Spatial interactions between grey wolves and Eurasian lynx in
Białowieża Primeval Forest, Poland

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Abstract

Various species of large predators are reported to influence each other through interference or exploitation competition that may affect demography and survival of the subordinate species. We analyzed spatial relationships between grey wolf *Canis lupus* and Eurasian lynx *Lynx lynx* in Białowieża Primeval Forest (BPF, eastern Poland) to determine how they partitioned the space. The wolves (*n*=8) and lynx (*n*=14) were radio-tracked in 1991-1999. Three wolves and seven lynx were radio-tracked simultaneously in 1994-1996. Territories of wolf packs and home ranges of lynx overlapped considerably (76% of wolf territories and 50% of lynx home ranges, on average). In three cases, their core areas were also overlapping. Wolf–lynx dyads with overlapping home ranges were simultaneously located at distances from 0 to 28 km from each other. We found neither avoidance nor attraction between wolves and lynx occupying the same areas. We concluded that in BPF, the two large predators coexist due to specialisation on different preferred prey and heterogeneous habitat.

Key words: *Canis lupus*, coexistence, exploitation competition, interference competition, *Lynx lynx*, spatial overlap

Introduction

What enables various carnivorous mammals to coexist and how they interact with each other when occurring sympatrically has been a subject of numerous studies. Rosenzweig (1966) suggested that coexistence results from size differences between predator species. Felids and canids seem to be particularly predisposed to “peaceful coexistence” (Major and Sherburne 1987) through separation of their ecological niches, which likely resulted from evolution of their different social systems (Kleiman and Eisenberg 1973).
On the other hand, the competitive exclusion was recently suggested between tigers *Panthera tigris* and wolves *Canis lupus* even despite of extreme size differences (Miquelle et al. 2005). Cases of interspecific killing are common among predators, including felids and canids (review in Palomares and Caro 1999). In some instances intraguild predation may have serious consequences on demography and survival of the inferior species, as it has been suggested for cheetahs *Acinonyx jubatus* (Laurenson 1995) and African wild dogs *Lycaon pictus* (Creel and Creel 1996, Carbone et al. 1997).

Grey wolves and Eurasian lynx *Lynx lynx* are sympatric across most of their vast geographical ranges, which stretch from Eastern Europe to the Far East of Asia (Bibikov 1985, Nowell and Jackson 1996). The spatial interactions between these species, however, have not yet been studied. Anecdotal information on their interspecific relationships (based on harvest data and incidental observations) are available from the Russian part of their ranges and from Fennoscandia. According to those reports, coexistence of the two large carnivores is often characterized by negative influences of wolf on lynx (Pulliainen 1965, Myrberget 1970, Matyushkin 1985, Malafeev et al. 1986, Matyushkin and Vaisfeld 2003). Dynamics of wolf and lynx population numbers reported there suggest that lynx may reach higher numbers only when wolves are rare. Cases of wolves killing lynx were also reported (see Matyushkin and Vaisfeld 2003 for review). On the other hand, it has also been suggested that the relationships between the two species may vary with ecological circumstances (Matyushkin 1985). Indeed, in some areas populations of both predators existed in large numbers without apparent reciprocal influence (e.g. Upper Volga Region: Zheltukhin 1986) or even increased simultaneously (West Siberia: Azarov and Shubin 2003; Eastern Poland and Western Belarus: Jędrzejewska and Jędrzejewski 1998). Snow-tracking data from several study areas in Eurasia (e.g. Upper Volga Region: Zheltukhin 1986; North-West Russia: Danilov et al. 2003; Far East of Asia: Matyushkin et al. 2003) showed that lynx and wolves do not avoid using the same
sites and do not exhibit any particular interest in each other, which suggests a lack of interference competition (*sensu* Case and Gilpin 1974).

Wolves and lynx also have similar diets across their common range (see Matyushkin and Vaisfeld 2003 for review). Therefore, one can expect that the wolves may limit lynx populations through exploitation of the common food resources (exploitation competition), as suggested by Litvaitis and Harrison (1989) for sympatric bobcat *Lynx rufus* and coyote *Canis latrans* in Maine (USA).

In Białowieża Primeval Forest (BPF, E Poland) the two predators coexist and no negative relationship between their long-term dynamics was noted – the wolf and lynx densities were found to be significantly correlated in time (Jędrzejewska and Jędrzejewski 2005). Their numbers were simultaneously shaped by temporarily varying hunting harvest. The ecology of both species in BPF has been studied in detail (Jędrzejewski et al. 1996, Okarma et al. 1997, Schmidt *et. al.* 1997, Okarma et al. 1998, Schmidt 1999, Jędrzejewski et al. 2000, Theuerkauf et al. 2003), but their interspecific interactions have not been analyzed.

The feeding niches of the two carnivores partly overlap, as wolves primarily prey on red deer *Cervus elaphus* and supplement their diet with wild boar *Sus scrofa* and roe deer *Capreolus capreolus* (Jędrzejewski et al. 2000), whereas lynx feed mainly on roe deer with the addition of female and young red deer (Okarma et al. 1997). Given the high densities of ungulates in BPF (Jędrzejewski et al. 2002), exploitation competition is not very likely.

The aim of this study was to analyze fine scale spatial interactions between radio-tracked wolves and lynx inhabiting the Białowieża Primeval Forest. We investigated these relationships at three spatial scales: (1) the study area level - utilization of the forest by both species, (2) home range level – degree of overlap between lynx and wolf home ranges and (3) individual level – dynamic interactions between dyads of lynx and wolf individuals located at the same time. This way we intended to determine if wolves and lynx tended to be spatially
segregated and show any signs of exclusion of one by the other (interference competition) in
the BPF.

Material and methods

Study area

The study was conducted in Polish part of the Białowieża Primeval Forest (BPF), Eastern
Poland (52°30’-53° N, 23°30’-24°15’ E). The BPF is a temperate mixed lowland forest located
on the Polish-Belarussian border and characterized by a high percentage of natural stands
(Faliński 1986). The whole forest covers nearly 1500 km² and its Polish part about 600 km².
Most of the Polish part of the BPF (500 km²) is managed by State Forestry, while the rest is
protected as the Białowieża National Park (BNP, 100 km²) with a 50-km² area of strict
reserve, where no human interference is allowed except for tourism and research. A network
of small reserves with partial protection is located within the managed part of the BPF
(Wesołowski 2005). The dominating tree species are: pine *Pinus silvestris*, spruce *Picea
abies*, oak *Quercus robur*, hornbeam *Carpinus betulus*, black alder *Alnus glutinosa*, ash
*Fraxinus excelsior*, lime *Tilia cordata*, birches *Betula verrucosa* and *B. pubescens*, aspen
*Populus tremula* and maple *Acer platanoides*. Despite of timber exploitation, the BPF
maintains a unique character in comparison to other European forest in terms of: (1) tree
diversity (with 26 tree and 55 shrub species forming a mosaic of diverse tree communities),
(2) a multi-storey profile of stands, (3) relatively large amount of dead wood and (4)
outstanding diversity of flora and fauna (Wesołowski 2005). The climate of BPF is temperate
with transitional character between Atlantic and continental ones with clearly marked warm
and cold periods (average temperatures during the study period were -3.9º C in January and
19.1º C in July; average annual precipitation was 622 mm; snow cover persisted for an
average of 96 days per year from November to March). Wolf and lynx are currently the only
large predators in BPF. The community of ungulate mammals consists of: red deer *Cervus
elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scropha*, moose *Alces alces*, and
European bison *Bison bonasus*. However, only three species – red deer, roe deer and wild
boar – play an important role in both predators’ diets (Jędrzejewski et al. 1993, Jędrzejewski
et al. 2000).

Radio-tracking

The study was a part of a larger research project on wolf and lynx ecology in BPF conducted
in 1991-1999 (Schmidt et al. 1997, Jędrzejewski et al. 2002). The principal data for this paper
originates from 1994-1996, when both wolf and lynx were studied by radio-tracking: 3 female
wolves belonging to 2 packs and 7 lynx (2 M, 5 F) (Appendix I). Five lynx provided
sufficient number of locations taken simultaneously with those of wolves for calculating
dynamic interactions between the species. Locations of wolves and lynx taken before and
after 1994-1996 were, however, used for general assessment of the forest use by both species
(9 wolves and 16 lynx). We acknowledge that the sample of studied animals is low and we
didn’t monitor whole the populations of both predators. However, the information obtained
during this study provided minimum estimates of their spatial overlap and existing potential
for interactions between them. Moreover, both wolves and lynx use large home ranges (173-
294 km$^2$ in wolves: Okarma et al. 1998 and 133-248 km$^2$ in lynx: Schmidt et al. 1997), so that
the total area used by simultaneously radio-tracked wolves and lynx covered a representative
portion of the study area. We estimated that during the study, the population of wolves in
Polish part of BPF consisted of 3-4 packs of wolves containing 2-8 individuals each
(Jędrzejewski et al. 2000). Lynx were estimated at 6 – 18 adult individuals (Jędrzejewski et.
al. 1996).
The wolves were captured both with “fladry” (a rope with strips of cloth that is used to limit and drive wolves’ movements) and a net system (Okarma and Jędrzejewski 1997) or foot snare traps (equipped with alarm-system) and fitted with VHF radio-collars made by Telonics Inc., (Mesa, Arizona, USA), AVM Instrument Co. (Livermore, California, USA), Telemetry Systems (Mequon, Wisconsin, USA), and Advanced Telemetry Systems (Isanti, Minnesota, USA). Lynx were captured with snare traps set at fresh kill and marking sites or in a box trap (equipped with alarm-system) and fitted with VHF radio-collars made by Wagener Temetrieanlagen HF-NF Technik, (Köln, Germany) or AVM Instrument Co. The range of the collars was 1 – 2 km. Both wolves and lynx were immobilized with a mixture of ketamine hydrochloride (wolves: 3.4-4.5 mg/kg, lynx 5 mg/kg of body weight) and xylazine hydrochloride (wolves: 5-6.5 mg/kg, lynx 6 mg/kg of body weight).

We located radio-collared animals 2-5 times per week by triangulation from the forest roads. Additionally, each month we conducted sessions of continuous 24-h radio-tracking lasting 2-7 days, during which we located animals every 30 min. During these sessions we focused on one individual of a given species, although we recorded locations of the second species if it was present nearby until the animals separated such that following two of them simultaneously was too difficult. Locations were plotted on forest maps with 533x533 m square grid (according to the forest division compartments marked in the terrain). Positions of the animals were determined in the center of a square, in the middle of one of its sides or in the corner between four adjacent squares. Their estimated locations could then differ from the actual ones by a maximum of 373 m. We aimed at reducing the error by taking bearings from points on the forest roads closest to animals (≥100 m). During continuous radio-tracking, however, the observer usually stayed 500-1000 m from the focal animal to avoid disturbing it.

For a general assessment of space use by both species and their spatial relationships in the study area we overlaid all locations of wolves (8 individuals with 28857 locations) and
lynx (14 individuals with 7521 locations) recorded between 1991-1999 on the forest map using program Biotas™ v.1.03.1 Alpha (Ecological Software Solutions, Urnäsch, Switzerland). To estimate an extent of overlap of both species’ occurrence in the entire study area we calculated 95% minimum convex polygon ranges for pooled locations of all individuals in the two species. Using 95% MCP, in this case, allowed us to maximise the studied area used by both species as well as for excluding large portions of non-forested areas that were not visited by them. We also calculated 75% fixed kernel ranges for the same data to find out if there is an overlap of most frequently used areas by all radio-tracked lynx and wolves. The fixed kernel ranges where estimated with a level of smoothing selected by least-squares cross-validation method and the chosen bandwidth was 750 m.

We also examined static and dynamic interactions (Macdonald et al. 1980) between wolves and lynx. Static interactions were determined by calculating overlaps of lynx home ranges with territories of wolves. We calculated an average overlap both between an individual lynx home range and all available pooled wolf territories, between an individual wolf pack territory and all available pooled lynx home ranges as well as between dyads of lynx and wolves. We included all lynx radio-tracked simultaneously with wolves for the pooled lynx home ranges, despite the low number of locations for some individuals (see Appendix). The discrepancy in sample size, however, should not significantly affect the results, because our aim was to estimate a minimum value of the overlap between wolf territory and all detected home ranges of lynx inhabiting a common area. The home ranges were estimated with 100% minimum convex polygon method using the program Biotas™ v.1.03.1 Alpha, for all locations recorded during a simultaneous period of radio-tracking and for a sub-sample of both species’ locations taken on the same day only (on average within 1 h, max 12 h). This way we accounted for potential bias, resulting from a higher probability of finding two animals with decreasing distance between them. The 100% MCP was used to
To ensure detecting maximum potential overlapping area used by wolf and lynx dyads. To determine core areas used by particular lynx and wolf individuals we calculated 50% fixed kernel ranges (with the same smoothing parameters as for general – species’ level assessment).

To determine if two predators ignore, avoid or attract each other, we examined their dynamic interactions (Macdonald et al. 1980, Kenward 1992) using the program Ranges 6 v. 1.08 (R. Kenward, A. South and S. Walls, Anatrack Ltd. Dorset, UK). The program compares observed and expected distances between locations of two animals. The expected distances were estimated as a mean distance between each location of one animal and all locations of another animal. The observed and expected distances were then compared with Jacobs’ index ($D$) (Jacobs 1974):

$$D = \frac{d_E - d_O}{d_E + d_O}$$

where $d_E$ is expected distance and $d_O$ is observed distance between pairs of simultaneous locations of a wolf-lynx dyad with overlapping home ranges. $D$ ranges from -1 in case of mutual avoidance, to 0 if the animals move independently, to +1 if they are attracted to each other.

**Results**

Wolves and lynx utilized the study area in nearly the same extent (Fig. 1). Although the eight wolves of four packs were more intensively radio-tracked than the 14 lynx, the minimum convex polygons with 95% of pooled locations of all individuals in the two species overlapped in 88%. Most frequently used areas by both predators (75% fixed kernel) also showed a substantial spatial overlap: wolves on 18% of lynx core area, and lynx on 32% of wolves’ core area. It is striking that both wolves and lynx were utilizing mostly the main solid
forest body, leaving it only occasionally. However, wolves seemed to wander out of the forest
slightly more readily than lynx (note westernmost locations of wolves on Fig. 1).

Home ranges of lynx individuals and territories of wolf packs overlapped each other
extensively (Fig. 2). Territory of each of the studied wolf packs was on average, covered by
home ranges of radio-collared lynx by 76% (Table 1). Home range of each lynx was covered
by wolf territories by 50%, on average. Smaller overlap (mean 12-14%) was recorded
between core areas (Table 1). These measures of overlap are certainly underestimated, since
in both years shown in Fig. 2, there were other (non-collared) wolf packs and lynx individuals
recorded by snow-tracking in the nearest vicinities of the territories/home ranges of radio-

When found at approximately the same time, particular dyads of wolves and lynx with
overlapping home ranges were located at an average distance from 4.4 to 11.0 km apart
(Table 2). It is noteworthy that occasionally they were found at the same location as the
minimum recorded distance was 0 or 0.3 km in some dyads. According to analysis of
dynamic interactions (based on Jacobs’ index, $D$) conducted for pairs of simultaneous
locations of wolves and lynx, the animals showed neither avoidance nor attraction to each
other (Table 2). A slight attraction was recorded in the case of a dyad L4-W3, which also
showed the most extensive overlap of their home ranges.

A male lynx L4 and a pack of wolves with female W3 were radio-tracked
simultaneously on three separate occasions, in which the animals were found at very short
(less than 1 km) distances from each other for longer periods (Fig. 3). On 23 May 1995, the
lynx approached the site where the wolf pack stayed and remained there in close proximity to
wolves (0.25 – 0.8 km) for 5 h. The lynx left that area in the evening and headed in the
opposite direction to the one he arrived. On 22 June 1995, both lynx and wolf were at
approximately the same location (maximum 0.25 km from each other) for 1 h. Afterwards,
they split, however, they still remained close by (0.25 – 1.4 km) in an area of about 0.8 km² for the subsequent 8 h, before the lynx departed. On another occasion, 23/24 October 1995, the female wolf with her pack and the lynx moved along nearly the same route over 13 km for 22 h. During this time, the animals rested four times, each time in different place, at a distance of 0.5 – 1.5 km from each other. After the resting bouts that took from 0.5 to 2.5 h, they moved alternately following each other, heading approximately in the same direction until early morning, when they went separate ways (Fig. 3).

Discussion

The competition between two species of predators may be mitigated by various factors, such as differences in size (Rosenzweig 1966) and social organization (Kleiman and Eisenberg 1973). Therefore, it is difficult to predict the effect of interactions between given species at given site. Grey wolf inhabiting BPF is nearly twice as heavy as Eurasian lynx (on average, 45 and 35 kg, for adult male and female wolves, respectively: Jędrzejewski et al. 2007; 22 and 17 kg for male and female lynx, respectively: Schmidt et al. 1997). Size difference may lead to interference competition through interspecific killing, as suggested by Palomares and Caro (1999). On the other hand it may diminish exploitive competition through partitioning of prey resources (Scognamillo et al. 2003). Different life habits of canids and felids – sociality and coursing hunting behaviour of wolves versus solitary life and stalking hunting common in felids – may farther ease resource partitioning, as found by Husseman et al. (2003) for sympatric wolves and cougars *Puma concolor*.

Our study showed that the wolves and the lynx did not exclude each other spatially in the Białowieża Primeval Forest. They behaved neutrally, neither avoiding nor attracting each other, which suggests that they used the available area completely independently. Cases of
extensively overlapping core areas and parallel travelling recorded during this study are also
indicating that individuals of the two species do not particularly tend to separate from each
other while using the same area. The patterns of their activity were also greatly overlapping
(compare Schmidt 1999 and Theuerkauf et al. 2003), because wolves were active throughout
the day with peaks at dawn and dusk, while in lynx the most active period covered the whole
night including dawn and dusk. Moreover, except one record by Gavrin and Donaurov (1954)
of lynx remains in the wolf scats, we did not obtain any recent or other past reports on lynx
being killed by wolves or vice versa in BPF.

How is the “peaceful coexistence” (Major and Sherburne 1987) possible between the
wolf and the lynx in Białowieża Forest? The separation of ecological niches in community of
carnivores often lies in different diets (Sunquist et al. 1989, Jędrzejewska and Jędrzejewski
1998, Karanth and Sunquist 2000, Ray and Sunquist 2001). However, in sympatric bobcats
and coyotes, no interference competition was even found in situations, where their diets
overlapped almost completely (Major and Sherburne 1987). In BPF, red deer and roe deer are
essential prey species of wolves and lynx. Lynx highly prefers roe deer, taking them more
often than expected from their share in the ungulate community (Okarma et al. 1997). Red
deer, on the other hand, were taken more often than expected from their abundance by wolves
(Jędrzejewski et al. 2000). The diet of both predators, however, overlapped partly due to less
frequent predation of lynx on red deer (22% of prey killed) and wolves on roe deer (17% of
prey killed). Although wolves appeared to be strongly dependent on red deer in BPF, these
canids are also well suited to kill and sustain themselves on the smaller species, e.g. roe deer.

In areas where red deer are absent or very rare the roe deer may become a staple food of
wolves (Valdmann et al. 2005). Nevertheless, there is probably quite wide range of densities
at which the wolves focus their predation on red deer. In the Western Carpathian Mountains
wolves were found to prey predominantly on red deer, despite its relatively low (21%) share
in ungulates community (Nowak et al. 2005). Thus, it seems that possibility for exploitive
competition between wolves and lynx is low. It would be, however very likely only in case of
a severe alteration of red and roe deer proportions in the living ungulate community (e.g. due
to hunting harvest). For example, the coyotes occurring sympatrically with Canada lynx *Lynx
canadensis*, were suggested to influence lynx densities through heavy exploiting the
snowshoe hares *Lepus americanus* (Buskirk et al. 2000).

Yet another way of avoiding competition are differences in hunting behaviour between
wolves and lynx. As a solitary predator, the lynx is able to conceal itself as well as its prey,
making it less detectable for wolves, as suggested by Stander et al. (1997) for African
leopards *Panthera pardus*. Lynx usually drag their kills into thick vegetation and cover it with
available material (leaves, snow etc.) (Jędrzejewski et al. 1993). In BPF, wolves were rarely
recorded scavenging at kills made by lynx (Jędrzejewski et al. 1993, Selva et al. 2005). Lynx
were also never found feeding on kills made by wolves (Selva et al. 2005).

According to Matyushkin (1985), direct competition between wolf and lynx is
possible, but the relationships between these two species vary depending on the circumstances
in which they share resources. Similarly, based on interactions among African wild dogs and
larger carnivores, Creel (2001) proposed that the effect of competition on carnivores’
population dynamics may be significantly modified by several factors, including habitat
characteristics. Although the Białowieża Forest is characterized by lack of topographic
heterogeneity that would ensure escape avenues, it offers heterogeneous habitat, which may
facilitate the coexistence of these two large carnivores. The lynx were found to select specific
habitat features (fallen logs, uprooted trees and dense thickets) when hunting and resting
(Podgórski et al. 2008). In a study on sympatric wolves and cougars, Husseman *et al.* (2003)
showed that the two carnivores used the habitat in different ways when hunting. Ambushing
cougars focused on small patches facilitating stalking, whereas coursing wolves pursued their
prey irrespective of specific habitat type. Wolves, in contrast to lynx, were also occasionally
found outside of the forest during this study. Therefore, wolves may probably do well in less
diverse habitat, while lynx may need heterogeneous environment to escape competition with
stronger predator.

In conclusion, differences in morphology, diet, habitat use and hunting behaviour all
contribute to allow grey wolf and Eurasian lynx to coexist wherever local habitat and
available prey resources fulfil both predators’ requirements.

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Table 1. Spatial overlap among home ranges of 7 lynx and territories of 3 wolf packs radio-tracked simultaneously in the Białowieża Primeval Forest in 1994-1996. The overlaps were calculated for combinations of particular wolf pack territories with all lynx home ranges and for particular lynx home ranges with all wolf packs monitored concurrently. See Appendix for number of locations of individual lynx and wolves.

<table>
<thead>
<tr>
<th>Pair of species, territory/home range estimate</th>
<th>Percentage overlap (percent of territory/home range of the first species overlapped by all radio-tracked individuals of the second species)</th>
<th>N cases</th>
<th>Mean ± SE</th>
<th>(min – max)</th>
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<tbody>
<tr>
<td>Wolf pack – lynx, MCP 100%</td>
<td></td>
<td>3</td>
<td>76 ± 7</td>
<td>(68 – 89)</td>
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<td>Wolf pack – lynx, Kernel 50%</td>
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<td>12 ± 12</td>
<td>(0 – 36)</td>
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<td>Lynx – wolf packs, MCP 100%</td>
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<td>50 ± 12</td>
<td>(13 – 99)</td>
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<td>14 ± 10</td>
<td>(0 – 70)</td>
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<td>Dyads</td>
<td>Percentage overlap</td>
<td>Distance between individuals (km)</td>
<td>Jacobs’ index</td>
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<td>Mean ± SE (min-max)</td>
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<td></td>
<td>territory home range</td>
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<tr>
<td>W1 – L1</td>
<td>3 5</td>
<td>6.9±0.2 2.3-18.4</td>
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<td>(159)</td>
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<tr>
<td>W1 – L2</td>
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<td>(424)</td>
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<td>W2 – L3</td>
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<td>W3 – L4</td>
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Figure captions:

Figure 1. Distribution of all radio-locations of lynx ($n=7521$ of 14 radio-tracked individuals in 1991-1996) and wolves ($n=28857$ of 8 individuals belonging to 4 packs radio-tracked in 1994-1999) in the Białowieża Primeval Forest and most frequently used areas (75% fixed kernel) estimated for all locations pooled for each species. Question marks denote area where lynx were not trapped for radio-collaring.

Figure 2. Territories (100% MCP) and core areas (50% fixed kernel) of wolf packs ($n=3$) and home ranges of lynx ($n=7$) radio-tracked in the Białowieża Primeval Forest in 1994-1996.

Figure 3. Examples of movement routes of a pack of wolves (with the female W3) and male lynx (L4) recorded during simultaneous, continuous radio-tracking of both carnivores in BPF.
Figure 1.
Figure 2.
Figure 3.

<table>
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<tr>
<th>Animal</th>
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<th>Age</th>
<th>Time of simultaneous radio-tracking</th>
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