

Population dynamics (1869–1994), demography, and home ranges of the lynx in Białowieża Primeval Forest (Poland and Belarus)

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Population dynamics, demography and home ranges of the Eurasian lynx *Lynx lynx* were studied in Białowieża Primeval Forest (BPF, 1250 km²), the best preserved mixed and deciduous forest in the lowlands of Europe, 40% of BPF area belongs to Poland and 60% to the Belarus Republic. Results of radiotelemetry of lynx (1991–1994) were combined with the Polish and Belarussian game departments' inventories of lynx numbers (1946–1994), archival hunting statistics (1869–1989), observations and snowtracking of lynx.

In 1991–1994, 12 lynx were radiocollared. Their home ranges covered from 50 to 246 km² (mean 147 km²), depending largely on the time the lynx was radiotracked. During a given period, i.e. the autumn–winter seasons (1 October–30 April), the home ranges were largest in adult males (90–148 km²), then in adult females (82–108 km²), and smallest in subadult lynxes (39–55 km²). Home ranges overlapped extensively.

In winters 1992/93 and 1993/94, 21 and 29 lynxes, respectively, were recorded by the mapping of radiotracked and snowtracked individuals in the Polish part of BPF. Of them, 40% were 'transborder' individuals utilising both Polish and Belarussian parts of BPF. Winter densities were c. 3 adult lynx 100 km⁻² and 5 lynx 100 km⁻² if kittens were included. Adult males formed, on average, 29% and reproducing females 23% of all lynx. Subadults and kittens constituted, respectively, 12% and 35% of the population. Sex ratio was 1:1. During the first 3 months of kittens' life, on average 3.3 kittens/mother were recorded, only 1.6 young/mother survived till independence. Mortality of kittens was at least 48%, and the rate of mortality was highest during the early stage of kittens' life. Mean annual reproduction rate of lynx population was 0.59. In the protected population, annual mortality rate of subadult and adult lynx was on average 0.37. Poaching was the most important factor contributing 71% to the total annual mortality rate.

During the last 125 years (1869–1994), three periods with relatively low harvest of lynx by man and thus with fairly natural functioning of lynx population, were recorded: before 1875 (density 2–3 lynx 100 km⁻²), in 1920–1959 (4–6 lynx 100 km⁻²) and after 1970 (2–5 lynx 100 km⁻²). The levels of lynx densities were most probably determined by the varying abundance of roe deer *Capreolus capreolus* and red deer *Cervus elaphus* (lynx's main prey) in the ungulate community in BPF. Two periods of near extermination of lynx occurred (1890–1914 and 1960–1970), both caused by deliberate persecution of lynx. As soon as persecution was abandoned, lynx population recovered rapidly, mainly due to immigration from vast continuous forests in the east and north-east.

Review of the long-term data on lynx dynamics in the Palaearctic revealed that in the Far North-East (Yakutia), the 10-year cycles of lynx and the blue hare *Lepus timidus*, its main prey, were recorded. Towards west the cycle period becomes shorter.

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(5–6 years in the Komi region) In the SW regions of the Palaearctic, where lynx relies on ungulates, lynx numbers are more stable but, periodically also more affected by man

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The 200-year population dynamics of the Canadian lynx *Lynx canadensis* in North America has become the classic example of cycles driven by the cyclic abundance of prey, the snowshoe hare *Lepus americanus* (Elton and Nicholson 1942, Quinn and Parker 1987). Eurasian lynx *Lynx lynx*, although much less publicised than its American congeneric, is still more interesting in this respect. In its, originally vast, geographic range covering all types of Palaearctic forests from the northernmost taiga to the steppe woodland, the lynx shows clear latitudinal gradient in its foraging. In the boreal forests, lynx hunt mainly for the blue hare *Lepus timidus*, whereas in the nemoral boreal forests they rely on ungulates (Jędrzejewski et al. 1993). Moreover, the boreal Siberian populations of lynx follow in numbers the 10-year cycles of blue hare (e.g. Tavorovskii et al. 1971). Southern and western populations of lynx hunting for ungulates (mainly the roe deer *Capreolus capreolus*, see Jędrzejewski et al. 1993), do not show multiannual cycles. Instead, in many regions, they are most seriously affected by man hunting policy, predator controls, poaching and availability of forested habitats (e.g. Novikov 1967). Thus, lynx is a good subject for studying the predator population dynamics in the gradient of prey resources changing from clearly cyclic (hare) to relatively stable (ungulates).

Spatial structure of Eurasian lynx populations is poorly known. Data on lynx home range size are scanty and show enormous variation from 10–20 km² (Heptner and Sludskii 1972) to 1862 km² (Breitenmoser and Haller 1993), which seems to question the applicability of a simple territoriality scheme to lynx ecology. In contrast to the well studied Canadian lynx (e.g. Brand and Keith 1979), demography of Eurasian lynx remains unknown.

In this paper, we analysed population dynamics of lynx in Białowieża Primeval Forest located on the Polish–Belarussian border. It is the best preserved temperate lowland forest of its size in Europe. By combining the results of radiotelemetry of lynx (in 1991–1994), with the game departments' inventories of lynx numbers (1946–1994), hunting statistics (from 1869 until 1989 when lynx became protected), observations, snowtracking and all available reports on lynx, we aimed at showing: 1) the spatial structure of lynx population and

size of home ranges, 2) sex and age structure of population, litter size and mortality of lynx, and 3) dynamics of harvest and lynx numbers in 1869–1994. We analysed how man and natural factors had affected the functioning of lynx populations during the last 125 years. Finally, we reviewed the available long-term data on lynx population dynamics from Palaearctic to show the gradient from cyclicality in the parts of lynx range where blue hare dominates its diet, to potential stability (though disturbed by man) in the parts, where lynx relies on ungulates.

The study was part of a long-term research on predator-prey relationships in Białowieża Primeval Forest (e.g. Jędrzejewski et al. 1992, Jędrzejewski and Jędrzejewska 1993, Jędrzejewska et al. 1994). Feeding ecology of lynx and its choice and utilisation of ungulate prey was described in detail by Jędrzejewski et al. (1993).

Study area

Białowieża Primeval Forest (BPF 52°30'–53°N 23°30'–24°15'E) located on the Polish–Belarussian border, is a vast woodland connected continuously with other large forest tracts (Pruzhana Forest in NE, Shershevo Forest in SE, Knyszyn Forest in NW) (Fig. 1). It lies in the boreal nemoral zone, and is composed of rich multispecies tree stands. In its historical borders, BPF covers 1 250 km², but in the recent decades its administrative coverage increased to nearly 1 500 km² due to amencement (in both Polish and Belarussian parts) of peripheral woods and woodlots, mostly of secondary origin.

From the 15th to the end of 18th century, BPF was protected as the royal hunting forest of Polish kings. In the 19th century and until 1914 (under the Russian rule), it became a protected forest for monarchical hunts of the Russian tsars. Industrial scale exploitation of timber in BPF was begun only in 1915 (during World War I) by German occupants. After WW I, Polish state forestry and the English company "The Century European Timber Corporation" continued exploitation. In 1921, the most valuable and nearly untouched oldgrowth (47.5 km²) located in the heart of BPF was proclaimed as Białowieża National Park. The remaining part of BPF underwent economic exploitation of timber until 1941.

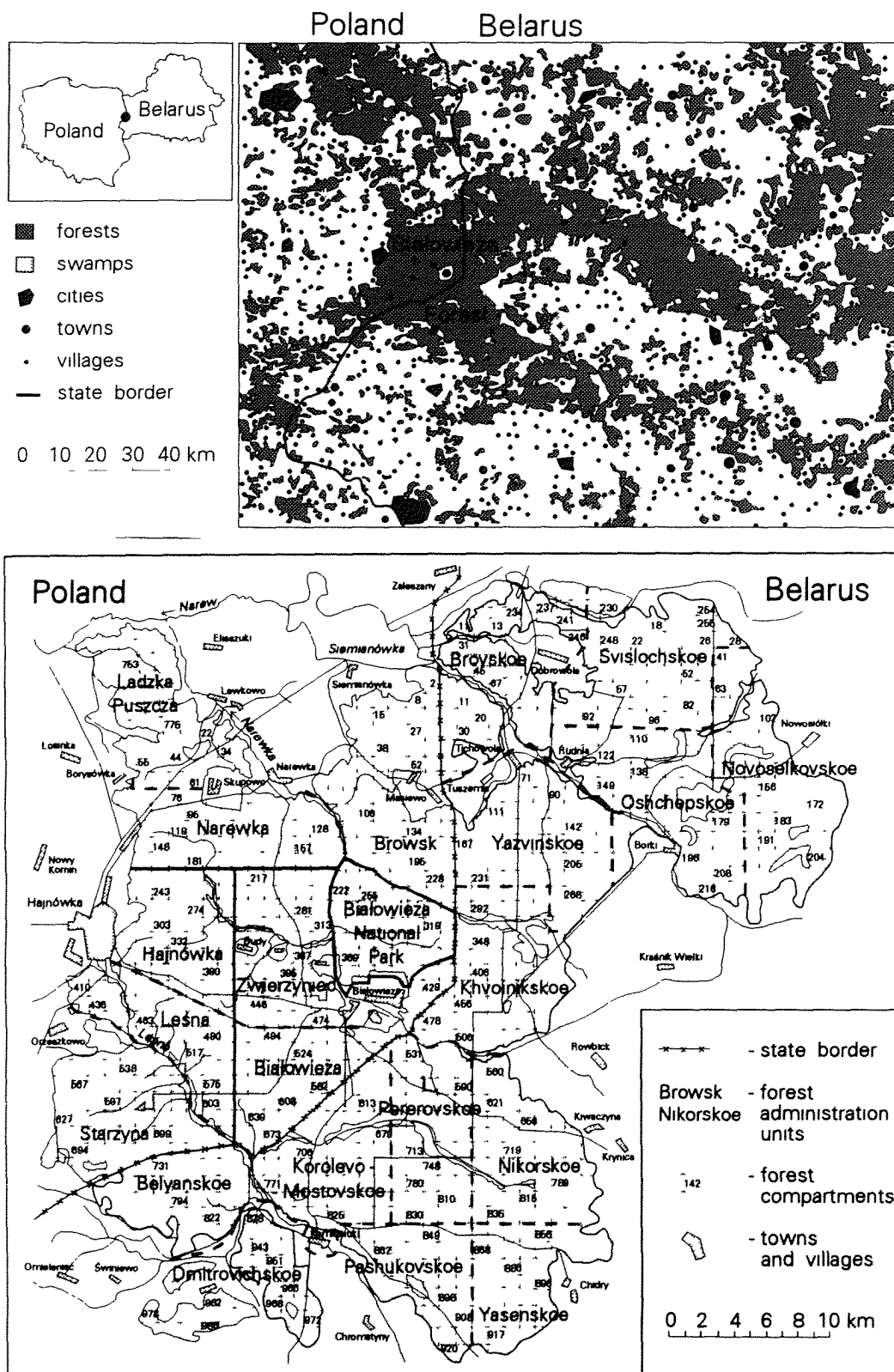


Fig 1 Upper panel Białowieża Primeval Forest among the woodlands of eastern Poland and western Belarus Lower panel schematic map of BPF with division into forest administration units

In 1945 the new state border between Poland and the Soviet Union (Belarussian SSR) divided the BPF into two parts (Fig. 1) with different management rules. In 1981 the Soviets built a 2.5-m high wire fence along the border, and it became a real barrier to ungulate movements. Lynx and wolves can cross the border.

The Polish part of BPF (580 km²) includes Białowieża National Park (BNP, 47.5 km²) and the exploited forests administered by the State Forestry (530 km²). BNP is a strict reservation where no hunting, timber exploitation and motor transportation is allowed. The rich deciduous tree stands dominated by oak *Quercus robur*, lime *Tilia cordata* and hornbeam *Carpinus betulus* cover 48% of the park's area. Mixed coniferous forest dominated by pine *Pinus silvestris* and spruce *Picea abies* (with admixtures of oak) cover 17% and wet alder *Alnus glutinosa* and ash *Fraxinus excelsior* forests – 18%. The average age of tree stands is 130 years. In the 1970's the park became UNESCO's Man & Biosphere Reserve and World Heritage Site.

The exploited forests on the Polish side of the border are managed by means of small clear cuts and selective cutting of large trees, and replantation. Mixed coniferous forests dominated by pine and spruce (with admixtures of oak) cover 54% of the area of exploited forest, alder and ash forests 20%, and oak-lime-hornbeam forests 13%. Mean age of tree stands is 72 yr.

The Belarussian part of BPF (670 km²) has been partially protected since 1945. Cutting is small and selective (dead and dying trees only, no clearcuts). Coniferous forests dominated by pine and mixed coniferous forests composed of pine and spruce (with admixtures of oak) cover 69% of area, oak-lime-hornbeam forests 6%, and wet alder-ash forests 16%. The average age of tree stands is 100 yr. In 1991, the whole Belarussian part of BPF became the State National Park (with some strict reserves and mostly with partial protection regime) and the UNESCO's Man & Biosphere Reserve. More detailed information about vegetation of BPF is given by Falinski (1986).

BPF harbours a rich community of ungulates consisting of European bison *Bison bonasus*, moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, and wild boar *Sus scrofa*. Large predators include lynx and wolf *Canis lupus*. The native brown bear *Ursus arctos* was exterminated in the 2nd half of the 19th century. Few reintroduced bears lived in BPF from 1938 till 1950 (Buchalczyk 1980, Bunevich unpubl.).

History of lynx management in Białowieża Primeval Forest

In BPF, lynx was neither protected nor particularly persecuted until the 2nd half of the 19th century. As elsewhere in the Polish-Lithuanian Commonwealth, it

was valued for its fur and hunted sustainably by the local game wardens Jarocki (1830), after having visited the Forest and talked to the wardens, reported 'The lynx (*Felis lynx*) although appears here quite often, is a transitive rather than native inhabitant of the Forest'. In the 1860's the Russian administration of BPF began the 'modern' game management (Karcov 1903). In 1869 predator control (aimed at extermination of brown bear, wolf and lynx) began and lasted until 1914. In 1869–1876, from 14 to 23 drive hunts against wolves were organized annually, during which all lynx seen were also shot. In 1877–1882 additionally, strychnine balls were laid out in the Forest to poison wolves and lynx (Karcov 1903). Since 1889 bounties were paid for killed predators. First (1889–1890) bounties were rather high (20 rubels for a lynx) then (1891–1895) much lower (3 rubels) which made the predator extermination markedly less effective. In 1896, bounties raised to 10 rubels for a lynx. During that period the salary of forestry administration officer was 203 rubels per year and that of a game warden 93 rubels (Karcov 1903). Complete extermination of wolves and lynx from BPF was difficult because they continuously immigrated from surrounding forests, but the campaign was, nonetheless, effective enough. Karcov reported in 1903 'Game wardens no longer find ungulates mutilated by wolves and lynx'.

Detailed game management reports are not available from 1903–1914 but it is known that extermination of wolves and lynx as a measure of protection and promotion of ungulates was conducted till 1915, when German army invaded Białowieża. During 1915–1918, German administration of BPF focused at fast and large scale exploitation of timber. Game was practically not protected and poaching (especially by the end of WW I and during the Polish-Soviet war in 1919–1920) was disastrous for ungulates (Jędrzejewska et al. 1994). Beginning from 1915, tracks of lynx and wolves were often seen in BPF (Voit 1917). In 1919–1939, the whole BPF was again under the Polish rule. The Forest became a place of diplomatic hunts for the Polish president invited politicians and monarchs (Więcko 1984). Lynx were valued trophies of the hunts. In 1939–1941 BPF passed under the Soviet rule, and in 1941–1944, it was established the 'Reichjagdgebiet' by the Nazi occupants. By the end of World War II, the numbers of wolves and lynx were very high.

After 1945, when the new Polish-Soviet border divided BPF, game management rules were different in each part. In the Belarussian part, from 1946 till 1955, lynx was a subject of sustainable hunting harvest. In 1956–1980, it was treated as pest but the deliberate persecution occurred in 1956–1967 only, mainly by drive hunts like those in the second half of the 19th century. In 1981–1992, lynx was a subject to occasional sport hunts. In 1993, it was included into Red Data Book of the Republic of Belarus as a rare species.

(Chyrvonaya Kniga Respubliki Belarus 1993) In the Polish part of BPF, the lynx was fully protected in 1946–1953, hunted (under a licence system) in rather small numbers in 1954–1988, and again protected since 1989

Methods and material

Radiotracking

From February 1991 through March 1994, in the Polish part of BPF, 12 lynxes were captured with spring-powered footsnare traps at fresh kills or marking places (12 captures, including 2 recaptures to change collars) and in a large double-door box trap (3 captures, including 1 recapture). All traps had radio alarm systems that signalled the capture of an animal and shortened the time lynx spent in a trap to 1–2 h. A captured lynx was immobilized with a 0.4–1.0 ml of Ketamin/Xylazin mixture (583 mg Bayer ‘‘Rompun’’ dissolved in 4 ml Parke-Davis ‘‘Ketavet 100 mg 1 ml’’). (Seal and Kreeger 1987). We determined the sex, age (based on tooth wear), and weight of a lynx, and fitted it with a radiocollar (150–200 g). After handling, the lynx was injected 0.4–1.0 ml of Effortil to help recover the normal heart action. Data on collared lynx are given in Appendix I.

Five to 7 days a week we tried to locate the radio-marked lynxes from the church tower (33 m high) in Białowieża village. The audibility range of signal from the tower was 6–10 km. After getting an approximate position of a lynx we localised it precisely from the ground (signal range 1–3 km). Searching for lynxes not previously located from the tower was conducted by driving the system of forest roads (see map in Fig. 1). In 1991–1993, the radiotracking was done in the Polish part of BPF (few localisations from the Belarussian part made from the church tower are included). In the winter of 1993/94, once a month, a search of radiocollared lynxes was also conducted in the Belarussian part. The terrain of BPF is flat but the dense, not easily accessible forest made our efforts of daily locating of lynxes successful on 19%–50% (on average 41%) of all days the lynxes lived in BPF and wore active collars. In 1993–1994, in addition to daily locations, a continuous 5-day radiotracking (with locations at 30-min intervals) of one randomly chosen lynx was conducted once a month.

For estimating home ranges, all daily localisations of the autumn-winter seasons (1 October–30 April) and the whole periods of radiotracking of each lynx were included. From the series of continuous tracking, one location per day was taken if lynx was more or less stationary, and two extreme localisations if it moved. Home range size was calculated by Minimum Convex Polygon method using a program Tracker (A. Angerbjörn, Sweden). Detailed analysis of home range shape and size variation will be presented elsewhere.

Snowtracking

Snowtracking was a supplementary method of estimating lynx numbers and densities. Snowtracking of individual lynxes was done in the Polish part of BPF, first (1991/92) to locate non-collared lynx for livetrapping. In 1992/93 and 1993/94, all lynx tracks noticed during any field work were recorded. Some trails were followed for few kilometers. The total length of snowtracking of non-collared lynx was 20 km in 1991/92, 90 km in 1992/93 and 230 km in 1993/94. There were c. 75 days with snow cover in 1990/91 and 1993/94 and c. 52 days in 1991/92 and 1992/93.

We visited the central part of BPF more often than peripheral parts. The numbers of lynxes walking together and their marking behaviour were recorded. Size of the foot print and the pace length were assessed visually. Snowtracking of radiocollared lynxes of known sex and age showed that adult males had distinctly larger footprints and a long pace. Moreover, most of the captured lynx were snowtracked before capturing. In all such cases, the sex/age determined by snowtracking proved to be correct when an individual was trapped. Tracks of radiocollared lynxes were distinguished from those of non-collared individuals by radio-localisations done concurrently with snowtracking. Adult females were determined as such when leading young, the number of kittens was also counted during snowtracking. Lonely adult females could be difficult to distinguish from adult males by their tracks. However, adult females with no kittens were obviously very rare (no such females were recorded among captured individuals). For density estimation, all records of radio-tracked and snowtracked lynxes were mapped for each winter, with an attempt to distinguish all individuals present in the Polish part of BPF.

Additionally, we used data on the snowtracking of lynx in Białowieża National Park collected in 1956/57–1961/62 (courtesy of A. Kawecki), and 1985/86–1991/92 (see details in Jędrzejewski and Jędrzejewska 1993). Lynx were surveyed on the grid of transects covering 47.5 km² (entire BNP) in 1956–1962 and 11.2 km² (SW part of BNP) in 1985–1992. The mean index (N tracks km⁻¹ d⁻¹) for the entire study area for each winter was calculated and used for estimating the lynx densities according to the method by Prisklonsky (1965). For detailed description of rationale of Prisklonsky's method see Jędrzejewski and Jędrzejewska (1993).

Long-term dynamics of lynx population – sources of data and methods of inventories

Information on predator control conducted in 1869–1902 was taken from Karcov (1903). Game department documents from 1920–1939 archived by the Polish State Forestry Administration were destroyed by Soviet

managers in 1939. Only few information were derived from the articles on diplomatic hunts published in the foresters' monthly journal (Anonymous 1937a,b, 1938). We are not aware of any German game archives from 1941–1944. Data from 1869–1938 are listed in Appendix II.

In 1946–1994, hunting quotas and lynx number estimates in the Belarussian part of BPF were archived by the Game Management Department of the State National Park Belovezhskaya Pushcha (before 1991: Game Hunting Preserve Belovezhskaya Pushcha). Each winter, the inventories of lynx were done by game wardens. After new snow fall, the snowtracking on all accessible forest compartment lines ($1066 \times 1066 \text{ m} = 1 \times 1 \text{ verst}$) was conducted twice (usually on two consecutive days to get a reliable estimate). Tracks of lynx crossing the lines and their direction were noted. Then, all tracks were mapped and, by drawing the reconstructed routes of lynx movements, the places of lynx daily rest sites were determined (i.e. forest compartments, where a track went into but not out of it). Some of the data on lynx numbers were published by Filonov (1989).

In the Polish part of BPF, data on lynx numbers and hunting quotas were collected and archived by the Game Department of the Białowieża State Forest Administration, but only the archives from 1958–1994 persisted. Some earlier information (1946–1950) were found in the typescript of memoirs (archived at the Library of Białowieża National Park) of the late director of Game Department, Edmund Wagner. In the Polish part of BPF, inventories of lynx (conducted by game wardens) were done by snowtracking.

Because of the political isolation in 1945–1990, there was no exchange of information about predator numbers and hunting policy between the respective Game Departments in the Polish and Belarussian parts of BPF. Thus, the data from the two parts can be treated as independent. All data from 1946–1994 are listed in Appendix III.

Totally, during the 125 years, the estimates of lynx numbers in the whole BPF or part of it, are available for 51 years (41%), and data on lynx hunting statistics for 83 years (66%). Reconstruction of lynx population size was possible for nearly the whole series of 1869–1994, based on regression between number of lynx killed during the years of persecution and estimated numbers of lynx and between independent censuses of lynx in the Polish and Belarussian parts of BPF (see details in Appendices II and III).

Demographic parameters

Information on females with kittens (from snowtracking and visual observations) were gathered by the Belarussian game wardens and scientists during any field work. Available archives of their reports covered years

1947–1951 and 1982–1994. In the Polish part of BPF, data gathered in the same way by State Forest game wardens, wardens of BNP, and zoologists covered years 1957–1959 and 1986–1994. One earlier information (from the 1930's) was derived from a documentary photograph taken of lynx litter by J. J. Karpiński (Anonymous 1937b). Totally, 61 observations (visual observations or snowtracking) of 47 litters were documented (if any litter was observed more than once, the earliest observation and the latest one were taken).

Data about non-harvest mortality of lynx was collected in the Polish part of BPF during radiotracking of lynxes and by autopsies of any dead lynx reported to us by forestry services (full data in Appendix IV). Annual mortality rates were calculated for the radiotracked sample of lynx population in 1991/92–1993/94 according to the method by Heisey and Fuller (1985).

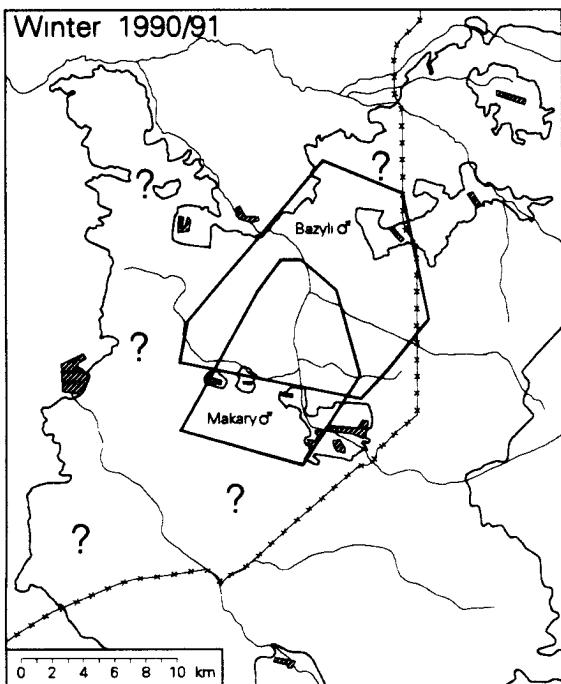
Results

Spatial structure of lynx population in 1990/91–1993/94

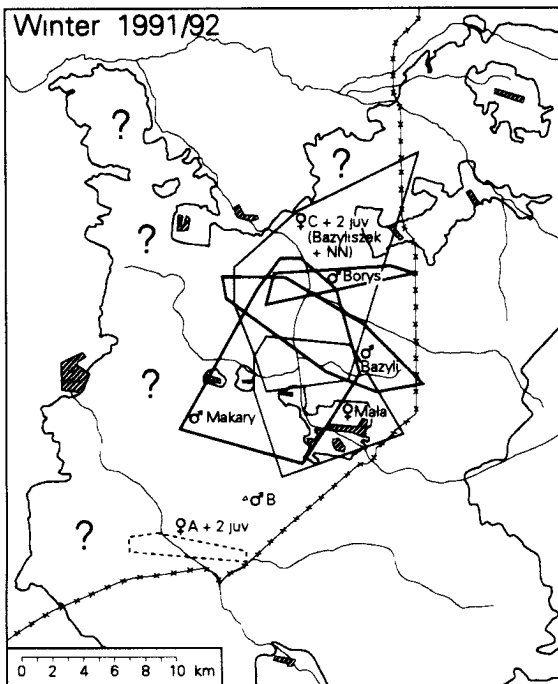
During winter 1990/91, only two adult males were radiotracked, Bazyli and Makary. Their ranges overlapped considerably (Fig. 2).

In winter 1991/92, we captured 3 lynxes. An adult male Borys, trapped north of BNP, most likely visited this area during the mating season only. Later he was recorded mainly in the western part of BPF (Fig. 2). A juvenile male Bazyliszek, captured in early February, stayed with his mother and a sibling till March 21, so we could estimate the home range of his mother. A juvenile female Mała, trapped in December, was probably a daughter of a female that had led 2 kittens and was shot in the Belarussian part of BPF (near the border) in October/November 1991. Makary was not radiotracked during that winter because of collar failure, but tracks of a single male were recorded in his former home range. We interpreted those as Makary's tracks, because in the following year, he was recaptured in the same area. Bazyli was found dead in a snare in late December 1991, and Mała disappeared from the study area by the end of January 1992. Additionally, a male and a female with two kittens were recorded by snowtracking during 1991/92 (Fig. 2).

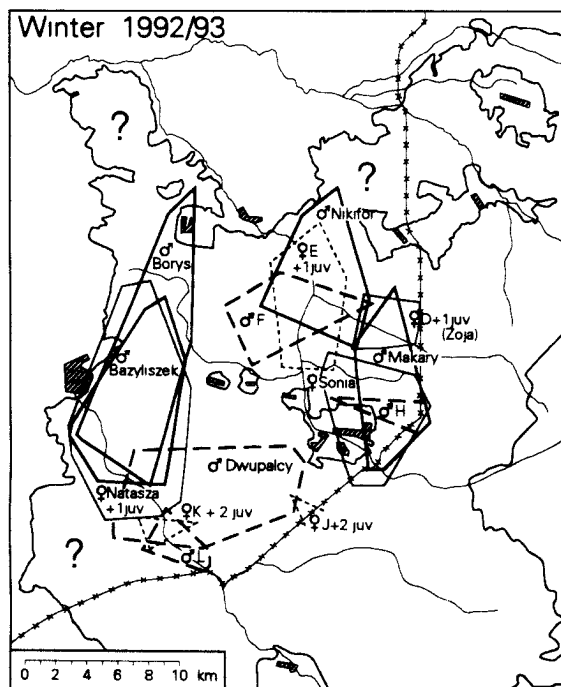
In winter 1992/93, we radiotracked 7 lynxes, including 4 newly captured ones. Adult male Borys and subadult male Bazyliszek had overlapping territories and they were occasionally found close to each other. In December 1992, Borys was poached. After a female Natasza had been radiocollared in February 1993, Bazyliszek was recorded to accompany her several times. Their home ranges overlapped considerably. Makary stayed farther east than in 1990/91 (Fig. 2). He often accompanied females Sonia and D, the latter one



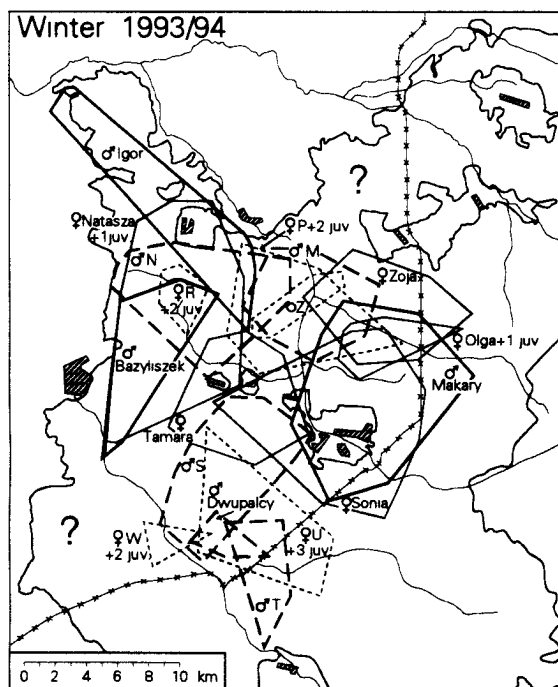
♂ Bazyli 24 Feb - 30 Apr 91
♂ Makary 10 March - 30 Apr 91



♂ Makary 9 March - 30 Apr 91
♂ Bazyli 1 Oct - 23 Dec 91
♂ Borys 8 Feb - 30 Apr 92
♀ Mala 11 Dec 91 - 21 Jan 92
♀ C + 2 juv 9 Dec 91 - 28 March 92
(♂ Bazyli + NN)
♂ B 31 Jan 92
♀ A + 2 juv 21 Jan - 3 Feb 92



♂ Borys 1 Oct - 7 Dec 92
♂ Bazyli 1 Oct 92 - 30 Apr 93
♂ Nikfor 25 Jan - 23 Feb 93
♂ Makary 27 Feb - 30 Apr 93
♀ D + 1 juv 29 Dec 92 - 30 Apr 93
♀ Sonia 12 Jan - 30 Apr 93
♀ Natasza + 1 juv 3 Feb - 30 Apr 93
♂ F 15 Dec 92 - 31 March 93
♂ L 29 Dec 92 - 3 March 93
♂ H 2 Jan 93
♂ Dwupalcy 9 Feb - 30 March 93
♀ E + 1 juv 14 Dec 92 - 3 Feb 93
♀ J + 2 juv 19 Feb 93
♀ K + 2 juv 3 - 30 March 93



♂ Bazyli 1 Oct 93 - 21 Nov 94
♂ Makary 1 Oct 93 - 30 Apr 94
♂ Igor 22 March - 30 Apr 94
♀ Natasza + 1 juv 1 Oct 93 - 28 March 94
♀ Zoja 1 Oct 93 - 30 Apr 94
♀ Sonia 1 Oct 93 - 30 Apr 94
♀ Tamara 17 Nov 93 - 30 Apr 94
♀ Olga + 1 juv 16 Feb - 30 Apr 94
♂ S 12 Nov 93 - 8 March 94
♂ M 16 Nov 93 - 18 March 94
♂ N 16 Nov 93 - 21 March 94
♂ T 4 - 28 March 94
♂ Dwupalcy 7 - 8 March 94
♀ P + 2 juv 1 Nov 93 - 28 March 94
♀ Z 7 Nov 93 - 4 March 94
♀ R + 2 juv 16 Nov 93 - 10 March 94
♀ W + 2 juv 24 Nov 93 - 9 March 94
♀ U + 3 juv 3 Feb - 8 Apr 94

Table 1 Home ranges of lynx in Białowieża Primeval Forest estimated by the Minimum Convex Polygon with 100% localisations. Life-time home range: total area utilised by a lynx during the whole period of radiotracking (dates given in Appendix 1). Winter home ranges: size of area utilised by a given lynx during 1 October–30 April (calculated only for individuals the radiotracking of which during any cold season spread >3 months and included 25 or more localisations). Numbers of localisations in parentheses.

Lynx sex, age at capture, and name	Life-time home range (km ²) (N localisations)	Winter home range size (km ²)			
		1990/91	1991/92	1992/93	1993/94
M, ad, Bazyli	222.2 (152)	148.2 (36)	–	–	–
M, ad, Makary	245.9 (200)	90.3 (25)	–	–	91.2 (68)
F, ad, Mother of Bazyłiszek ¹	99.2 (38)	–	99.2 (38)	–	–
M, subad, Bazyłiszek ²	185.6 (134)	–	–	55.1 (32)	–
M, ad, Borys	239.9 (58)	–	–	–	–
F, subad, Sonia	118.7 (255)	–	–	38.5 (62)	108.4 (131)
F, subad, Zoja	49.7 (54)	–	–	–	47.1 (26)
F, ad, Natasza	158.2 (209)	–	–	82.1 (67)	98.1 (55)
F, subad, Tamara	73.1 (94)	–	–	–	49.0 (41)
M, subad, Igor	76.3 (28)	–	–	–	–

¹ This female was not radiocollared. Her home range was calculated based on radiolocations of her offspring (Bazyłiszek) while it had stayed in a family group.

² Included are only localisations taken after he had become independent.

leading a radiocollared kitten Zoja. Adult male Nikifor was radiotracked for one month (25 Jan–23 Feb) and disappeared. Ten months later he was killed as rabid on a farm yard in Knyszyn Forest, 60 km N from the place of capture. Probably, he came to Białowieża Forest only for the mating season, when he was recorded together with the female E leading a kitten.

By snowtracking, we mapped 4 males and 3 females with kittens. Male H was recorded once, as he came from the Belarusian part (Fig. 2). He was distinguished from Makary by obviously larger tracks and pace length. Another male lacked two toes on his foot print (Dwupalcy = two-toed in Polish). His tracks were often recorded together with the tracks of Natasza and Bazyłiszek (Fig. 2).

In winter 1993/94, 8 lynxes were radiotracked, including 3 newly trapped ones. Makary was found in the same area as in the former winter. He visited females Sonia, Zoja, and a newly captured female Olga with a kitten. Home ranges of subadult Zoja and adult Olga overlapped extensively. Three lynxes were radiotracked in the western part of the Forest (Fig. 2). The range of male Bazyłiszek overlapped that of female Natasza with a kitten. In the end of December 1993, Bazyłiszek was poached. Afterwards, Natasza moved north-east. In March, she was observed without a kitten and was leaving blood on her trail. No prey of her own were found, but she scavenged on prey remains of female R.

with 2 kittens. In late March 1994, we lost contact with Natasza. A subadult male Igor was trapped in the central part of the Forest in late March 1994. Later he moved to the NW part and stayed there. The home range of a subadult female Tamara was located most centrally.

Additionally, snowtracking revealed the presence of 5 males, 4 females with kittens, and one lonely individual with distinctly small tracks (lynx Z in Fig. 2). Male Dwupalcy was recorded on 2 days only, he probably came from the Belarusian part for the mating season.

In winters 1992/93 and 1993/94, 43% and 38% (on average 40%) of all lynxes recorded in the Polish part, respectively, were found either on the state border or in the Belarusian part of the Forest (Fig. 2).

Home range size

For 10 lynxes, Minimum Convex Polygon home ranges estimated for the entire periods of radiotracking covered, on average, 147 km² (SD 73) (Table 1). The average home range of males was 194 km² (SD 70, n = 5) and that of females 100 km² (SD 42, n = 5). However, the size of home range increased with the number of days the lynx wore active collars ($Y = 80.8 + 0.23X$, n = 10, $R^2 = 0.473$, $p = 0.028$). The above given estimates of home range size corresponded to an

Fig. 2 Spatial distribution of lynx in the Polish part of BPF. Solid lines (and all names of lynx except of Dwupalcy) denote radiotracked lynxes (thick lines – males, thin lines – females). Periods of radiotracking (and snowtracking if tracks of a given lynx were recorded prior to capture) given under each map. Minimum Convex Polygon home ranges are plotted for all radiotracked lynxes irrespectively of the numbers of localisations. Broken lines (lynx Dwupalcy and lynxes denoted by letters) denote non-collared individuals recorded by snowtracking (thick lines – males, thin lines – females). Periods of snowtracking given under the maps. Polygons of 'ranges' embraced all tracks that were unambiguously prescribed to a given lynx.

Table 2 Winter densities of lynx in BPF, estimated by various methods (see Fig. 2 for distribution of recorded lynx) MCP – minimum convex polygon. Methods (1) and (2) yielded underestimated measures of density, whereas method (3) is most reliable. In method (3), the numbers of lynx in early winter and late winter (the latter in parentheses) are given.

Method	Winter	N lynx recorded	Area (km ²)	Density (N 100 km ⁻²)
(1) N adult lynx per whole Polish part of BPF	1992/93	14	580	2.4
	1993/94	18	580	3.1
	1992/93	21	580	3.6
	1993/94	29	580	5.0
(2) N adult lynx corrected by transborder lynx per whole Polish part of BPF	1992/93	11	580	1.9
	1993/94	14.5	580	2.5
	1992/93	16.5	580	2.8
	1993/94	23.5	580	4.0
(3) N adult lynx per MCP area utilised by them	1991/92	6 (6)	216.3	2.8 (2.8)
	1992/93	14 (12)	430.7	3.2 (2.8)
	1993/94	18 (16)	562.0	3.2 (2.8)
	1991/92	11 (10)	216.3	5.1 (4.6)
	1992/93	21 (19)	430.7	4.9 (4.4)
	1993/94	29 (27)	562.0	5.2 (4.8)

average of 360 days in males and 215 days in females. The trend of increasing size of home range with longer time of radiotracking occurred both in males and females, but the regressions were not significant due to the small sample sizes (5 male and 5 female ranges).

During the autumn-winter seasons (i.e. equal periods of radiotracking), the ranges were smaller, and their sizes were largely determined by lynx body mass ($Y = -118.1 + 12.0X$, $n = 11$, $R^2 = 0.58$, $p = 0.006$). Adults of both sexes held large ranges, on average 110 km² in males (SD 33, $n = 3$ ranges) and 97 km² in females (SD 33, $n = 3$). Subadults had much smaller ranges, in females on average 45 km² (SD 6, $n = 3$), and in a male 55 km² (one case only) (Table 2). Average autumn-winter home range of all lynx was 82 km² (SD 33).

Winter densities of lynx in 1991–1994

During the four years of livetrapping and radiotracking of lynx, only a part of BPF area was censused and an unknown proportion of lynx population was recorded. Thus, we estimated the density by 3 methods: 1) total number of recorded lynx divided by the whole area of the Polish part of BPF, 2) the number of recorded lynx corrected by the percent of 'transborder' lynxes (i.e. by 20% lower) divided by the whole area of the Polish part of BPF, and 3) total number of recorded lynx divided by the area covered by their home ranges (that area was estimated as Minimum Convex Polygon). In

all three methods, density was calculated first for adult and subadult lynx and then for all lynxes (kittens included) (Table 2).

The densities of adult lynx were from 1.9 to 3.2 lynx 100 km⁻², and those of all lynx (kittens included) from 2.8 to 5.2 inds 100 km⁻² (Table 2). In winter 1993/94, when the study was most intense and covered the largest area, the 3 methods yielded similar density estimates. The most reliable estimate (method 3) gave similar results in all years: 2.8–3.2 adult lynx 100 km⁻² and c. 5 lynx 100 km⁻² including kittens. These are estimates for beginning of each cold season. If all cases of mortality and disappearance are considered, the densities (representative of late winter) were 2.8 adult lynx 100 km⁻² and 4.4–4.8 lynx 100 km⁻² including kittens (Table 2).

By extrapolating the density estimates on the whole BPF, we can assess that during 1992–1994, 1 250 km² harboured 24–35 adult lynx and 35–62 lynx including kittens. In the same years, the inventories by game departments reported 29–44 lynx, if Polish and Belarussian estimates are summed, or 27–41 lynx, if a correction for double-counted transborder lynx is made (i.e. numbers of lynx in the Polish part of BPF lowered by 20%). Therefore, the game departments' estimates are within the range of densities calculated from radiotracking and snowtracking. Both game departments' inventories and radio- and snowtracking showed a 10%–30% increase in adult lynx numbers in 1992–1994.

Table 3 Sex and age structure of lynx population in BPF in 1990/91–1993/94 R - radiocollared lynx, S - lynx recorded by snowtracking (see Fig. 2 for distribution of all lynx) Mean body masses of lynx of each age sex group (in kg) are given in parentheses (data averaged from live-captured lynxes)

Winter		Recorded numbers of				
		Ad, M (21.2)	Ad F (15.7)	Subad (15.0)	Juv (9.0)	Undet
1990/91 1991/92	R	2				
	R	2			2	
	S	2	2		3	
1992/93	R	3	1	2	1	
	S	4	4		6	
	Total	7 (33%)	5 (24%)	2 (10%)	7 (33%)	
1993/94	R	2	2	4		
	S	5	4		11	1
	Total	7 (24%)	6 (21%)	4 (14%)	11 (38%)	1 (3%)
Mean percent (1992/93–1993/94)		29%	23%	12%	35%	1%

Sex and age structure, reproductive parameters, and mortality rate of lynx population

Data on sex and age of lynxes radiotracked and snow-tracked in winters 1990/91–1993/94 is given in Table 3. In 1992/93–1993/94, adult males formed on average 29% and reproducing females 23% of all lynx. Subadult individuals constituted 12% and kittens 35% of the lynx population (Table 3). Sex ratio was 1:1. Mean number of young was 1.4 kittens per reproducing female (1.2 kittens/female including subadult non-reproducing females) in 1992/93, and 1.8 kittens per reproducing female (1.2 kitten/female) in 1993/94. Totally, in 1991–1994, 13 females were leading 21 kittens, i.e. 1.6 kittens per reproducing female. One orphan kitten, Mała, was recorded.

Long-term data on lynx litter size showed that during the first 3 months of kittens' life, there were on average 3.3 young/mother and the rate of mortality was higher during the early period of kittens' life than during their older age (Fig. 3). Mortality of young before independence amounted to 48%, but it may be somewhat underestimated, because snowtracking and visual observations could not reveal females that lost entire litters especially during the first weeks of kittens' life.

Mortality of subadult and adult lynx was estimated in the Polish part of BPF. Totally, in 1978–1994, 11 cases of mortality were recorded (Appendix IV), including 6 poached lynxes (54%), 1 shot after it had come to the farmyard, 1 rabied, 1 dead from gun-wounds, and 2 from unknown causes. Natural factors were responsible for 9% only (or 27% if unknown causes of deaths were included) of the recorded deaths. On average annual mortality rate of radiotracked lynx was 0.372, in other words 37% of subadult and adult lynx died each year (Table 4), 71% of that mortality was due to poaching. Natural mortality was low, on average 5% per year.

Total mortality after 3 yr was 0.763, i.e. only c. 24% of initial number of lynx survived 3 years (Table 4). Annual mortality rates were compared to the annual rate of increase due to reproduction (calculated as number of young produced per year by one individual in a population). On average, the annual increase rate was 0.593 (Table 4). Thus, during the three years of our study when no hunting harvest took place, the increase rate overcompensated for the mortality.

Dynamics of lynx harvest and population numbers in 1869–1994

In 1946–1994 (49 years), three independent counts of annual numbers of lynxes in BPF were done: in the Belarussian part (data for 44 years) in the exploited forests of the Polish part (42 years), and in Białowieża National Park (11 yr) (Appendix III, Fig. 4). The results of these censuses are correlated, thus verifying the reliability of lynx number estimates (numbers of lynx in the Belarussian and Polish parts: $r = 0.59$, $n = 38$ years, $p < 0.0005$, numbers in BNP and Belarussian part: $r = 0.75$, $n = 11$, $p = 0.008$, numbers in BNP and exploited forests of the Polish part: $r = 0.55$, $n = 10$, ns).

Hunting for and persecution of lynx in the Belarussian part of BPF affected its numbers in the whole Białowieża Forest. During the period of the most intense persecution, lynx in the Polish part declined earlier and recovered later than in the Belarussian part, which adjoins other continuous forests inhabited by lynx. BNP, a strict reserve, where hunting was never permitted, is too small (47.5 km²) to serve as a refuge for lynx. Numbers of lynx in BNP underwent dramatic fluctuations linked with those in the Belarussian part.

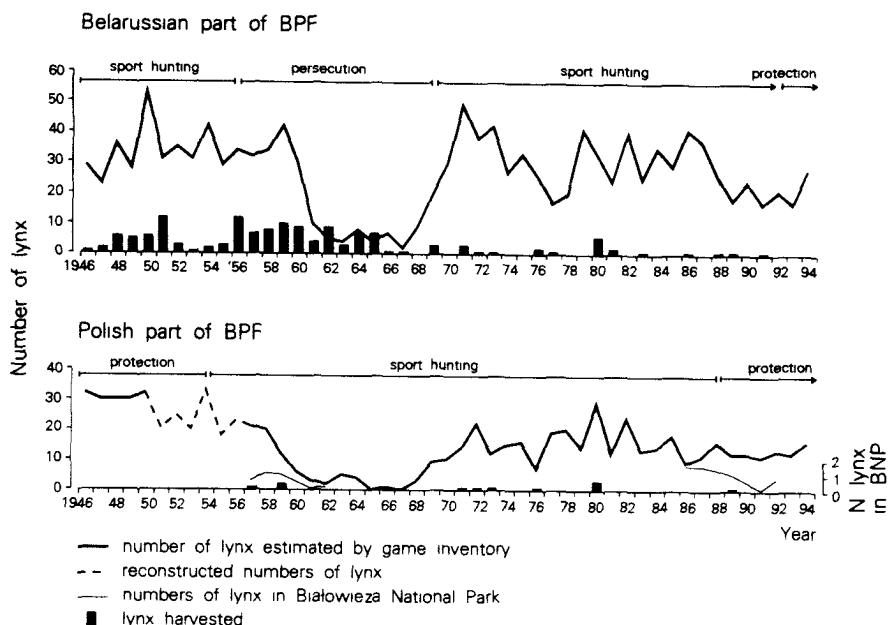


Fig. 4 Dynamics of lynx numbers (censused by snowtracking), and hunting harvest of lynx in the Belarussian and Polish parts of BPF in 1946–1994 (data in Appendix III)

recorded in times of political chaos and economic regression that affected local people. Recently, an exponential increase of numbers of poached ungulates found by game wardens has been recorded after 1989 in the Polish part of BPF (Okarma et al 1995). Similarly, in the Spanish population of fully protected *Lynx pardina* annual mortality rate was 0.37, and 50% of that mortal-

ity was due to poaching and another 17% due to traffic accidents (Ferrerías et al 1992).

Prospects of lynx survival in Białowieża are good because the Forest joins other large forest tracts in the North (Knyszyn Forest) and especially in the East (various Belarussian forests), which are populated by lynx and where lynx is protected.

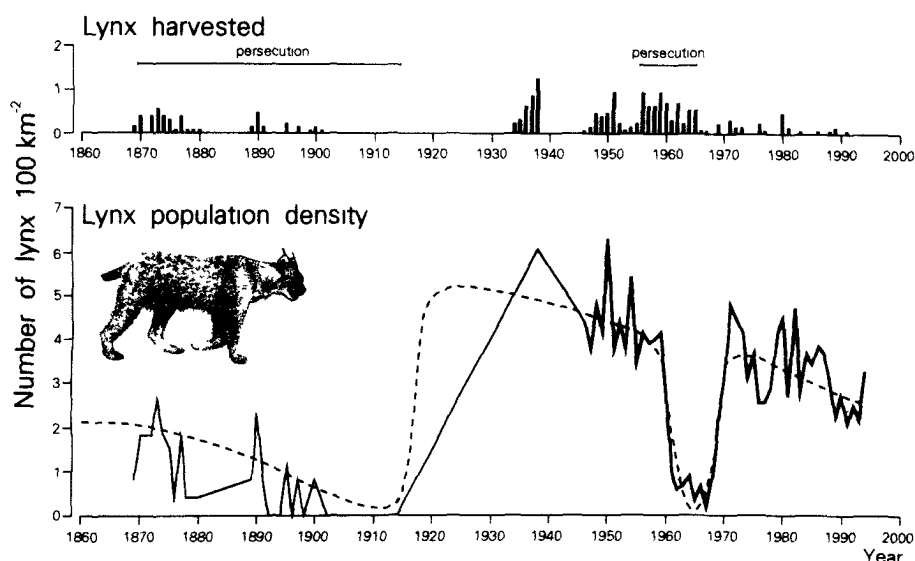


Fig. 5 Long-term dynamics of lynx density and hunting harvest in BPF (1869–1994). Density in 1869–1946 (thin line) reconstructed based on regression between numbers shot and population size in 1958–1967. Density in 1946–1994 (thick line) – snowtracking censuses, numbers of lynx recorded in the Belarussian part combined with those in the Polish part corrected by 20% ('transborder' lynx, see text). Broken line – smoothed population dynamics. Data in Appendices II and III.

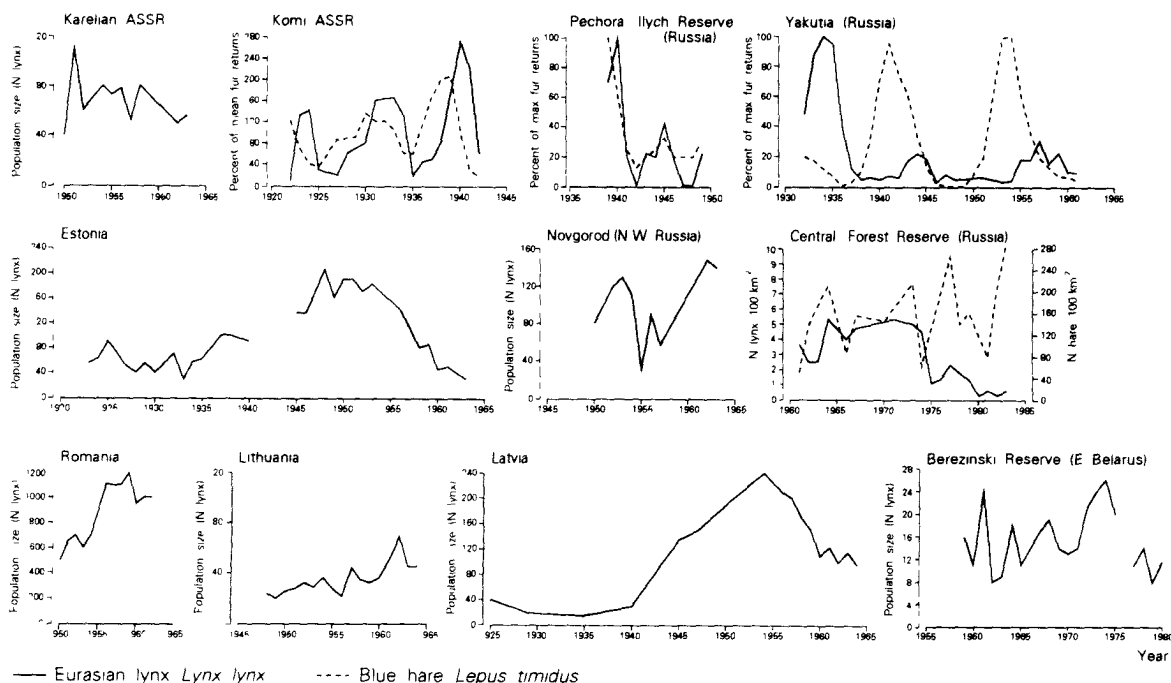


Fig. 6 Population dynamics of lynx (and in some regions of the blue hare *Lepus timidus*) in the Palaearctic region from north-east Asia (Yakutia) to south-central Europe (Romania). Sources of data: Yakutia - Tavrovskii et al. (1971), Pechora-Ilych reserve and Komi ASSR - Teplov and Teplova (1947, cited after Heptner and Sludskii 1972) and Naumov (1947), Central-Forest Reserve - Zheltukhin (1986), Karelia, Estonia, NW Russia, Lithuania, Latvia - Novikov (1967), Berezinski Reserve - Geltman and Dolbik (1983), Romania - Kratochvil (1968).

Dynamics of lynx population in Białowieża Primeval Forest

During the three periods of fairly undisturbed functioning of lynx population in the last 125 yr the levels of lynx density differed markedly. We think that the numbers of lynx were determined by availability of prey. In the first half of the 19th century and until 1890, ungulate community in BPF consisted of 4 species only (in order of decreasing abundance) wild boar, roe deer, European bison, and moose. The native red deer became extinct by the end of the 18th century (Brincken 1828, Jarocki 1830). Numbers of wolves were very high (up to 8 inds 100 km^{-2}) (Jędrzejewska et al. unpubl.) and brown bear (also preying on ungulates) still occurred in small numbers (Karcov 1903). Thus, the roe deer must have been the staple prey to both lynx and wolves, although the latter hunted also for wild boar, moose and European bison (Karcov 1903).

After 1920, ungulate community changed in favour of the lynx preferred prey. Roe deer, red deer (the latter one reintroduced in 1890), and wild boar inhabited BPF, whereas European bison and moose were temporarily exterminated (Gavrín and Donaurov 1954, Więcko 1984, Pucek 1992). Wolves were so heavily persecuted after 1946 (Gavrín and Donaurov 1954), that already by 1950 their numbers were much lower

than those of lynx. That period was characterised by the highest recorded numbers of lynx.

In 1970–1994, densities of lynx were somewhat lower than during its best years. The structure of ungulate community has gradually changed. Red deer became the dominant species, followed by roe deer and wild boar. European bison was restituted and moose recovered, but the two latter species are still the least numerous ungulates in BPF (Jędrzejewska et al. 1994, Okarma et al. 1995). Although up to 20 wolves are still harvested annually in the Belarussian part, their numbers are quite stable at 2–4 inds 100 km^{-2} , i.e. comparable to those of lynx (Jędrzejewska et al. unpubl.).

In Białowieża, the impact of man heavy enough to disturb the lynx-ungulate relationships occurred rather late in comparison to other European regions and it was restricted to c. 40 yr in the 19th century and some 20 yr in the 20th century.

Patterns of population dynamics of lynx in the Palaearctic region

Eurasian lynx shifts from the blue hare *Lepus timidus* as basic prey in the north and north-east to ungulates at more southern and south-western latitudes of the Palaearctic region (Jędrzejewski et al. 1993). Long-term

data from fur returns, hunting statistics and inventories show, that there is a clear geographic gradient in the cyclicity of blue hare and, consequently, of the Eurasian lynx populations (Fig 6). The 10-yr cycles occur in north-east Siberia (Yakutia). Towards west, the cycle length becomes shorter (5–6 yr in Komi territories). In the northern part of Europe and at southern latitudes in the whole Palaearctic, fluctuations of blue hare numbers are irregular and do not drive fluctuations in lynx numbers (e.g. Central-Forest Reserve), because lynx utilises ungulates as alternative and – still more south – as primary prey. However, in regions, where lynx depend primarily on ungulates (e.g. Latvia, Estonia, Lithuania, Romania), its long-term dynamics can be quite strongly affected by human policy of game management.

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Appendix I

Lynxes captured and radiotracked in Białowieża Primeval Forest in 1991–1994. If not stated otherwise, the radiotracking was continued after 30 April 1994.

Name, age, sex	Body mass (kg)	Dates of radiotracking	Cause of untimely end of radiotracking and other notes
Bazyli, ad. M	20	24 Feb–23 Dec '91	poached
Makary, ad. M	19	9 March–3 July '91	transmitter failure
	23 ¹	27 Feb '93–30 Apr '94	
Mała, juv. F	9	11 Dec '91–21 Jan '92	disappeared
Bazyliśzek, juv. M	11	7 Feb '92–21 March '92	stayed with mother and another kitten
subad. M	14 ²	28 March '92–21 Nov '93	poached
Borys, ad. M	24	8 Feb–7 Dec '92	poached
Nikifor, ad. M	21	25 Jan–23 Feb '93	killed as rabid in Knyszyn Forest (31 Dec '93), 60 km N from capture place
Sonia, subad. F	15	30 Jan '93–30 Apr '94	
Zoja, juv. F	10	5 Jan '93–Apr '93	stayed with mother
subad. F	?	Apr '93–30 Apr '94	
Natasza, ad. F	16.5	3 Feb '93–28 March '94	disappeared
Olga, ad. F	15	16 Feb–30 Apr '94	
Igor, subad. M	16	22 March–30 Apr '94	
Tamara, subad. F	15	29 March–30 Apr '94	

¹ captured on 15 December 1993 for collar change, body mass 20 kg.
² captured for collar change in June 1992 (weighed at the time of capture)

Appendix II

Numbers of lynx killed in BPF (1250 km²) in 1869–1938, numbers of lynx estimated by game wardens (1928, 1935), and reconstructed population numbers (the latter in *italics*) Sources of data in Methods and material Reconstruction of numbers was done for years of intense persecution of lynx and was based on regression between the number of lynx killed and estimated population size in 1958–1961, 1966–1967 (i.e. years with reliable data for both Belarussian and Polish part of BPF, data in Appendix III) $Y = -0.066 + 4.783X$, $R^2 = 0.87$, $p = 0.007$, $n = 6$? – reliable reconstruction of lynx numbers not possible or available data uncertain

Year	Yearly number of killed lynx	Reconstructed number of lynx	Year	Yearly number of killed lynx	Reconstructed number of lynx
1869	2	<i>10</i>	1892	0	<i>0</i>
1870	5	<i>24</i>	1893	0	<i>0</i>
1871	0	<i>?</i>	1894	0	<i>0</i>
1872	5	<i>24</i>	1895	3	<i>14</i>
1873	7	<i>33</i>	1896	0	<i>0</i>
1874	5	<i>24</i>	1897	2	<i>10</i>
1875	4	<i>19</i>	1898	0	<i>0</i>
1876	1	<i>5</i>	1899	1	<i>5</i>
1877	5	<i>24</i>	1900	2	<i>10</i>
1878	1	<i>5</i>	1901	1	<i>5</i>
1879	1	<i>5</i>	1902	0	<i>0</i>
1880	1	<i>5</i>	1928	<i>?</i>	<i>30</i>
1881	0	<i>?</i>	1934	3	<i>?</i>
1882	0	<i>?</i>	1935	4	<i>95?</i>
1889	2	<i>10</i>	1936	8	<i>?</i>
1890	6	<i>29</i>	1937	11	<i>?</i>
1891	2	<i>10</i>	1938	16	<i>76</i>

Appendix III

Number and harvest of lynx in the Polish part (exploited forests 530 km², and Białowieża National Park 47.5 km²) and the Belarussian part of BPF (670 km²) in 1946–1994 Numbers of lynx censused numbers are in Roman type, reconstructed numbers in *italics* (reconstruction of numbers in 1951–1957 in the Polish part and in 1983, 1985, 1990 in the Belarussian part based on regression of lynx numbers in the Belarussian and Polish parts ($Y = 3.36 + 0.414X$, $R^2 = 0.352$, $n = 38$, $p < 0.0005$) Question marks denote numbers of lynx censused but strongly departing from the long-term trend (and thus thought to be unreliable), for such years numbers estimated from the above regression equation are given in parentheses Sources of data and methods of censuses described in Methods and material

Year	Lynx in the Polish part of BPF			Lynx in the Belarussian part of BPF	
	Numbers in the exploited forests	N killed	Numbers in BNP	Numbers	N killed
1946	32	0		29	1
1947	30	0		23	2
1948	30	0		36	6
1949	30	0		28	5
1950	32	0		53	6
1951	<i>20</i>	0		31	12
1952	25	0		35	3
1953	<i>20</i>	0		31	1
1954	33	0		42	2
1955	<i>18</i>	0		29	3
1956	23	0		14 [?] (34)	12
1957	<i>21</i>	1	0.6	32	7
1958	20	0	1.1	34	8
1959	12	2	1.0	42	10
1960	6	0		30	9
1961	3	0	0.1	10	4
1962	2	0	0.2	5	9

Appendix III (cont.)

Year	Lynx in the Polish part of BPF			Lynx in the Belarussian part of BPF	
	Numbers in the exploited forests	N killed	Numbers in BNP	Numbers	N killed
1963	5	0		4	3
1964	4	0		8	7
1965	0	0		4	7
1966	1	0		7	1
1967	0	0		2	1
1968	3	0		9	0
1969	9	0		20	3
1970	10	0		30	0
1971	14	1		49	3
1972	22	1		38	1
1973	12	1		42	1
1974	15	0		62? (27)	0
1975	16	0		33	0
1976	7	1		26	2
1977	19	0		17	1
1978	20	0		20	0
1979	14	0		41	0
1980	29	3		33	6
1981	12	0		24	2
1982	24	0		40	0
1983	13	0		25	1
1984	14	0		35	0
1985	18	0		29	0
1986	9	0	1 6	41	1
1987	11	0	1 6	37	0
1988	16	0	1 4	26	1
1989	12	1	1 1	18	1
1990	12	0		24	0
1991	11	0	0 1	17	1
1992	13	0	0 8	21	0
1993	12	0		17	0
1994	16	0		28	0

Appendix IV

Cases of non-harvest mortality of lynx from the Polish part of BPF r – river, v – village, names of forest administration units (in parentheses) as in Fig. 1. Names of lynxes refer to radiocollared individuals (see Appendix I).

Date	Place	Description of lynx	Cause of death
Winter 1978	E of Białowieża v (Białowieża)	Adult male	Poached with two dogs (Kossak 1988)
1986	Sacharewo v (Lesna)	?	Shot in a farmyard
April 1988	W of Krzywiec v (Ladzka Puszcza)	?	Poached, probably poisoned
April-May 1990	Przewłoka (Białowieża)	?	Found decayed, cause of death unknown
Winter 1990/91	(Browski)	Adult male	Found dead from gun-wounds
Winter 1990/91	Nowosady v (Narewka)	?	Poached
December 1991	Hwozna r (BNP)	Adult male Bazyli	Poached with snare
December 1992	W of Nowosady v (Narewka)	Adult male Borys	Poached with snare
December 1993	Skryplewo v (Narewka)	2 5-yr old male Bazyłszek	Poached, its collar (destroyed) found on 4 January 1994
December 1993	Knyszyn Forest	Adult male Nikifor	Killed in a farmyard, rabied
April 1994	N of Pogorzelle v (Zwierzyniec)	Adult male	Found dead, decayed, cause unknown

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