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Original article

Foraging sites of Eurasian lynx *Lynx lynx*: relative importance of microhabitat and prey occurrence

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The choice of foraging areas by large carnivores can be driven both by prey abundance and landscape attributes and it is likely that the relative importance of these two components changes on different spatial scales. In the Bohemian Forest (southwestern Bohemia, Czech Republic), we focused on the effect of microhabitat. We tested if Eurasian lynx *Lynx lynx* hunted merely in areas where its main prey, roe deer *Capreolus capreolus* and red deer *Cervus elaphus*, occurred ('prey-occurrence hypothesis') or if there were fine-scale habitat features that increased prey catchability ('landscape hypothesis'). Fine-scale habitat features were recorded at sites where an ungulate had been killed and located using telemetry or by chance (in winter: $N = 29$ roe deer, $N = 18$ red deer; in summer: $N = 33$ roe deer, $N = 5$ red deer). We compared these features with those recorded at locations where live red or roe deer were recorded using telemetry ($N = 100$ per species per six-month period). In winter, lynx killed both roe and red deer at sites where there was a greater heterogeneity in terms of visibility than at sites where live ungulates were recorded, i.e. at kill sites there were both good stalking cover and good visibility. In addition, the risk of predation for red deer was negatively correlated with tree density. In summer, the risk of predation for roe deer was not associated with any of the habitat variables measured. Thus, the presence of a kill was associated with particular fine-scale habitat features in winter, while in summer it was simply associated with where prey occurred. A deeper understanding of the type of habitat favoured by lynx is fundamental to the management and conservation of this species. Based on our results, forest management should ensure that the level of habitat heterogeneity is favourable for lynx.

Key words: Eurasian Lynx, Lynx lynx, microhabitat, predation, red deer, roe deer, stalking cover

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Hunting success is one of the most important factors determining the fitness of carnivores (Pyke et al. 1997, Sunde & Kvam 1997, Melville et al. 2004) and is dependent upon several factors, including the quality of foraging habitats (Krofel et al. 2007). Carnivore foraging decisions are driven by natural selection to optimise nutrient intakes at the minimum energy expenditure and at the least risk to the predator (Krebs & Davies 1993). The choice of the most suitable hunting areas can be driven both by prey abundance ('prey-abundance hypothesis'; Hopcraft et al. 2005) and landscape attributes influencing prey catchability ('landscape hypothesis'; Hopcraft et al. 2005). In the literature, there are several studies supporting the first hypothesis (e.g. Litvaitis et al. 1986, Murray et al. 1994, Palomares et al. 2001, Spong 2002, Keim et al. 2011) and the second hypothesis (e.g. Hebblewhite et al. 2005, Hopcraft et al. 2005, Balme et al. 2007, Fuller et al. 2007, Maletzke et al. 2008).

This indicates that the ideal strategy is a combination of these two factors and that their relative importance depends on the species, the environmental conditions (Fuller et al. 2007) and the spatial scale considered (Bowyer & Kie 2006, Panzacchi et al. 2009). In fact, as suggested by the concept of hierarchical selection (Johnson 1980), the same animal species may even select certain habitat features on one spatial scale and avoid them on another scale (Rachlow & Bowyer 1998, reviewed in Bowyer & Kie 2006). Thus, for a better understanding of the habitat requirements of a species it may be necessary to sample on different scales (Bowyer & Kie 2006). There are several studies that show that investigating habitat selection only on a large scale can mask the importance of small-scale differences in habitat (e.g. Bowyer et al. 1999, reviewed in Bowyer & Kie 2006, Panzacchi et al. 2009) and lead to wrong management decisions.

Characteristics of the microhabitat are likely to be more important in the case of stalking predators (most felids) than of coursing predators, such as canids (Husseman et al. 2003). In the last decade, several studies have dealt with microhabitat selection by large felids, including all species belonging to the genus *Lynx*: Iberian lynx *Lynx pardinus* (Palomares 2001), bobcat *Lynx rufus* (Kolowski & Woolf 2002), Canadian lynx *Lynx canadensis* (Maletzke et al. 2008) and Eurasian lynx *Lynx lynx* (Podgorski et al. 2008).

The Eurasian lynx is a forest species (Niedzialkowska et al. 2006, Basille et al. 2008, 2009, Rozylowicz et al. 2010) and its main prey in most of Europe is roe deer *Capreolus capreolus* (Jedrzejewski et al. 1993, Okarma et al. 1997, Sunde & Kvam 1997, Jobin et al. 2000). On a subhome-range scale, Basille et al. (2009) found that lynx preferred areas that include large proportions of forest and areas where roe deer are abundant. On a large scale, therefore, both prey density and habitat features play a role in habitat selection by lynx. To date, there is only one study on habitat selection by Eurasian lynx carried out on a fine spatial scale (Podgorski et al. 2008). This study indicates that both habitat complexity and visibility are important for lynx when hunting prey. Krofel et al. (2007) also describe the microhabitat at lynx kill sites in Slovenia and report that they occur mainly in moderately rugged terrain with sparse cover. Nevertheless, this second study only considers habitat characteristics and does not investigate habitat selection, i.e. it does not compare microhabitat features at kill sites with those at random sites.

Although these two studies indicate that habitat features are important in determining where lynx hunt for prey, none of them tested for the potential effect of microhabitat use by the prey. In fact, certain habitat features may actually help lynx to successfully stalk and kill prey. However, it is also possible that such features are attractive for their prey, and therefore lynx select such habitats because that is where they are most likely to encounter ungulates (Krofel et al. 2007). Indeed, there are studies which suggest that features like big rocks, uprooted trees or dense clumps of shrubs can allow a predator to approach prey without being noticed (Palomares 2001, Podgorski et al. 2008). Therefore, these features may be avoided by prey (Moreno et al. 1996). On the other hand, other studies indicate that the same features may represent shelter or important sources of food for ungulates (Pierce et al. 2004, Mao et al. 2005, Ratikainen et al. 2007, Adrados et al. 2008). Consequently, even on a fine scale, the high frequency of certain habitat features at lynx kill sites recorded by Podgorski et al. (2008) and Krofel et al. (2007) may be explained in two ways; these features may: 1) increase prey catchability ('landscape hypothesis') or 2) may be correlated with a higher occurrence of ungulates ('prey-abundance hypothesis' or, more properly on this scale, 'prey-occurrence hypothesis').

In our study, we attempted to distinguish between these two alternatives. We determined whether the microhabitat features that provided lynx with good stalking cover were also frequently found in the places used by the lynx's main prey, roe and red deer *Cervus elaphus*, thus supporting the 'prey-occurrence hypothesis', or if they were more often present at places where lynx successfully killed ungulates, thus supporting the 'landscape hypothesis'. In addition, we determined whether there were any differences between the seasons, associated with changes in the diet of lynx (Fejklová 2002, Odden et al. 2006) or with different weather conditions (such as snow cover; Ratikainen et al. 2007, Kittle et al. 2008).

Material and methods

Study area

Our study was conducted during 2007-2009, mainly in the Czech part of the Bohemian Forest (48°55'-49°17'N, 13°13'-13°47'E) on the mountain range along the border between the Czech Republic and Germany. The core area of the Bohemian Forest (the Šumava Mountains) includes a typical relict high mountain plateau surrounded by deep valleys of brooks and rivers with rocky slopes. It encompasses two adjoining national parks, Šumava and Bavarian Forest, with a total area of ca 1,000 km^2. Both national parks are surrounded by a Protected Landscape Area (on the Czech side) and nature parks (on the Bavarian side) which together cover ca 4,300 km^2. Even though the foothills surrounding the Protected Landscape Area host several small human settlements, the mean human population density is low (about 20 individuals/km^2 and only 1.9 individuals/km^2 in the central parts; Wölfl et al. 2001, Mašková et al. 2003).

On the Czech side, the altitude of the Bohemian Forest ranges between 600 and 1,378 m a.s.l. At the lowest altitude, the first snow cover generally appears at the end of October, while in the highest areas it appears as early as the first half of September; its average duration is seven months. Strong windstorms frequently occur in this region, often resulting in the creation of almost treeless areas in spruce stands. The forest cover of the whole area is ca 60%, but reaches 90% in the central parts (Svobodová 2001, Zatloukal 2001). Most of the original natural mixed forests were replaced by Norway spruce *Picea abies* plantations. The remains of the native forest ecosystem survived as a network of islands of different forest types (e.g. natural climax spruce forests, mixed beech *Fagus silvatica*-silver fir *Abies alba*-Norway spruce forests and relict pine *Pinus silvestris* forests). Large parts of forest as well as some secondary forestless areas are left to natural succession.

The Eurasian lynx is the only large carnivore species currently living in this area (Koubek & Červený 1996) and the whole study area is permanently occupied by this species. Wolves *Canis lupus* occasionally occur as single migrants (Bufka et al. 2005), while the most common carnivore is the red fox *Vulpes vulpes*, which is present in relatively high numbers throughout the whole region (Anděra & Červený 1994). The primary species of wild ungulates are red deer, roe deer and wild boar *Sus scrofa*. All these ungulate species are widely distributed in our study area and have coexisted with the lynx since the 1980s, when it was reintroduced into the Šumava National Park (Červený & Bufka 1996). In the Bohemian Forest, roe and red deer are the main prey of lynx, representing $>$ 80% of lynx kills (Fejklová 2002, Mayer et al. 2012, J. Červený, L. Bufka & E. Belotti, unpubl. data).

Data collection

Between November 2007 and May 2009, we recorded the habitat features at all locations where a dead ungulate was found and predation by lynx was determined as the cause of death (Molinari et al. 2000). The locations of ungulate kills were obtained from the following four different sources: 1) locating roe deer by radio-telemetry (radio-collared deer that were killed by lynx) between 2005 and 2008 ($N=5$), 2) locating lynx by radio-telemetry between 2000 and 2008 (prey killed by radio-collared lynx; $N = 5$), 3) occasionally finding and verifying lynx kills between 1998 and 2008 ($N = 59$) and 4) locating prey of one adult female and two adult male lynx which were monitored using GPS-telemetry between February and November 2007 and between November 2008 and May 2009 ($N = 16$). For killed prey found in previous years, we used general descriptions and photographs to verify that the habitat had remained the same and all the locations were revisited by at least one of the people who had found the kill. We excluded all the places that had undergone significant changes, which resulted in the data set described above.

To determine the effect of 'season', we divided the year into two periods, hereafter referred to as summer (from 15 April to 14 October) and winter (from 15 October to 14 April). This division was based on three factors: 1) red deer are known to use different areas in summer and winter (Georgii &

Schröder 1983, Mysterud et al. 2001, Jarnemo 2008), 2) the composition of the diet of lynx differs in summer and winter (Fejklová 2002, Odden et al. 2006) and 3) in our study area, as in the whole of Central Europe, there are big differences in the habitat features between the two seasons, especially in the deciduous shrub layer in forests and herbaceous layer in open areas. Altogether, we located 85 kill sites for at least 10 different lynx. In particular, we found 33 roe and five red deer kills in summer and 29 roe and 18 red deer kills in winter.

We recorded the same habitat features at kill sites and at two sets of locations where live roe deer and red deer were found using telemetry. In doing this, we were not interested in determining the habitat preferences of roe and red deer, which are also likely to be influenced by other habitat features, but, rather, we aimed to verify whether certain habitat features were more frequently associated with lynx kill sites or whether they were linked only to the presence of the prey. We chose the set of locations of red deer from the positions of four GPS-collared adult females, as predation by lynx on red deer is mostly limited to adult females and calves (Nowicki 1997, Okarma et al. 1997). We randomly selected 25 locations per season per animal. We therefore analysed 100 red deer locations in summer and 94 in winter (six of the 100 initial locations were inaccessible in winter due to deep snow, thus it was impossible to record the environmental data). In the case of roe deer prey, lynx did not seem to select any particular sex or age class (e.g. Okarma et al. 1997). Therefore, in order to compile the set of roe deer locations, we used the data for 25 animals (reduced to 10 in summer because some animals died during a harsh winter and some collars failed) which were studied using VHF-telemetry from 2005 to 2008. Given a total number of 100 roe deer locations per season, the number of locations for each animal was proportional to the ratio between the tracking time for this animal and the overall tracking time for all animals.

Habitat analysis

At all locations, we recorded the fine-scale habitat features that we assumed important for lynx that are hunting for prey. This was done for each location by the same person (E. Belotti) and in the proper season, according to the date when the telemetry position was recorded or the killed ungulate was found. All this data were downloaded to a portable GPS (hand-held Trimble Juno ST). We described the vegetation structure (shrub cover and tree density; Table 1) in plots of a 20-m radius, which is the distance within which more than two thirds of the attacks by lynx are successful (Haglund 1966). We recorded the presence of particular features, such as rocks, uprooted trees or coniferous branches at a height of < 1.5 m from the ground (see Table 1). We further measured the 'visibility' at each location (in terms of both whether the lynx could remain hidden from, yet see, its approaching prey) using the 'pole method' (Pierce et al. 2004): we put a 2-m-high wooden pole, divided into 10 coloured segments, at the centre of each location and then counted how many segments were $> 50\%$ hidden when observed from each cardinal direction at a distance of 20 m and a height of 1 m. We created two indices ('ground cover' and 'average deviation in stalking cover index', hereafter 'AverDevSCI'; see Table 1), representing,

Table 1. Description of the eight environmental variables that were used for the comparison of kill and live ungulate sites.

Name of variable	Unit	Description
Slope	°	Calculated using ArcGIS 9.2 (ESRI 2009) and a specific GIS layer with a 15 × 15 m-resolution (source: Český Úřad Zeměměřický a Katastrální, ČUZK, Praha, Czech Republic)
Shrub_cover	%	Mean percentage of the 20-m segment in each cardinal direction (2-m buffer) covered by shrubs
Tree_density	N/m^2	Total number of coniferous and deciduous trees/area in the 20-m radius plot
Ground_cover	index (0-4)	Number of cardinal directions in which the three lowest segments of the wooden pole (one segment = 20 cm) were completely hidden[a]
Average deviation in stalking cover index (AverDevSCI)	index (0-4.5)	Average deviation of the four values registered in the 20-m radius plot using the 'pole method' (each of the four values = number of pole segments hidden for $> 50\%$)[a]
Rocks	Categorical	P = presence of rocks ≥ 30 cm; A = absence of rocks (or presence of very small rocks)
Conifer_branches	Categorical	P = presence of coniferous branches at a height of < 1.5 m above the ground; A = absence of coniferous trees or presence of trees without branches < 1.5 m above the ground
Uprooted_trees	Categorical	P = presence of uprooted trees; A = absence of uprooted trees

[a] When observed at a distance of 20 m and at a height of 1 m.

respectively, the level of ground cover and the heterogeneity in terms of visibility at each location (i.e. presence of areas where the visibility was good and others where there was good cover for stalking).

Obviously, biases in field measurements caused by imprecision due to failure of the collars or the portable GPS had no influence on the location of kill sites (found directly in the field). In the case of live roe deer, only VHF-telemetry locations were available for our study area. Although this technique can be subject to measurement error, we were confident that the data were suitable for achieving the objective of our study because: 1) the individuals located using VHF-telemetry used our study area very compactly, which resulted in the different VHF locations forming 'dense clusters'; therefore, in the surroundings of our randomly chosen VHF locations there were, in most cases, several other VHF locations, which may partially compensate for imprecision, 2) in several cases, roe deer were actually located visually during VHF-telemetry and 3) when visiting roe deer VHF locations in the field, we found roe deer faeces at the point indicated by VHF-telemetry, which at least demonstrated that the location was actually used by a roe deer, if not specifically by the collared individual. Finally, in the case of the locations of red deer, we estimated that the possible imprecision in recordings of the collars or portable GPS could result in the position recorded in the field differing from the actual position by up to 15 m when using GPS-collars and 5 m when using portable GPS (Šustr et al. 2007, E. Belotti, pers. obs.). Therefore, the actual position would still be inside the measured plot (40-m diameter), even if part of the actual plot was excluded.

In summary, we believe that the size we chose for the plots was precise enough and, at the same time, small enough to allow us to detect, in the field, all the habitat features important for our study.

Finally, for each point we also calculated the slope (see Table 1) using ArcGIS 9.2 (ESRI 2009).

Statistical analysis

We tested for differences between locations where there were kills and those with live ungulates in terms of the eight environmental variables described in Table 1. Because some of the kill sites were found by telemetry and others by chance, we first tested for differences in the two types of sites using generalised linear models (GLM; binary response variable: 1 = located using telemetry, 0 = found by chance). We did not detect any differences in the microhabitat characteristics that were used in subsequent analyses ($P > 0.4$), apart from a marginal difference in the presence of uprooted trees, which tended to be present more often at sites located using telemetry ($P = 0.1$). Therefore, we did not distinguish between kill sites located by different methods.

Our data set included data for roe deer kill sites that were found in winter and summer and data for red deer kill sites only found in winter. Only a few red deer kills were recorded in summer ($N = 5$), hence we did not include them in the data set. Due to these limitations, we used the following modelling strategy: species-specific models were fitted separately to the roe and red deer data in the first step. Interaction effects between 'season' and all other variables (specified in Table 1) were considered in the case of roe deer in order to test for the dependence of individual variables on the context of summer vs winter. For red deer, this was not applicable, hence we focused just on the model including main effects for this species. In the next step, red and roe deer data sets for winter were merged, and all main effects and their interactions with species type were used to evaluate variation in the risk of predation. Predation models were fitted using GLM with binomial errors and a logit link function. The response variable was binary (i.e. 1/0; kill sites vs telemetry locations of live ungulates). Explanatory variables were transformed before computation, if necessary.

The correlation between explanatory variables was generally low. The absolute value of the correlation coefficient ranged between 0.001 and 0.25, with the exception of a relatively high correlation between 'shrub cover' and 'ground cover' ($r = 0.46$). Nevertheless, the variance inflation factors that were computed for every explanatory variable included in the initial model were low (i.e. ranging between 1.07 and 1.73), suggesting a low risk of problems associated with multicollinearity.

We used an automatic procedure to fit and compare all potential candidate models (i.e. including all possible combinations of explanatory variables) as implemented in R package MuMIn version 1.7.0 (Barton 2012). To avoid model overfitting and to model space on a reasonable scale, fitted models were limited to a maximum of six estimated parameters. We assessed the adequacy of candidate models on predation risk using the Akaike Information Criterion with the correction for small sample size (AIC_c; e.g. Burnham & Anderson 2002) and Akaike weights (w). All models that differed from the best supported model (i.e. the model with the lowest AIC_c) by a factor $\Delta AIC_c < 2$ were considered to be similarly supported (Burnham & Anderson 2002). We computed average estimates (± SE) and the cumulative weight of evidence (cw; i.e. sum of model weights over all models containing a given predictor) for all predictors that were considered in a given group of models.

The results of these predation models may have been confounded by pseudo-replication since our set of live ungulate locations included more than one telemetry location for the same individual. Given the structure of our data (i.e. no pseudo-replication for kills but many for telemetry data), most of the statistical models that are generally used to deal with this problem (e.g. mixed effect models) were not applicable. Hence, to address this concern, for each collared ungulate, we computed the means of values of the variables that were identified as potentially important based on the GLM. These subject-specific mean values for each collared ungulate were compared with values recorded for killed individuals using simple tests such as t-test or Wilcoxon rank test. All analyses were run using R 2.13.1 (R Development Core Team 2011).

Results

The number of roe deer kills that were found in winter and summer were 29 and 33, respectively. We found 18 red deer kills in winter but only five in summer, suggesting that predation risk for red deer increases considerably compared to roe deer during winter (χ^2 test: df = 1, $\chi^2 = 5.514$, P = 0.018).

Roe deer (winter and summer)

When analysing roe deer data, we produced several models with a level of support that was similar to that of the best supported model (i.e. 13 candidate models with $\Delta AIC_c < 2$; Table 2). Consequently, the information value of most predictors was low and the only predictor that received substantial support, based on cw and averaged parameter estimates, was the interaction between season and AverDevSCI (Table 3 and Fig. 1). Although there was no relationship between predation risk and AverDevSCI in summer for roe deer, there was a strong positive association between these two variables in winter (see Fig. 1).

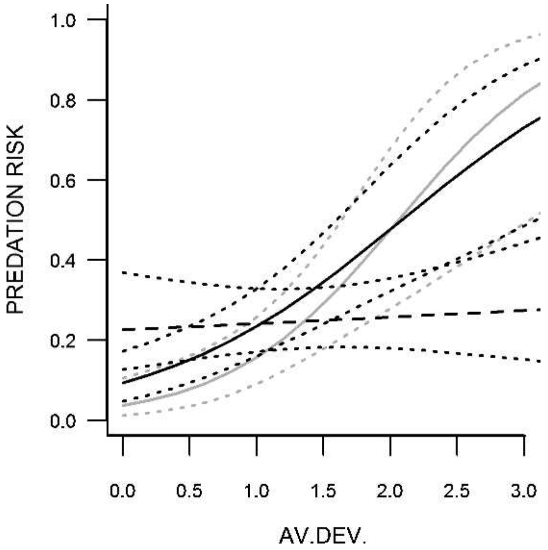

Figure 1. Relationship between risk of predation and AverDevSCI (GLM based estimate ± 95% CI) for roe deer in winter (solid black line) and summer (dashed black line) and for red deer in winter (grey line).

Red deer (winter)

As in the previous case, there were several 'best candidate' models for the red deer data (i.e. five candidate models with $\Delta AIC_c < 2$; see Table 2). Consistent with the results obtained for roe deer, based on cw and averaged parameter estimates, there was high support for a positive association between predation risk and AverDevSCI (see Table 3 and Fig. 1). Unlike the roe deer data, there was a negative association, with a high level of support, between tree density and predation risk (see Table 3 and Fig. 2).

Roe and red deer (winter)

There was a much higher level of support for the best supported model of the pooled roe and red deer winter data sets than for the alternative models ($\Delta AIC_c = 4.21$, w = 0.68, evidence ratio = 8 compared to the second best model; see Table 2). This model was in accordance with our previous results, i.e. consistent with the species-specific models, it included AverDevSCI as the main effect (see Tables 2 and 3 and Fig. 1) and the interaction between species type and tree density (see Tables 2 and 3 and Fig. 2). In addition, based on the structure of the best supported model and relatively high cw, there was relatively good support for an association between predation risk and the presence of uprooted trees. In particular, predation risk decreased by 56.1% at sites where there were uprooted trees (deduced from the fact that

Table 2. Results of model fitting for the risk of deer being killed by lynx in the Bohemian Forest. Groups of models were fitted separately to the roe deer data (winter and summer), red deer data (winter only) and roe deer and red deer data (winter only). Models were compared based on the number of parameters, model deviance (Deviance), Akaike's Information Criterion corrected for sample size (AIC_c), the difference in AIC_c from that of the best-fitting model (ΔAIC_c) and model weight (w). Only the models that had $\Delta AIC_c < 2$ or $w \geq 0.05$ are presented.

Data set	Model	Deviance	AIC_c	ΔAIC_c	w
Roe deer (winter and summer)	AverDevSCI + Season + AverDevSCI*Season	263.10	271.25	0.00	0.07
	AverDevSCI + Season + Uprooted_trees + AverDevSCI*Season + Season*Uprooted_trees	258.96	271.29	0.04	0.07
	AverDevSCI + Conifer_branches + Season + AverDevSCI*Season	261.56	271.79	0.54	0.05
	AverDevSCI + Season + Shrub_cover + AverDevSCI*Season	261.76	272.00	0.74	0.05
	AverDevSCI + Season + Slope + AverDevSCI*Season	261.82	272.06	0.80	0.05
	AverDevSCI + Season + Uprooted_trees + AverDevSCI*Season	262.08	272.31	1.06	0.04
	AverDevSCI + Conifer_branches + Season + Slope + AverDevSCI*Season	260.22	272.55	1.29	0.04
	AverDevSCI + Conifer_branches + Season + Shrub_cover + AverDevSCI*Season	260.33	272.66	1.40	0.04
	AverDevSCI + Season + Shrub_cover + Slope + AverDevSCI*Season	260.46	272.79	1.53	0.03
	AverDevSCI + Season + Slope + Uprooted_trees + AverDevSCI*Season	260.46	272.79	1.54	0.03
	AverDevSCI + Season + Shrub_cover + Uprooted_trees + AverDevSCI*Season	260.49	272.82	1.56	0.03
	AverDevSCI + Conifer_branches + Season + Uprooted_trees + AverDevSCI*Season	260.58	272.91	1.66	0.03
	AverDevSCI + Season + Tree_density + AverDevSCI*Season	262.91	273.15	1.89	0.03
Red deer (winter)	AverDevSCI + Ground_cover + Tree_density + Uprooted_trees	50.73	61.35	0.00	0.10
	AverDevSCI + Tree_density + Uprooted_trees	53.32	61.73	0.38	0.09
	AverDevSCI + Ground_cover + Tree_density	53.79	62.19	0.84	0.07
	AverDevSCI + Tree_density	56.44	62.68	1.33	0.05
	AverDevSCI + Ground_cover + Rocks + Tree_density + Uprooted_ trees	50.34	63.21	1.86	0.04
Roe deer and red deer (winter)	AverDevSCI + Species + Tree_density + Uprooted_trees + Species*Tree_density	166.28	178.66	0.00	0.68
	AverDevSCI + Species + Tree_density + AverDevSCI*Species + Species*Tree_density	170.49	182.87	4.21	0.08
	AverDevSCI + Ground_cover + Species + Tree_density + Species*Tree_density	170.84	183.21	4.56	0.07

Table 3. Model-averaged parameter estimates (Coeff. = coefficient, SE, Z and P) and cumulative weights (cw) of the predictors from models of predation risk for roe deer data (winter and summer), red deer data (winter only) and roe deer and red deer data (winter only). Predictors whose cw was > 0.7 at least in one case are shown here. Lines corresponding to predictors which proved significant (P < 0.05) in a given group of models are in italics for the corresponding group of models. Averaged parameter estimates for all predictors are available in Appendix I.

	Roe deer (winter and summer)					Red deer (winter)					Roe deer and red deer (winter)				
Variable	Coeff.	SE	Z	P	cw	Coeff.	SE	Z	P	cw	Coeff.	SE	Z	P	cw
(Intercept)	*-1.241*	*0.485*	*2.547*	*0.011*	*1.00*	-1.229	0.866	1.403	0.161	1.00	-1.301	0.898	1.445	0.148	1.00
AverDevSCI	0.054	0.526	0.102	0.919	1.00	*3.630*	*1.332*	*2.701*	*0.007*	*0.98*	*2.998*	*0.757*	*3.950*	*0.000*	*1.00*
Tree_density	0.592	3.547	0.166	0.868	0.14	*-126.500*	*41.240*	*3.033*	*0.002*	*1.00*	*-99.220*	*35.490*	*2.786*	*0.005*	*0.91*
Uprooted_trees-present	-0.058	0.297	0.193	0.847	0.26	-9.620	1393.000	0.007	0.995	0.57	-2.094	24.500	0.009	0.993	0.75
Season-winter	*-1.371*	*0.650*	*2.102*	*0.036*	*0.98*	-	-	-	-	-	-	-	-	-	-
Species	-	-	-	-	-	-	-	-	-	-	-1.461	1.055	1.382	0.167	0.96
AverDevSCI* season-winter	*2.228*	*0.819*	*2.712*	*0.007*	*0.97*	-	-	-	-	-	-	-	-	-	-
Species- roe_deer* tree_density	-	-	-	-	-	-	-	-	-	-	*105.300*	*33.500*	*3.129*	*0.002*	*0.86*

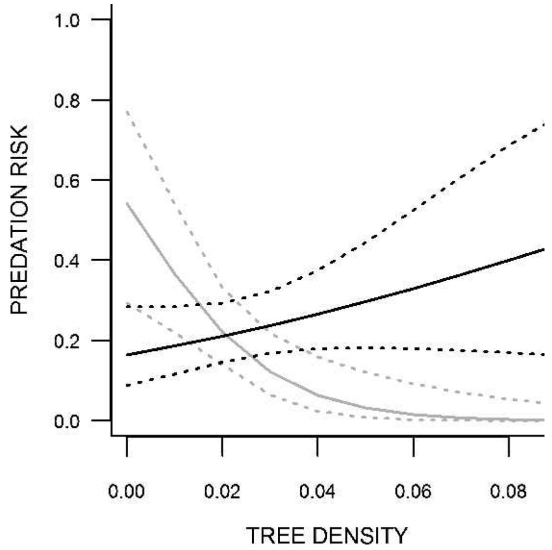

Figure 2. Relationship between risk of predation and tree density (GLM based estimate ± 95% CI) for roe deer (black lines) and red deer (grey lines) in winter.

the proportion kill sites/all sites was 23.5% for locations where uprooted trees were absent compared to 10.3% for locations where uprooted trees were present; see Table 4).

Kills vs subject-specific means for collared deer

AverDevSCI was significantly higher at sites where kills of both prey species were recorded compared to individual specific means from telemetry data during winter (Welch's t-test: df = 69, t = 54.655, P < 0.001), but not in summer (Welch's t-test: df = 41, t = 0.572, P = 0.570). We found no difference between the tree density at sites where roe deer kills were recorded vs individual specific means of tree density as computed based on roe deer telemetry data (Welch's t-test: df = 45, t = 1.578, P = 0.121), yet tree density at red deer kill sites was significantly lower than the individual specific means computed for locations of collared red deer (Welch's t-test: df = 20, t = 4.862, P < 0.001). Finally, and consistent with the GLM, the Wilcoxon rank test indicated that the presence of uprooted trees decreased predation risk in winter (P < 0.001). The mean values of the environmental variables that proved significant are given in Table 4.

Discussion

Regarding our two initial hypotheses, the analysis of summer data supported the 'prey-occurrence hy-

Table 4. Mean values (± SE) or frequencies of each significant environmental variable calculated for locations of live roe deer (ROED), roe deer kills (KROE), live red deer (REDD) and red deer kills (KRED). S = summer and W = winter.

		Tree density (N/ha)		AverDevSCI		Uprooted trees
Type of location	N	Mean	SE	Mean	SE	% Present
ROED-S	100	250.90	17.62	1.36	0.09	0.14
KROED-S	33	268.23	43.56	1.44	0.19	0.18
ROED-W	100	223.05	19.73	0.54	0.14	0.26
KROE-W	29	284.49	36.44	1.49	0.19	0.21
REDD-W	94	301.38	16.43	0.67	0.06	0.31
KRED-W	18	175.47	24.46	1.66	0.26	0.00

pothesis', indicating that lynx hunt in an opportunistic way in summer. The analysis of winter data revealed significant differences between the kill locations and those of live ungulates of both species, suggesting that the locations of lynx kills are not a mere consequence of habitat use by its prey, which supports the 'landscape hypothesis'. This is a counterintuitive result, as one might have expected that, in winter, when snow cover reduces ungulate mobility (Ratikainen et al. 2007, Kittle et al. 2008) and both prey species are likely to be in a poorer physical condition (e.g. Okarma 1984), the chances of a successful hunt by lynx will increase independently of habitat features. In particular, we found that in winter, the risk of predation for both prey species was correlated with certain habitat features, while others influenced only the risk of predation for red deer, which are probably more difficult to catch due to their large size. In fact, predation risk was negatively correlated with tree density only for red deer. A high density of trees might constitute an obstacle to movement and limit the space for manoeuvre. In addition, it may make the environment unsafe for the predator during the attack, which could be much more violent when the prey is red deer. Accordingly, Podgorski et al. (2008) reported a lower density of trees at lynx kill sites than at random locations in winter, and Krofel et al. (2007) found that lynx killed prey in forests with a sparse or moderate tree density (although their study is just descriptive). Balme et al. (2007) reported similar results for the leopard *Panthera pardus*, another large felid which prefers to hunt in habitats with a medium vegetation density, even if the highest prey densities occur where the vegetation is densest. As we found no significant difference in tree density in the case of roe deer, and as collared red deer were located in areas where the density of trees was higher than at the roe deer locations, a possible alternative explanation is that lynx might simply select the best places to hunt roe deer (their main prey) and hunt red deer (mainly calves) when they encounter them by chance in similar places. Nevertheless, our data indicate that the first explanation is most likely to be correct because tree density was even lower at red deer kill sites than at roe deer kill sites.

Unlike those of Podgorski et al. (2008), our results also suggest a negative correlation between the predation risk for red deer in winter and the presence of uprooted trees. Mao et al. (2005) reported that uprooted trees were avoided by wolves hunting red deer, probably because they are an obstacle to movement. Although the hunting strategies of canids and felids generally differ (e.g. Kruuk & Turner 1967, Kruuk 1986), this explanation may also apply in the case of lynx, similar to the above interpretation regarding tree density. On the other hand, based on the GLM results, uprooted trees was the only habitat feature that tended to differ between the kill sites that were located using telemetry and those found by chance, although this difference was not significant. Based on field observations and the above-mentioned GLM results, it is legitimate to state that most of the microhabitat features considered in our study were similarly present at all kill locations, independent of the method used to find the kill. In fact, old remains of man-made structures, dense clumps of shrubs, rocks and irregularities in the terrain (which all provide good stalking cover) can be found in both accessible and inaccessible places throughout our study area. The only exception may be uprooted trees, which are much more common in natural forests regularly frequented by red deer (Jedrzejewski et al. 1993), but less accessible to people. Therefore, the fact that most of the kills (69%) were found by chance (i.e. they were probably in more accessible areas) may have biased the result regarding this particular habitat feature. Nevertheless, unpublished data from an ongoing telemetry study in the Bohemian Forest suggest that uprooted trees are more often present at sites where lynx rest than at kill sites (E. Belotti & L. Bufka, unpubl. data), which indicates that this aspect needs further study.

A common feature of all the winter kill sites, regardless of prey species, was the higher level of heterogeneity (i.e. presence of both areas with dense cover and areas with good visibility at the same site) compared to the locations of live ungulates. Spatial heterogeneity has proved to correlate with lynx occurrence on a medium scale (Rozylowicz et al. 2010) and lynx choice of hunting areas on a fine scale (Podgorski et al. 2008). Areas characterised by high heterogeneity in visibility likely enable a predator to remain hidden and, at the same time, follow the prey's movements. Accordingly, during winter, both roe and red deer selected habitats characterised by similar values of visibility in all four cardinal directions and, in general, occurred in plots where the visibility was good (E. Belotti, pers. obs.). Ratikainen et al. (2007) also suggested that roe deer, when threatened by a stalking predator like lynx, may use more open habitats when not constrained by deep snow.

Using our data set, the risk of predation in summer could only be measured for roe deer and the analysis indicated that it was not associated with any of the habitat parameters measured. Podgorski et al. (2008) reported that summer kill sites were characterised by more habitat complexity than random sites. This difference may be because Podgorski's study area was mainly forested. In our study area, lynx also killed prey in open habitats, therefore, we included such habitats where, in summer, the strong growth of vegetation may have 'homogenised' the habitat features in the 20-m radius plots.

In addition, the differences in the selection of hunting areas by lynx in winter and summer may be due to the greater importance of small, non-ungulate prey in summer (Bufka & Červený 1996, Fejklová 2002). In fact, in summer, small prey is likely to be more abundant due to their reproductive cycles (e.g. Lincoln 1974) and the higher temperature allows the utilisation of a killed prey for a shorter time than in winter, independent of its size. Therefore, these two factors may induce the lynx to adopt a more opportunistic hunting strategy during summer months. A similar switch in lynx diet between winter and summer was also reported by Odden et al. (2006). Nevertheless, it is interesting to note that the mean value of the heterogeneity index (AverDevSCI) at roe deer kill sites was only slightly lower in summer than in winter, whereas for live roe deer locations in summer, it was more than twice that recorded in winter. Our results for summer may, therefore, also be due to a change in the behaviour of roe deer, in that they occurred in more heterogeneous areas in summer than in winter. Tufto et al. (1996) studied summer habitat selection by female roe deer and found that they spent more time near habitat edges in summer, which may account for the higher heterogeneity in visibility at roe deer locations recorded in our study.

Finally, the large difference in the number of red deer killed in summer and winter may also be a direct consequence of the above-mentioned switch in lynx diet. In fact, based on our results, the predation risk for this species seems to increase greatly from summer to winter (five killed red deer in summer and 18 in winter). This may be due to: 1) their more aggregated distribution in winter than in summer (Putman & Staines 2004), which may make it easier for lynx to locate red deer, 2) the presence of snow, which might result in more favourable conditions for lynx, as deer are less mobile in deep snow (Mech et al. 1987, Kittle et al. 2008) and lynx do not sink to the same depth in snow as deer (Nilsen et al. 2009) and 3) the condition of red deer, which deteriorates in winter. In particular, the young animals are more adversely affected then by the difficult terrain and weather conditions (Bergerud 1971), thus their vulnerability may increase. In fact, the lynx in our study area showed a strong selection for red deer calves. Similar results are reported for other areas in Central Europe (Jedrzejewski et al. 1993, Nowicki 1997, Okarma et al. 1997), and Okarma (1984) reports that red deer killed by lynx in winter were all calves in a very poor physical condition.

We are aware that the places where prey are found may not correspond exactly with where they are killed by lynx (Červený & Okarma 2002, Podgorsky et al. 2008), even if, in most cases, this felid leaves the prey where it was killed or moves it a short distance (Jedrzejewski et al. 1993). The data we have for red deer indicate the carcasses were not moved and therefore the sites where red deer kills were found were the places where they were killed. Regarding the roe deer kills, in five cases we could clearly determine both the site where the prey was killed and the site where it was cached. The distance between the two places was generally short (about 20 m) and therefore, in most cases, the plots of the caching sites (40-m diameter) also included the actual kill site. Furthermore, the correlation between the risk of predation and the heterogeneity in visibility index (AverDevSCI) was significant both in the case of red deer kills (not cached) and of roe deer kills (sometimes cached). Therefore, caching the prey did not seem to have a strong effect on this relationship. The correlation between risk of predation and tree density was significant only in the case of red deer. Nevertheless, tree density rarely changes significantly at the distances over which lynx usually drag their prey. Therefore, our two main results are unlikely to be biased by the way lynx caches its prey. It would be interesting to investigate differences between the actual kill sites and caching sites, but unfortunately the sample was too small ($N = 5$ clear cases).

As we do not have any information on the habitat features at sites where lynx hunted unsuccessfully, we could not determine whether the higher heterogeneity in visibility at winter kill sites was found as a result of an active selection by lynx (i.e. lynx selected particular areas for hunting) or because of an actual increase in prey catchability (i.e. because of the higher heterogeneity in visibility, lynx were more successful when hunting ungulates in those areas). Nevertheless, both alternatives would lead to the same conclusion: in winter, the probability of finding killed prey is correlated with habitat features linked to heterogeneity in visibility, independent of the habitat used by the prey. This is a step forward in our understanding of the mechanisms determining habitat choice by lynx. Such information is needed to develop strategies of forest and game management that will result in an increased chance of survival for this species, both in and outside protected areas. Based on our findings, forest management that results in a good level of habitat heterogeneity should be adopted to favour hunting lynx. Furthermore, the presence of particular microhabitat features could benefit lynx even in non-optimal macrohabitat conditions. Therefore, special attention should also be given to preserve such features in mosaic landscapes.

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Appendix I. Model-averaged parameter estimates (Coeff. =coefficient, SE, Z and P) and cumulative weights (cw) of the predictors from models of predation risk for roe deer data (winter and summer), red deer data (winter only) and roe deer and red deer data (winter only). Lines corresponding to predictors which proved significant (P < 0.05) in a given group of models are in italics for the corresponding group of models.

	Roe deer (winter and summer)					Red deer (winter)					Roe deer and red deer (winter)				
Variable	Coeff.	SE	Z	P	cw	Coeff.	SE	Z	P	cw	Coeff.	SE	Z	p	cw
(Intercept)	*-1.241*	*0.485*	*2.547*	*0.011*	*1.00*	-1.229	0.866	1.403	0.161	1.00	-1.301	0.898	1.445	0.148	1.00
AverDevSCI	0.054	0.526	0.102	0.919	1.00	*3.630*	*1.332*	*2.701*	*0.007*	*0.98*	*2.998*	*0.757*	*3.950*	*0.000*	*1.00*
Conifer_branches-present	-0.107	0.261	0.411	0.681	0.25	-0.048	0.335	0.142	0.887	0.21	-0.429	0.429	0.995	0.320	0.05
Ground_cover	-0.009	0.057	0.156	0.876	0.15	0.294	0.401	0.729	0.466	0.49	0.391	0.231	1.685	0.092	0.12
Rocks-present	-0.006	0.144	0.044	0.965	0.13	0.133	0.478	0.276	0.783	0.24	-0.115	0.470	0.244	0.807	0.03
Shrub_cover	0.181	0.461	0.392	0.695	0.23	0.112	0.792	0.140	0.888	0.21	0.848	0.890	0.949	0.343	0.05
Slope	0.007	0.020	0.369	0.712	0.24	-0.008	0.029	0.287	0.774	0.24	0.002	0.032	0.063	0.949	0.03
Tree_density	0.592	3.547	0.166	0.868	0.14	*-126.500*	*41.240*	*3.033*	*0.002*	*1.00*	*-99.220*	*35.490*	*2.786*	*0.005*	*0.91*
Uprooted_trees-present	-0.058	0.297	0.193	0.847	0.26	-9.620	1393.000	0.007	0.995	0.57	-2.094	24.500	0.009	0.993	0.75
Season-winter	*-1.371*	*0.650*	*2.102*	*0.036*	*0.98*	-	-	-	-	-	-	-	-	-	-
Species	-	-	-	-	-	-	-	-	-	-	-1.461	1.055	1.382	0.167	0.96
AverDevSCI*Season winter	*2.228*	*0.819*	*2.712*	*0.007*	*0.97*	-	-	-	-	-	-	-	-	-	-
Conifer_branches-present*Season-winter	-0.006	0.111	0.055	0.956	0.02	-	-	-	-	-	-	-	-	-	-
Ground_cover*Season-winter	0.011	0.089	0.121	0.903	0.02	-	-	-	-	-	-	-	-	-	-
Rocks-present*Season-winter	-0.003	0.082	0.034	0.973	0.01	-	-	-	-	-	-	-	-	-	-
Season-winter*Shrub_cover	-0.001	0.177	0.006	0.995	0.02	-	-	-	-	-	-	-	-	-	-
Season-winter*Slope	0.001	0.010	0.088	0.930	0.02	-	-	-	-	-	-	-	-	-	-
Season-winter*Tree_density	-0.020	1.700	0.012	0.991	0.01	-	-	-	-	-	-	-	-	-	-
Season-winter*Uprooted_trees-present	-0.100	0.420	0.237	0.813	0.07	-	-	-	-	-	-	-	-	-	-
Species-roe_deer*Tree_density	-	-	-	-	-	-	-	-	-	-	*105.300*	*33.500*	*3.129*	*0.002*	*0.86*
AverDevSCI*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	-1.908	1.359	1.398	0.162	0.08
Species-roe_deer*Uprooted_trees-present	-	-	-	-	-	-	-	-	-	-	15.900	121.000	0.013	0.990	0.03
Ground_cover*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	-0.200	0.364	0.547	0.584	0.00
Slope*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	0.108	0.059	1.825	0.068	0.00
Shrub_cover*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	0.121	1.654	0.072	0.942	0.00
Conifer_branches-present*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	-0.156	0.810	0.192	0.848	0.00
Rocks-present*Species-roe_deer	-	-	-	-	-	-	-	-	-	-	0.139	0.891	0.155	0.877	0.00