

BOOK REVIEW

**Semiaquatic Mammals**

Semiaquatische Säugetiere. Materialien des 2. Internationalen Symposiums "Semiaquatische Säugetiere" in Osnabrück vom 9.6 bis 12.6.1992. R. Schröpfer, M. Stubbe and D. Heidecke, eds. Wissenschaftliche Beiträge, Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, 1992, 468 pp. ISBN 3-86010-362-8.

This book is the next issue of series entitled "Kongreß- und Tagungsberichte der Martin-Luther-Universität Halle-Wittenberg" published by the Institute of Zoology of this university. It constitutes the proceedings of the 2nd Symposium of Semiaquatic Mammals (2nd SSM), which took place in Osnabrück (northwestern Germany) in June 9 – 12, 1992. It contains 42 papers presented at the meeting, as well as editors' foreword, protocols of 2 workshops (one on European mink and another on European beaver), obituary of Leonid S. Lavrov – Russian beaver-specialist, and lists of symposium participants and sponsors.

The published papers, were mostly presented as lectures during 2nd SSM, but some posters are also included. The authors of works come from 11 European countries: Germany (20 papers), Russia (6), Spain (4), Slovak Republic (3), Belarus and Latvia (each 2), Austria, Denmark, Iceland, the Netherlands, and Poland (each 1). The majority of papers is published in German with English summary (23) or in English (12), and only 9 are solely in German. They present studies carried out on 15 semiaquatic mammal species. Papers on beaver (13), otter (9), and 2 species of minks (7) prevail. On the other hand, single papers concern animals as rare as Russian desman *Desmana moschata* and Tibetan water shrew *Nectogale elegans*. The other objects of presented researches are 2 *Neomys* species, 2 *Arvicola* species, nutria, muskrat, and Norway rat. Papers about ecology, protection, and reintroduction of species mentioned above predominate, but several studies are focused on ethology, biology, morphology and diseases/parasites. Five papers concerns more general problems (see below).

The advantage of this publication is that reports of quite many investigations of European semiaquatic mammals are collected in one volume. Moreover, the majority of papers contains references of other related publications what constitutes an additional source of information. Unquestionable good point of these proceedings is quite numerous papers written by East European authors, which until now were usually published in their native languages. The presence of some review-papers can be interested also for mammalogists not working with semiaquatic mammals (e.g. Schröpfer R. and Stubbe M. "The diversity of European semiaquatic mammals within the continuum of running water system", and Danilov P. I. "Introduction of North-American semiaquatic mammals in Karelia and its consequences for aboriginal species") or professionalists of nature protection and environment planning (e.g. Heidecke D. and Klenner-Fringes B. "Studie über die Habitatnutzung des Bibers in der Kulturlandschaft").

However, some slight faults crept in the publication. There are some spelling errors in the text, and mistakes regarding names of paper authors and in participants list. The references of the proceedings of the 1st SSM are advertised insufficiently (mentioned only in the editors' foreword), and unfortunately, with a mistake ("27. Jahrgang" instead of correct "72. Jahrgang").

In the proceedings of 1st SSM [Vorträge aus dem Symposium über "Semiaquatische Säugetiere und ihre Lebensräume" in Osnabrück vom 28. bis 30.8.1984. Z. Angewandte Zool. 72 (1-2), 1985], 20 works carried out on 7 semiaquatic mammal species by authors from only 4 countries (Germany, France, Great Britain, and the Netherlands) were published mostly in German with English summary (13 papers). In comparison to this, the proceedings of 2nd SSM show the increase of importance of the symposium – doubling of participants number and internationalization. We should wish ourself that these trends will be maintained during the 3rd SSM.

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## Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints

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Lynx *Lynx lynx* (Linnaeus, 1758) – ungulate relationships were studied in the exploited (530 km<sup>2</sup>) and pristine (47.5 km<sup>2</sup>) parts of Białowieża Primeval Forest during 1985 through 1992. In pristine forest, *Sus scrofa* (54%) and *Cervus elaphus* (35%) predominated in the ungulate community. In exploited forest, *C. elaphus* (36%) and *Capreolus capreolus* (33%) were most abundant. Scat analysis indicated that cervids comprised 87% of biomass consumed by lynxes in the cold season; *Lepus europaeus* were 11%, and *S. scrofa* 2%. Hare was 2.5 times higher in the lynx diet in the exploited forest than in the pristine forest. Among 138 carcasses of ungulates killed by lynx in exploited forests in cold seasons, 76% were roe deer. In the pristine forests, red deer (61%) and roe deer (28%) were equally positively selected. Lynx did not select roe deer for any sex/age class but did select red deer fawns. Snowtracking showed that lynx attempted 1 attack on deer, 2 on medium-sized prey, and 6 on rodents in their daily route. Lynx fed an average of 3 – 4 days on a killed deer. Eight species of scavengers (mainly wild boar and red fox) fed on lynx's kills. Analysis of 1090 ungulate carcasses found in Białowieża Forest showed that predation was responsible for 75% of known natural mortality in red deer (66% by wolf *Canis lupus* Linnaeus, 1758; 9% by lynx), 62% in roe deer (37% by lynx, 25% by wolf), 27% in moose (all by wolf), and 12% in wild boar (11% by wolf, 1% by lynx). Review of studies from the Palaearctic region revealed that the share of hare in lynx diet positively correlated with latitude, whereas the share of ungulates was inversely related to latitude. From Palaearctic ungulates that ranged from 15 kg body mass (*Moschus moschiferus*) to 920 kg (male *Bison bonasus*), the lynx selected the smallest species available. Mean electivity index (D) for 9 ungulate species was negatively correlated with their log body mass. In the Palaearctic region, predation contributed, on average, 1% to the natural mortality of European bison, 25% to that of wild boar, 59% of moose, 80% of red deer, and 85% of roe deer. Of total predation-caused mortality, the average share caused by lynx was 46% in roe deer, 14% in red deer and little or none in wild boar, moose, and bison.

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Key words: *Lynx lynx*, *Canis lupus*, feeding habits, prey choice, predator-prey relationships, ungulate mortality, Białowieża Primeval Forest, Palaearctic

## Introduction

The effect of large predators on ungulates has received much interest in North America and the former Soviet Union (e.g. Pimlott 1967, Filonov 1989), where both predator and ungulate populations are relatively well preserved. In western Europe, where large predators have mostly been exterminated, predation on ungulates has received little study. However, recent efforts to reintroduce lynx to western Europe (Breitenmoser and Haller 1987a), the increase and spread of brown bear and wolf populations in central Europe (Jakubiec and Buchalczyk 1987, Okarma 1989) and the growing concern about protection of large predators (Schonewald-Cox *et al.* 1991) has revived the questions of predators' effect on local ungulate population and their general role in evolution and current performance of ungulates (Kruuk 1986, Skogland 1991, Jędrzejewski *et al.* 1992).

We present the results of a 7-year study of lynx *Lynx lynx* (Linnaeus, 1758) and ungulates in the relatively well preserved Białowieża Primeval Forest, eastern Poland. We investigated: (1) lynx feeding habits and prey selection; (2) the role of lynx predation in the mortality of ungulates; (3) differences in lynx–ungulate relationships between the protected, pristine and the man-transformed, logged portions of the Białowieża Forest; and (4) difference in prey selection between lynx and wolf *Canis lupus* Linnaeus, 1758. Results were then compared to other studies conducted in the Palearctic region, mainly in various game reserves in the former Soviet Union. By use of this comparison, we hoped to draw more general conclusions about the lynx's adaptation to exploit various prey communities and its role in ungulate mortality.

The study was part of a long-term research on vertebrate predator–prey relationships in Białowieża Primeval Forest (Jędrzejewski *et al.* 1989, Jędrzejewski and Jędrzejewska 1993).

## Study area

The 1250 km<sup>2</sup> Białowieża Primeval Forest is located on the Polish–Belarussian border and is the best preserved woodland in lowland temperate Europe. Mature stands of lowland type forests in the nemoral boreal zone are dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, black alder *Alnus glutinosa*, spruce *Picea abies*, and pine *Pinus sylvestris*. More detailed description of vegetation was provided by Faliński (1986). In 1945, the Białowieża Forest was divided between the USSR (670 km<sup>2</sup>) and Poland (580 km<sup>2</sup>). This study was conducted only in the Polish portion, most of which (530 km<sup>2</sup>) undergoes timber harvest, reforestation, and game management. It has been commercially logged since 1915. Replanting of small clearcuts (predominantly with pine and spruce) decreased the proportion of deciduous stands (at present 46% of area) below their potential representation in the forest. The average age of tree stands in the managed forest is 72 years.

A small (47.5 km<sup>2</sup>) strictly protected area forms Białowieża National Park (BNP), where neither exploitation nor hunting has been allowed since its establishment in 1921. BNP (UNESCO's Man and Biosphere Reserve and World Heritage Site) protects the best preserved part of the Białowieża Forest, where most of the tree stands are of natural origin and bear few signs of human impact. Most of BNP (73%) is covered by deciduous stands (oak, hornbeam, black alder, maple *Acer platanoides* and lime

*Tilia cordata*). The average age of tree stands is 130 years. Animals move freely between BNP and the exploited forest.

Since 1981, Polish and Belarussian parts of Białowieża Primeval Forest are separated by a 2.5-m tall, thick wire fence built by the Soviets along their state border. Ungulates can no longer cross the border, though lynx and wolves are often reported to cross.

The contemporary community of ungulates consists of five species: red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, moose *Alces alces*, and European bison *Bison bonasus*. The bison is protected in the Polish part of Białowieża Forest and its number is kept stable (ca 250) by yearly culling. The four other species of ungulates are hunted in the exploited part of the forest but not in BNP. The guild of large predators was impoverished in the 19th century by extermination of brown bear *Ursus arctos*, and today it contains two species, lynx and wolf. During the last 150 years, their numbers were subject to changes including temporary exterminations due to predator control and intensive hunting. Lynx numbers have been relatively stable since 1970 and wolf numbers since 1980 (Miłkowski 1986). We estimated that about 10 lynxes and 15 wolves inhabited the Polish part of the forest during the study.

The climate of Białowieża Forest is transitional between continental and Atlantic types. Mean temperature for January (the coldest month) during the last 3 decades varied from  $-13.4^{\circ}\text{C}$  (in 1963) to  $1.3^{\circ}\text{C}$  (in 1984). The depth of snow during winter may vary from 0 to  $> 100$  cm.

## Methods and material

### Estimation of ungulate numbers and causes of mortality

Censuses of ungulates were designed to estimate the species structure of the community, sex and age structure of red and roe deer populations, and approximate density of each species. In January 1991, a drive census (Pucek *et al.* 1975) of ungulates was conducted on  $11.2\text{ km}^2$  in BNP (24% of its area) and in March 1991, a drive census was conducted in the exploited forest on  $55.3\text{ km}^2$  (10% of its total area). The area driven in BNP was a rectangle app.  $3 \times 4$  km, whereas the censused area in exploited forests consisted of 50 randomly selected forest compartments, mostly  $1066 \times 1066$  m ( $1 \times 1$  verst) each. The measure of density used here was the total number of censused ungulates divided by the sampled area (to obtain an average of  $n$  animals/ $\text{km}^2$ ). More detailed analysis of spatial variability of ungulate density in BPF will be presented elsewhere.

Sex and age (fawn or adult) of red and roe deer were recorded during the census in the exploited forest. Results of the drive censuses conducted during 1991 were used as measures of species structure of ungulate communities for the entire study period (1985 through 1992). The results were similar to those obtained in the early 1970s by Pucek *et al.* (1975) and species structure was considered stable (Jędrzejewski *et al.* 1992).

During 7 autumn-winter seasons (1985/86 through 1991/92), searches for ungulate carcasses were conducted in the exploited forest (mainly by game wardens) and in BNP (by MRI staff). In total, 1090 carcasses were analysed: 227 from BNP and 863 from the exploited forest. Cause of death was recorded at each carcass and, if predators were involved, the species was identified by tracks and signs on snow. For analysis, carcasses were classified as: (1) killed by lynx; (2) killed by wolves; (3) dead from causes other than predation. The latter category included animals which died from undernutrition and disease and did not bear visible signs of predators' action, accidents or poaching. Road and railway kills (very few), and all other cases of man-caused death (e.g. hunting, poaching) were excluded. Age (juvenile or adult) and sex of dead ungulates were determined in the field based on size and external features. Additionally, after 1990, the jaws of red and roe deer found by MRI staff were extracted for aging on the basis of tooth-wear (Lochman 1985, Pielowski 1988).

Although the 1090 analysed carcasses constituted an unknown percentage of the total natural mortality of ungulates in cold seasons, we believe that they were a representative and random sample of the total number of ungulates dead from natural causes.

### Lynx feeding habits

Analysis of lynx diet was based on 76 scats collected during autumn and winter; 55 were collected in BNP during 1985/86 through 1991/92, and 21 were collected in the exploited forest during 1990/91 and 1991/92. Twenty of 55 scats gathered in BNP were found at one red deer kill site utilized by a family of lynxes. These scats contained only the remains of red deer, so their weights were averaged and they were treated as one scat. Thus, the total material consisted of 36 scat samples from BNP and 21 from the exploited forest. Though the lynxes moved freely between BNP and the exploited forest, we believe that the scats represented the lynx's prey captured in the same part of the Białowieża Primeval Forest as the scat location. Our data from snow and radiotracking indicated that lynx remained near a kill site for several days and that the lynxes which utilized the National Park most often stayed there for some time.

The analysis of scats followed standard procedure (Lockie 1959, Goszczyński 1974). Prey were identified on the basis of bony remains (Pucek 1984) and macro- as well as microscopic analysis of hair (Dziurdzik 1973, Debrot 1982). Because only small bone fragments were recovered from lynx scats, in contrast to wolf scats (see Jędrzejewski *et al.* 1992), neither species of deer nor their age could be determined. Prey groups in lynx diet were expressed as percent of occurrence in scats and percent of mean biomass consumed per scat. The food biomass consumed by lynx was estimated using the coefficients of digestibility from Goszczyński's (1974) work on foxes. Coefficients obtained for domestic cats (Liberg 1982) were not used because of the lack of ungulate carcasses in Liberg's trials. Food niche breadth was calculated ( $B = 1 / \sum p_i^2$ , where  $p_i$  – percent biomass of a given prey) according to Levins (1968).

To assess relative prey selection by lynx of ungulate species, Ivlev's selectivity index (D) was calculated (as modified by Jacobs 1974):  $D = (r - p) / (r + p - 2rp)$ , where:  $r$  – the fraction of a given species in a total number of ungulates killed by lynx (data from carcasses found);  $p$  – the fraction of a species in an ungulate community (data from drive census). D ranges from -1 (total avoidance of a species), through 0 (killing proportional to occurrence), to 1 (maximum positive selection). Lynx selection of sex and age classes from deer population was assessed by comparison of age and sex structure of carcasses of deer killed by lynx and those of living populations (data from drive census in the exploited forest).

Information about lynx hunting and feeding modes and presence of scavengers was read from the signs and tracks on snow whenever possible at carcasses of ungulates killed by lynx and found in BNP and from radiotracking of lynxes in both parts of Białowieża Forest. All non-ungulate prey found during radiotracking was also recorded. Radiotracking of lynxes only occurred in 1991 and 1992. Data on modes of area searching and hunting behaviour of lynx were gathered by snowtracking of individual lynxes in pristine forests of BNP in 1986/87 through 1988/89. The length of trail was measured by pacing and all detectable activities of lynx were recorded during 25874 m of tracking.

## Results

### Density and species composition of ungulates

In January – March 1991, the average density of ungulates per km<sup>2</sup> in the entire Białowieża Primeval Forest was: 6.4 red deer, 5.9 wild boar, 4.7 roe deer, 0.5 European bison, and 0.3 moose. Red deer and wild boar were more abundant in BNP (11.4 and 17.9 inds/km<sup>2</sup>, respectively) than in the exploited forests (5.4 and 3.5 inds/km<sup>2</sup>, respectively). Roe deer had higher density in exploited forest (4.9 inds/km<sup>2</sup>) than in BNP (3.7 inds/km<sup>2</sup>).

Species structure of ungulates differed significantly between the exploited and pristine forests ( $G = 33.07$ ,  $df = 4$ ,  $p < 0.001$ ,  $G$ -test) (Fig. 1). The percentages of

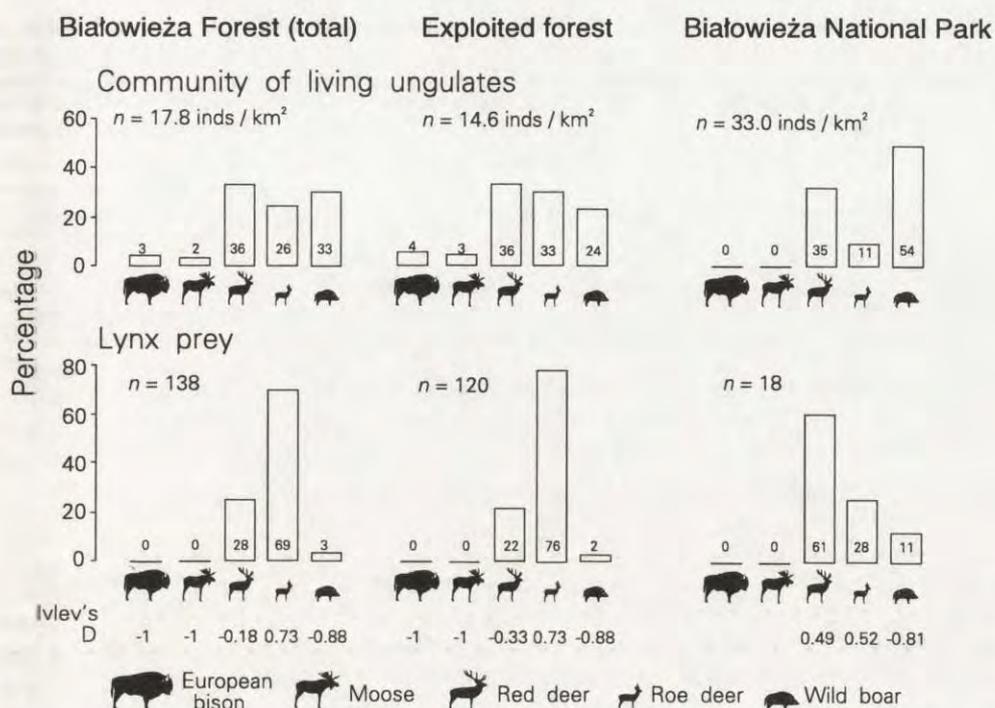


Fig. 1. Species structure of the ungulate community and prey of lynx in the entire, exploited, and pristine portions of Białowieża Primeval Forest.  $n$  – upper panel: mean number of all ungulates per  $\text{km}^2$  (taken as 100% in each graph); lower panel: number of lynx prey found (taken as 100% in each graph). D – Ivlev's selectivity index.

roe deer and wild boar were responsible for this difference ( $G = 11.51$ ,  $df = 1$ ,  $p < 0.001$  in roe deer;  $G = 11.8$ ,  $df = 1$ ,  $p < 0.001$  in boar) (Fig. 1).

#### Autumn and winter diet of lynx

The most important prey found in lynx scats was *Cervidae*, followed by brown hare *Lepus europaeus* (Table 1). Wild boar was only 2% of food biomass eaten by lynx. Hare was a significantly higher portion of lynx diet in exploited forests than in BNP ( $G = 5.64$ ,  $df = 1$ ,  $p < 0.025$ ,  $G$ -test for % biomass). It was mainly the higher proportion of hare that made the food niche of lynx wider in the exploited forest than in the pristine forest (Table 1).

In 8 (14%) of 57 analysed scats, plant material from stomachs of cervids was detected and constituted from 1 to 93% of dry weight of all food remains (20.4% on average,  $SD = 33.7$ ). For all 57 scats, the mean value was 3%.

#### Analysis of ungulates killed by lynx

Among 138 ungulates killed by lynx, roe deer predominated (69%), followed by red deer (28%) (Fig. 1). Wild boar formed 3% of ungulate prey, and neither bison

Table 1. Autumn and winter diet of lynx in exploited, pristine, and the entire forest of Białowieża as determined by scat analysis. Data pooled for 1985 – 1992. *n* – number of scats. %O – percent occurrence in scats, %B – percent of mean biomass consumed per scat. + – traces (< 0.05). B – niche breadth calculated according to Levins (1968). For calculation of niche breadth, *Cervidae* were partitioned into roe and red deer classes proportionally to their shares in the carcasses of cervids killed by lynx in the respective parts of Białowieża Forest (Fig. 1).

Food item	Entire Białowieża Primeval Forest <i>n</i> = 57		Exploited forest <i>n</i> = 21		Pristine forest of BNP <i>n</i> = 36	
	%O	%B	%O	%B	%O	%B
<i>Cervidae</i>	84.2	87.0	80.9	78.8	86.1	89.1
<i>Sus scrofa</i>	5.3	2.0	–	–	8.3	2.5
<i>Lepus europaeus</i>	17.5	10.9	28.6	20.9	11.1	8.3
<i>Canidae</i>	1.8	+	4.8	0.1	–	–
<i>Sciurus vulgaris</i>	1.8	+	4.8	+	–	–
<i>Micromammalia</i>	5.3	0.1	4.8	0.1	5.6	+
of this:						
<i>Microtus</i> sp.	1.8	+	–	–	2.8	0.1
<i>Clethrionomys glareolus</i>	1.8	+	4.8	0.1	–	–
<i>Soricidae</i>	1.8	+	–	–	2.8	+
Birds	1.8	+	–	–	2.8	+
Mean biomass consumed per scat (g)	469.6		269.4		586.5	
B (niche breadth)	2.5		2.8		1.5	

nor moose were recorded as lynx prey. Although the number of ungulate prey found in BNP was small, their species structure differed from those found in the exploited forest ( $G = 48.9$ ,  $df = 2$ ,  $p < 0.001$ ) (Fig. 1). Ivlev's selectivity indices showed that the roe deer was the most preferred ungulate in both exploited and pristine forests (Fig. 1). In BNP, where roe deer density was lower, lynxes also killed red deer more often than expected based on their occurrence in the community. Wild boar was consistently avoided (Fig. 1).

Table 2. Sex and age structure of roe and red deer populations inhabiting Białowieża Primeval Forest (data from drive census, sex and age of 269 roe deer and 297 red deer identified visually) and those killed by lynx (carcasses of 94 roe deer and 36 red deer). D – Ivlev's selectivity index.

Parameter	Roe deer			Red deer		
	Juvenile	Adult female	Adult male	Juvenile	Adult female	Adult male
Population (%)	29	46	25	27	46	27
Lynx prey (%)	26	57	17	64	36	0
D	–0.08	0.22	–0.23	0.66	–0.20	–1

No significant difference ( $G = 2.87$ ,  $df = 2$ ,  $p > 0.1$ ) was observed between the sex and age structure of roe deer killed by lynx and that of the living population. However, the sex and age structure of red deer killed by lynx differed greatly from that of the living population ( $G = 54.14$ ,  $df = 2$ ,  $p < 0.001$ ). Lynx selected juvenile red deer for their prey and completely avoided adult stags (Table 2).

Of 15 jaws from roe deer killed by lynx and collected during snow and radiotracking, 4 were juveniles (< 1 year), 2 were 1–2 yrs old, 4 were 2–3 yrs, 1 was 3–4 yrs, 1 was 4–5 yrs, 1 was 7–8 yrs, 1 was 9–10 yrs, and 1 was > 10 yrs old. Among 9 red deer jaws, 3 were juveniles, 1 was 1–2 yrs old, 3 were 2–3 yrs old, 1 was 3–4 yrs, and 1 was 5 yrs old. The 2 wild boar killed by lynx that were aged were both adults.

During radiotracking of lynxes and on lynx trails on snow, the following non-ungulate prey were found: 4 hares, a pine marten *Martes martes*, a hazel hen *Tetrastes bonasia*, and a great spotted woodpecker *Dendrocopos major*.

#### Foraging behaviour of lynx

Data on searching and hunting behaviour of lynx (recorded by snowtracking) were recalculated per 10 km of lynx trail which approximates the daily route of lynx (Goszczyński 1986). When moving through the mature, pristine forests, lynx very often used fallen trees and their root plates (Table 3). These natural features helped lynx remain partly concealed while stalking prey. The root plates of uprooted trees (mainly spruce) were also used as marking posts. Frequent walking on fallen logs (Table 3) widened the lynx's field of vision for spotting prey. When not hunting, lynx moved on forest paths and frozen streams that made walking in snow less strenuous. The estimated daily hunting effort included 1 failed attack on ungulate prey, 2 failed attacks on medium-sized prey, 6 attacks on small rodents, and twice feeding on a previously killed deer (Table 3).

During the search for carcasses of ungulates killed by lynx, the place of kill was exactly determined in 31 cases. In 21 of those (68%), the lynx moved the carcass from 2 to 75 m ( $\bar{x} = 14$  m,  $SD = 18.1$ ) from the kill site. Roe deer were moved significantly more often (17 of 21) than red deer (3 of 10) ( $G = 7.7$ ,  $df = 1$ ,  $p < 0.01$ ). An adult wild boar was moved 8 m from the kill site. The carcass was usually moved to dense vegetation (12 cases) or under a fallen log (3). In addition, the lynx frequently covered the carcass with soil, leaves, moss, deer hair or snow (21 cases of 31) to protect it from scavengers. Normally, lynxes fed on an ungulate prey for several consecutive days (Table 4). Although roe deer were much smaller than red deer, the time lynx spent utilizing their carcasses did not significantly differ ( $U_s = 60$ ,  $p > 0.1$ , Mann-Whitney  $U$ -test).

Snowtracking made it possible to record scavenging by other animals at lynx kills. Sixteen (80%) of 20 carcasses were fed upon by 1 to 5 species of scavengers (2 on average). The most common scavenger was wild boar (8×, 40% of prey). Wild boar was the only species that was able to appropriate a fresh kill from lynx and

Table 3. Lynx hunting behaviour and activities associated with modes of searching for prey as revealed by 25874 m of snowtracking of individual lynxes in BNP in 1986 – 1989. Figures in parentheses indicate unsuccessful attacks. <sup>a</sup> lynx stalked a group of deer by staying hidden behind fallen trees and attacked by jumps over fallen logs; <sup>b</sup> lynx attacked a roe deer lying (sleeping?) on the ground and chased it 30 m before giving up; <sup>c</sup> both raccoon dogs escaped into a cavity at the bottom of tree; <sup>d</sup> both attacks at trees, squirrels escaped up the tree; <sup>e</sup> attacks on rodents by scratching through snow; <sup>f</sup> in one case, 2 lynxes fed on a female red deer on 6 consecutive days; in another case, 2 lynxes returned to the female red deer.

Activity	Number (n/10 km of trail)	Length (m/10 km of trail)	Total n of prey
Modes of movement and area searching			
Walking along a fallen tree	40	126	
Crouching under a fallen tree	68	88	
Close approaching the root plate of uprooted tree	75		
Walking on a fallen log	185	274	
Climbing the root plate of uprooted tree	3		
Following a forest path		1681	
Following frozen stream		58	
Moving with another lynx		651	
Searching for prey			
Inspecting: wild boar lair	1.2		
red fox den	0.4		
raccoon dog den	1.6		
Following: ungulate trail	42.0	710	
hare trail	1.0	44	
Attacks and feeding			
Attacks on: red deer	0.4		1(1) <sup>a</sup>
roe deer	0.4		1(1) <sup>b</sup>
raccoon dog	0.8		2(2) <sup>c</sup>
red squirrel	0.8		2(2) <sup>d</sup>
woodpecker	0.4		1
small rodent	6.0		15(?) <sup>e</sup>
Feeding on previously killed red deer	2.0		2 <sup>f</sup>

Table 4. Number of consecutive days lynx returned to ungulate kills and fed. \* – kills appropriated by a group of wild boar.

Prey species	Number of prey at which lynx spent:						Mean (SD)
	1	2	3	4	5	6 day(s)	
Roe deer (n = 15)	1*	5	4	2	2	1	3.1 (1.4)
Red deer (n = 6)	1*	–	1*	1	2	1	4.0 (1.8)

consume it completely (Table 4). Other scavengers were: *Vulpes vulpes* (7×), *Corvus corax* (7×), *Nyctereutes procyonoides* (4×), *Martes martes* (3×), *Garrulus glandarius* (3×), *Canis lupus* (3×), and *Meles meles* (1×).

**Importance of lynx predation in the ungulate mortality**

Three causes of natural mortality of ungulates were distinguished: lynx predation, wolf predation, and non-predatory factors (undernutrition and/or disease).

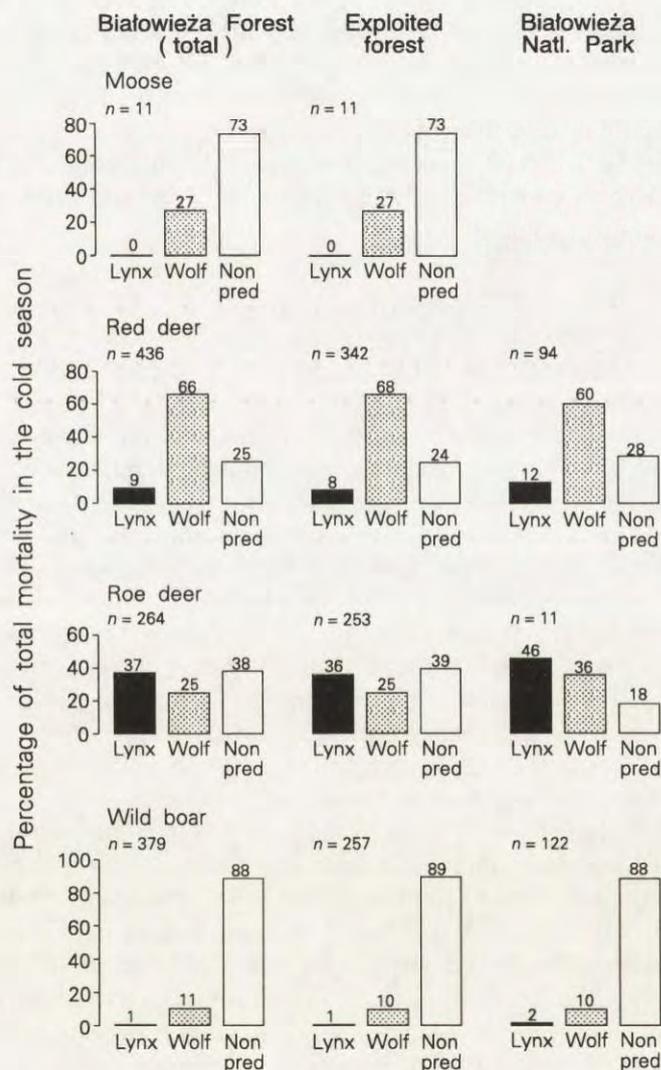


Fig. 2. Percent contributions of lynx and wolf predation and non-predatory causes to the total known natural mortality of four species of ungulates in Białowieża Primeval Forest during cold seasons of 1985 – 1992. n – total number of carcasses found (taken as 100% in each graph).

The effects of these factors on four species of ungulates (moose, red and roe deer, wild boar) in Białowieża Primeval Forest were highly heterogeneous ( $G = 172.16$ ,  $df = 6$ ,  $p < 0.001$ ) (Fig. 2). Lynx predation varied significantly among ungulate species ( $G = 75.16$ ,  $df = 3$ ,  $p < 0.001$ ); it was most important in roe deer mortality, less so in red deer, negligible for wild boar and none for moose.

The role of lynx predation in the ungulate community was different than that of wolf ( $G = 58.73$ ,  $df = 3$ ,  $p < 0.001$ ). Wolf predation occurred more equally on all species but was most important in red deer and moose mortality (Fig. 2). Deaths from non-predatory causes and lynx predation also differed greatly among various species of ungulates ( $G = 95.8$ ,  $df = 3$ ,  $p < 0.001$ ). Wild boar and moose suffered most from nonpredator-caused mortality (Fig. 2). Non-predatory factors were most important in roe deer mortality in exploited forests, whereas lynx predation was most important in BNP ( $G = 11.14$ ,  $df = 2$ ,  $p < 0.005$ ) (Fig. 2). There were no significant differences in mortality factors in red deer and wild boar inhabiting pristine forests and exploited forests.

## Discussion

### Lynx in Białowieża Primeval Forest

In the virgin deciduous forests of Białowieża National Park, the lynx availed itself of the specific structure of dense, pristine woodland to stalk ungulates and it relied primarily on red deer and, to a lesser extent, roe deer. We believe that lynx foraging described from BNP represented its ancestral habits in undisturbed forests of central European lowlands. The large-scale exploitation of timber that has occurred in Białowieża since 1915, has led to (1) 'thinning' and 'opening' of forest structure (open clearcuts, young-age classes interspersed with mature stands), and (2) significant 'borealisation' of species composition (fast growing spruce and pine in place of potentially dominant oak-lime-hornbeam stands). These man-made alterations to forest habitats, typical of the recent history of most European woodlands, were followed by changes in animal communities. The densities of wild boar and red deer (species indicative of mature deciduous forests) were lower in exploited forest than in pristine forest of Białowieża. By contrast, the roe deer, an ungulate inhabiting boreal and nemoral forests as well as forest-field mosaic and farmlands (Heptner *et al.* 1961, Pielowski 1988), increased in absolute density and also relative to other ungulates in exploited forest. Brown hare, which prefer open areas (Bresiński and Chlewski 1976), were also more numerous in exploited forest than in pristine forest. Snowtracking on transects in 1986/87 through 1988/89 (W. Jędrzejewski, unpubl.) yielded about 10 times as many hare tracks along the edge of forest and open meadows as deep in the forests of BNP. Therefore, the more intense consumption of roe deer and hare by lynx in the exploited than in the pristine forest coincided with differences in prey abundance in the two parts of Białowieża Primeval Forest.

Although capable of seizing ungulates as big as adult female red deer and wild boar, the lynx specialised on hunting the smallest ungulates available. We think that two factors were conducive to such preferences: (1) small body size and the solitary hunting style of the lynx, and (2) competition with scavengers and wolves. Young lynxes beginning their independent life weighed about 10 kg, whereas the largest adult male was 24 kg (authors' unpubl. data). To such "small" large predators, roe deer (newborns 1.6 kg, adults ca 20 kg, Pielowski 1988) and red deer fawns (newborns ca 6.5 kg, 1-year-olds ca 80 kg, Dzieciolowski 1969, Staines 1991) were the easiest prey to kill.

Competition with scavengers, which fed on lynx kills or even appropriated them, appeared to be intense in Białowieża. According to Haglund (1966), a normal meal for lynx consists of about 2 kg of meat, so a large carcass (e.g. red deer) would provide this predator with food for many days, especially during the cold season, when meat remains unspoiled for long periods. We documented, however, that after having killed a red deer (3 – 5 times heavier than roe deer), the lynx was able to secure and utilize it only 1.3 times longer (Table 4) than the roe deer carcass. Red deer were more difficult for lynx to drag and hide. Therefore, scavengers, mainly wild boar (and in summer fast decay of meat), made the lynx's hunting for large ungulates unrewarding in comparison to hunting smaller prey (cf Pulliainen 1981).

Competition with wolves, which in Białowieża specialised on red deer (Jędrzejewski *et al.* 1992), might also contribute to lynx shifting to smaller prey. In the pristine forests of BNP, where roe deer and hare were rare, the food niches of wolf and lynx overlapped almost completely (Pianka's index 0.99, calculated for scat content; acc. to Pianka 1973; data on wolf diet from Jędrzejewski *et al.* 1992; proportion of red to roe deer in lynx scats assumed to be the same as among lynx kills). In the exploited forests, this dietary overlap (ungulate prey only) was lower (0.5), and in the whole Białowieża Forest it approached 0.6. Thus, potentially, competition between lynx and wolf is strong and lynx, as the smaller predator, may try to avoid competition whenever smaller ungulates are available.

We did not estimate the role of lynx in regulating ungulate numbers. Nonetheless, the 37% contribution of lynx predation to the natural mortality of roe deer suggests potentially significant impact of lynx on population dynamics and density of this species.

#### Lynx in the Palaearctic region

Numerous studies conducted in the Palaearctic region reported ungulates and hare as the most important prey to lynx. Their relative contributions to lynx diet were determined by latitude (Fig. 3): the share of hare was highest in the north, declining towards the south, whereas the opposite trend was observed in ungulate occurrence in lynx diet. From 52 – 54°N southward ungulates began to be dominant in the lynx diet. Semi-domestic reindeer *Rangifer tarandus* were the most

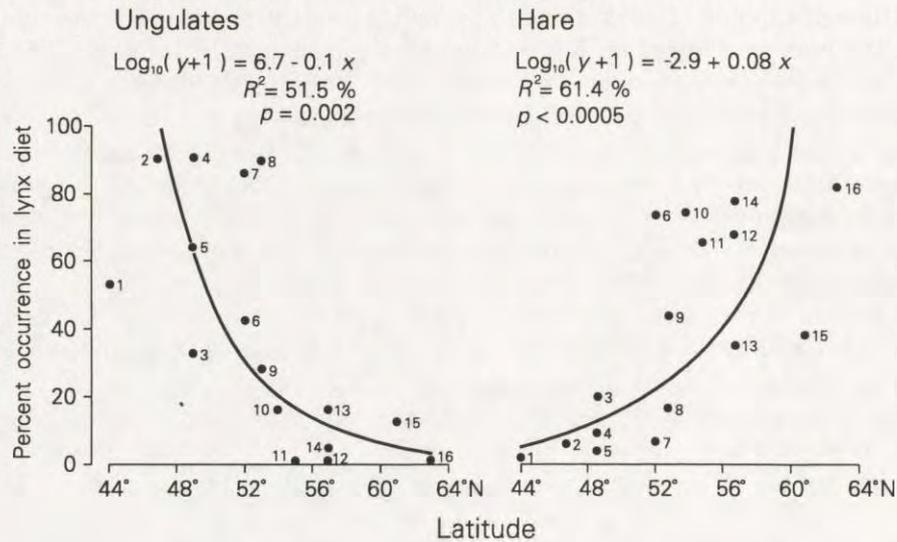


Fig. 3. Relationships between the latitude and the occurrence of wild ungulates and hare in lynx stomachs, scats or among prey remains in Palaearctic. Data sources: (1) Caucasian reserve (Kotov 1958), (2) Northern Alps (Breitenmoser and Haller 1987b), (3) Carpathian Mts (Lindemann 1956), (4) W Carpathians, Slovakia (Hell 1978), (5) Bavarian Forest (Hucht-Ciorga 1988), (6) Western Zabaykal'e (Smirnov 1978), (7) NW Altay Mts (Dul'keit 1953), (8) Western Białowieża Primeval Forest (this paper), (9) Eastern Białowieża Primeval Forest, Belarus (Nikitenko and Kozlo 1965), (10) Il'men reserve, S Urals (Davydov 1979), (11) Tatar SSR (Popov 1952), (12) Tomsk region, W Siberia (Šubin 1967), (13) Central Urals (Malafeev *et al.* 1986), (14) Central-Forest reserve, Volga-Western Dvina watershed (Želtuhin 1979), (15) Karelia, St. Petersburg, Pskov and Novgorod regions, NW Russia (Danilov *et al.* 1979), (16) SE Finland (Pulliainen and Hyypia 1975).

numerous prey of lynx in two northernmost Scandinavian localities (not included in Fig. 3) (Haglund 1966, Birkeland and Myrberger 1980).

Such a geographic pattern of hare and wild ungulates in lynx diet coincides with the north-south gradient of their abundance in woodlands. The blue hare *Lepus timidus* inhabits boreal forests of Europe and Asia down to 53°N in Eastern Europe and 50°N in Western Siberia (Pucek 1984). Further south, the range of the brown hare extends into the zone of mixed and deciduous forests, but in contrast to blue hare, it is an open-habitat animal, living in farmlands and steppes. Its densities in woodlands are very low, so it is not a dependable food to the lynx, strictly a forest predator. The abundance and number of species of ungulates increases from north to south (Heptner *et al.* 1961).

Tetraonid birds (*Tetrastes bonasia*, *Lyrurus tetrax*, and *Tetrao urogallus*) were significant prey of lynx only in boreal and montane forests. They constituted over 20% of lynx prey in NW Russia (Danilov *et al.* 1979) and the Central Urals (Malafeev *et al.* 1986), and 14–16% in Sweden (Haglund 1966), the S Urals (Davydov 1979), and the Carpathian Mts (Lindemann 1956). The maximum share of these

birds in lynx diet (50% occurrence in scats) was reported from a boreal forest in western Siberia (Šubin 1967).

Thus, in the zone of mixed and deciduous forests of the Palaearctic region, the lynx (adult body mass 16 – 34 kg, Pucek 1984) primarily hunts ungulates. This distinctly differentiates *L. lynx* from *L. canadensis* (adult body mass 5 – 17 kg, Saunders 1963), which feeds almost exclusively on snowshoe hare *Lepus americanus* throughout its range (review: Quinn and Parker 1987). Also, the Spanish lynx *L. pardina* (smaller than *L. lynx*) relies primarily on rabbits *Oryctolagus cuniculus* (Delibes 1980).

Studies done in six other localities in the Palaearctic region also compared the choice of ungulate prey by lynx with the species structure of the ungulate community (Table 5). Lynx coexisted with 10 species of ungulates ranging in adult body mass from 15 kg (Siberian musk deer) to 920 kg (male European bison). It preyed on all but bison, and in each place the smallest ungulate was highly selected (Table 5). Mean selectivity index negatively correlated with  $\log_{10}$  body mass of ungulates: Kendall's tau =  $-0.889$ ,  $p < 0.01$  (body masses as in Table 5; middle values between min and max were used for calculation).

Roe deer, the most preferred ungulate prey of the lynx, has a vast geographical range covering the zone of nemoral and southern boreal forests from the Atlantic shore in Europe to the Sea of Japan (with a break in the Volga river plain) (Heptner *et al.* 1961). It was also the most common ungulate prey for the lynx in that zone (references in Table 5, and Dul'keit 1953, Nikitenko and Kozlo 1965, Smirnov 1978, Malafeev *et al.* 1986, Breitenmoser and Haller 1987b, Hucht-Ciorga 1988, localities listed in Fig. 3; and the Stolby Reserve in Krasnoyarsk region: Zyrjanov 1979; Angara river region: Elskij and Šišikin 1979). In montane forests of Europe, the chamois contributed considerably to lynx prey (Kotov 1958, Breitenmoser and Haller 1987b). In eastern Siberia (east of Yenisey river), Siberian musk deer, the range of which stretches over boreal and nemoral forests of eastern Asia (Heptner *et al.* 1961), was an important prey for the lynx (Zyrjanov 1979, Filonov 1989).

Despite the lynx's obvious preference for the smallest ungulate in the community, larger species of ungulates are regularly reported in its diet. Of those, however, invariably a strong selection for young is documented. In the Belarussian part of Białowieża Forest, Šostak and Bunevič (1986) determined sex and age of 29 red deer killed by lynx. Twenty (69%) were < 1 year, 3 were adult males and 6 were adult females. In the Polish Carpathian Mts, Okarma (1984) also found a strong selection for young red deer in lynx hunting. Moose killed by lynx (Danilov *et al.* 1979, Birkeland and Myrberget 1980, Malafeev *et al.* 1986, Filonov 1989) were young or sick individuals. Rakov (1970) reported that all wild boar (14) killed by lynx in the basin of Amur river were < 1 year.

#### Role of lynx in ungulate mortality

Game management in exploited and protected woodlands of Central Europe and the former Soviet Union has included a continuous registration of dead

Table 5. Selection of prey by lynx from the living community of ungulates in 7 localities in Palaeartic. L – percent share of each ungulate species in the community, K – percent share in the total number of ungulates killed by lynx,  $n$  – number of lynx prey found. Body masses (kg, given under each species name) are min weight of adult female and max weight of adult male (after Heptner *et al.* 1961, Kotov 1966, Dzieciolowski 1969, Pucek 1984, Krasńska 1988, Pielowski 1988). <sup>a</sup> *Capra caucasica*, <sup>b</sup> *Capra sibirica*. D – Ivlev's selectivity index, calculated as mean for indices of all localities. Data from: this paper (Białowieża, Poland), Kerečun 1979 (E Carpathian Mts, Ukraine), Filonov 1989 (Altay Mts, Bashkir, Il'men, Mordovian and Caucasian reserves, Russia), and Kotov 1958 (Caucasian reserve).

Locality		<i>Bison</i>		<i>Alces</i>		<i>Sus</i>		<i>Cervus</i>		<i>Capra</i>		<i>Cervus</i>		<i>Rupicapra</i>		<i>Capreolus</i>		<i>Moschus</i>	
		<i>bonasus</i>	<i>alces</i>	<i>scrofa</i>	<i>elaphus</i>	sp.	<i>nippon</i>	<i>capreolus</i>	<i>capreolus</i>	<i>capreolus</i>	<i>moschiferus</i>								
		300 – 920	195 – 382	85 – 320	80 – 224	30 – 155	25 – 131	25 – 36	17 – 26	15 – 17									
Białowieża $n = 138$	L	3	2	33	36	–	–	–	26	–									
	K	0	0	3	28	–	–	–	69	–									
Carpathian Mts $n = 149$	L	–	–	24	21	–	–	–	55	–									
	K	–	–	5	31	–	–	–	64	–									
Caucasian Res. $n = 73$	L	5	–	9	15	48 <sup>a</sup>	–	22	1	–									
	K	0	–	8	16	36	–	33	7	–									
Mordovian Res. $n = 17$	L	–	45	8	13	–	34	–	–	–									
	K	–	0	0	0	–	100	–	–	–									
Bashkir Res. $n = 19$	L	–	53	1	41	–	–	–	5	–									
	K	–	6	0	68	–	–	–	26	–									
Il'men Res. $n = 221$	L	–	5	1	–	–	4	–	90	–									
	K	–	0	0	–	–	1	–	99	–									
Altay Mts Res. $n = 85$	L	–	4	9	69	8 <sup>b</sup>	–	–	5	5									
	K	–	0	0	15	0	–	–	68	17									
D mean		–1	–0.98	–0.81	–0.20	–0.62	0.20	0.27	0.71	0.59									
(SD)		(0)	(0.05)	(0.35)	(0.61)	(0.54)	(1.14)	–	(0.25)	–									

ungulates by game wardens, by use of the same basic methods over decades [e.g. data analysed by Filonov (1989) dates back to the 1930s] and – in exceptional cases, such as European bison in Białowieża Primeval Forest – since the beginning of the 19th century (Karcev 1903, Krasinski 1967). We reviewed these sources to examine the role of predation, especially that by lynx, in the natural mortality of European bison, moose, red deer, roe deer, and wild boar.

The majority of roe deer and red deer deaths were due to predation in all locations (Table 6). Moose died from non-predatory factors nearly as often as from predation, and in wild boar an average of only 25% of deaths were caused by predators. Predation played a negligible role in European bison mortality. This fact is only partially explained by special protection measures undertaken to restore the bison in a few European woodlands. The data from 1809 – 1902 showed that in Białowieża Primeval Forest only 15% of bison deaths were caused by predation (685 carcasses examined), although the abundance of wolves, presence of brown bear and temporary extinction of red deer then facilitated predation on bison (Karcev 1903).

In bovine and cervid ungulates, the percent contribution of predation to total mortality decreased with increasing body mass of the ungulate:  $Y = 96.5 - 0.15$  (Body mass),  $n = 4$  species,  $R^2 = 97\%$ ,  $p = 0.017$  (body masses as in Table 5; middle values between min and max were used for calculation). In wild boar, the role of

Table 6. Predation as a percentage of the natural mortality of ungulates in woodlands of Palaearctic. Only localities of sympatric occurrence of lynx and wolf are included. Non-predatory mortality factors included disease, starvation, and traumas. Figures in parentheses are total numbers of examined carcasses. Sources: this paper (Białowieża Primeval Forest, Poland), Rakov 1970 (Amur river region, Russia), Okarma 1984 (W Carpathian Mts, Poland), Filonov 1989 (Berezina river reserve, Belarus; Darvinskii, Il'men, Mordovian, Oka river, Pechora-Ilych rivers, Bashkir, Altay Mts, Stolby and Caucasian reserves, Russia).

Locality	European bison	Moose	Red deer	Roe deer	Wild boar
Białowieża	0	27 (11)	75 (436)	62 (264)	12 (379)
W Carpathian Mts	–	–	96 (47)	–	–
Berezina Res.	–	86 (225)	93 (31)	74 (8)	66 (105)
Darvinskii Res.	–	83 (560)	–	–	10 (51)
Mordovian Res.	–	56 (63)	–	–	0 (8)
Oka Res.	–	76 (245)	–	–	–
Pechora-Ilych Res.	–	54 (325)	–	–	–
Caucasian Res.	2 (82)	–	83 (145)	–	–
Bashkir Res.	–	76 (45)	87 (186)	100 (58)	–
Il'men Res.	–	17 (12)	–	94 (989)	–
Stolby Res.	–	–	46 (227)	–	–
Altay Mts Res.	–	–	78 (318)	97 (30)	–
Amur river	–	–	–	–	36 (834)
Mean percentage	1	59	80	85	25
(SD)	(1.4)	(25.9)	(16.7)	(16.6)	(26.6)

Table 7. Percent contribution of lynx predation to the total predator-caused mortality of ungulates. Figures in parentheses are the total numbers of ungulates killed by predators. Sources: this paper and Karcev 1903 (data from 1809 – 1902 on European bison, Białowieża), Filonov 1989 (Tab. 2.8; Berezina, Oka, Mordovian, Bashkir, Altay Mts, and Il'men reserves), Kerečun 1979 (E Carpathians), Okarma 1984 (W Carpathians), and Rusakov 1979 (NW USSR: Karelia, Murmansk, Novgorod, Pskov, and St. Petersburg regions, Russia).

Locality	European bison	Moose	Red deer	Roe deer	Wild boar
Białowieża	0 (101)	–	12 (326)	59 (163)	9 (44)
W Carpathians	–	–	24 (45)	–	–
E Carpathians	–	–	35 (130)	62 (155)	26 (27)
Berezina Res.	–	1 (196)	0 (28)	–	0 (70)
NW USSR	–	2 (442)	–	33 (37)	–
Oka Res.	–	0 (184)	–	–	–
Mordovian Res.	–	0 (36)	–	–	–
Bashkir Res.	–	3 (33)	8 (163)	9 (58)	–
Il'men Res.	–	–	–	23 (938)	–
Altay Mts Res.	–	–	5 (261)	92 (63)	–
Mean percentage	0	1	14	46	12
(SD)	–	(1.3)	(13.1)	(30.4)	(13.2)

predation was disproportionately small in comparison with other ungulates of similar body size. We think that this results from both strong avoidance of boar by lynx and wolves and high susceptibility of boar to infectious diseases that often decimate their numbers under unfavourable environmental conditions (e.g. Caboń 1958).

In five European species of ungulates, the contribution of lynx to the total predator-caused mortality was related to ungulate body mass (Table 7); it decreased from an average of 46% in roe deer to 0 in bison ( $Y = 91.1 - 34.5 [\log_{10} \text{body mass}]$ ,  $n = 5$ ,  $R^2 = 96\%$ ,  $p = 0.004$ ).

The role of lynx in shaping the densities of ungulates (*sensu* Peek 1980), particularly the roe deer, is unknown. Indirect evidence was presented by Gaross (1979), who concluded that predation was an important factor influencing the number of roe deer in Latvian forests. He compared the densities of roe deer in 107 randomly selected forest administration units in Latvia with the presence and density of lynx and wolf in those forests. In forests with no predators, the mean density of roe deer was 7.8/km<sup>2</sup>. In units with low density of lynx (1 – 2 lynx/100 km<sup>2</sup>) and without wolves, the mean density of roe deer was 4.2/km<sup>2</sup>. Forests with numerous lynx ( $\geq 3/100 \text{ km}^2$ ) supported 2.8 roe deer/km<sup>2</sup>. In forests, where both wolves and lynx were present in low numbers (pooled density 1 – 4/100 km<sup>2</sup>), the mean density of roe deer was 3.6/km<sup>2</sup>. High density of predators ( $\geq 5/100 \text{ km}^2$ ) coincided with the lowest mean density of roe deer (2.1/km<sup>2</sup>) which was only 27% of that in predator-free forests.

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## References

- Birkeland K. H. and Myrberget S. 1980. The diet of the lynx *Lynx lynx* in Norway. *Fauna Norv.*, Ser. A 1: 24 – 28.
- Breitenmoser U. and Haller H. 1987a. The reintroduction of the lynx (*Lynx lynx*): An assessment after 15 years of experience in Switzerland. *Ciconia* 11: 119 – 130.
- Breitenmoser V. and Haller H. 1987b. Zur Nahrungsökologie des Luchses *Lynx lynx* in den schweizerischen Nordalpen. *Z. Säugetierk.* 52: 168 – 191.
- Bresiński W. and Chlewski A. 1976. Tree stands in fields and spatial distribution of hare populations. [In: Ecology and management of European hare populations. Z. Pielowski and Z. Pucek, eds]. Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa: 185 – 193.
- Caboń K. 1958. Das Massensterben von Wildschweinen im Naturstaatspark von Białowieża im Winter 1955/1956. *Acta theriol.* 2: 71 – 82.
- Danilov P. I., Rusakov O. S. and Tumanov I. L. 1979. [Predatory animals of the North-West USSR]. Nauka, Leningrad: 1 – 163. [In Russian]
- Davydov V. G. 1979. [On the food of lynx in the Southern Urals]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. Izd. Nauka, Moskva: 261 – 262. [In Russian]
- Debrot S. 1982. Atlas des poils de Mammifères d'Europe. Peseux, Suisse: 1 – 208.
- Delibes M. 1980. Feeding ecology of the Spanish lynx in the Coto Doñana. *Acta theriol.* 25: 309 – 324.
- Dul'keit G. D. 1953. [Role of lynx and wolverine as predators in the nature of Altay boreal forest]. [In: Transformation of vertebrate fauna of our country. Biotechnological procedures. A. A. Nasimovič, ed]. Izd. Mosk. Obsč. Ispyt. Prirody, Moskva: 147 – 152. [In Russian]
- Dzięciółowski R. 1969. [The weight of our lowland deer]. *Łowiec pol.* 19(1358): 4. [In Polish]
- Dziurdzik B. 1973. Key to the identification of hairs of mammals from Poland. *Acta zool. Crac.* 18: 73 – 91.
- Elskij G. M. and Šišikin A. S. 1979. [Relationships of predatory and herbivorous mammals in places of their winter concentrations in Angara river region]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. Izd. Nauka, Moskva: 265 – 266. [In Russian]
- Faliński J. B. 1986. Vegetation dynamics in temperate lowland primeval forest. Dr W. Junk Publishers, Dordrecht, *Geobotany* 8: 1 – 537.
- Filonov K. P. 1989. Ungulates and large predators in wildlife reserves. Nauka, Moskva. [In Russian]
- Gaross V. Ja. 1979. [Impact of lynx and wolves on the Latvian population of roe deer]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. Izd. Nauka, Moskva: 257 – 261. [In Russian]
- Goszczyński J. 1974. Studies on the food of foxes. *Acta theriol.* 19: 1 – 18.
- Goszczyński J. 1986. Locomotor activity of terrestrial predators and its consequences. *Acta theriol.* 31: 79 – 95.
- Haglund B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. *Viltrevy* 4: 81 – 310.

- Hell P. 1978. Die Situation des Karpatenluchses (*Lynx lynx orientalis*, *natio carpathicus* Krat. et Stoll., 1963) in der Tschechoslowakei. [In: Der Luchs. Erhaltung und Wiedereinbürgerung in Europa. U. Wotschikowsky, ed]. Mammerdorf, Berhard.
- Heptner V. G., Nasimovič A. A. and Bannikov A. G. 1961. [Mammals of the Soviet Union I. Even-toed and odd-toed ungulates]. Gos. Izd. Vysšaja Škola, Moskva: 1 – 776. [In Russian]
- Hucht-Ciorga I. 1988. Studien zur Biologie des Luchses: Jagdverhalten, Beuteausnutzung, innerartliche Kommunikation und an den Spuren fassbare Körpermerkmale. Schr. Arbeitskr. Wildbiol. u. Jagdwiss. Justus-Liebig-Univ. Giesen 19: 1 – 177.
- Jacobs J. 1974. Quantitative measurements of food selection; a modification of the forage ratio and Ivlev's Electivity index. *Oecologia* 14: 413 – 417.
- Jakubiec Z. and Buchalczyk T. 1987. The brown bear in Poland: its history and present numbers. *Acta theriol.* 32: 289 – 306.
- Jędrzejewski W. and Jędrzejewska B. 1993. Predation on rodents in Białowieża primeval forest, Poland. *Ecography* 16: 47 – 64.
- Jędrzejewski W., Jędrzejewska B., Okarma H. and Ruprecht A. L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. *Oecologia* 90: 27 – 36.
- Jędrzejewski W., Jędrzejewska B. and Szymura A. 1989. Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. *Acta theriol.* 32: 337 – 348.
- Karcev G. 1903. [Belovezha Primeval Forest. Its historical description, contemporary game management, and monarchical hunts in the Forest]. A. Marks, St. Petersburg: 1 – 414. [In Russian]
- Kerečun S. F. 1979. [Impact of predators on ungulate numbers in the Carpathian zone]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. Izd. Nauka, Moskva: 43 – 44. [In Russian]
- Kotov V. A. 1958. [Food of lynx in the Caucasian Reserve]. *Tr. Kavkaz. gos. Zapovednika* 4: 214 – 217. [In Russian]
- Kotov V. A. 1966. The size and weight of *Capra caucasica* Guld. *Zool. Ž.* 45: 1229 – 1234. [In Russian with English summary]
- Kraśńska M. 1988. Hybrids of European bison and domestic cattle. *Ossolineum, Prace Habilitacyjne*, Wrocław: 1 – 188. [In Polish with English summary]
- Kraśński Z. 1967. Free living European bison. *Acta theriol.* 12: 391 – 405.
- Kruuk H. 1986. Interactions between *Felidae* and their prey species: a review. [In: Cats of the World. Biology, conservation and management]. National Wildlife Federation, Washington, D.C.: 353 – 374.
- Levins R. 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton: 1 – 120.
- Liberg O. 1982. Correction factors for important prey categories in the diet of domestic cats. *Acta theriol.* 27: 115 – 122.
- Lindemann W. 1956. Der Luchs und seine Bedeutung im Haushalt der Natur. *Kosmos* 52: 187 – 193.
- Lochman J. 1985. [Red deer]. *Statni zemedelske nakladatelstvi, Praha*: 1 – 352. [In Czech]
- Lockie J. D. 1959. The estimation of the food of foxes. *J. Wildl. Manage.* 23: 224 – 227.
- Malafeev Ju. M., Križimskij F. B. and Dobrinskij L. N. 1986. [Analysis of lynx population of the Central Urals]. *Akad. Nauk SSSR, Uralskij Naučnyj Centr, Sverdlovsk*: 1 – 120. [In Russian]
- Milkowski L. 1986. [Wolf and lynx in Białowieża Primeval Forest]. *Łowiec pol.* 1986/10: 18 – 19. [In Polish]
- Nikitenko M. F. and Kozlo P. G. 1965. [Ecological-morphological description of lynx inhabiting Belovezha Primeval Forest]. [In: Ecology of vertebrate animals of Belarus]. A. N. Belarusskoj SSR, Minsk: 56 – 63. [In Russian]
- Okarma H. 1984. The physical condition of red deer falling a prey to the wolf and lynx and harvested in the Carpathian Mountains. *Acta theriol.* 29: 283 – 290.
- Okarma H. 1989. Distribution and numbers of wolves in Poland. *Acta theriol.* 34: 497 – 503.

- Peek J. M. 1980. Natural regulation of ungulates (What constitutes a real wilderness?) *Wildl. Soc. Bull.* 8: 217 – 227.
- Pianka E. R. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4: 53 – 74.
- Pielowski Z. 1988. [Roe deer]. 3rd edn. Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa. [In Polish]
- Pimlott D. 1967. Wolf predation and ungulate populations. *Amer. Zool.* 7: 267 – 278.
- Popov V. A. 1952. [Results of investigation and reconstruction of the fauna of terrestrial vertebrates during 30 years of the TASSR]. *Izd. Kazanskogo filiala A. N. USSR, Ser. biol.* 3: 183 – 206. [In Russian]
- Pucek Z. 1984. [Key to identification of mammals of Poland]. PWN – Polish Scientific Publishers, Warszawa: 1 – 387. [In Polish]
- Pucek Z., Bobek B., Łabudzki L., Miłkowski L., Morow K. and Tomek A. 1975. Estimates of density and number of ungulates. *Pol. ecol. Stud.* 1(2): 121 – 135.
- Pulliaainen E. 1981. Winter diet of *Felis lynx* L. in SW Finland as compared with the nutrition of other northern lynxes. *Z. Säugetierk.* 46: 249 – 259.
- Pulliaainen E. and Hyypia V. 1975. Winter food and feeding habits of lynxes (*Lynx lynx*) in south-eastern Finland. *Suomen Riista* 26: 60 – 63. [In Finnish with English summary]
- Quinn N. W. S. and Parker G. 1987. Lynx. [In: Wild furbearer management and conservation in North America. M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, eds]. *Min. Natural Resources, Ontario*: 683 – 694.
- Rakov N. V. 1970. Causes of mortality of the wild boar and its interrelation with predators in the Amur territory. *Zool. Ž.* 49: 1220 – 1228. [In Russian with English summary]
- Rusakov O. S. 1979. [Predators as a factor in the dynamics of ungulate numbers in the North-West USSR]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. *Izd. Nauka, Moskva*: 61 – 62. [In Russian]
- Saunders J. K. 1963. Movements and activities of the lynx in Newfoundland. *J. Wildl. Manage.* 27: 390 – 400.
- Schonewald-Cox C., Azari R. and Blume S. 1991. Scale, variable density, and conservation planning for mammalian carnivores. *Conserv. Biol.* 5: 491 – 495.
- Skogland T. 1991. What are the effects of predators on large ungulate populations? *Oikos* 61: 401 – 411.
- Smirnov M. N. 1978. [Roe deer in western Zabaikal'e]. *Izd. Nauka, Sibirskoe Otd., Novosibirsk*: 1 – 189. [In Russian]
- Šostak S. V. and Bunevič A. N. 1986. [The impact of lynx on red deer population]. *IV S'ezd Vsesojuznogo Teriologičeskogo Obščestva, Moskva*: Vol. 3, 76 – 77. [In Russian]
- Staines B. W. 1991. Red deer *Cervus elaphus*. [In: The handbook of British mammals. 3rd edn. G. B. Corbet and S. Harris, eds]. *Blackwell Scientific Publ., Oxford*: 492 – 504.
- Šubin N. G. 1967. [Material on ecology of lynx in Western Siberia]. [In: *Problemy ekologii*]. *Tomsk*: 240 – 246. [In Russian]
- Želtuhin A. S. 1979. [Winter food and hunting behaviour of lynx in the Central-Forest reserve]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. *Izd. Nauka, Moskva*: 266 – 267. [In Russian]
- Zyrjanov A. N. 1979. [Lynx and wolverine in the Krasnoyarsk country]. [In: Ecological fundamentals of protection and rational utilisation of predatory mammals. V. E. Sokolov, ed]. *Izd. Nauka, Moskva*: 267 – 269. [In Russian]