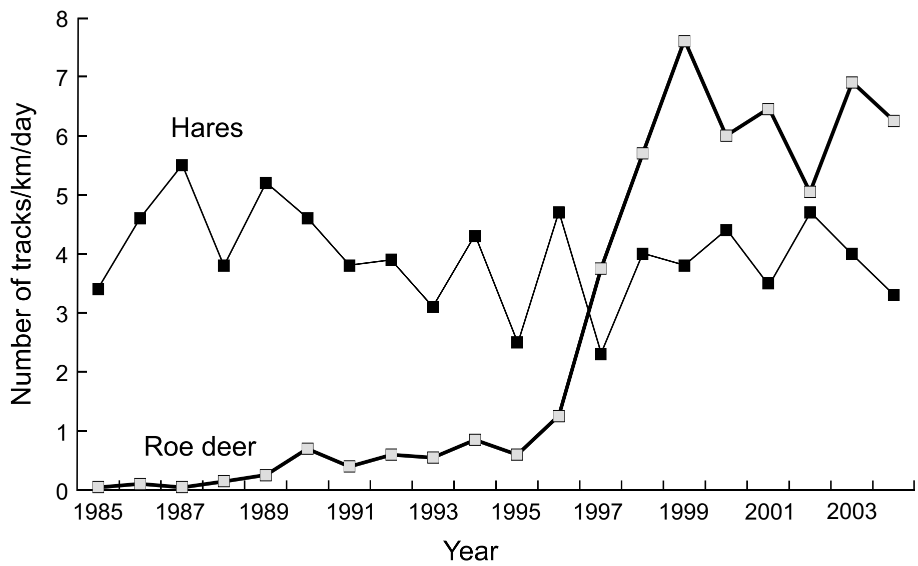

Fig. 1. Population dynamics of hares (mainly mountain hare) and roe deer in the woodlands of northern Belarus, Vitebsk region, in 1985–2004. Average numbers of the species tracks recorded on transects divided by number of kilometres inspected and the number of days since the last snowfall. The dates signify winter at the end of preceding year and the beginning of a given year.

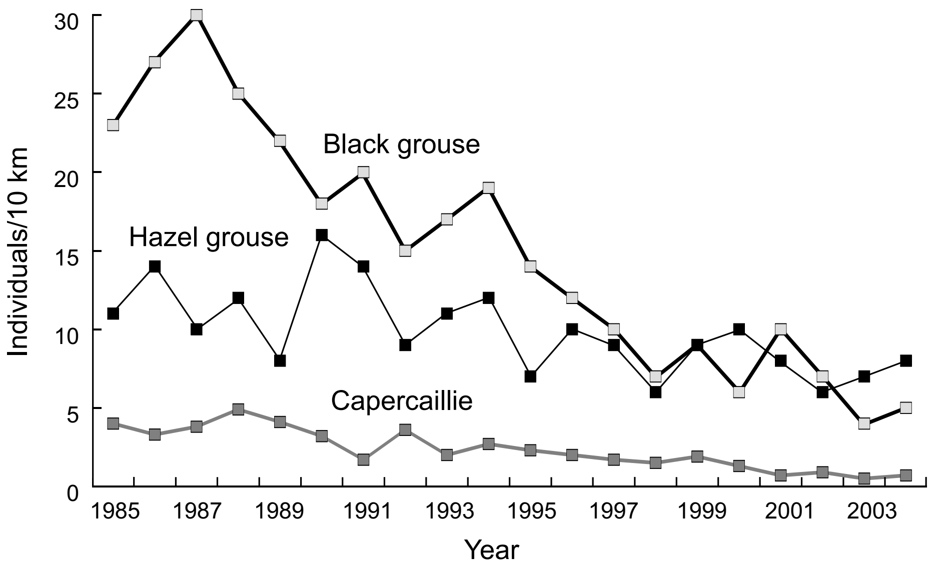

Fig. 2. Dynamics of the tetraonids populations in the woodlands of northern Belarus, Vitebsk region, in 1985–2004. Average numbers of individuals recorded on every 10 km of the transects. The dates signify winter at the end of preceding year and the beginning of a given year.

Table 1. Diet of lynx in northern Belarus in the warm (April–October) and cold (November–March) seasons, 1985–2004. %OC – frequency of prey occurrence in the diet expressed in %; %BC – ratio of prey biomass consumed expressed in %.

Prey item	Warm season		Cold season	
	%OC	%BC	%OC	%BC
Fish	1.3	0.3	–	–
Hedgehog	0.7	0.2	0.4	0.2
Small rodents	5.4	1.1	13.2	5.1
Muskrat	1.3	0.4	–	–
Hares	79.9	39.1	78.8	45.7
Beaver	2.7	1.5	0.8	0.5
Red squirrel	2.0	0.7	1.6	1.0
Polecat	1.3	0.6	4.0	2.7
Pine marten	2.7	1.3	0.8	0.4
Raccoon dog	6.0	3.2	4.4	2.5
Red fox	4.7	2.1	2.0	1.9
Roe deer	32.2	18.8	31.6	21.4
Wild boar	2.7	1.5	4.4	3.0
Goat	0.7	0.3	–	–
Domestic dog	2.0	0.8	1.2	0.7
Domestic cat	6.0	2.1	1.2	0.5
Small birds	12.8	3.7	2.0	0.9
Tetraonids	41.6	17.3	19.6	12.2
Other medium-sized birds	11.4	4.7	1.6	1.2
Herbs	3.4	0.3	0.4	0.1
Number of scats analysed	149		250	
Food niche breadth, Levin's index *B*	5.07	4.45	3.60	3.63

Table 2. Diet of lynx in northern Belarus in the conditions of different prey supply: 1985–1996 – low density of roe deer and fairly high density of tetraonids, 1997–2004 – increased roe deer numbers, but decline in tetraonids. %OC – frequency of prey occurrence in the diet expressed in %; %BC – ratio of prey biomass consumed expressed in %.

Prey item	1985–1996		1997–2004	
	%OC	%BC	%OC	%BC
Fish	–	–	1.1	0.3
Hedgehog	0.5	0.2	0.6	0.1
Small rodents	14.1	4.3	5.6	1.6
Muskrat	0.9	0.4	–	–
Hares	88.6	52.1	78.9	37.1
Beaver	0.9	0.8	2.2	1.4
Red squirrel	1.4	0.4	2.2	0.7
Polecat	3.2	1.0	2.8	0.8
Pine marten	1.4	0.8	1.7	0.9
Raccoon dog	0.9	0.7	10.0	5.3
Red fox	3.7	2.0	2.2	1.1
Roe deer	14.1	10.2	64.4	32.5
Wild boar	4.1	2.4	3.3	1.9
Goat	–	–	0.6	0.3
Domestic dog	1.8	1.0	1.1	0.5
Domestic cat	2.3	0.7	3.9	1.3
Small birds	4.6	1.9	7.8	2.0
Tetraonids	36.1	19.0	17.8	8.8
Other medium-sized birds	3.7	1.8	7.2	3.0
Herbs	3.2	0.3	5.6	0.4
Number of scats analysed	219		180	
Food niche breadth, Levin's index *B*	3.48	3.11	4.35	3.99

In 1997–2004, when the density of roe deer was relatively high, this prey occurred markedly more often (5.1 fold) in the lynx diet than in 1985–1996 ($G = 41.6$, $p < 0.01$) (Table 2). In contrast, since late 1990's when tetraonids appeared to be less common, frequency of their occurrence in the lynx diet was 2.0 fold lower than during the first period ($G = 6.3$, $p = 0.02$). There was also a notable increase of consumption of raccoon dogs *Nyctereutes procyonoides* by lynx ($G = 7.1$, $p < 0.01$) during the second period; however, no data on their abundance are available. In general, fairly high overlap was found ($\alpha = 0.85$) between the two periods when diet was compared by frequency of prey occurrence. Nevertheless, it was significantly different when compared with the G-test ($G = 57.8$, $p < 0.001$).

Similar overlap ($\alpha = 0.86$) between periods was found where diet was determined as %BC: values were not significant, when compared with the G-test ($G = 23.8$, $p = 0.25$). However, there was a pronounced difference in consumption of roe deer between the periods (3.5 fold; $G = 12.2$, $p < 0.01$). The other notable changes, though not significant, were found in case of hare (1.4 fold lower), raccoon dog (7.9 fold higher) and grouse (2.1 lower) in 1997–2004 in comparison to the previous period.

Relationship between lynx and prey population dynamics

Monitoring of lynx abundance showed an increase of its population since mid 1990's (Fig. 3).

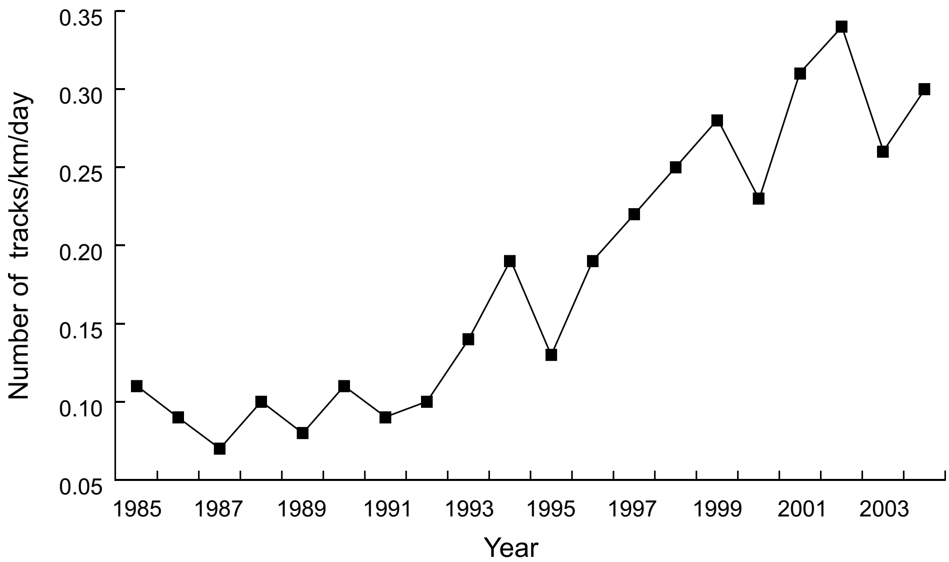

Fig. 3. Dynamics of the Eurasian lynx population in the woodlands of northern Belarus, Vitebsk region, in 1985–2004. Average numbers of lynx tracks recorded on transects divided by number of kilometres inspected and the number of days since the last snowfall. The dates signify winter at the end of preceding year and the beginning of a given year.

The trend was statistically significant ($r_s = 0.92$, $p < 0.001$). The difference of the mean abundance of lynx between the periods of 1985–1996 and 1997–2004 was about 2.3 fold (0.23 versus 0.54 tracks/km/day) and was highly significant ($U = 88.0$, $p = 0.002$).

By comparing the changes in lynx abundance with the variations in abundance of the main prey, the following correlations were found: hares – $r_s = -0.25$, $p = 0.29$; roe deer – $r_s = 0.91$, $p < 0.001$; black grouse – $r_s = -0.89$, $p < 0.001$; capercaillie – $r_s = -0.84$, $p < 0.001$; hazel grouse – $r_s = -0.58$, $p = 0.007$.

Lynx population dynamics in relation to winter severity

The lynx population abundance was also analysed in relation to climatic data with and without 1 year time lag, however, no significant correlation was found in any of parameters examined: duration of period with presence of snow cover in forest habitats ($r_s = -0.23$, $p = 0.34$ and $r_s = -0.02$, $p = 0.94$), mean depth of snow cover in forest habitats ($r_s = -0.06$, $p = 0.80$ and $r_s = -0.06$, $p = 0.80$), and mean night air temperature during snow cover period ($r_s = 0.03$, $p = 0.91$ and $r_s = -0.10$, $p = 0.66$).

Discussion

The main advantage of this study was that it provided a unique opportunity to follow the dynamics of the Eurasian lynx population and its prey over a long period with simultaneous monitoring of the lynx diet. This allowed me to make an attempt to answer important questions concerning the status and ecology of lynx in Belarus: (1) what is the reason for the increase in lynx numbers in northern Belarus; (2) which prey species or group of species is crucial to lynx and (3) how the observed changes in prey abundance affect the lynx population in northern Belarus?

There are several factors, which could be related to the observed increase in lynx numbers. Three factors seem to be most likely: (1) climatic changes, (2) better protection, and (3) improved prey availability. The climatic data presented in this paper showed no apparent trend during the study period, thus there was no relationship between climate and either lynx or prey population increase. The lynx became a protected species in Belarus since 1985 (included in the national red list of endangered species). Therefore, one cannot exclude a possibility that the increase of its population could have been, at least, partly caused by stronger protection. However, during my 19-year study, which covered the entire time of protection, there were no changes in conservation policy, which could affect the efficiency of preservation. Although poaching might have occurred occasionally, protective actions by hunting wardens, forest guards and nature conservation police are quite effective in the area all the time. Although I do not have data to quantitatively measure the efficiency of conservation, it seems unlikely that it could affect lynx numbers in such an extent.

Most likely the cause of the lynx population increase seems to be changes in roe deer availability. Among the three groups of prey species, which were found to constitute most of the lynx diet in Europe (hares, cervids, mainly roe deer and tetraonids) (Jędrzejewska and Jędrzejewski 1998, Matyushkin and Vaisfeld 2003, and references therein), only the roe deer population experienced a multiple increase in northern Belarus in 1997–2004. One can assume that the magnitude of that 12-fold increase determined using relative index of roe deer abundance is equal to at least several times higher prey biomass available to the predator. The 2.4-fold parallel increase of lynx numbers seems to follow accurately the roe deer dynamics. It is noteworthy to mention that this positive trend in the predator population happened despite that populations of other important potential prey species remained stable or even declined.

The data on lynx diet obtained in this study showed that roe deer are more favoured prey by lynx than hares. This contrasts to the fact that hare is preferred by this predator in northern areas of Russia (Matyushkin and Vaisfeld 2003, and references therein) and also in northern Belarus in 1985–1996 before proliferation of the roe deer population. Regardless of stability in the populations of hares, their share in biomass consumed by lynx dropped 1.4 times during the period of high density of roe deer. Conversely, at the same time the proportion of roe deer in prey biomass consumed by lynx increased 3.5 fold.

Several studies have already shown the importance of roe deer and other medium-sized ungulates to lynx (Birkeland and Myrberget 1980, Pulliainen 1981, Jędrzejewski *et al*. 1993, Okarma *et al*. 1997, Jobin *et al*. 2000, Sunde *et al*. 2000). However, in most cases, roe deer were preferred, when other typical prey species (hares and grouse) were uncommon. According to the review by Jędrzejewski *et al*. (1993), the share of ungulates in Eurasian lynx diet in the

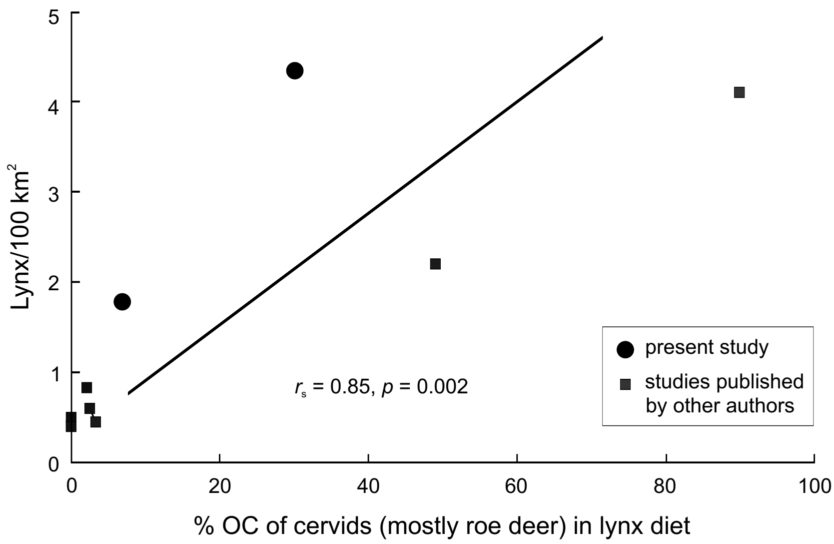

Fig. 4. Correlation between the lynx density and proportion of cervids (mainly roe deer) (determined as frequency of occurrence in the scats analyzed) in the predator diet in Europe. The points denote following localities (taken from Jędrzejewska and Jędrzejewski 1998, Matyushkin and Vaisfeld 2003 and this study): northern Belarus, Białowieża Forest in eastern Poland, Estonia, and Karelia, Udmurtia, Leningrad, Novgorod, Pskov, Kostroma and Tula regions in Russia.

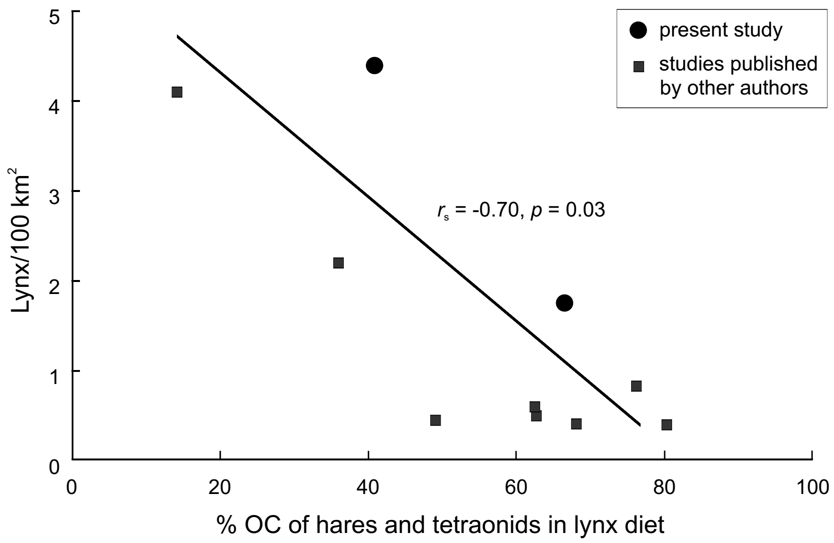

Fig. 5. Correlation between the lynx density and pooled proportion of hares and tetraonids in the predator diet in Europe (determined as frequency of occurrence in the scats analyzed). The points denote following localities (taken from Jędrzejewska and Jędrzejewski 1998, Matyushkin and Vaisfeld 2003 and this study): northern Belarus, Białowieża Forest in eastern Poland, Karelia, Leningrad, Novgorod, Pskov, Kirov and Tver regions in Russia.

Palearctic is determined by latitude and increases with decreasing abundance of hares. However, during my study lynx was strongly dependent on roe deer despite the hare population being relatively high and remaining stable over time.

The role of the roe deer in shaping lynx populations may be better understood when looking at their relationships on a European scale. For that reason, I compared the data on lynx population density and the predator diet in Europe available in literature (based on reviews in Jędrzejewska and Jędrzejewski 1998 and Matyushkin and Vaisfeld 2003) (Figs 4 and 5). In the analysis, I also included the data that I obtained during this study after recalculating the indirect index of lynx abundance into the absolute density, based on Priklonsky's formula (Priklonsky 1965). There were 1–3 (average, 1.8) individuals/100 km^2 in 1985–1996, and 3.4–5.4 (average, 4.3) individuals/100 km^2 in 1997–2004 in northern Belarus (U = 88.0, p = 0.002).

The lynx densities increased significantly along the gradient of increasing share of roe deer in its diet in Europe (Fig. 4). In contrast, the lynx densities were lowest, when hares and tetraonids constituted the majority of its diet (Fig. 5). However, this correlation was significant only if both hares and grouse were pooled in the analysis. This comparison shows that the Eurasian lynx is a highly specialised predator of small ungulates. Although it may survive on a diet consisting of small vertebrates, like hares or grouse, the lynx population is not able to reach as high densities as when relying on ungulates. This sharply contrasts with the situation in the Canada lynx *Lynx canadensis* or bobcat *Lynx rufus*, which are highly dependent on hares or other lagomorphs and small vertebrates and may reach densities up to 5 times higher than those of its Eurasian counterpart (Larivière and Walton 1997, Mowat *et al*. 2000). The reason for this relationship is probably due to body size of the Eurasian lynx, which is twice as large as the Canada lynx. The large size of the Eurasian lynx and resulting energy requirements may be too high for this predator to sustain itself solely on smaller prey. The result of my study can be regarded as a confirmation of the work of Pulliainen (1981), who stated that the large body size of the Eurasian lynx in contrast to the Canada lynx or Iberian lynx *Lynx pardinus*, is an adaptation to hunting large prey.

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Appendix 1. Parameters of winter severity in northern Belarus during the period of study on the lynx ecology, Vitebsk region, 1984–2004 (according to the data of the hydrometeorological service in northern Belarus).

Winter of the years	Duration of period with presence of snow cover in forest habitats (days)	Mean depth of snow cover in forest habitats (cm)	Mean night air temperature during snow cover period (°C)
1984–1985	130	37	–12.4
1985–1986	149	39	–9.4
1986–1987	162	42	–12.5
1987–1988	171	35	–6.6
1988–1989	154	20	–2.8
1989–1990	120	17	–2.5
1990–1991	181	39	–5.0
1991–1992	162	33	–4.0
1992–1993	181	40	–5.4
1993–1994	177	42	–6.5
1994–1995	153	30	–4.2
1995–1996	160	45	–12.2
1996–1997	147	27	–6.6
1997–1998	164	30	–5.8
1998–1999	146	35	–7.0
1999–2000	149	33	–4.2
2000–2001	156	36	–5.2
2001–2002	132	29	–6.1
2002–2003	167	43	–9.6
2003–2004	150	38	–6.4