

Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability

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The distribution and abundance of food resources is a major factor influencing animal populations. I studied the effect of a roe and red deer population decline on diet composition, home range size and foraging pattern in the Eurasian lynx *Lynx lynx* (Linnaeus, 1758) in the Białowieża Primeval Forest (BPF), eastern Poland. The population of cervids in BPF experienced a nearly two-fold reduction in size from 1991 through 2006 due to severe hunting pressure between 1991 and 1996. Comparison of published data on lynx diet during the high abundance of ungulates with new data obtained for the low abundance period showed that despite a significant decline in their availability, cervids (roe and red deer) continued to form the majority of the diet of lynx, with roe deer being most preferred in both periods. Home range sizes of lynx showed a tendency to increase with declining prey densities, as indicated by relative percentage increases in average yearly home range sizes amongst different sex/age groups. In response to lower availability of their main prey, lynx increased their daily straight-line movement distances by 44% and doubled the ranges covered in 5-day periods. This illustrated that, with declining prey abundance, the lynx increased their hunting efforts by either spending more time actively searching for prey or continuing foraging even after a successful hunt. Spatial analysis of the distribution of ungulates and lynx indicated that deer were evenly distributed throughout lynx ranges in BPF and spatial proximity of the predator to prey sites did not play an important role in the efficiency of hunting. Lynx may adapt to changing prey availability by increasing search effort, but this was not sufficient to prevent the negative influences of the prey decline on the lynx population. Prey depletion has an immediate effect on lynx spatial organization and, in consequence, on their density. This information has to be considered in prioritizing lynx conservation measures and management of ungulates.

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Introduction

The distribution and abundance of food resources are among the most important factors

influencing animal distributions, spatial requirements, movements (Macdonald 1983, Manly *et al.* 2002, Ranta *et al.* 2006) and population densities (Hayward *et al.* 2007). Animals may

use different strategies in exploiting available resources to satisfy their survival or reproductive requirements, but the quality and quantity of the resources should chiefly determine their home ranges (Mitchell and Powell 2004). Theoretical models predict that home range size should increase with decreasing quantity and clumped distribution of food resources (Mitchell and Powell 2004), as has been found with African lions (van Orsdol *et al.* 1985). Spatial dispersion patterns of food should also have an effect on animal foraging patterns (Andersson 1981, Stephens and Krebs 1986, Brandt and Lambin 2007).

The relationships between size and use of home ranges and food availability are of particular interest in large carnivores due to their large spatial requirements and resulting management and conservational challenges. Carnivores may limit the populations of animals of interest to humans (Messier 1991, Wehausen 1996, Turner and Morrison 2001), while their rarity and vulnerability may be related to human regulation of their prey resources (Karanth and Stith 1999, Mishra *et al.* 2003, Johnson *et al.* 2006).

Field studies of various carnivore species to date provide inconsistent evidence regarding the relationship between home range size and prey abundance. Data on African lions *Panthera leo* (van Orsdol *et al.* 1985), wolves *Canis lupus* (Wydeven *et al.* 1995, Fuller 2003, Jędrzejewski *et al.* 2007), coyotes *Canis latrans* (Patterson and Messier 2001), pumas *Puma concolor* (Grigione *et al.* 2002), and bobcats *Lynx rufus* (Litvaitis *et al.* 1986, Knick 1990) have shown a clear negative correlation between home range size and prey availability. No such relationship, however, was found by Logan and Swenar (2001) in their in-depth research on puma or by Palomares *et al.* (2001) for Iberian lynx *Lynx pardinus*. Also, several studies on Canada lynx *Lynx canadensis* (reviewed in Mowat *et al.* 2000) failed to find a linear relationship between lynx home range size and snowshoe hare *Lepus americanus* density, even though the predators did increase home range sizes immediately after crashes in hare abundance. Thus, additional field research on novel species in varying ecological conditions is necessary to increase our understanding of this relationship.

Inter- and intra-specific comparisons of predator-prey relationships become even more complicated when their spatial distributions are considered. At the extreme point is the situation when predators have to cope with migratory herbivores, leading to either following or prey-switching strategies (Scheel and Packer 1995, Ballard *et al.* 1997, Pierce *et al.* 1999). Studies of the spatio-temporal relationships between more sedentary predator and prey have also revealed considerable variability in foraging strategies. Patterson and Messier (2001) found that coyotes sometimes preferred hunting in areas with low densities of white-tailed deer *Odocoileus virginianus*, suggesting that their hunting efficiency was also dependent on factors other than local prey abundance. In contrast, Branch *et al.* (1996) implied that puma may actively search for sparsely distributed clumps of plains vizcacha *Lagostomus maximus* colonies during a period of overall population decline of the prey. A study on jaguars *Panthera onca* by Weckel *et al.* (2006) provided indirect clues that high spatial overlap of the predators with potential prey species does not necessarily result in selection of those prey as food. For these reasons, predator and prey spatial relationships remain an intriguing subject for further ecological research.

The Eurasian lynx *Lynx lynx* (Linnaeus, 1758) has been reported to forage on a variety of animals (Jędrzejewski *et al.* 1993, Okarma *et al.* 1997, Sunde and Kvam 1997, Valdmann *et al.* 2005, Odden *et al.* 2006), however it has been shown to specialize on medium-sized ungulates (Jędrzejewski *et al.* 1993, Pedersen *et al.* 1999, Jobin *et al.* 2000). In central Europe and southern Scandinavia, roe deer *Capreolus capreolus* is the main prey of lynx even at low herbivore density (Jędrzejewski *et al.* 1993, Odden *et al.* 2006, Sidorovich 2006). Along with their diets, home range sizes of lynx vary greatly throughout Europe and may be linked with prey availability (Linnell *et al.* 2001). Indeed, home range sizes of lynx have recently been shown to correlate negatively with indices of food availability at two spatial scales – European and regional (Norway) (Herfindal *et al.* 2005). The European scale analysis, however, was based on an indirect index of environmental productivity, whereas the re-

gional, based on an index of roe deer harvest, actually considered two different study areas. Although the results of that study fit very well into the existing predictions of home range size, there is still unexplained variation due to other factors acting locally, such as topography, habitat structure, local variation in prey density or the predator's social structure (McLoughlin and Ferguson 2000). There are no data on the local home range dynamics of Eurasian lynx reflecting temporal changes in food availability.

Lynx foraging patterns can be also affected by spatial distribution of the roe deer, as shown by Moa *et al.* 2006. However, that study concerned areas with very low density and clumped distribution of roe deer. It is unknown how lynx behave amongst more homogeneously dispersed herbivore populations and how they adjust to changes in temporal prey distribution and abundance. Lynx appear to be flexible predators that sometimes react unexpectedly to temporal changes in local conditions by, for instance, shifting to alternative prey in areas with migratory reindeer *Rangifer tarandus*, instead of following its locally preferred ungulate prey as was expected (Danell *et al.* 2006).

In this study I took advantage of a dramatic decrease of ungulate populations that occurred in the Białowieża Primeval Forest (BPF), Poland due to enormous hunting pressure aimed at reducing their numbers (Jędrzejewski *et al.* 2002b). Roe deer, red deer *Cervus elaphus* and wild boar *Sus scropha* were subjected to culling from 1991/1992 to 1995/1996 (Jędrzejewski *et al.* 2002b). The large predators, lynx and wolf *Canis lupus*, were not hunted in that period, and their predation contributed significantly to the ungulate population crash (Okarma *et al.* 1997, Jędrzejewski *et al.* 2002b) and to maintaining low densities of ungulates for subsequent years. Since 1996/1997, the ungulate harvest was markedly reduced or even abandoned in some years (Jędrzejewski *et al.* 2002b). As ecological research on the lynx has been conducted there during (1991–1996: Jędrzejewski *et al.* 1993, Okarma *et al.* 1997, Schmidt *et al.* 1997) and after (2003–2006: this study) the culling period, this provided an opportunity to observe the response of this predator to changes in food avail-

ability at a local scale. The objective of this study was to find out how, if at all, lynx have responded to temporal declines of their main prey – the roe deer and the red deer in the Białowieża Primeval Forest. To answer this I addressed the following questions: (1) Did the prey decline cause changes in the diets of lynx? (2) Was there a negative relationship between the home range sizes of lynx and prey abundance? (3) Did prey abundance affect foraging patterns of lynx? (4) Did the spatial distribution of prey during periods of high and low abundance affect use of home ranges by lynx?

Material and methods

Study area

The study was conducted on the Polish side of the Białowieża Primeval Forest (BPF), eastern Poland (52°30'–53°N, 23°30'–24°15'E) located on the Polish-Belarusian border. The BPF is a temperate mixed lowland forest and is characterized by a high percentage of natural stands (Faliński 1986). The Polish side of the BPF covers about 600 km², whereas the whole forest is nearly 1500 km² and has connections to other forests in Belarus. Most (500 km²) of the Polish side of the BPF is managed by state forestry, while the rest is protected as the Białowieża National Park (BNP, 100 km²) with a 50-km² area of strict reserve, where no human interference is allowed except for tourism and research. A network of small reserves with partial protection is located in the managed part of the BPF (Wesołowski 2005). Game hunting (particularly of ungulate mammals) is allowed outside the protected zones. The forest consists of a variety of tree associations. The original association was a deciduous oak-lime-hornbeam forest (*Quercus robur*, *Tilia cordata*, *Carpinus betulus* with admixture of maple *Acer platanoides* and spruce *Picea abies*) which is today largely restricted to the protected areas. The managed part is now dominated by planted pine *Pinus silvestris*, and spruce. Other typical associations in BPF include bog alder *Alnus glutinosa* wood on wet areas with stagnating water, and ash *Fraxinus excelsior* – alder forests associated with small river banks. The area is flat (134–186 m a.s.l.) and the forest stands are quite continuous with only a few glades occupied by villages, marshes and open river valleys. It is easily accessible for vehicles by a dense network of dirt roads that usually follow a regular grid of square forest compartments (1066 × 1066 m). The climate of BPF is temperate with transitional character between Atlantic and continental ones with clearly marked warm and cold periods (average temperatures during the study period were –3.9°C in January and 19.1°C in July; average annual precipitation was 622 mm; snow cover persisted for an average of 96 days per year from November to March).

The community of ungulate mammals in BPF consists of: red deer, roe deer, wild boar, moose *Alces alces*, and European bison *Bison bonasus*. However, only the three former species have been recorded as prey of lynx in the BPF (Jędrzejewski *et al.* 1993, Okarma *et al.* 1997). Grey wolves also occur in the area.

Lynx diet

I examined the diet of lynx based on analysis of 92 fecal samples and 113 lynx-killed prey collected between 2001 and 2006, and compared the results with published data covering the period 1985–1996 by Okarma *et al.* (1997). To analyse the feces, I followed the standard method of drying and washing through a 0.5-mm-mesh sieve (Goszczyński 1974). Prey were identified by bone, hair, and feather remains according to the taxonomic keys of Pucek (1981) and Debrot *et al.* (1982), and by comparison with the reference material stored at the Mammal Research Institute PAS, Białowieża, Poland. I presented the relative amount of prey as the percentage occurrence in the total number of fecal samples and the percentage of biomass consumed by lynx. To calculate the biomass of each prey species I multiplied the weight of prey remains recovered from feces by coefficients of digestibility determined by Goszczyński (1974). Microscopic analysis of hair did not allow for unambiguous identification of deer species. Therefore, to obtain information on relative share of roe deer and red deer in the lynx diet I used data from remnants of kills made by lynx. The lynx kills were recovered during both snow- and radio-tracking.

Lynx capturing and radio-tracking

Lynx were captured during winter using foot-snare traps (Jackson 1989) set at fresh ungulate kills and marking sites and using a wire box-trap. All traps were equipped with radio-alarm systems (Wagener Telemetrieanlagen HF-NF Technik, Köln, Germany) that allowed us to release the captured animals from the traps within 15 minutes to 1 hour, although lynx captured in the box-trap stayed in the trap for up to 3 h. Lynx were immobilized with a mixture of ketamine hydrochloride (5 mg/kg of body weight) and xylazine hydrochloride (6 mg/kg of body weight) and equipped with radio-collars (Wagener Telemetrieanlagen and AVM Instrument Co. California, USA) that weighed approximately 230 g (that is 1–2% of the lynx body mass). During the lynx captures in 2003–2006, the effect of xylazine was reversed with atipamezole hydrochloride (0.5 mg/kg). The procedures were approved by Polish Experimental Animal Ethics Committee (approval number DB/KKE/PL-110/2001).

Data on 13 lynx captured in 1991–1996 and 6 lynx captured in 2003–2006 have been used in this study. From 1991–1996, the radio-collared lynx were searched 5 to 7 times a week. Additionally, each month one individual was monitored every 30 min for 5 consecutive days. I used all lo-

cations collected during this period for home range estimation, whereas for other purposes I selected only one location per day. In 2003–2006, the lynx were monitored 1–2 times a day, but I used one location per day for all analyses except home range size. Although the radio-tracking was facilitated by a dense network of forest roads, approximately 20% of searches failed to locate the animals due to large sizes of lynx home ranges. In total, 4338 locations were collected in 1991–1996 and 1404 in 2003–2006. Locations were taken by triangulation. In 1991–1996 the locations were superimposed on a forest map 1:100 000 with the aim at determining the position of the animals in a forest compartment of the size 533 × 533 m and measured with accuracy estimated at 373 m (Jędrzejewski *et al.* 2002a). In 2003–2006 the topographic maps 1:50 000 were used, so that the locations were recorded to the nearest 50 m.

Ungulates abundance and distribution

Data on ungulate abundance were made available by the State Forestry General Administration in Białystok for 1991–1995 and 2004–2006. The estimates of ungulate densities were made by drive censuses in late winter (Kossak 1995). Censuses were not conducted in 1994 and 1996.

Data on spatial distribution of ungulates were collected by the team of the Mammal Research Institute, Poland, during the radio-tracking studies by noting the locations and number of observed animals while driving the forest roads in search of radio-collared lynx. The locations were noted according to the grid of forest compartments and recorded on topographic maps, as in case of lynx locations. In 1991–1995, a total of 527 cervids (126 roe deer and 401 red deer) were noted. In 2005–2006 a total of 911 cervids (240 roe deer and 671 red deer) were recorded. I assumed that the results of these surveys reliably reflected the true pattern of ungulate distribution, because they were conducted systematically using regular grid of forest roads that covered the majority of the forest area with equal efficiency. Moreover, as the ungulate surveys were conducted simultaneously with the lynx searching, mapping their records provided a comparable data set of their distribution within the lynx home ranges.

Data analysis

I investigated the relationship between the home range sizes of lynx and ungulate abundance using the yearly data on densities of roe and red deer (data for 7 years were available: Appendix 1). In the remaining analyses I considered the period 1991–1995 as the ‘high’ and 1996–2007 as ‘low’ ungulate’ abundance periods, respectively. Although data on ungulates densities for 1985–1990 (that included period of scat and kills collection) were not available, I consider that period as ‘high’ abundance, because no ungulate culling was conducted at that time. I calculated the annual home range sizes of lynx with 100% MCP (minimum convex

polygon) using BiotasTM (2003) software. Due to low sample sizes and large differences in home range sizes between males and females, I transformed the direct values into percentage increases of the home range sizes relative to the first recorded home range sizes for four sex/age classes separately: adult males, subadult males, adult females and subadult females (Appendix 1). For regression analysis, I averaged the home range sizes for particular sex/age classes in each year (in total 16 yearly home ranges sizes of 13 lynx) to reduce a possibility of a negative bias that could have resulted from including underestimated home ranges. The home range and ungulate density data were log-transformed.

To quantify the foraging patterns of lynx in both periods, I calculated the daily straight-line movement distances (SLD) and 5-day movement ranges (areas of activity within 5-day periods). I assumed that these characteristics of lynx behaviour should be most sensitive to possible changes in prey availability. As the lynx hunts ungulate prey by active searching (Jędrzejewski *et al.* 2002a), I predicted that the distances moved by the predator should increase with low availability of prey. Lynx spend on average 5.4 days on searching and feeding on killed large prey (Okarma *et al.* 1997). Therefore, I assumed that they should spend more time in the vicinity of kills in the period of high ungulate availability and, consequently, the movement ranges during the 5-day periods should be smaller than at low prey densities. In contrast, at low densities the following factors should contribute to enlarged 5-day ranges: (1) lynx may still roam around the prey in an attempt to secure more food even after a successful kill or (2) the prey searching time may exceed 5 days so that more distant locations should be recorded within that period. I calculated both indices to increase the chance of detecting a behavioural response by lynx to low prey availability. In analyses of both SLD and 5-day ranges, I included data on 11 lynx radio-tracked during the period 1991–1995 (high ungulate abundance) and 8 lynx radio-tracked during the period 1996–2007 (low ungulate abundance). Two lynx (males: Trofim and Iwan) that were monitored at the turn of 1995–1996 were included to the second period as it was the last season of the ungulate culling and their numbers were believed to be extremely low in 1996, though no census was conducted in that year (the census in 1997–1998 showed the lowest recorded densities: 115 roe deer and 286 red deer/km²; Jędrzejewski *et al.* 2002b). The same two individuals were also included in the low ungulate abundance period in the spatial analysis, although it must be noted that the data on ungulate distribution in that period were collected in 2005–2006 only. Nevertheless, I assumed that the data from this period reflected the distribution of cervids more reliably with regard to these two males than the data from high abundance time.

I carried out the analysis of spatial association of lynx radio-locations with locations of the observed roe deer and red deer (pooled) in both periods of high and low ungulate densities using the BiotasTM (2003) software to test if the distribution of cervids influenced space use by lynx. Before the spatial association analysis, I tested data sets on distribution of roe deer and red deer with the Morishita (1959)

dispersion index (I_δ) to determine if they were distributed patchily, according to formula:

$$I_\delta = q \sum_{i=1}^q \frac{x_i(x_i - 1)}{n(n-1)}$$

where q is the number of analyzed quadrats, x_i is the number of records in i th quadrat and n is the total number of records. The spatial distribution of locations is clumped, random or uniform, if $I_\delta > 1$, $I_\delta = 1$ or $I_\delta < 1$, respectively.

I conducted the association analyses between relocations of individual lynx and observations of ungulates within their home ranges using Ochiai's and Dice's pair-wise association coefficients (Janson and Vegelius 1981) and with multivariate covariance analysis (Schluter test: Schluter 1984). The analyses were performed based on a square grid by comparing the presence and absence (pair-wise) or densities (Schluter test) of points in each square (Fig. 2). The size of squares was set at 2×2 km for all samples, because the animals were observed along the roads only and the lynx were mostly located ≤ 1 km on either side of the nearest road. I assumed that size of the square was adequate to consider the proximity of a predator located within the limits of the same square as ungulates. The Ochiai's and Dice's coefficients of association may range from 0 (no association) to 1 (maximum association). The significance of association is tested with χ^2 -test by comparing the distribution of studied samples with all possible pairs of point patterns. The Ochiai's coefficient formula is:

$$r_O = \frac{A}{\sqrt{A+B} \times \sqrt{A+C}}$$

and the Dice's coefficient formula is:

$$r_D = \frac{2 \times A}{2 \times A + B + C}$$

where A is the number of squares where both lynx and ungulates were present, and B and C are the numbers of squares where only one of them was present. The multivariate covariance analysis (Schluter 1984) provides a variance ratio (V) between the variance in compared samples (species) (S_T^2) and variance in sampling units (grid squares) (σ_i^2) that is used as an association index:

$$V = S_T^2 / \sum \sigma_i^2$$

where

$$S_T^2 = (1/N) \sum_j^N (T_j - t)^2$$

where N is the number of sampling units j (grid squares), T is the number of compared samples (species) and t is the observed mean number of all records (lynx and ungulates pooled) per sampling unit, and

$$\sigma_i^2 = (1/N) \sum_j^N (X_{ij} - t_i)^2$$

where X_{ij} is the density of a sample i (lynx or ungulates) in a sampling unit j , and t is the observed mean density of sample i (lynx or ungulates).

The expected value of V under the null hypothesis of independent distribution of samples is 1. The significance of deviation from 1 ($V < 1$: avoidance and $V > 1$: association) is measured with a statistic W that is a modification of the association index (V):

$$W = S_T^2 N / \sum \sigma_i^2.$$

Interpretation of this statistic is based on the χ^2 distribution. The null hypothesis is rejected if W does not fall within the limits of critical values: $\chi^2_{0.025, N} \leq W \leq \chi^2_{0.975, N}$. Before conducting the spatial association analyses I overlaid the compared pairs of samples in the BiotasTM (2003) software and selected only the points that were included within the overlapping zone of each lynx's home range with the area of ungulates' distribution.

Results

Abundance of ungulates

According to the results of ungulate census, the period 1991–1995 was generally characterized by decreasing numbers of cervids (with exception of 1995), but the yearly average was still 78% higher than during the period 1996–2006 (Appendix 1). The decrease in ungulate abun-

dance was also remarkable in average number of animals observed per group. The average (\pm SD) number of roe deer decreased significantly from 2.3 (\pm 1.6) in 1991–1995 to 1.6 (\pm 0.8) individuals per record in 2005–2006 (Mann-Whitney U -test: $Z = 3.16$, $n_1 = 98$, $n_2 = 232$, $p < 0.01$) and that of red deer (though not significantly) from 4.1 (\pm 5.2) to 2.9 (\pm 2.5) individuals per record ($Z = 0.96$, $n_1 = 54$, $n_2 = 145$, $p > 0.1$) in the respective periods.

Composition of lynx diet during high and low ungulate abundance

The diet of lynx was very similar during the periods of high and low ungulate abundance (Table 1). It is conspicuous that during both periods cervids (roe and red deer) constituted the majority of the diet of lynx. Although the composition of prey items determined by percentage of occurrence in the scats was different between periods (replicated goodness-of-fit test: $G = 22.8$, $df = 8$, $p < 0.01$), this was caused by high predation on small mammals (micromammalia) during this

Table 1. Dietary composition of Eurasian lynx in the Białowieża Primeval Forest in two periods: 1985–1995 (high ungulate abundance) – data from Okarma *et al.* (1997) and 2001–2006 (low ungulate abundance) based on scats analysis and lynx prey remains found in the field. % Occ – percentage of occurrence in scats, % Bio – percentage of total biomass consumed by lynx. Scats were collected in the winter period only (October–April), whereas lynx kills include data from the whole year. Other mammals include: pine marten *Martes martes*, raccoon dog *Nyctereutes procyonoides*, domestic dog *Canis familiaris* and unidentified mammals. ¹ Okarma *et al.* 1997, ² this study, + trace amount.

Prey species	Scats analysis				Kills found (%)	
	High ungulate density ¹ ($n = 127$)		Low ungulate density ² ($n = 92$)		High ungulate density ¹ ($n = 172$)	Low ungulate density ² ($n = 113$)
	% Occ	% Bio	% Occ	% Bio		
Cervidae	87.4	89.9	85.9	94.5	84.0	89.4
Roe deer <i>Capreolus capreolus</i>	–	–	–	–	62.0	69.9
Red deer <i>Cervus elaphus</i>	–	–	–	–	22.0	19.5
Wild boar <i>Sus scrofa</i>	3.9	1.0	3.3	0.3	1.0	0.9
Micromammalia	0.8	+	12.0	0.3	–	–
Brown hare <i>Lepus europaeus</i>	11.0	6.0	1.1	4.5	9.0	7.9
Squirrel <i>Sciurius vulgaris</i>	0.8	+	1.1	0.1	0.5	0.9
Birds	3.9	0.5	2.2	0.3	4.0	0.9
Insects	0.8	+	1.1	+	–	–
Amphibians	0.8	+	–	–	–	–
Plant material	0.8	+	–	–	–	–
Other mammals	3.2	2.4	15.2	–	1.5	–

study that made no difference when converted to the biomass consumed ($G = 1.2$, $df = 6$, $p > 0.1$). In both periods, roe deer were more frequently captured by lynx than red deer (Table 1). Diets determined from the lynx kill remains found during radio-tracking were not different between the two periods ($G = 4.9$, $df = 6$, $p > 0.1$).

Relationship between lynx home range and prey density

The regression analyses showed that the index of lynx home range increase was weakly ($r^2 = 0.33$), but significantly ($p = 0.05$) negatively correlated with density of both cervids pooled after log-transformation (Fig. 1). The relationship was slightly stronger for the roe deer and weaker for the red deer densities taken separately. The relationships suggest that lynx responded to the decrease of cervids (especially roe deer) abundance by increasing their home range sizes.

Lynx foraging pattern relative to prey densities

The average SLD for all lynx was 44% longer during the period of low ungulate availability than during high ungulate abundance and this

difference was highly significant (Table 2). However, when analyzed separately in different sex/age groups the significance of the difference was maintained only in adult females, which had 45% longer SLDs when prey was scarce. The SLD moved by adult males and subadult females were also longer in the same period, but only by 10 and 20%, respectively and these differences were not significant (Table 2).

Similarly, the 5-day ranges were on average 2.2 times larger during the period of prey scarcity than in the preceding period for all lynx (Table 2). When analyzed separately, the significance of the difference again held in adult females only. The adult males doubled their 5-day ranges when prey was scarce compared to the period of deer abundance, but these differences were not significant. The same trend occurred in subadult females, but with yet smaller differences.

Spatial association between the lynx and its prey

Roe and red deer showed relatively clumpy distribution in both periods. The Morishita indices (I_δ) were 2.09 and 1.83 in 1991–1995 and

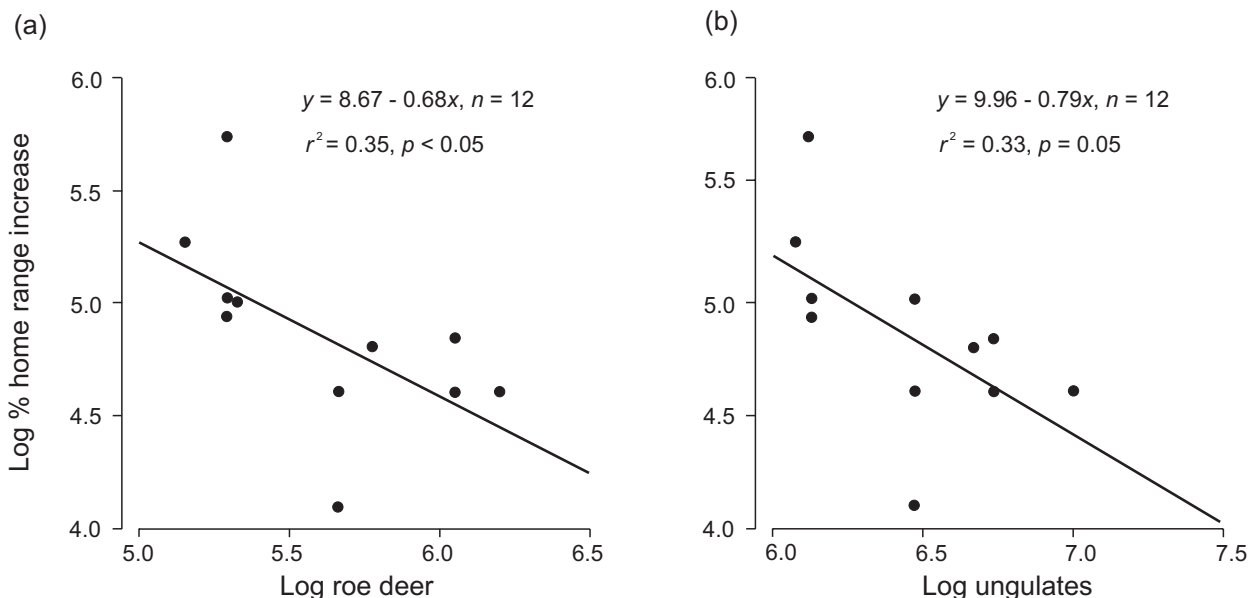


Fig. 1. Relationship between the home range size (expressed as percentage increase of yearly average home range sizes for given sex/age class relative to the first year it was calculated) of Eurasian lynx and the density of roe deer (a) and total cervids' density (b – roe and red deer pooled) in the Białowieża Primeval Forest, Poland.

Table 2. Variation in straight-line distance movements and 5-day ranges of Eurasian lynx in two periods: 1991–1995 (high ungulate density) and 1996–2006 (low ungulate density) in the Białowieża Primeval Forest, Poland. n_1 – number of individuals in 1991–1995, n_2 – number of individuals in 1996–2006, n_3 – number of records.

Sex/age group of lynx (n_1, n_2)	Straight-line distance (m)			5-day range (km ²)		
	High ungulate density	Low ungulate density	Mann-Whitney <i>U</i> -test	High ungulate density	Low ungulate density	Mann-Whitney <i>U</i> -test
	Mean ± SD (min–max) n_3	Mean ± SD (m) (min–max) n_3		Mean ± SD (min–max) n_3	Mean ± SD (min–max) n_3	
Adult males (3, 5)	2992 ± 2920 (0–14596) 168	3298 ± 3309 (0–18040) 721	$Z = -0.83$ $p = 0.41$	5.44 ± 6.13 (0–20.65) 34	11.10 ± 14.18 (0–63.41) 36	$Z = -1.73$ $p = 0.08$
Adult females (4, 1)	1480 ± 1602 (0–9072) 303	2147 ± 2368 (0–11702) 168	$Z = -2.59$ $p < 0.01$	2.55 ± 3.03 (0–12.82) 70	5.92 ± 8.48 (0–40.41) 39	$Z = -2.11$ $p = 0.035$
Subadult females (3, 2)	2035 ± 1987 (0–9958) 262	2462 ± 2677 (0–12731) 188	$Z = -1.18$ $p = 0.24$	4.59 ± 5.96 (0–26.41) 60	6.29 ± 9.79 (0–41.50) 43	$Z = -0.52$ $p = 0.60$
Subadult males (2)	2172 ± 2156 (0–10826) 231	–	–	5.37 ± 8.64 (0–45.01) 47	–	–
All lynx pooled	2060 ± 2174 (0–14596) 964	2972 ± 3109 (0–18040) 1077	$Z = -5.83$ $p < 0.0001$	4.22 ± 6.06 (0–45.01) 211	9.22 ± 12.73 (0–63.41) 218	$Z = -4.14$ $p < 0.0001$

2003–2006, respectively. However, this result does not demonstrate how the cervids were distributed within the lynx home ranges. Therefore, I attempted to evaluate the spatial association of individual lynx radio-locations relative to spatial distribution of roe and red deer pooled during the periods of high and low ungulate abundances (Fig. 2). In general, the mean (\pm SD) coefficients of association in pair-wise association analysis (related to area overlap) between lynx and both cervids were relatively high (0.67 ± 0.14 and 0.53 ± 0.13 , respectively, for Ochiai's and Dice's coefficient), suggesting a moderate association in space (Table 3). In other words, the area of ungulates' distribution coincided with lynx locations quite evenly throughout the lynx home ranges. In contrast, when accounting for density, the associations calculated with Schluter test showed no significant tendencies for grouping of locations of lynx with those of their prey (Table 3).

Although the associations were overall weaker in 1991–1995 than 1996–2007, the differences were not significant. The average (\pm SD) Ochiai's coefficients in the respective periods were: 0.62 ± 0.16 and 0.72 ± 0.11 ; t -test: $t = -1.57$, $df = 14$, $p = 0.14$). In case of Dice's coefficient, which was more conservative, the averages (\pm SD) were: 0.48 ± 0.12 and 0.60 ± 0.14 , in two periods, respectively; $t = -1.38$, $df = 14$, $p = 0.18$).

The multivariate covariance Schluter test (accounting for density) found no significant associations between the lynx and cervids during both the high and low ungulate abundance (Table 3). The variance ratio (V) was close to 1 in all analyzed lynx individuals, indicating an independent distribution of lynx locations relative to the deer spatial arrangements. In other words, the lynx showed no tendency for staying in close proximity to aggregations of deer (Fig. 2).



Fig. 2. Examples of data used for analysis of association between lynx and ungulates with BiotasTM software, illustrating the distribution of ungulate observations in the forest within the lynx home range: a – lynx locations (female “Jagna”: squares) and b – ungulate observations, roe and red deer pooled (triangles). Different intensity of shading is relative to the number of points, recorded in each grid square. Solid line denotes shape of the forest. Note strong overlapping of lynx and cervids’ general distributions and different intensity of the square use by the predator and its prey.

Discussion

The relationships between food resources and various life history traits are predictable with theoretical models (Mitchell and Powell 2004) and have been studied empirically with various tools including indirect measures of resources such as latitude (Gompper and Gittleman 1991) or environmental productivity (Herfindal *et al.* 2005, Zalewski and Jędrzejewski 2006). As ecological conditions vary greatly both among and within species however, detailed field research may still provide new insights into these complex interactions. This study provided data on how Eurasian lynx adjusted their spatial and

foraging behaviour to decreasing availability of prey in one locality over time.

The results of the dietary comparison conducted in this study highlighted two important points. Firstly, it is striking that despite the declining availability of cervids, lynx remained highly specialized in hunting them, and roe deer in particular. Although no quantitative data on alternative prey abundance were available for both periods, field observations indicate that hare numbers increased during the period of low ungulate densities (K. Schmidt, pers. obs.), providing an opportunity for prey switching and a higher predation rate on them. However, regardless of the reliability of this observation,

Table 3. Results of the analysis of association among locations of radio-tracked lynx and observations of ungulates in the Białowieża Primeval Forest during periods of high (1991–1995) and low ungulate density (1996–2006). The Schluter (1984) test shows association based on density of points in the grid squares with the variance ratio $V = 1$ indicating independent distribution. The pair-wise associations (Janson and Vegelius 1981) are based on presence and absence of points in each grid square with Ochiai and Dice coefficients ranging from 0 (no association) to 1 (maximum association). The two coefficients are given for comparison, with the Dice coefficient being more conservative than Ochiai's. See Methods for more details. n_1 – number of lynx locations, n_2 – number of ungulate observations. W – test statistic (Schluter 1984).

Lynx identity (sex)	n_1, n_2 (sampled units)	Multivariate Covariance Schluter Test				Pair-wise association analysis			
		Variance ratio V	W	$\chi^2_{0.025}$	$\chi^2_{0.975}$	Association coefficients		χ^2	p
						Ochiai	Dice		
1991–1995									
Bazyli (M)	85, 268 (81)	1.17	94.77	58.00	107.78	0.32	0.44	9.03	0.003
Bazyliszek (M)	173, 367 (99)	1.24	122.28	73.36	128.42	0.75	0.60	20.57	<0.001
Borys (M)	35, 361 (132)	1.04	136.76	102.09	165.70	0.50	0.28	12.75	<0.001
Diana (F)	41, 294 (64)	1.06	68.00	43.78	88.00	0.54	0.35	2.92	0.09
Makary (M)	147, 252 (81)	1.27	102.96	58.00	107.78	0.70	0.54	16.30	<0.001
Natasza (F)	124, 213 (66)	1.12	73.68	45.43	90.35	0.62	0.45	6.85	0.009
Sonia (F)	261, 144 (48)	1.15	55.10	30.76	69.02	0.75	0.59	11.09	0.001
Tamara (F)	89, 114 (36)	1.27	45.80	21.34	54.44	0.75	0.60	5.35	0.02
1996–2006									
Trofim (M)	184, 628 (110)	1.08	118.82	82.87	140.92	0.71	0.55	12.00	0.001
Iwan (M)	138, 86 (40)	0.99	39.52	24.43	59.34	0.55	0.37	4.40	0.04
Jurand (M)	176, 562 (140)	1.19	166.32	109.14	174.65	0.80	0.66	76.51	<0.001
Jagna (F)	284, 518 (108)	1.18	127.62	81.13	138.65	0.78	0.63	29.36	<0.001
Maćko (M)	229, 646 (192)	1.12	215.55	155.52	232.27	0.60	0.42	26.09	<0.001
Jula (F)	173, 532 (140)	1.07	150.75	109.14	174.65	0.67	0.51	22.06	<0.001
Dana (F)	84, 208 (36)	1.17	42.16	21.34	54.44	0.86	0.75	8.66	0.003
Zbyszko (M)	141, 127 (63)	1.14	71.90	42.95	86.83	0.80	0.67	30.17	<0.001

hares became even less important food for lynx during that period. The high specialization of lynx in hunting roe deer, despite their very low density, has been reported by Odden *et al.* (2006), but that study was particularly concerned with the winter period when this ungulate was distributed in a highly clumped manner, making it more predictable in time and space. In the BPF, roe and red deer were relatively evenly dispersed, so that lynx would be forced to make extra efforts to locate them during their population declines. The second point is of importance for justification of other analyses in this study as it suggests that these ungulates were equally important as prey of the lynx in both study periods. Therefore, one can assume that the observed changes in lynx behaviour reflected its efforts to maintain a deer diet while experiencing this food shortage, rather than just a general adaptation (that could, for instance, include prey shifting) to the main prey decrease. A strong reliance on one type of prey – the rabbit *Oryctolagus cuniculus*, regardless of their density was also reported for the Iberian lynx (Gil-Sanchez *et al.* 2006).

The response of lynx to decreasing ungulate abundance by increasing their home range sizes was clear, but the relationship was quite weak. The relatively low explanatory power of the regression most likely resulted from low sample sizes and the fact that the study area was cut by the state border, so that the sizes of home ranges might have been underestimated in some cases. If that was the case, yet farther lynx movements could have not been discovered particularly at low prey abundances. Another reason for dilution of this relationship is a possible inconsistency in the ungulate censuses. For instance, the red deer numbers provided in 2006 seem to be overestimated in comparison to previous year, based on their reproductive potential determined in BPF (46% of adult females with 0.9 juvenile per female: Okarma *et al.* 1997). On the other hand, the fact that this relationship turned out to be quantitatively discernible, despite of the dilutive effects, seems to show a real trend.

There are few studies that have investigated the dynamics of carnivore home range sizes in

response to changes in local prey abundance. Although predicted from theoretical models and large-scale comparative studies, only a few field studies have proven the existence of a direct response of the home ranges of a carnivore to a prey population decline (eg Knick 1990, Wydeven *et al.* 1995, Grigione *et al.* 2002). Other research has failed to find a clear relationship (Mowat *et al.* 2000, Logan and Sweanor 2001, Palomares *et al.* 2001). This inconsistency probably results from the complex nature of this relationship, as there are numerous additional factors that may contribute to the unexplained portion of home range variability. This calls for further field research that may account for these lacking variables by studying various predator-prey associations at different ecosystems.

An increase in home range size over time in a local population cannot continue without affecting its social and spatial organization (Mitchell and Powell 2004). The influence of population density of carnivores may have even stronger effect on home range size than food supply, as was recently found in a bobcat population living with relatively stable food resources (Benson *et al.* 2006). Thus, it is easy to predict that at declining food resources, the increasing home range of the predator should yet more strictly parallel the decreasing density. Although there are no firm data available on lynx density in the BPF, snow-tracking combined with radio-telemetry allowed approximate estimates of lynx numbers, suggesting they were 30–35% lower in 2003–2006 compared to the previous period (Jędrzejewski *et al.* 1996, K. Schmidt and R. Kowalczyk, unpubl.). This emphasizes the importance of maintaining suitable prey resources for conservation of this large predator.

Like most felids, lynx forage by active searching for their prey (Jędrzejewski *et al.* 2002a, Sunquist and Sunquist 2002) and they spend considerable amounts of time at kill sites with large ungulate prey (Okarma *et al.* 1997). Therefore, it was reasonable to expect that at declining prey availability the lynx should change its foraging behaviour to acquire enough food, assuming that it does not shift to alternative prey. This study, indeed, showed significant changes in lynx behaviour that emphasize strong de-

pendence of lynx on roe deer. Earlier investigations in the same lynx population, but still at high ungulate abundance, demonstrated that, after killing a large prey item, lynx increased their foraging activity day by day (Schmidt 1999, Jędrzejewski *et al.* 2002a). This was explained by decreasing amount of food that evoked a stronger hunting efforts, and the same is also valid at the population scale that has been considered in this study. The general increase of daily movements (SLD) and the 5-day ranges associated with the drop of prey availability indicated that when the prey availability is low, lynx either have to spend more time actively searching or continue foraging even after successful hunts to secure more food. I collected anecdotal observations showing both patterns during the period of low prey abundance. On several occasions, I found the lynx traveling long distances between bouts of feeding at recently killed large prey, whereas in a number of other instances lynx moved for several days covering large portions of their home ranges, without returning to the same spot (suggesting there was no active kill site). The changes in lynx foraging pattern in connection with stability of its diet despite declining prey abundance clearly illustrate the adaptation of this strongly specialized predator to low food availability.

Another important aspect of lynx foraging highlighted by this research is that adult females reacted more strongly to the prey shortage than did males and subadult females. This is in concordance with predictions made by Sandell (1989) saying that females' reproductive strategy in solitary carnivores is shaped by reliance on food resources, while that of males relies on distribution of females. In the Eurasian lynx, such divergence related to the reproductive strategies have been observed both at a local scale (differences in home range size, movement and activity patterns: Schmidt *et al.* 1997, Schmidt 1999, Jędrzejewski *et al.* 2002a; and diet: Okarma *et al.* 1997, Sunde and Kvam 1997, Jobin *et al.* 2000) and larger geographical scales (Herfindal *et al.* 2005). The results of this study emphasize that prey depletion may have a particularly profound effect on lynx conservation through affecting reproducing females. As the

females are tending kittens for most of the year (Schmidt 1998) and are solely burdened with providing them with food, prey shortage may first impede their ability to do so. This may directly influence survival of kittens. Indeed, monitoring of the lynx population in the BPF in 1991–1996 indicated that the number of kittens per female dropped after the reduction of ungulates occurred (Jędrzejewska and Jędrzejewski 1998).

The analysis of spatial association of lynx with ungulates showed that the areas utilized by both the predator and its prey substantially overlap in the BPF. However, when variation in density was accounted for, the analysis provided no indication of association of predator and prey. Both results indicate that despite of tendency for grouping, roe and red deer are relatively evenly available within the lynx home ranges. Therefore, lynx have access to prey throughout their entire home ranges and do not specifically select sites with the highest prey densities, especially given they are capable to cover long distances within their ranges in a short time (Jędrzejewski *et al.* 2002a). On the other hand, they should seek habitats, where prey is easier to capture (Hopcraft *et al.* 2005) and, indeed, the lynx were found to be highly selective towards specific microhabitat structures during hunting in the BPF (Podgórski *et al.* 2008).

My results are in contrast with those of Moa *et al.* (2006) who showed a clear preference of lynx for the roe deer patches. This is, however, to be expected as the roe deer in their study area were distributed in a highly clumped manner. I am convinced that, in BPF and other similar predator-prey systems, the spatial proximity of the predator to prey sites does not play an important role in hunting. Predators may cope with declining prey abundance by increasing their search effort by covering longer distances or larger areas, as was found here. Such a strategy may be a consequence of behavioral depression of prey availability (Charnov *et al.* 1976, Brown *et al.* 1999) that may possibly be manifested by increased ungulate vigilance after a predator's visit. Furthermore, I suggest that, in turn, the relatively homogeneous distribution of cervids in the BPF could be caused by incessant

risk associated with constant presence of large predators.

According to the present study, Eurasian lynx are distinguished by having a high threshold of tolerance towards densities of their main prey, in terms of maintaining their specialization in hunting the roe deer. The behavioural mechanisms may help individuals to adapt to changing prey availability, although they are not sufficient to prevent the negative influence of prey declines on lynx populations. The results also emphasize that prey depletion has an immediate effect on lynx spatial organization and, in consequence, on their density. This information has to be considered in prioritizing lynx conservation strategies and management of ungulates.

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Appendix 1. Data on lynx home range sizes and ungulate densities ($n/100 \text{ km}^2$) in the Białowieża Primeval Forest in 1991–2006 used for regression analysis. ¹ – mean home range size of lynx of particular sex/age class (Ad M – adult male; Ad F – adult female; Subad M – subadult male, Subad F – subadult female) in a given year. ² – percent increase of average yearly home range size for a given sex/age class in relation to previous year (the home range recorded in the first year is taken as 100%). n – number of locations

Year	Lynx identity	Age/sex	n	Home range (km^2)	Mean home range ¹	% increase ²	Roe deer density	Red deer density	Ungulates total
1991	Bazyli	Ad M	228	222			492	607	1099
	Makary	Ad M	146	165	193.5	100			
1992	Borys	Ad M	187	245	245.0	126.6	425	416	841
	Bazyliszek	Subad M	475	268	268.0	100			
1993	Makary	Ad M	268	112			288	359	647
	Bazyliszek	Ad M	96	120	116.0	59.9			
	Natasza	Ad F	522	113	113.0	100			
	Sonia	Subad F	461	101	101.0	100			
1995	Iwan	Ad M	957	193			324	463	787
	Trofim	Ad M	998	279	236.0	122.0			
2004	Jagna	Ad F	246	220	220.0	194.7	173	262	435
2005	Jagna	Ad F	131	171	171.0	151.3	199	260	459
	Jurand	Ad M	278	270	270.0	139.5			
	Jula	Subad F	220	312	312.0	308.9			
2006	Maćko	Ad M	308	423			205	443	648
	Zbyszko	Ad M	221	158	290.5	150.1			