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Microhabitat selection by Eurasian lynx and its implications for species conservation

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We studied microhabitat selection of the Eurasian lynx *Lynx lynx* (Linnaeus, 1758) at 116 hunting and 88 resting sites in Białowieża Primeval Forest (Poland) to describe its characteristics and determine the importance of habitat structure for stalking prey and for security during resting. We identified lynx-used sites by radio-tracking 3 male and 3 female lynx. When hunting, the lynx did not select for any type or age class of forest. During both summer and winter, the lynx selected sites characterized by high complexity (number of structures useful for stalking: fallen logs and branches, root plates, patches of dense bushes) and low visibility. In summer, hunting sites were often located in the vicinity of small forest glades that provided good stalking opportunities for lynx and rich foraging resources for roe deer – the main prey of lynx. The habitat at kill sites was more open than at sites where the prey was cached, with higher visibility, lower density of trees and poorer undergrowth. The most important characteristic of resting sites was very low visibility that resulted mainly from using young pine or spruce thickets in the winter and dense undergrowth of oak-lime-hornbeam and ash-alder forests in the summer. The information provided by this study could have direct implications for Eurasian lynx conservation by guiding forest restructuring to better suit the species' biological requirements.

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Introduction

If not harvested, populations of large carnivores are limited mainly by prey abundance and habitat alteration and fragmentation (Nowell and Jackson 1996, Karanth and Stith 1999, Hayward *et al*. 2007). Large carnivores are particularly susceptible to the fragmentation of habitat into small unconnected patches due to their great spatial requirements (Seidensticker 1986, Crooks 2002, Haskell *et al*. 2002). Thus,

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large-scale assessments of habitat availability have been proposed for a number of species in order to identify their potential to persist or recover (Beier 1993, Smith *et al.* 1998, Riley and Malecki 2001, Woolf *et al.* 2002, Kramer-Schadt *et al.* 2004, Hoving *et al.* 2005). However, large-scale approaches may disregard fine-scale landscape patterns that can benefit the predator population through increasing carrying capacity of the habitat (Litvaitis *et al.* 1996, Funston *et al.* 2001, Fernández *et al.* 2003). Thus, it is essential to increase our knowledge of the detailed habitat requirements of particular species of concern.

The Eurasian lynx *Lynx lynx* (Linnaeus, 1758) is a felid that, in European conditions, is closely tied to forest habitat and is reluctant to cross open, human-dominated landscapes (Schmidt 1998). However, empirical data on the habitat preferences of the species are scarce. A recent, large-scale analysis of lynx distribution and habitat availability in Poland (Niedziałkowska *et al.* 2006) showed that forest cover and connectivity to the core lynx population were most important. Another large-scale model developed for a reintroduced population in the Swiss Jura Mountains (Zimmermann and Breitenmoser 2002) predicted that the presence of lynx was indirectly correlated with forest cover. The lynx in the boreal-alpine zone of central Norway preferred lowland forest types (Sunde *et al.* 2000b). Such large-scale approaches, however, cannot identify variation between different forests in terms of the availability of specific environmental structures suitable as stalking cover or resting sites. More detailed studies provided characteristics of lynx den sites (Boutros 2002) and documented features of lynx resting sites allowing them to tolerate human presence (Sunde *et al.* 1998). Nevertheless, in-depth knowledge of Eurasian lynx microhabitat requirements is still limited.

Hunting is a fundamental biological function in predators. Factors affecting hunting success also affect the time and energy individuals spend foraging (Stephens and Krebs 1986). Therefore, knowledge on habitat characteristics associated with hunting may improve the success of species conservation measures. When hunting, most felids stalk their prey, taking advantage of physical features in the environment to approach the prey undetected before launching an attack (Sunquist and Sunquist 1989). It is important that habitat provides both sufficient cover for the predator as well as good visibility of the prey (Balme *et al.* 2007). Such conditions are met at habitat edges, especially on the border between forested and open areas, which can also act as areas of high herbivore prey concentration (Holmes and Laundre 2006). The preferred prey of the Eurasian lynx, the roe deer *Capreolus capreolus* (Okarma *et al.* 1997, Sidorovich 2006), is known to select habitat edges (eg forest clearings) for foraging (Cederlund 1983, Tufto *et al.* 1996). Indeed, lynx in Norway tend to concentrate their hunting efforts in such areas (Sunde *et al.* 2000a).

Another biological function that may affect habitat use in felids is resting (Kolowski and Woolf 2002). The Eurasian lynx spend a major part of their day inactive (on average 17 hours: Schmidt 1999), so that they require secluded sites providing security for long periods. Therefore, habitat features that create favorable conditions for resting may play an important role in the individual's security and may also be subject to intra-specific competition. Decreasing population density resulting from limited numbers of sites suitable for resting has been observed for some mustelids (Mustelidae) (Beja 1996, Halliwell and Macdonald 1996, Fournier *et al.* 2007).

Although the Eurasian lynx appears to have increased in number and is now abundant in northern Europe, its populations elsewhere are locally declining or occur at low density (eg Poland and Lithuania, Linnell *et al.* 2006). In Poland, the lynx population inhabits areas of fragmented habitat and has recently suffered range contraction despite receiving full legal protection (Jędrzejewski *et al.* 2002). Therefore, a well-designed conservation plan for the species in the region will require actions at various scales for population maintenance and development. As most lynx range falls outside protected areas, detailed knowledge of its microhabitat requirements may allow forest managers to predict the effects of forestry activities on the population. The aims of this study were to characterise the habitat features at lynx kill and resting sites in the Białowieża Primeval Forest, Poland, and determine which of them are most important for stalking prey and providing security during resting.

Material and methods

The study was conducted in the Polish side of the Białowieża Primeval Forest (BPF: 600 km^2), eastern Poland (52°30'–53°N, 23°30'–24°15'E) located on the Polish-Belarussian border. The whole continuous BPF (including both sides) covers nearly 1500 km^2. The two parts are separated with a barbed-wire fence along the state border.

The BPF is a temperate mixed lowland forest and its Polish side is characterized by a high percentage of natural stands (Faliński 1986). Most of the Polish side of the BPF (84%) is managed by the State Forestry, while the rest is protected as the Białowieża National Park (BNP) with a 50-km^2 area of strict reserve, where no human interference is allowed except for tourism and research. There is also a number of small nature reserves with partial or strict protection in the managed part of the BPF (Wesołowski 2005). Sixteen forest communities have been distinguished in the BPF (Kwiatkowski 1994). Originally a deciduous oak-lime-hornbeam forest (*Quercus robur*, *Tilia cordata*, *Carpinus betulus*) with admixture of maple *Acer platanoides* and spruce *Picea abies* constituted the majority of the forest, but today this habitat is largely restricted to the protected areas. The managed part is now dominated by planted Scots' pine *Pinus silvestris*, and spruce. There are also natural coniferous pine and/or spruce forests. Other common associations in BPF include bog alder *Alnus glutinosa* wood in wet areas with stagnating water, and ash *Fraxinus excelsior* – alder forests associated with banks of small rivers. The BPF is unique among other European woodlands due to high tree diversity (26 tree and 55 shrub species constituting a mosaic of tree communities), a multi-storey profile of stands, relatively large amount of dead wood and outstanding diversity of flora and fauna (Faliński 1986, Wesołowski 2005).

The area is flat (134–186 m a.s.l.) and the forest stands are quite continuous with only a few glades occupied by villages, marshes and open river valleys. It is easily accessible for vehicles by a dense network of dirt roads that usually follow a regular grid of square forest compartments (1066 × 1066 m). The climate of BPF is temperate with a transitional character between Atlantic and continental ones with clearly marked warm and cold periods (average temperatures during the winter were –3.9°C (January) and during the summer 19.1°C (July). Average annual precipitation was 622 mm and snow cover persisted for an average of 96 days per year from November to March.

Data collection

We used snow- and radio-tracking to locate lynx kill and resting sites. Data came from six radio-collared lynx (3 males and 3 females) and a few (probably 3–4) unmarked, snow-tracked animals. The cats were captured during winter from 2003 to 2006 with foot-snare traps (Jackson 1989) set at fresh ungulate kills. The traps were equipped with a radio-alarm system (Wagener Telemetrieanlagen HF-NF Technik, Köln, Germany) and monitored by researchers 1–1.5 km from the trap-site. This allowed us to release captured animals from traps within 15 minutes. The lynx were immobilized with a mixture of ketamine hydrochloride (5 mg/kg of body weight) and xylazine hydrochloride (6 mg/kg of body weight) (Seal and Kreeger 1987) and equipped with radio-collars (Wagener Telemetrieanlagen) that weighed 220 g. The effect of xylazine was reversed with atipamezole hydrochloride (0.5 mg/kg).

The radio-collared lynx were located twice a day – once during daylight hours and once at dusk or at night. The radio-tracking was facilitated by a network of forest roads and forest compartment lines (grid 533 × 533 m). Locations were taken by triangulation. If possible, we aimed at determining as precise a position of the lynx as possible by approaching the animals up to 100 m while still staying on the road. Resting sites were determined in cases when lynx stayed in one location inactively for ≥ 1 hour during daylight hours. Potential kill sites were determined by a lynx remaining active in the same location for ≥ 2 nights. Usually more than 3 bearings were taken and superimposed on 1:50 000 topographic maps to the nearest 50 m.

After the lynx left the site we searched it for remnants of kills or signs of resting lynx (tracks in snow, lynx hair at a bed site). Once kill remains were found, we tried to determine the actual location of the kill site, as lynx may drag prey carcasses several tens of meters to conceal them (Jędrzejewski *et al*. 1993). If no actual kill site could be found, we focused on the site of kill consumption, as this was easy to discern, even if prey had been completely eaten, due to the large amount of hair plucked by lynx from their prey. Since around seventy percent of successful lynx hunts are performed over a distance of 20 m (Haglund 1966), we described environmental characteristics of the site in a radius of 50 m from the kill to ensure that all potentially important features are considered.

In the case of resting sites, we aimed to find the exact lynx bed site. However, if that was not possible due to impenetrability of the area (very dense thickets), we described its characteristics at the nearest accessible spot assuming that it was representative for the actual bed site, due to homogeneity of the habitat. Resting sites of females rearing young kittens (before they started to follow the mother) were not taken into consideration in this study.

A total of 116 hunting and 88 resting sites were found (Fig. 1). Forty four hunting and 28 resting sites were of males, while 56 hunting and 57 resting sites were of females. The remaining 16 hunting and 3 resting sites were of lynx of unknown sex. We described the sites in a radius of 50 m from a focal spot (kill or bed site) with the following seven characteristics:

(1) Forest type – of 16 forest associations found in the BPF (Kwiatkowski 1994, Matuszkiewicz 2001), six general types were distinguished for easy identification, based on fertility, humidity and dominant tree species:
  (a) oak-lime-hornbeam forest – occurring on fertile, humid soil, dominated by lime, hornbeam and oak;
  (b) ash-alder forest – occurring along rivers on fertile and humid soil, dominated by ash and black alder;

(c) bog alderwood – occurring on fertile soil inundated during most of the year with stagnant water, dominated by black alder and ash trees;

(d) coniferous forest – occurring usually (except in plantations) on arid soil, dominated by Scots pine and Norway spruce;

(e) mixed forest – consisting of both deciduous and coniferous trees;

(f) other (including rare habitats: eg marshy pine forest, marshy spruce forest, birch *Betula* sp. forest).

(2) Forest age class – four classes were distinguished: I – thicket (5–20 years old); II – young stand (20–50); III – middle-aged stand (50–100); IV – mature stand (> 100 years old).

(3) Glade – presence and type of forest glade. Small glades (≤ 1 ha) of different character (fresh clear-cut, old regenerating clear-cut, meadow, hunting plot, crop field) were considered. Three classes were distinguished: 0 – no glade, 1 – glade overgrowing with vegetation or regenerating trees, 2 – fresh clear-cuts without cover.

(4) Tree density – we estimated visually the tree density according to a subjective scale of the span among trees from 0 to 10 with increasing values expressing an increasing span.

(5) Undergrowth – degree of undergrowth development; we established a subjective scale of intensity of undergrowth layer that included herbaceous vegetation, brushwood and shrubs: 0 – no cover, 1 – sparse cover, 2 – medium cover, 3 – intensive cover, noted with accuracy of 0.5 degree.

(6) Complexity – a scale expressing number of structures that may potentially facilitate stalking prey that included: uprooted trees, fallen logs and clumps of dense shrubs. The complexity was given as 0 (no structures) or 1 – 3 (representing the number of types of structure present). We used this trait only when analysing hunt-

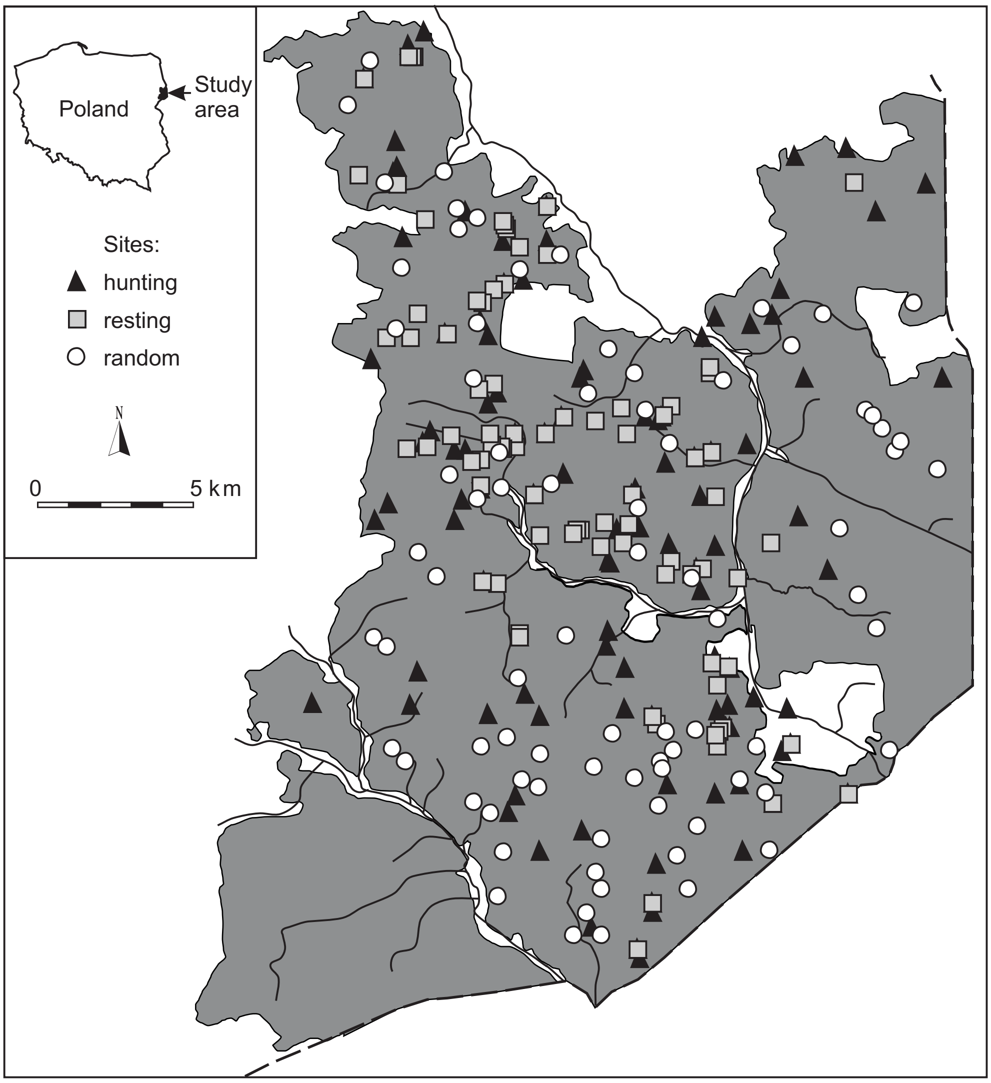

Fig. 1. Map of the study area – the Białowieża Primeval Forest, Poland showing distribution of hunting and resting sites of Eurasian lynx (determined by radio-tracking 3 males and 3 females and snow-tracking) and random sites.

ing sites because we considered it to be specifically related to this behaviour.

(7) Degree of visibility – percentage of a 0.5 × 1 m board (with 10 red and white rectangles, each representing 10%) visible from a distance of 50 m in four directions: N, S, W, E. The board was placed exactly at the prey, bed or random site. Visibility was measured with an accuracy of 5% and was averaged from all directions (Nudds 1977).

For comparison with hunting and resting sites, we generated a set of random points within an area formed by geographic coordinates of real lynx-sites using a Microsoft Excel software spreadsheet. After excluding the points that fell outside the forest area (eg villages and crop-land), 81 points were taken for analysis (Fig. 1). The coordinates were imported to a GPS receiver and the points were located in the field with an accuracy of approximately 10 m and the site character described. We described each random site twice – in the summer (May–October) and in the winter (November–April), in order to consider changes in habitat characters dependent on the development of foliage and vegetation.

Statistical analysis

We pooled data from both sexes, because the number of individuals was too low for conducting analyses in males and females separately (Manly *et al*. 2002). To test for differences between habitat variables at lynx-used sites and random sites we applied a Mann-Whitney *U*-test (in the case of continuous variables) and a *G*-test for goodness of fit (in the case of categorical variables) in both seasons separately.

For an estimation of the relative importance of variables at lynx-used sites we conducted a forward stepwise logistic regression analysis (LRA) (Manly *et al*. 2002). We aimed at constructing a model including the most powerful variables that predict the uniqueness of the lynx sites. We set a tail probability for inclusion of variables into the model at $p < 0.01$.

Results

Summer hunting sites

Only three habitat variables at hunting sites in the summer were different from those at random sites: complexity, glade and visibility (Table 1). The hunting sites were characterized by significantly higher complexity (Mann-Whitney *U*-test: $Z = -3.35$, $n_1 = 46$, $n_2 = 81$, $p < 0.001$). In the majority of hunting sites (57%, $n = 66$, two seasons pooled due to a lack of differences) there were two or three types of structures whereas in 70% ($n = 57$) of random sites none or one type was observed only (*G*-test for goodness of fit: $G = 14.6$, df = 1, $p < 0.001$) (Fig. 2). In the summer, lynx hunting sites were located in the vicinity (0 – 50 m) of forest glades more frequently than expected from their availability ($G = 21.2$, df = 1, $p < 0.001$) (Table 2). Furthermore, the majority (91.7%) of glades associated with hunting sites

Table 1. Habitat characteristics (mean ± SD) associated with lynx summer ($n = 46$) and winter ($n = 70$) hunting sites vs random sites ($n = 81$) in Białowieża Primeval Forest, Poland, 2004–2006. [1] – number of structures at the site, [2] – scale from 0–3 with accuracy of 0.5 degree, [3] – *G*-test for goodness of fit, [4] – Mann-Whitney *U*-test.

Variable	Hunting site		Random site			*p*	
	Summer	Winter	Summer	Winter	Whole year	Summer	Winter
Forest type (%)							
oak-lime-hornbeam	43	39			38	> 0.5[3]	> 0.5[3]
bog alderwood	13	14			14		
ash-alder	8	7			9		
coniferous	15	29			22		
mixed	21	11			17		
Forest age class (%)							
I	10	11			9	> 0.5[3]	> 0.9[3]
II	27	22			25		
III	43	36			37		
IV	20	31			29		
Glade (%)	52	30			21	< 0.001[3]	> 0.2[3]
Complexity[1]	1.7 (± 0.94)	1.7 (± 0.88)			1.1 (± 0.85)	< 0.001[4]	< 0.001[4]
Tree density (m)	3.5 (± 1.82)	4.1 (± 1.87)			3.5 (± 1.46)	> 0.5[4]	< 0.05[4]
Undergrowth[2]	1.8 (± 0.98)	1.1 (± 0.89)	1.6 (± 0.94)	0.8 (± 0.76)		> 0.2[4]	< 0.05[4]
Visibility (%)	23 (± 26.0)	37 (± 29.1)	33 (± 29.1)	54 (± 31.8)		< 0.05[4]	< 0.01[4]

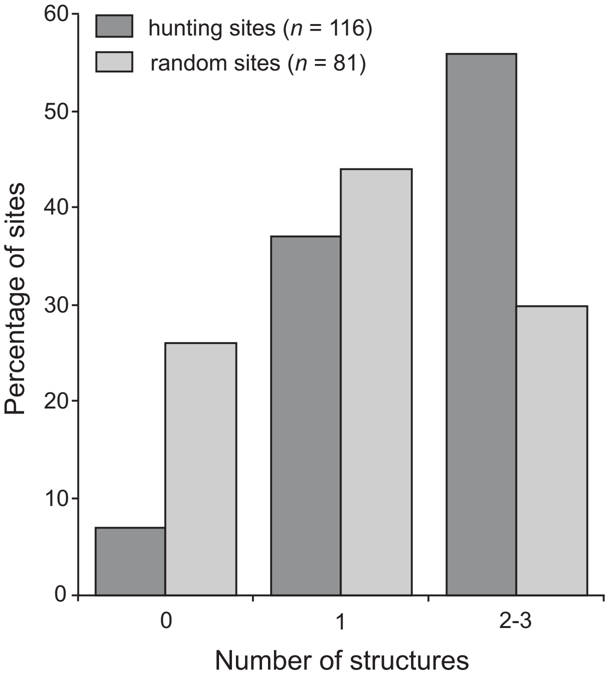

Fig. 2. Percentage of lynx hunting sites and random sites in relation to complexity of the environment (number of structures at the site which facilitated the stalking of prey) in Białowieża Primeval Forest, Poland, 2004–2006.

were small, old clearcuts overgrown with regenerating woody species and herbaceous vegetation, or other forest glades with herb cover. On the other hand, nearly equal percentages of random sites occurred at overgrowing glades and fresh clear-cuts, which differed significantly from the hunting sites (G = 8.3, df = 1, $p < 0.01$) (Table 2). Mean (± SD) area of the glades (n = 39, two seasons pooled) associated with hunting sites was 0.6 ± 1.1 ha (range: 0.01–5 ha). Majority of glades (71%) were ≤ 0.5 ha. The visibility at hunting sites was significantly lower than at random sites ($Z = -2.12$, $n_1 = 46$, $n_2 = 81$, $p < 0.05$) (Table 1). No preference for type or age of forest was found.

The best model of the forward stepwise LRA produced in the third step contained two variables contributing significantly to the classification of summer hunting sites: complexity and glade (Table 3). Based on that model, 58% of the hunting sites and 90% of random sites were classified correctly.

Winter hunting sites

Hunting sites during winter were characterized by higher complexity ($Z = -6.80$, $n_1 = 70$, $n_2 = 81$, $p < 0.001$), richer undergrowth ($Z = -2.01$, $p < 0.05$), lower visibility ($Z = -3.19$, $p < 0.01$) and lower density of trees ($Z = -2.16$, $p < 0.05$) than at random sites (Table 1). No particular forest type or age was selected. In contrast to summer, forest glades did not appear to significantly affect the choice of hunting sites in winter (G = 2.14, df = 1, $p > 0.1$).

The best model provided in the second step of the LRA contained only one variable contributing to the classification of lynx hunting sites in the winter: complexity (Table 3). It classified correctly 70 and 71% of hunting and random sites respectively.

Kill sites vs caching sites

At 25 hunting sites we were able to determine exact kill sites of large prey by lynx and compare their characteristics to those sites where prey was cached. Due to the small sample size, we pooled these records from both seasons

Table 2. Comparison of the location of Eurasian lynx hunting sites and random sites relative to glades inside the forest (numbers in parentheses are percentages).

Site	Glade		No glade	Total
	Overgrowing	Fresh clear-cut		
Hunting				
Summer	22 (48)	2 (4)	22 (48)	46 (100)
Winter	17 (24)	4 (6)	49 (70)	70 (100)
Random	9 (11)	8 (10)	64 (79)	81 (100)

Table 3. Results of logistic regression analysis of habitat variables describing the Eurasian lynx summer (n = 46) and winter (n = 70) hunting sites and random sites (n = 81) in Białowieża Primeval Forest, Poland.

Variable	Wald statistic	p	% of correct classifications	
			Hunting	Random
	Summer			
Complexity	11.7	0.0006	58	90
Glade	11.6	0.0007		
	Winter			
Complexity	18.1	< 0.0001	70	71

for analysis. The comparison revealed significant differences in tree density, undergrowth and visibility between kill and caching sites (Table 4). Kill sites were characterized by greater mean distance between trees and poorer undergrowth cover, which results in generally higher visibility than at caching sites. On the other hand, the complexity at both sites was equal. Carcasses (n = 25) were dragged from 2 to 150 m (mean ± SD: 33 ± 39.2 m) from kill sites. Kill sites from which prey was pulled further than the average dragging distance (n = 8) were characterized by higher visibility (mean ± SD: 67 ± 20.6%) than those with shorter than average dragging distance (n = 17; 39 ± 30.4%) (U = 31, $p < 0.05$).

Summer resting sites

Summer resting sites were characterized by considerably lower visibility and higher tree density than random sites (Mann-Whitney U-test: $Z = -6.24$, $n_1 = 46$, $n_2 = 81$, $p < 0.001$, $Z = -4.08$, $p < 0.001$ respectively) (Table 5). The undergrowth was more open than random sites ($Z=-2.61$, $p < 0.01$), but was significantly richer when compared to winter resting sites ($Z = -2.03$, $n_1 = 46$, $n_2 = 41$, $p < 0.05$) (Table 5). The share of forest types was different between resting and random sites ($G = 10.6$, df = 4, $p < 0.05$), with a relatively higher proportion of oak-lime-hornbeam and ash-alder forest at resting sites (Table 5). The coniferous and bog alderwood forests were used less than found at random. There was a significant difference in the distribution of forest age classes between the two samples of sites ($G = 30.7$, df = 3, $p < 0.001$ Table 5), with the class I clearly selected for resting ($G = 29.0$, df = 1, $p < 0.001$).

The best model produced in the fourth step of the LRA contained three variables contributing significantly to the classification of lynx resting sites in the summer: visibility, undergrowth and coniferous forest (Table 6). Seventy six percent of resting sites and 91% of random sites were classified correctly based on that model.

Table 4. Microhabitat characteristics (mean ± SD) associated with the ungulate killing and caching sites of Eurasian lynx. The differences were tested with Wilcoxon test.

Variable	Site		p
	Killing	Caching	
Tree density (m)	4.1 ± 2.1	3.5 ± 1.7	0.046
Undergrowth	1.2 ± 1.0	1.5 ± 1.1	0.028
Complexity	1.5 ± 0.7	1.5 ± 0.9	0.827
Visibility (%)	47 ± 30	29 ± 30	0.003

Table 5. Habitat characteristics (mean ± SD) associated with lynx summer (n = 46) and winter (n = 41) resting sites vs random sites (n = 81) in Białowieża Primeval Forest, Poland, 2004–2006. [1] – scale from 0–3 with accuracy of 0.5 degree, [2] – *G*-test for goodness of fit, [3] – Mann-Whitney *U*-test.

Variable	Resting sites		Random sites			p	
	Summer	Winter	Summer	Winter	Whole year	Summer	Winter
Forest type (%)							
oak-lime-hornbeam	51	35			38	< 0.05[2]	< 0.05[2]
bog alderwood	6	6			14		
ash-alder	17	4			9		
coniferous	13	38			22		
mixed	13	17			17		
Forest age class (%)							
I	41	54			9	< 0.001[2]	< 0.001[2]
II	18	19			25		
III	18	16			37		
IV	23	11			29		
Glade (%)	17	5			21	> 0.5[2]	< 0.02[2]
Tree density (m)	2.4 (± 2.04)	1.5 (± 1.13)			3.5 (± 1.46)	< 0.001[3]	< 0.001[3]
Undergrowth[1]	1.1 (± 1.20)	0.5 (± 0.98)	1.6 (± 0.94)	0.8 (± 0.76)		< 0.01[3]	< 0.01[3]
Visibility (%)	5 (± 14.2)	6 (± 15.2)	33 (± 29.1)	54 (± 31.8)		< 0.001[3]	< 0.001[3]

Winter resting sites

All variables recorded at resting sites during winter differed from those at random sites (Table 5). The resting sites were characterized by much lower visibility (Mann-Whitney *U*-test: $Z = -7.25$, $n_1 = 41$, $n_2 = 81$, $p < 0.001$) (Table 5), higher tree density ($Z = -6.45$, $p < 0.001$) and poorer undergrowth ($Z = -2.87$, $p = 0.004$) than random sites. Visibility at resting sites did not differ between seasons ($Z = 0.34$, $n_1 = 46$, $n_2 = 46$, $p = 0.73$), whereas it did at random sites, as expected from seasonal differences in vegetation and foliage (Wilcoxon test: $Z = 6.9$, $p < 0.001$). The share of forest types at winter resting sites did not correspond to their availability observed in a random sample ($G = 9.7$, df = 4, $p < 0.05$ Table 5). This was mostly due to heavy use of coniferous forest and under-represented bog alderwood and ash-alder forest for resting sites. There were also differences in forest age classes between lynx and random sites ($G = 53.4$, df = 3, $p < 0.001$ Table 5), which resulted from overrepresentation of thickets (forest age class I) mostly consisting of pine and spruce plantation. Over a half (54%) of winter resting sites were found in thickets, whereas only 9% of random sites were located in this age class ($G = 50.7$, df = 1, $p < 0.001$). Lynx rested in thickets more frequently during winter than summer (Table 5) although this difference was not statistically significant ($G = 3.4$, df = 1, $p = 0.066$).

The LRA provided the best model in the third step that contained only two variables contributing significantly to classification of lynx resting sites in the winter: forest age class I and visibility (Table 6). Eighty three percent of the resting sites and 93% of random sites were classified correctly based on that model.

Choice of resting sites in relation to kill sites

In 30 cases, we were able to determine distance between resting site and the currently-used kill. As visibility was one of the most important habitat features for resting lynx, we compared it between kill sites located close (< 50 m) and far (> 50 m) from the resting site to show if conditions at kill sites determined the choice of resting site. Lynx rested from 0 to 2000 meters from their prey. Visibility at kill sites when lynx rested further than 50 m away (n = 9) was 39 ± 26.0% (mean ± SD), which was three times greater than at kill sites when lynx stayed close to it during the day (n = 21; 13 ± 20.0%, Mann-Whitney *U*-test: $U = 30$, $p < 0.01$).

Table 6. Results of a logistic regression analysis of habitat variables describing Eurasian lynx summer (n = 46) and winter (n = 41) resting sites and random sites (n = 81) in Białowieża Primeval Forest, Poland, 2004–2006.

Variable	Wald statistic	p	% of correct classifications	
			Resting	Random
	Summer			
Visibility	19.9	< 0.0001		
Undergrowth	9.1	0.0025		
Coniferous forest	7.1	0.0078	76	91
	Winter			
Visibility	16.3	0.0001		
Age class I	11.3	0.0007	83	93

Discussion

Habitat use has often been the subject of research for various felid species, most likely because of a strong conviction that habitat fragmentation and alteration is one of the most serious threats to carnivores (Seidensticker 1986, Logan and Sweanor 2001). So far, numerous studies have been devoted to this problem (eg Koehler and Hornocker 1991, Poole *et al*. 1996, Dickson and Beier 2002, Mowat and Slough 2003, Kautz *et al*. 2006, Niedziałkowska *et al*. 2006), however, they mostly considered habitat selection at broad scales, such as state, population or home range. Our study is among relatively few which provide data on detailed micro-habitat use by large felids (Anderson 1990, Palomares 2001, Kolowski and Woolf 2002), and is the only study to date on the Eurasian lynx which identifies habitat characteristics at hunting and resting locations.

In most cases, we were not able to determine precisely the sites where the prey was actually attacked and killed, so that the general description of hunting sites has been focused on the surroundings of sites where prey was cached. However, because we noted the habitat characteristics within a radius of 50 m from the prey, they could also embrace potential kill sites, as lynx usually drag their prey for less than 50 m (Jędrzejewski *et al*. 1993, this study). Therefore, the traits of the kill site were most likely included. Nevertheless, as shown by the comparison between a sub-sample of real killing sites with caching sites, some differences were still discernible. The trees were sparser and undergrowth more open at kill sites, which resulted in higher visibility than at caching sites. The differences are reasonable because these traits provide a better chance to spot prey, as well as enough space for manoeuvering and safety for the predator during a violent attack. This finding is concordant with observations made by O'Donoghue *et al*. (1998), who found that Canada lynx *Lynx canadensis* and coyotes *Canis latrans* are ineffective at hunting in very dense habitats. In contrast, pumas *Puma concolor* were reported to hunt preferably in areas with dense undergrowth and poor visibility (Husseman *et al*. 2003). We suppose, however, that this might have resulted from the assessments done at caching rather than kill sites, since in our study the general visibility at hunting sites was also lower than in a random sample.

Both killing and caching sites were commonly characterized by equally high complexity. Complexity (which included a number of different structures such as root plates, fallen logs and branches, shrub patches) was clearly the most significant difference between hunting sites and random sites during both winter and summer. This corresponds very well with the typical felid hunting technique of approaching prey undetected and launching an attack from as close as possible (Haglund 1966, Kruuk 1986, Sunquist and Sunquist 1989). The importance of various physical structures as cover for stalking has been suggested in various cat studies (Koehler and Hornocker 1991, Murray *et al*. 1995, Dickson and Beier 2002). An earlier study on lynx in BPF, based on snow-tracking by Jędrzejewski *et al*. (1993), showed the extensive use of root plates and fallen logs by foraging lynx. However, our research was first to assess the selection for these structures relative to their availability in hunting felids.

Site complexity also appears to be critical for caching prey as it was the only characteristic that did not differ from kill sites. The importance of complexity (eg with numerous fallen trees that resulted in generally poor visibility) was also seen by the fact that lynx dragged their prey away from those kill sites characterized by high visibility. This strategy, which involves caching prey in secluded places, has likely evolved in various felids, which usually do not consume the entire carcass immediately after a kill, in order to minimize losses of large prey to scavengers (see Sunquist and Sunquist 2002 for review). In the BPF, 40–80% of lynx prey was found to be utilized by various scavengers, 60% of which were wild boar (*Sus scrofa*) that were able to consume it entirely (Jędrzejewska and Jędrzejewski 1998, Selva *et al*. 2005).

In the summer, lynx selected sites in the vicinity of forest glades for hunting. This can be explained in two ways. Firstly, forest edge may serve as effective cover for a predator approaching from inside the forest, making it hard to be detected by ungulates foraging in the open. Furthermore, the prey can be easily seen by the predator, thus increasing the likelihood of the prey's successful capture. Secondly, forest glade (among other ecotone zones) is a favorable habitat for roe deer, the lynx's main prey in BPF (Jędrzejewski *et al*. 1993, Okarma *et al*. 1997), as it provides high quality forage and shelter (Cederlund 1983, Tufto *et al*. 1996). These resources are particularly abundant in glades with well developed vegetation cover. Indeed, a majority (92%) of glades where lynx hunted consisted of old clear-cuts overgrown with herbs and regenerating trees, as well as other types of forest glades with herb cover (eg forest meadows). The value of glades as foraging areas for herbivores is supported by the fact that they were not selected by lynx during winter when vegetation cover was largely not available there. Using edges adjacent to open habitat was also reported for pumas (Logan and Irwin 1985, Dickson and Beier 2002) and Canada lynx (Poole *et al*. 1996). Mowat *et al*. (2000) also concluded that regrowth of vegetation on previously logged areas may provide quality habitat for Canada lynx due to its use by snowshoe hares *Lepus americanus*.

The characteristics of resting sites that were most important in our analyses suggest that these sites provided lynx with security and shelter against unfavorable weather conditions. This result is all the more understandable taking into consideration that lynx spend a considerable part of the day inactive (Schmidt 1999), when they are thus vulnerable to disturbance or weather extremities for long periods. Very poor visibility at resting sites, which makes lynx virtually undetectable from a very short distance, was the strongest variable describing lynx resting sites in both seasons. However, different factors contributed to low values of this characteristic in each season. While in winter it was clearly related to location of resting sites in dense thickets, poor visibility in summer most likely resulted from the use of both thickets and dense undergrowth to similar extents. Nevertheless, the role of the undergrowth can be misleading when taking the results of the LRA and pair-wise comparisons directly, as in fact the undergrowth appeared to be more open at summer resting sites relative to random ones. In reality, the undergrowth was still relatively dense compared to winter resting sites, but its average low value resulted from the fact that the lynx also heavily used thickets lacking undergrowth. On the other hand, lynx also frequently used oak-lime-hornbeam and ash-alder forests during summer when these habitats had a particularly dense undergrowth (Matuszkiewicz 2001). Fallen dead trees could also have contributed to low visibility in a number of cases, but we didn't specifically account for this during our survey of resting sites.

Studies conducted on other lynx species (Iberian lynx *Lynx pardinus*, bobcat *Lynx rufus* and Canada lynx) also showed that sites characterized by dense vegetation cover, such as thick undergrowth, tree plantations and naturally regenerating thickets, were preferred by these species for resting (McCord 1974, Anderson 1990, Palomares 2001, Kolowski and Woolf 2002, Chamberlain *et al*. 2003, Mowat and Slough 2003). Our results on Eurasian lynx fit very well into this pattern. The particular importance of coniferous thickets (pine and spruce plantations) in winter in our study may reflect its protective value against harsh weather conditions, but also the lack of other suitable cover due to missing foliage.

In contrast to our results, some observations of the resting sites of lynx (as well as other large cats) based on snow-tracking (eg Pikunov and Korkishko 1992, Matyushkin and Vaisfeld 2003) seem to suggest that they always have good visibility to allow the predator to watch for potential prey or danger. This discrepancy likely arises from the fact that snow-tracking does not account for time spent utilizing the site, so that these descriptions may have involved short rest events during hunting or vigilance at kill sites. During a real sleep, which sometimes takes several hours, as recorded by radio-tracking (Schmidt 1999), the resting site has to be hardly accessible from all directions to ensure full security for an unaware lynx.

Killing large ungulate prey by lynx is followed by a decrease in activity that may last several days (Okarma *et al*. 1997, Schmidt 1999). Whether this inactivity near a carcass may be partly related to safeguarding the kill from scavengers, is unclear. We attempted to answer this by comparing resting sites at kill sites with those that were far away from them. We found that, when characteristics of caching sites were suitable for resting (ie low visibility), the lynx remained there for the diurnal rest. Otherwise, they preferred to rest in more distant places which offered secure concealment, thus putting a higher price on their own safety. Therefore, we suggest that if lynx remain at a kill site, it does not result from a need to guard prey, but is rather caused by sufficient cover providing the predator with safe resting conditions.

It is remarkable that lynx in BPF didn't show a particular preference for any of the forest types during hunting. This result is, however, due to the fact that, despite the high diversity of forest types, the environment inside the forest block is relatively homogenous in terms of its general formation. Fine variations in habitat structure seem to play a more important role by meeting some specific requirements for lynx. Similarly, the selection by lynx of oak-lime-hornbeam, ash-alder and coniferous forests for resting in particular seasons seems to be an effect of vegetation structure rather than species composition. For instance, the use of coniferous forest in winter for resting was driven by the selection of thickets of pine and spruce plantations.

Another important issue that emerges from our research is that none of the identified characteristics would be significant by themselves. High quality habitat for lynx is represented by a diversity of forest components interspersed with one another. Other than structural complexity (expressed by an abundance of fallen logs and branches, root plates, and patches of shrubs), such a mosaic should consist of small glades (subject to natural succession) and more open stands to allow effective hunting, as well as dense thickets and undergrowth for secure resting. Although we were not able to show if the availability of those sites may limit the lynx population, we are convinced that co-occurrence of various suitable habitats providing both hunting and resting conditions is one of essential factors for lynx survival. If the lynx has to travel long distances from the kill to the resting site, it will increase its energetic expenditure and the risk of loosing the food caches to scavengers.

The limited availability of suitable stalking cover may affect hunting success, home range size and population numbers in felids, even if prey populations are not limited (Kruuk 1986). Furthermore, restricted access to good quality resting sites is very likely to affect populations of carnivores (Beja 1996, Halliwell and Macdonald 1996). Thus, improved knowledge of Eurasian lynx habitat requirements is of great importance for the conservation of the species. We believe that lynx preferences observed in BPF, on account of its unique diversity, can be regarded as the benchmark and their implications should be kept in mind whenever conservation measures are taken. The information presented here could have direct conservation applications through guiding the appropriate restructuring of simplified forest stands to better meet the biological requirements of the Eurasian lynx. The results, however, should not be misinterpreted as the absolute conditions for lynx survival, as this felid is known to occur in diverse habitats (Nowell and Jackson 1996). They should rather be understood as conditions for increasing the carrying capacity of the deciduous forest habitat (Fernández *et al*. 2003) that may appear particularly limiting, when acting in concert with such factors as habitat fragmentation or prey depletion.

As Linnell *et al*. (2001) have shown for Scandinavia, the sizes of protected areas are not sufficient for effective conservation of the lynx and the same is very likely to be true for other parts of Europe. Thus, the conservation of this felid will mostly occur in managed forests, where the structure of stands is usually much simpler than that potentially encountered in protected habitats. We suggest the following measures, which take into account lynx requirements, that should be employed by forest managers in regions where Eurasian lynx are to be conserved:

(1) enriching forest stands with undergrowth,
(2) retaining a substantial amount of fallen dead wood (*sensu* Czeszczewik and Walankiewicz 2006),
(3) logging using only small (< 0.5 ha) clear-cuts,
(4) leaving small forest glades (including clear-cuts) for natural regeneration or replanting according to local habitat conditions,
(5) diversifying the age structure and density of stands,
(6) restructuring the forest stands to create a mosaic of all forest components.

These measures should be considered both for the restoration of modified habitats and the planning of ecological corridors to improve habitat connectivity. We believe that modifying forest management according to lynx habitat requirements may be an important factor influencing lynx density in areas where the species still occurs and facilitating the expansion of the species' range. An assessment of the availability of microhabitat features in the landscape should be also considered before the implementation of future Eurasian lynx reintroduction projects (eg Hetherington and Gorman 2007).

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