

Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present

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Abstract

Winter climate at northern latitudes is a challenge to small-bodied ungulates, and they modify behaviour to save energy and to increase the likelihood of survival. Also, the ongoing expansion of large carnivores in several European countries can lead to the recovery of (potentially energetically costly) anti-predator behaviours. In an area recently recolonized by Eurasian lynx *Lynx lynx*, we snow-tracked radio-collared roe deer *Capreolus capreolus* in order to investigate their bedding and feeding behaviour during winter, and assess how environmental factors affect their habitat use. We also tested the prediction that roe deer use more open sites than locally available in areas with a stalking predator such as the lynx. Our results showed that both bed sites and foraging sites had more cover, compared with random sites. Most of the variation in canopy cover and in the distance and foraging sites between bed sites and foraging sites was explained by prevailing weather. As the winter progressed, the presumed depletion of fat reserves promoted the use of more canopy cover at foraging sites by night, less by day and a decrease in the distance between beds, foraging sites and human activities. Males used artificial feeding sites less often and bedded further from humans than females. The data fit the hypothesis of tighter energy budgets for family groups (females with fawns) or that males are more cautious towards humans. There was no support for the hypothesis that roe deer used more open habitat than locally available in order to reduce their vulnerability to lynx predation. Owing to severe winter conditions and the danger of starvation, roe deer seem to be forced to accept a high risk when predators are present, not changing their main pattern of habitat use from comparative areas where predators are absent.

Introduction

Animal habitat selection results from the simultaneous consideration of many factors, including the need for forage and cover to avoid extreme weather and predators. Habitat selection is the outcome of the trade-offs between the costs and benefits connected with each habitat (Sih, 1980; Lima & Dill, 1990). Individuals may experience these trade-offs differently over time. Habitat selection may vary in relation to short-term (daily) variations in factors such as activity, time of day and weather; medium-term (seasonal) variations in environmental conditions and physiological status; and long-term (annual, decadal) variations in community structure and demographic and environmental parameters.

Roe deer winter survival strategies in northern ecosystems are relatively well studied (Markgren, 1966; Holand, 1990; Holand, 1992b; Mysterud & Østbye, 1995; Mysterud, Bjørnsen & Østbye, 1997; Mysterud, Lian & Hjermmann, 1999), and a number of behaviours consistent with energy

conservation have been identified at various scales. An important general strategy at fine scales seems to be the selection of cover in periods of harsh climate. However, as forage quality is the more important factor for the energy budget, they will expose themselves if the best forage is in open habitat (e.g. Moen, 1976; Mysterud *et al.*, 1999). Recent recolonization of large carnivores in much of Europe and North America has sparked considerable interest in determining how ungulate behaviour (Berger, Swenson & Persson, 2001; Sand *et al.*, 2006) and population dynamics (Nilsen *et al.*, 2005) are affected. Predation risk has been demonstrated to induce habitat shifts leading to a reduced intake of high-quality forage in ungulates (Hernandez & Laundre, 2005), and also a decrease in foraging rates through increased vigilance (Hunter & Skinner, 1998; Laundre, Hernandez & Altendorf, 2001; Wolff & Van Horn, 2003). Most of these studies have focused on wolves preying on either moose *Alces alces* or elk *Cervus elaphus*. Considering the ongoing expansion of the Eurasian lynx *Lynx lynx* across Europe

(Andersen *et al.*, 2003), it is of fundamental importance to understand the possible implications for their most abundant and widespread ungulate prey species: the roe deer *Capreolus capreolus*. However, little is known regarding the effects of lynx predation on prey behavioural decisions (Holand *et al.*, 1998).

The present study aims at investigating how roe deer use their winter habitat after lynx have returned to these ecosystems. In order to save energy, we predict that low temperature, deep snow or strong wind should favour the use of cover for protection and relief, and more so when they seek bed sites than when they forage (cfr. Moen, 1976). Such a pattern is expected to become stronger as the winter progresses, if fat resources become depleted. We also aimed to observe whether roe deer increase the use of open habitat as is expected when threatened by a stalking predator like lynx.

Materials and methods

Study area

The study was conducted in south-eastern Norway, in Akershus and Østfold counties (59–60°N; 11–12°E). The study area is dominated by commercially exploited boreal forest, mainly composed of Norwegian spruce *Picea abies*, Scots pine *Pinus sylvestris* and birch *Betula pubescens* interspersed with farmland. Artificial feeding sites for roe deer were found to be distributed throughout the area and were operational all winter. In 2004, the average temperatures were –5.0, –3.0 and 0.5 °C, in January, February and March, respectively. The mean snow depth at the closest weather station (nr. 2540 Høland-Føsser; Klimadivisjonen, Meteorologisk institutt) was 23.2 cm from January to the end of March, which is above average for this region in recent years.

In the study area, the main predator for roe deer in the winter is the lynx, while red fox *Vulpes vulpes* can prey on roe deer only in severe winters (Cederlund & Lindstrom, 1983). The annual hunting season for roe deer is from 10 August until 23 December; the period before September 25 is for male harvest only.

Capture and tracking of roe deer

Roe deer were captured and fitted with radio collars (Telvilt Int. Lindesberg, Sweden), mainly using box traps in winter, as a part of the ongoing 'lynx-roe deer project in south-eastern Norway' (Andersen *et al.*, 2005; Linnell *et al.*, 2005). No capture- or marking- related mortality was detected. The animals were collared for a wide range of purposes, including studies on long-term reproduction, survival and space use. These studies are still ongoing and therefore no attempt has been made to remove collars. For the purpose of this study, we selected 27 individuals [nine adult males, 14 adult females (five of them with fawns) and four orphaned fawns] whose home ranges were included within the area used by radio-monitored lynx. All groups that include fawns are considered families. During the study

period, one adult doe was killed by a lynx and one orphan fawn was killed by a red fox.

Tracking took place between 7 January and 4 March, 2004, whenever snow conditions allowed. The exact position of the roe deer was determined by a combination of close-approach radio-tracking and snow-tracking. If the bed site or feeding site was not found immediately, we back tracked the flushed deer until the site was found. Owing to bad snow conditions or problems with the radio tracking, the animals were not tracked an equal number of times (between eight and 15 times each). Locations were equally distributed between day and night.

Observed parameters

At each feeding site (either natural or artificial) and bedding site, we recorded data on habitat type, ground (or hiding) cover, canopy cover, topography and snow depth. To be able to compare the chosen bed site or the feeding site with the locally available habitat, all parameters were measured both at the bed sites and foraging sites and at a point 50 m away in a random direction.

The habitat type was classified as 'forest' or 'garden/field', and forest sites were further classified as 'conifer', 'deciduous' or 'mixed'. The closest tree was categorized as 'spruce', 'pine' or 'deciduous'. The distance to the closest conifer, its diameter at breast height (dbh) and the height of the lowest live branch were measured. Percentage canopy cover was measured using a spherical densiometer (model C; Lemmon, 1956). Ground cover was assessed by counting the number of hidden squares of a cover board (with a total of 80 squares of 5 × 5 cm) from a distance of 30 m from the bedding or feeding site in a random direction (Mysterud & Østbye, 1999). The observation of the cover board provides a good indication of the potential visibility and vulnerability of roe deer to lynx, as more than two-thirds of successful hunting attempts start from a distance of 20 m, while attacks initiated from more than 50 m are rarely successful (Haglund, 1966; J. Odden *et al.* unpubl. data).

Starting from each bedding site, we followed roe deer tracks backward in order to measure the distance to the closest feeding site and the canopy cover at this site. Long distances may be underrepresented because of difficulties in discriminating among several different tracks or because of poor snow conditions (21 of 144 attempts failed). Distance to the closest house was measured with a GPS.

Each site was classified according to the micro-topographical scale described in Mysterud & Østbye (1995). Hence, we considered the slope within 5–30 m between the closest topographic top and the closest bottom. Within this area, each site was defined as 'top', 'upper third', 'middle', 'lower third', 'bottom' or 'flat'. If the spot was more than 5 m from such a slope, it was characterized as flat.

In addition to the measurement of the snow depth recorded at the roe deer site, daily snow depth, wind speed and temperature were obtained from the closest weather station. As wind speed and temperature were measured three times a

day, we selected the measurements closest to the time when the roe deer was radio-monitored.

Statistical analyses

Habitat selection is defined as use relative to availability. There are a number of different statistical approaches to analyse habitat selection depending on the study design (see recent update in Thomas & Taylor, 2006). We use the following approaches. (1) We compare characteristics of bed sites and feeding sites with availability close by, and are thus assessing local habitat selection per definition, using Wilcoxon's signed rank tests. (2) We compare the results of bed sites and feeding sites, without an explicit statistical testing, with previous studies showing marked effects (e.g. Myrsterud & Østbye, 1995; Myrsterud *et al.*, 1999). (3) We explore variation in the same characteristics during the course of the winter (separately for bed sites and feeding sites), which, strictly speaking is habitat use. However, as availability of the habitat variables is stable during winter (at home range scales), any variation in use over time is likely due to variation in selectivity. This analysis is clearly more challenging, and we used the following approaches: a combination of linear mixed effects models (LME), linear models (LM) and general linear models (GLM) were used to assess the importance of different factors on the choice of foraging and bedding sites (Crawley, 2002). In order to obtain normality and to avoid heteroscedasticity, canopy cover data were transformed with $\arcsin[\sqrt{(\text{canopy cover}/100)}]$, distance to the nearest house was square root transformed and distances between foraging and bedding sites were \ln -transformed. Two-way interactions and second- and third-order polynomials were only included in the tests when it could be justified for biological reasons. The ground cover variable had properties that made it difficult to find an appropriate statistical model, due to an extremely skewed data distribution. The ground cover indexes were therefore categorized as either 'open' or 'hidden' based on whether more than half the cover board was hidden or not, and could then be analysed as a binomial variable in a GLM (i.e. logistic regression).

When model selection was performed, temperature and snow depth from the weather station were used. The reason for this is that we can then be sure that the temperature or snow depth in the analysis is not the effect of the choice of preferred microhabitat. Data from beds and foraging sites were used in paired comparisons with random sites. Because no males were associated with fawns, only one of the predictor variables 'family' or 'sex' was used in a model at the time, and the final model includes the parameter that yielded the most parsimonious model, or, if not necessary, none. In a similar manner, either the variable 'artificial feeding site' which indicate whether the feeding site used is artificial or not, or the variable 'canopy cover above feeding site' was used in the model because they are highly correlated. Interactions between continuous predictor variables were modelled by the multiplicative term of the standardized (st.) variables (Myrsterud *et al.*, 2000).

Model selection was aided by the Akaike information criterion adjusted for small sample sizes (AICc; Burnham & Anderson, 2002). The model with the lowest AICc value was chosen according to the parsimony principle. Model selections are shown in online Supplementary Material Appendices S2–S9. As AIC cannot be used in combination with mixed models (based on REML), we performed the model selection using LM. The final model (as defined by the AICc) was then analysed with LME with individual deer as a random variable, to check for the influence of repeated measurements of the same individuals. Diagnostic tests were performed on the best model in order to check for normality, constancy of variance and the influence of single observations. For logistic regression models, overdispersion was assessed by the statistical significance of the residual deviance of the fitted model. Categorical data were analysed with χ^2 tests. Statistics analyses were performed in S-plus (6.2 Professional edition). All means are given \pm SE (standard error).

Results

General results

The characteristics of foraging and bedding sites differed substantially. Canopy cover over beds [80.1% (\pm 21.1), $P < 0.001$, LME] was higher than over foraging sites [42.4% (\pm 0.33)]. This is reflected in a lower proportion of bedding sites (0.01) compared with foraging sites (0.29) in open habitat, and in a higher proportion of beds (0.73) versus foraging sites in coniferous forests (0.58). The mean distance between roe deer beds and foraging sites was 47.1 m (\pm 75.4), and ranged between 0 and 338 m. Roe deer walked significantly longer distances between artificial feeding and bedding sites than between other foraging sites and bedding sites (Table 1, Fig. 1). They also walked longer distances when snow was shallow (Table 1, Fig. 1). Early in the season, distances between bedding and foraging site were longer than at the end of the winter, but this effect was only evident when there was considerable snow (Table 1, Fig. 1). Families tended to walk shorter distances between bedding and foraging sites than single animals (Table 1). Both roe deer foraging sites and bed sites were placed on the micro topographic 'upper third' of slope more frequently than expected by chance (Fig. 2a and b; foraging sites: $\chi^2 = 24.798$, $P < 0.001$, beds: $\chi^2 = 60.427$, $P < 0.001$).

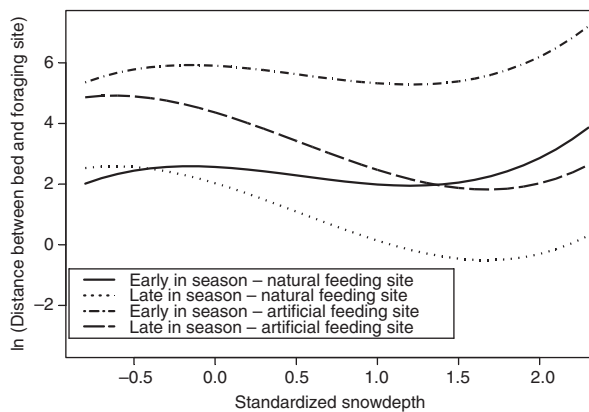
Foraging sites

Canopy cover at foraging sites was significantly higher compared with random points [30.6% (\pm 0.3); $n = 168$, $Z = 5.287$, $P < 0.001$]. Foraging sites were placed near a conifer more often than random points ($\chi^2 = 40.190$, $P < 0.001$) and were closer to live branches than expected by chance (Table 2). Roe deer foraged at sites with more canopy cover when the wind was strong compared with when it was absent, especially late in the season (Table 3; Fig. 3a). In strong wind, roe deer used foraging sites with higher (10 percentage

Table 1 Parameter estimation (estimate \pm standard error) for the most parsimonious linear model (LM) for canopy cover over bed sites, distances between foraging and bed sites and distances from bed site to the nearest house

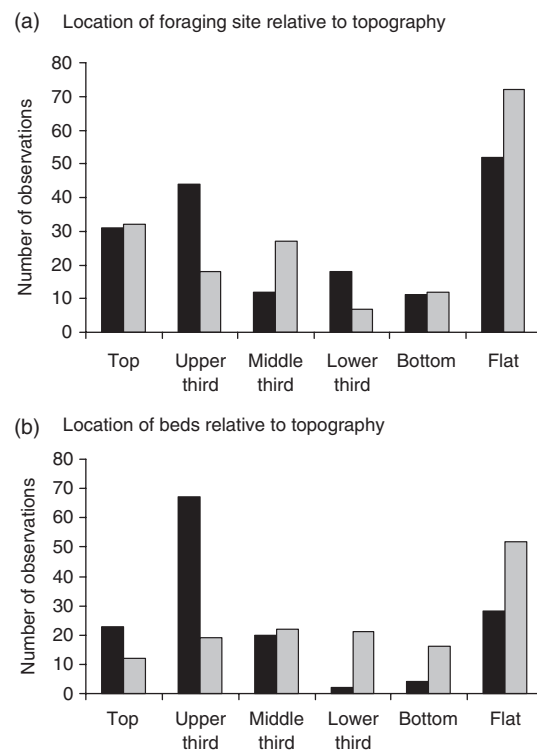
Predictor variable	Response variable		
	Canopy cover	Distances between foraging and bedding sites	Distances from the bed to the nearest house
Intercept	1.043 \pm 0.038	1.868 \pm 0.164	9.554 \pm 0.926
Time of day (night vs. day)		0.257 \pm 0.153	-0.542 \pm 0.320
St.snow depth	-0.064 \pm 0.037	-0.749 \pm 0.200	
St.snow depth ²	0.099 \pm 0.030	-0.822 \pm 0.284	
St.snow depth ³		0.523 \pm 0.141	
St.Juliandate		-0.19 \pm 0.152	0.048 \pm 0.022
Group type (family vs. single)		0.44 \pm 0.196	
Sex (males vs. females)			-0.741 \pm 0.307
St.windspeed	0.038 \pm 0.024	0.148 \pm 0.084	0.761 \pm 0.213
Artificial feeding site		2.994 \pm 0.202	
St.Juliandate \times st.snowdepth		-0.431 \pm 0.199	
St.Juliandate \times artificial feeding site		-0.309 \pm 0.177	
r^2	0.089	0.794	0.196
Sample size	144	121	144

For transformations of response variables, see the main text. Empty cells indicate that the effect is not included in the final model. Characters in bold indicate that the effect is significant both in the LM and in the corresponding linear mixed-effects model (LME) with individual as a random effect. Characters in italics indicate that the effect is significant only in the LM and not in the LME. The prefix 'st.' means that the variable has been standardized.

**Figure 1** Transformed canopy cover over roe deer *Capreolus capreolus* bed sites in Akershus and Østfold in relation to snow depth. Different line types represent different wind speeds. The lines indicate the predicted responses from the most parsimonious model presented in Table 1.

points more) canopy cover during cold temperatures; this was not observed when there was no wind (Table 3; Fig. 3a and b). Towards the end of the winter, roe deer started to forage with less canopy cover during the day compared with night (Fig. 3b, Table 3). Canopy cover above sites first increased, and then decreased as the season progressed (Table 3).

Ground cover at foraging sites [55.2 (\pm 35.4)] was significantly higher than at random points nearby [46.0 (\pm 37.4); $n = 168$, $Z = 3.490$, $P < 0.001$]. Feeding sites used by single animals were more 'hidden' than the ones used by families (Table 3).

**Figure 2** Number of roe deer *Capreolus capreolus* (a) foraging sites and (b) bed sites (both in black) compared with random sites (grey) in different micro-topographic categories.

Fourteen of the 27 animals were observed at artificial feeding sites during the study period, and females used artificial feeding sites more often than males (Table 3).

Table 2 Differences between climatic and environmental parameters recorded at foraging sites, bed sites and at the corresponding random sites

	Foraging site			Random site: mean	Bed site			Random site: mean
	Mean	<i>n</i>	<i>P</i>		Mean	<i>n</i>	<i>P</i>	
Snow depth (cm)	22.2	124	< 0.001	31.1	12.9	137	< 0.001	31.5
Temperature (°C)	-3.4	114	0.387	-3.6	-3.3	136	0.080	-3.4
Distance to conifer (m)	24.6	164	< 0.001	33.2	1.9	133	< 0.001	8.3
Dbh (cm)	27.2	143	< 0.001	26.2	23.3	117	< 0.001	18.2
Closest branch (cm)	1436.3	80	< 0.001	2427.5	151.1	91	0.054	264.9

Results from the Wilcoxon's signed rank test; significant *P*-values in bold characters.

Dbh, diameter of the trunk at breast height.

Table 3 Parameter estimation (estimate ± standard error) for the most parsimonious linear model (LM) explaining canopy cover at roe deer *Capreolus capreolus* foraging sites, the most parsimonious logistic regression models (GLM) explaining ground cover (open/hidden) and the use of artificial feeding sites

Predictor variable	Response variable		
	Canopy cover	Ground cover	Artificial feeding sites
Intercept	0.687 ± 0.048	-1.191 ± 0.205	0.588 ± 0.322
Time of day (night vs. day)	-0.044 ± 0.031		
St.temperature	0.020 ± 0.039		
St.Juliandate	-0.008 ± 0.038		
St.Juliandate ²	-0.091 ± 0.026		
Group type (family vs. single)	-0.175 ± 0.038	1.596 ± 0.401	
Sex (males vs. females)			-1.013 ± 0.448
St.windspeed	0.075 ± 0.042		
St.windspeed × st.temperature	-0.132 ± 0.045		
St.Juliandate × st.windspeed	0.094 ± 0.035		
Time of day × st.Juliandate	0.067 ± 0.032		
<i>r</i> ²	0.291		
Sample size	167	168	85

For transformations of response variables, see the main text. Empty cells indicate that the effect is not included in the final model. Characters in bold indicate that the effect is significant both in the LM/GLM and in the corresponding mixed-effects model with individual as a random effect. The prefix 'st.' means that the variable has been standardized.

The mean distance from human settlements to roe deer foraging sites was 151.2 m (± 121.7). However, none of the variables we tested could explain variations in this distance.

Bed sites

The mean canopy cover over roe deer beds was significantly higher than at random sites [44.3% (± 30.7); *n* = 145, *Z* = 9.182, *P* < 0.001]. Beds were placed below spruce trees more often than at random sites ($\chi^2 = 18.249$, *P* = 0.001). Roe deer bedded with significantly less canopy cover when the snow was deeper, and tended to choose beds with more canopy cover when the wind speed was high (Table 1).

Ground cover at roe deer beds [72.5 (± 20.4)] was also higher than expected by chance [62.6 (± 30.1); *n* = 144, *Z* = 2.898, *P* = 0.004]. Variation in ground cover could not be explained by any of the measured variables.

The mean distance from the bedding site to the nearest house was 168.1 m (± 98.3; range: 15–500 m), and increased as the season progressed (Table 1). Roe deer stayed further from houses when wind speeds were high (Table 1). Females maintained longer distances from humans than males, but

this effect was no longer significant in the mixed-effects model (Table 1).

Discussion

Earlier studies have shown that habitat use in ungulates is affected by prevailing weather (e.g. Lang & Gates, 1985; Mysterud & Østbye, 1995; Mysterud *et al.*, 1997). Snow increases the costs of moving around (Parker, Robbins & Hanley, 1984), and reduces the accessibility of forage (Mysterud *et al.*, 1997). Snow depths at foraging sites and bed sites were lower than expected from random choice, and roe deer bedded in areas with more canopy cover when the snow was deep. Increasing snow depth was correlated with decreasing distances between beds and foraging sites, suggesting that roe deer chose habitats to minimize travel costs. Possibly due to depleted fat reserves, the distances between bed and foraging sites were longer later in the season especially when snow depths were lower, indicating increased search effort.

Cover might protect against wind or low temperatures that will increase energy expenditure (Moen, 1973; Parker & Robbins, 1984). Canopy cover can also reduce night-time

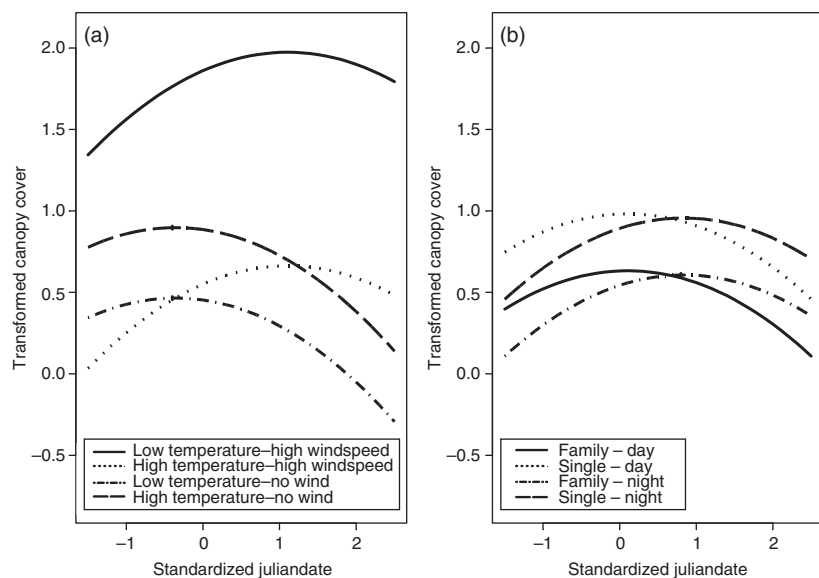


Figure 3 Transformed canopy cover over foraging sites in relation to date. In (a), different line types represent high wind speed and no wind, and high and low temperatures. In (b), different line types represent families and single animals, and day and night. The lines indicate the predicted responses from the most parsimonious model presented in Table 3.

loss of heat through thermal radiation, while it can hinder heating through solar radiation during the day late in the winter season (Moen, 1968; Moen, 1976). It is therefore interesting to observe that as the season progresses, there is a change in use of canopy cover over foraging sites during daytime. In the beginning of the season, there is no difference in the use of canopy cover during the day and night, but at the end of the season roe deer used less canopy cover during the daytime, presumably to make use of the stronger heat radiation from the sun. Consistent with earlier studies of roe deer, canopy cover was higher when temperatures were low, both over beds (Myserud & Østbye, 1995) and feeding sites (Myserud *et al.*, 1999). In addition, roe deer both forage and bed closer to a conifer with a larger diameter than expected from random.

Although sexual dimorphism is minimal in roe deer (Holand, 1990; Holand, 1992a), fawns have low fat reserves in late fall because they prioritize growth (Holand, 1990), which imparts a greater risk of dying from starvation. Indeed, families had less ground cover at foraging sites than single animals and walked shorter distances than other deer, suggesting that they traded off some safety. However, lynx predation has been demonstrated to be unselective for both age and sex (Andersen *et al.*, in press).

Trading starvation for predation?

Between 5 and 10% of the roe deer population in this study area are killed by lynx annually (Andersen *et al.*, 2005), and we would expect roe deer to respond by changing their habitat use. Despite differences in habitat and winter severity, patterns of roe deer selection of bed sites (Myserud & Østbye, 1995) and foraging sites (Myserud *et al.*, 1999) in similar areas before lynx recolonization were remarkably similar to those reported here. Beds were placed closer to conifers and with more canopy cover than expected by

chance, while feeding sites are in more open areas than beds, and distances to humans were less at night compared with that in the daytime in both studies.

The lynx is a stalking predator, and prefers to hunt in dense cover, which allows them to sneak up on their prey (Dunker, 1988). Logically, roe deer should avoid dense cover to be able to detect the lynx before it is too late. This has been observed in other deer species (LaGory, 1986; LaGory, 1987; Altendorf *et al.*, 2001; Stahl *et al.*, 2002). However, canopy and ground cover were higher at both foraging sites and bed sites than expected by chance. The lack of any marked effect of lynx presence may be caused by the relatively long and snowy winter during the study period. In addition to starvation, severe winters make roe deer more prone to predation by both red fox (Cederlund & Lindstrom, 1983) and lynx (Andersen *et al.*, 2005). High risks may therefore be unavoidable even if mistakes are fatal.

In the end, we will allow ourselves to speculate on the time scale of any predator avoidance. As 5–10% of roe deer are killed by lynx, and 66% of lynx attacks are successful (Andersen *et al.*, 2005), we estimate that the chance of an individual roe deer to be attacked by a lynx during each year is <15%. Owing to this rarity of attack for a given individual and severity of winter conditions, it may be useful to adjust the level of predator avoidance over short time scales only. Perhaps, roe deer seek open habitat when exposed to a lynx, but only when the immediate risk of attack is high. Also, the effects of lynx recolonization may potentially be stronger in areas with a lower roe deer density, where there is a much heavier predation pressure by lynx.

Thus, the pattern of habitat selection by roe deer seemed to be strongly influenced by climate, and may be viewed as a survival strategy. Roe deer seem to be forced to accept a high risk when predators are present, due to severe winter conditions and the danger of starvation.

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Supplementary material

The following supplementary material is available for this article:

Appendices S2–S9 Model selection procedure.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2007.00314.x>

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