

Winter habitat use of roe deer (*Capreolus capreolus*) in the presence of lynx (*Lynx lynx*).

Master of Science thesis

By

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Preface

This study was conducted under joint supervision from NINA and the University of Oslo. The study is part of the Lynx and Roe deer project of NINA (Norwegian Institutes for Nature Research) which in turn is part of Scand Lynx – a formal cooperation between Norwegian and Swedish lynx research projects, under the supervision of John Linnell and John Odden. Field work was conducted in collaboration with PhD student Manuela Panzacchi. Atle Mysterud from the University of Oslo contributed with huge amounts of experience and supervision of all analyses and subsequent work. Ivar Mysterud was the formal supervisor from University of Oslo.

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Abstract

Population sizes of large carnivores have increased in Scandinavia during the last century. Increases in predator population sizes can affect prey populations not only through increased mortality, but also through behavioural responses as prey redevelop anti-predator behaviours. In this study, the habitat use of roe deer (*Capreolus capreolus*) in an area with lynx (*Lynx lynx*) was investigated to assess the relative importance of predators and other factors in shaping their use of habitat and cover.

Bed sites had more cover than foraging sites; a difference that was also reflected in the different use of open habitats vs. forests for bedding and foraging. Activity type was not the only factor contributing to differences in habitat use. Local weather (snow depth, temperature and wind speed) explained much of the variation in canopy cover and distances between beds and foraging sites. Roe deer used sites with more canopy cover when temperatures were low and windspeed high. They also walked shorter from beds to foraging sites when snow was deep. As the winter progressed, fat reserves will deplete and the energy budget becomes tighter. That effect was expressed by the selection for more canopy cover at foraging sites by night, less by day, decreasing distance between beds and foraging sites, and from beds to humans, as the season progressed.

Data fits the hypothesis of tighter energy budgets for families (females with young at heel). They had higher canopy cover over foraging sites and walked shorter distances from beds to foraging sites. Males used artificial feeding sites less often, and bedded further from humans than females. These indications might suggest that males are more cautious towards humans compared to females, possibly because of a higher mortality due to hunting.

Few clear differences between the current study and earlier studies from areas without lynx were found. Two non-exclusive explanations are suggested. Despite the presence of resident lynx, few individual roe deer are ever attacked by lynx in this area, thus it will be highly adaptive to adjust trade-offs between predator avoidance and other factors like climatic stress and available forage in favour of the latter when predation risk is low. In addition, weather was quite severe in the winter when the study was conducted, further increasing the importance of avoiding climatic stress. To assess whether roe deer adjust their level of predator avoidance to the immediate predation pressure will require further studies on responses to predator presence.

Contents

Preface	i
Abstract	iii
Contents	1
1 Introduction	3
2 Materials and methods	8
2.1 Study area.....	8
2.2 Study animals.....	8
2.3 Tracking procedure.....	9
2.4 Local choice of bed or feeding site.....	9
2.5 General habitat classification.....	10
2.6 Cover characteristics.....	10
2.7 Topographic characteristics.....	11
2.8 Abiotic factors.....	11
2.9 Statistical analyses.....	11
3 Results	14
3.1 Foraging sites.....	14
3.1.1 Canopy cover.....	14
3.1.2 Ground cover.....	16
3.1.3 Use of artificial feeding sites.....	16
3.1.4 Distance to human settlements.....	16
3.1.5 Local scale selection.....	17
3.2 Bed sites.....	18
3.2.1 Canopy cover.....	18
3.2.2 Ground cover.....	19
3.2.3 Distance between bedding and foraging sites.....	19
3.2.4 Distance to humans.....	21
3.2.5 Local scale selection.....	22
4 Discussion	23
4.1 Predator avoidance behaviour.....	23
4.1.1 Hiding in cover or seeking the open?.....	25
4.1.2 Effects of humans versus lynx as a predator.....	26
4.1.3 Time scale of predator avoidance.....	28
4.2 Differences between bucks and does.....	29
4.3 Effects of weather.....	30
4.4 Variation in habitat use over the winter.....	32
5 Conclusions	33
6 References	34
Appendices	42
Appendix 1 - Model selection on canopy cover at foraging sites.....	42
Appendix 2 - Model selection on ground cover at foraging sites.....	43
Appendix 3 - Model selection on use of artificial feeding sites.....	44
Appendix 4 - Model selection on distance from foraging site to nearest house.....	45
Appendix 5 - Model selection on canopy cover at bed sites.....	46
Appendix 6 - Model selection on ground cover for beds.....	47
Appendix 7 - Model selection on distance between foraging and bedding sites.....	48
Appendix 8 - Model selection on distance from beds to humans.....	50

1 Introduction

When animals are selecting their habitats they have to simultaneously consider many factors. They need to feed, find mates, and avoid extreme weather while also avoiding predation, often from multiple predators, and accidents. These needs are often satisfied to varying degrees in different habitats, and habitat selection is thus often a trade-off between the costs and benefits for a given habitat (Lima & Dill, 1990; Sih, 1980). An animal may experience these trade-offs differently over time depending on current changes in the risk of being predated, resulting in variable habitat selection depending on short-term (daily) variation in factors such as activity, time of day, weather; medium-term (seasonal) variation in fat reserves; and also longterm (annual, decadal) variation in population size of the predator. In addition to this temporal scale of habitat choice, trade-offs may occur at different spatial scales (Boyce *et al.*, 2003; Jones & Hudson, 2002). Habitat selection may be viewed as a series of hierarchical questions ranging from the geographic range of species through home range and finally to the use of different habitats within that home range. When foraging sites are considered, there is also a fourth-order selection: which of the food items should be consumed of those that are available at the site (Johnson, 1980).

A common trade-off facing animals when choosing habitat is the one between foraging and avoiding predation. The most important key to avoid predation is often regarded as being cover. However, what is considered a good anti-predator tactic may vary depending on the hunting strategy of the various predators species. Felid and canid predators for example, use the habitat differently when approaching and catching prey (Murray *et al.*, 1995). In the presence of a predator many different animals prefer micro habitats with much cover, examples are snails (Turner, 1997), fish (Johnsson *et al.*, 2004), hares (Beaudoin *et al.*, 2004), and rodents (Hughes & Ward, 1993). This has also been observed in ungulates such as roe deer (*Capreoleus capreoleus*) (Chen *et al.*, 1999; Mysterud & Østbye, 1995). Another possible strategy would be to stay in an open area where they can detect the predator earlier, and thus avoid an attack. This is supported in studies of other ungulates like the white-tailed deer (*Odocoileus virginianus*) (LaGory, 1986, 1987) and mule deer (*Odocoileus hemionus*) (Altendorf *et al.*, 2001). Because roe deer have no avian predators (except very occasional kills by the golden eagle; *Aquila chryseatos*) canopy cover will not hide them and hence ground cover is more important with respect to predators. Another factor affecting predation risk can be topographic placing, as this can also hide and protect the animal from both

predators and weather, or give advantages such as good overview or an easy escape downhill (Mysterud & Østbye, 1995).

Roe deer winter survival strategies in the north are relatively well understood, but how predation affects the costs and benefits of these behavioural patterns is one of the missing aspects (Holand *et al.*, 1998). The effect of predation is becoming more important as the populations of large predators are increasing not only in Norway, but throughout Europe. During the last century lynx (*Lynx lynx*) populations in Norway have increased (Andersen *et al.*, 2003), and we know little about how these increasing populations affect the behaviour of their prey. When the European lynx have a choice, small ungulates like the roe deer are the most important prey (e.g. Breitenmoser & Haller, 1993; Dunker, 1988; Jobin *et al.*, 2000; Okarma *et al.*, 1997). In southern Norway the lynx is the most important natural predator of adult roe deer (Andersen *et al.*, 2005). The present study aims to investigate the effect lynx have on roe deer by affecting their habitat use, while also controlling for responses to climatic variables which have been shown to be of great importance during wintertime.

The purpose of this study was to examine the habitat use of roe deer in an area with predation from lynx, by snow-tracking radio-collared deer. The temporal scale of habitat use was examined by looking at use over the season, during night and day, and selection during different activities. This study considers the use of different micro-habitats within the home-ranges of the studied roe deer. Based on detailed measurements of cover characteristics, topography, climate, distance to humans and in foraging and bedding sites of roe deer, the following hypotheses and corresponding predictions are investigated:

- I. Antipredator behaviour will affect the use of foraging and bedding sites, and safer places will be preferred at the possible expense of forage quantity or thermal protection.
 - a. Hiding cover will be more important in an area with lynx
 - b. Topographic placement will be high in terrain.
- II. Temporal variation in the use of foraging and bedding sites are determined by the deers' energy budget. This energy budget will be tighter when fat reserves are lower or energy expenditure is high.
 - a. Effects of weather will influence habitat use more when roe deer are in poorer condition (i.e., late in the winter).
- III. Climatic variables will increase costs and hence alter the energy budget and subsequent choice of habitat.

- a. Deep snow will increase the costs of moving, and distances walked by deer will be shorter.
- b. Low operative temperature i.e. a product of temperature, wind and sun radiation, will increase the need for thermal cover.

Specific predictions from the hypotheses are outlined in table 1.

Table 1 An overview of all biological hypotheses to be tested in this study, how they are parameterized (predictor variable) and subsequently included in model selection. “+” indicating that response variable is predicted to increase with predictor variable, “-“ indicating the opposite. Open squares indicates no predicted response to predictor variable and the predictor variable is not included in model selection for this response variable. “F” = foraging sites, “B”= bedding sites. Bolded indicating statistically significant support to the predicted response in the analyses.

Predictor variable	Biological hypotheses	Qualitative predicted effect on increase in response variable							
		Canopy cover		Ground cover		Use of artificial feeding sites	Distance to humans		Distance from foraging site to bed♦
		F	B	F	B		F	B	
Night vs. Day	Higher net heat radiation from animals by night (Schmitz, 1991), lower visibility and less human activity, will increase benefit of canopy cover, decrease benefit of ground cover and decrease risk of humans.	+	+	-	-	+	-	-	+
Temperature	Higher temperature will decrease energy needs (Parker & Robbins, 1984).	-	-	-	-	-	+	+	-
Snowdepth	Deeper snow will increase energy expenditure of moving (Parker <i>et al.</i> , 1984), and decrease access to food (Mysterud <i>et al.</i> , 1997).	-	-	-	-	+	-	-	-
Snowdepth ²	Snow depths over a certain threshold value (chest height; Cederlund & Liberg, 1995) will restrict deer movement more strongly, this can be estimated by a 2 nd or 3 rd degree polynomial of response to snowdepth.	*	+ *	*	*	*	*	*	- *
Snowdepth ³	Previous studies have shown that snow depths over a certain threshold value will considerably restrict deer movement, this can be estimated by a 2 nd or 3 rd degree polynomial of response to snowdepth.	*	*	*	*	*	*	*	+ *
Juliandate	Due to diminishing fat reserves, increased date is predicted to be associated with higher energy needs (Mautz, 1978). Due to increased effect of sun radiation increased date can be associated with lower cost of less cover.	+	+	+	+	+	-	-	-
Juliandate ²	Fat reserves may be depleted to a certain level with low cost, but further depletion can result in death, resulting in a non-linear response to date.	- *	*	*	*	*	*	*	*
Juliandate ³	Fat reserves may be depleted to a certain level, but further depletion can result in death, resulting in a non-linear response to date.	*	*	*	*	*	*	*	*
Family vs. Single	Families take lower risks than single animals (Bleich <i>et al.</i> , 1997). In addition fawns have lower energy reserves and tighter energy budgets (Holand, 1990), and are thus expected to need more cover.	+	+	+	+	-	+	+	+
Male vs. Female	Males may take higher risks than females (Laundre <i>et al.</i> , 2001).	-	-	-	-	+ -	-	-	-
Windspeed	Increasing windspeed lowers operative temperature (Moen, 1973), and hence increases energy needs.	+	+	+	+	-	+	+	+

Night/Day*temperature	Higher net radiation from animals by night, increasingly important when temperatures are low, is predicted to increase protective gain from cover. (Schmitz, 1991)	*	*	*	*	*	*	*	*
Night/Day*Juliandate	Strength of sun radiation increases by date, only relevant at daytime. Open habitats may therefore be more attractive.	+*	*	*	*	*	*	*	*
Night/Day*windspeed	Higher net radiation from animals by night increases benefit of thermal cover	*	*	*	*	*	*	*	*
Temperature*Juliandate	Energy demands of low temperatures is more important when fat reserves are low.	*	*	*	*	*	*	*	*
Temperature*windspeed	The concept of operative temperature (Moen, 1973) is increasingly important as windspeeds increase or temperature decrease	-*	*	*	*	*	*	*	*
Snowdepth*Juliandate	Energy demands of deep snow is more important when fat reserves are low.	*	*	*	*	*	*	*	-*
Juliandate*Family	The proportionally higher energy demands of fawn is more important when fat reserves are low.	*	*	*	*	*	*	*	*
Juliandate*Sex	Energy demands of fawn is more important when fat reserves are low, this	*	*	*	*	*	*	*	*
Juliandate*windspeed	SEnergy demands of low operative temperatures is more important when fat reserves are low.	+*	*	*	*	*	*	*	*
Artificial feeding site vs. Natural feeding site	Artificial feeding sites are often placed in open areas near humans, thus they may be seen as higher risk than natural feeding sites.								+*
Canopycover at feeding site	Higher canopy cover at foraging site may reduce the benefit of walking to find more cover for bedding.								*
Night/Day*artificial feeding site	Human activity is lower by night, this is more important in artificial feeding sites.								*
Snowdepth* artificial feeding site	There is less snow in human vicinity (assuming artificial feeding sites are close to humans).								*
Juliandate* artificial feeding site	Artificial feeding sites may become more important as energy reserves are depleted.								*
Family* artificial feeding site	Females with offspring take lower risks than single animals, and artificial feeding sites can be seen as high risk because of human presence.								*
Sex* artificial feeding site	Females take lower risks than single animals, and artificial feeding sites can be seen as high risk because of human presence.								*
Windspeed* artificial feeding site	It is possible that roe deer use artificial feeding sites less when there is much wind, as these sites are typically more wind-exposed.								*

*Predicted response is dependent upon response of main variable(s), and can therefore not be unambiguously qualified. Predictions are clear from the column “biological hypothesis”. Given responses (+/-) are results from analyses, that are interpreted to be in a predicted direction.

◆Distance between beds and foraging sites are only expected to increase/decrease as a response to predictor variables if there is a trade-off between qualities of beds and foraging sites.

2 Materials and methods

2.1 Study area

The field work was conducted in South-eastern Norway, in the counties of Akershus and Østfold, in the area around the southern and eastern part of Lake Øyern, situated between approximately 69°-60°N and 11°-12°E. The study area is dominated by boreal forest, mainly Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The forest is intensively managed and clear cuts of varying sizes are found throughout the study area.

The average temperature from 1961 to 1990 was -5.5 °C in January, -5.0 °C in February and -1.0 °C in March. The average precipitation during these years was between 36 and 46 mm in January, February and March. In the study period, the average temperatures were -5.0 °C, -3.0 °C and 0.5 °C, in January, February and March, respectively. The snow depth at the weatherstation from where these data are obtained (2540 Høland-Fosser; Klimadivisjonen, Meteorologisk institutt) were between 0 and 50 cm during the study period.

The area was recolonized by roe deer around 1920 (Andersen *et al.*, 2004), after being extinct in this area since the seventeenth century (Ekman, 1919). Roe deer are the most important prey of lynx (Herfindal *et al.*, 2005), and except from humans, lynx are the most important predator of adult roe deer in this area. Lynx were responsible for more than 20 % of the adult radio-collared roe deer kills in the lynx and roe deer project (Andersen *et al.*, 2005). Other causes of death were human hunting (~30%), car accidents (~17%), other accidents or illness (~12%), dogs (~7%), foxes (*Vulpes vulpes*) (~6%), wolf (*Canis lupus*) (~1%) and unknown causes (~7%) (Andersen *et al.*, 2005).

In the period of this study, all roe deer were within the home range of at least one resident female and one resident male radio-collared lynx. In addition there may have been lynx without collar in the area. The annual lynx hunt started February 1st, and lasted only a few days. None of the adult lynxes in the study area were killed during this hunt. Roe deer are hunted from mid August until the end of December.

2.2 Study animals

Roe deer were captured with box-traps, drop-nets or as fawns and fitted with radio collars (Televilt Int.) as a part of the lynx and roe deer project (Andersen *et al.*, 2005). The animals included are distributed between age and sex groups as indicated in table 2. Of the fawns that were tracked, five were without mothers, two of these were sisters and treated as one

individual in the analysis, because they stayed together all the time. Two of the fawns had living mothers, but the mothers were not collared. I assumed they stayed together, and this was confirmed to a certain degree as their tracks always were seen together with tracks of at least one adult deer.

Two of the animals were killed during the study period, one adult female without fawns and one female fawn without a mother. The adult was killed by a lynx in the very beginning of February, and the fawn was killed by a fox in the same period.

Table 2. Distribution of study animals by age and sex.

	Males	Females	Total
Fawns without mother	2	2	4
Yearlings	3	2	5
Adults	6	12 (5 with fawns)	18
Total	11	16	27

2.3 Tracking procedure

Tracking took place between January 7th and March 4th 2004 whenever snow conditions allowed tracking. The animals were radio tracked at different hours, both during night and day. Of the 144 beds and 168 feeding sites found, 48 and 75 respectively, were found by night. The general positions of the animals were determined by triangulation. The animals were then approached and the exact position was determined by snow tracking. The snowtracks were followed until a bed site or a feeding site was found. To avoid scaring the animals too often, we did not approach the position immediately every time, so that the animal had time to move away. We were especially careful when the animals were at artificial feeding sites. Each animal was tracked between eight and fifteen times. Due to bad snow conditions or problems with the radio tracking, the animals were not always found, and hence all animals were not tracked equally.

2.4 Local choice of bed or feeding site

To be able to compare the chosen bed or the feeding site to the locally available habitat, all parameters were measured both at the site and at a point 50 m away in a random direction. This enables paired comparisons between each bed or feeding site and an associated random point.

2.5 General habitat classification

The habitat where the bed or foraging site was found was classified as “forest” or “garden/field”. All observations in forest were then classified again in different types (conifer, deciduous or mixed) and different cutting classes following the standard national forest evaluation of Norway: Clear cuts (class I), young plantations (class II), pole size stands (class III), medium-aged stands (class IV) and older mature stands (class V).

2.6 Cover characteristics

The closest tree was registered, and categorized as “spruce”, “pine” or “deciduous”. The distance to the closest conifer, the diameter at breast height (dbh), and distance to the closest live branch was measured. If the bed or feeding site was not in a forest, the distance to the closest 10 trees were registered.

Canopy cover was measured using a spherical densiometer (model C) (Lemmon, 1956, 1957). The densiometer was held horizontal, 30 cm above ground to simulate a bedding roe deer, and percentage cover was quantified. The densiometer contains a concave mirror that is divided into 24 squares. When quantifying the canopy cover each of these squares were divided into four and the number of small squares covered was counted. This is repeated in four directions (north, east, south and west) and the average was used. By multiplying the average with 1.04 an estimate of percentage cover is obtained.

Ground cover (also termed concealment cover, hiding cover, protective cover, security cover and escape cover) was measured by using a cover board (Myserud & Østbye, 1999; Nudds, 1977). The cover board was divided in 16x5 squares of 5x5 cm, and the number of squares seen 5 m and 30 m away in a random direction was counted. Studies of the lynx hunting techniques show that more than two thirds of successful hunts were less than 20 m long and attacks longer than 50 m are rarely successful (Haglund, 1966). Measures of ground cover at 30 m should therefore be a good indicator of anti-predator cover. Also, the sighting distance in the direction of the incoming tracks, and in the opposite direction was measured. This made it possible to check whether the roe deer had a better view in the direction from which it had walked into the bed, perhaps to discover predators that might follow its track.

For bedding sites, also the distance to feeding site (back tracking) was measured, and the canopy cover at this site was measured. Long distances may be underrepresented because it is sometimes difficult to backtrack the roe deer far, either because there were a lot of tracks or because of poor snow conditions.

2.7 Topographic characteristics

“Microtopography” was categorized as described in Mysterud and Østbye (1995). Microtopography is defined as a difference of 5-30 m between top and bottom. 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 characterised as flat. The slope in the point was also measured.

2.8 Abiotic factors

Temperature and snow depth were measured at the bed or foraging site. The temperatures varied between -18 and 8°C at the sites of beds and foraging. Snow depths varied between 0 and 61 cm. In addition, precipitation, wind speed and direction, snow depth and temperature were obtained from a weather station in the area (Weather station 2540 Høland – Fosser, 152 m a.s.l.). At this weather station wind speed and direction, and temperature was measured at 7:00 am, 13:00 pm and 19:00 pm every day, and precipitation and snow depth measured once every day. The measurement closest in time to the localizing of the animal was used in analyses. In the study period the temperature varied between -19.9 and 5.1°C, and snow depth was between 25 and 50 cm at the weather station. Wind speeds varied between 0 and 6.7 m/s. Exposition was measured in both beds and foraging sites as the direction with least topographic protection. This measure was then used to calculate wind exposition: the difference in degrees between the direction of the wind at the time of tracking and topographic exposure. This is only relevant when there is wind and “wind exposure” was only included in analyses if windspeed was 1 m/s or more.

2.9 Statistical analyses

A combination of Generalized Additive Models (GAM), 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). GAM was used to assess whether predictor variables was linearly or nonlinearly related to the response variable, thus enabling appropriate parametrization for LM and LME.

To obtain normality and to avoid heteroscedasticity, canopy cover data was transformed with $\arcsin[\sqrt{(\text{canopy cover}/100)}]$, distance to nearest house was transformed with square root, and distances between foraging and bedding sites were ln-transformed. The inclusion of two-way interactions and second and third order polynomials in the tests were

based on biological reasons. Parametrization and the variables biological meaning is shown in table 1.

The ground cover variables had properties making 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 analyzed 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 I then can be sure that the temperature or snow depth in the analysis is not the effect of the choice of preferred micro habitat, but rather an explaining variable. Because only one member of each family group is used in the analyses, all families are registered as “females”. Therefore, only one of the predictor variables “family” or “sex” were used in a model at the time, and the final model includes the parameter which gave the most parsimonious model, or, if not necessary, none. In a similar way, either the variable “artificial feeding site” which indicate whether the feeding site used is artificial or not, or the variable “canopy cover over feeding site” was used in the model because they are highly correlated.

Interactions between continuous predictor variables were assessed by the multiplicative term of the standardised (st.) variables (mean 0, variance 1). Standardising helps when interpreting interactions between continuous variables, because the interaction term is zero when the one variable in the interaction is average. The coefficient for a st. variable included in an interaction term is then the strength of this variable when the other is average (Myrsetad *et al.*, 2000).

Model selection was aided by the Akaike Information Criterion (AIC), adjusted for small sample sizes (Johnson & Omland, 2004) by adding the term $(2K(K+1) / (K-n-1))$ to the AIC-value (AICc) (Burnham & Anderson, 2002). The model with the lowest AICc value was chosen as it represents the best compromise between explaining as much variance as possible while using the smallest number of variables possible (parsimonious principle). Entire model-selections are shown in appendices 1-8. As AIC cannot be used in combination with mixed models (based on REML), I performed the model selection using LM. The final model (as defined by the AICc) was then analysed with LME with individual deer identity 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 influence of single observations (outliers, Cook's distance). Overdispersion (unaccounted heterogeneity) was assessed by the statistical significance of the residual deviance of the fitted model.

Initial modelling revealed that activity was a main factor in analysis of all response variables, and that different variables seemed to be important for different activities. Analyses were therefore split in two parts, one model for foraging sites and one for bed sites.

Analysis of the use of artificial feeding sites was done in two steps. First, model selection was used to find out if there were any patterns in which animals used the artificial feeding sites. The response variable in this model selection was whether individual animals had used an artificial feeding site at least once during the study period. To find more detailed information on when the artificial feeding sites were used, another model selection was performed on a limited dataset, only containing data from those animals that did use an artificial feeding site at least once during the study period.

Other continuous characteristics of beds and foraging sites were analysed by Wilcoxon signed rank tests to find differences between the preferred site and random points. Categorical data were analysed with chi-square tests.

Statistics and most subsequent graphical presentations were performed in S-plus (6.2 Professional edition). Statistical significance was set at $p < 0.05$. All means are given \pm SE (standard error). Plots are based on final models from model selection. Solid lines represent the predicted response, and dotted lines represent 2 SE (i.e. 95% confidence interval).

3 Results

Roe deer proportional use of habitats in Akershus and Østfold differed for foraging and bedding. Canopy cover over bed sites (transformed estimate: 1.155 ± 0.041 , $p < 0.0001$, LME) were higher than over foraging sites (transformed estimate: 0.651 ± 0.041 , $p < 0.0001$, LME). This is reflected in proportionally higher use of forests compared to fields/gardens when bedding compared to feeding (proportion beds in open habitat: 0.007, proportion foraging sites in open habitat: 0.293). This difference between foraging and bed sites is also reflected in proportional use of different forest habitats (0.727 of beds in coniferous forests, 0.580 foraging sites in coniferous forest), but not so much in differential use of different cutting classes (proportion beds in mature forest (class IV and V): 0.669, proportion foraging sites in mature forest: 0.672).

3.1 Foraging sites

3.1.1 Canopy cover

The mean canopy cover at roe deer feeding sites was $42.7 \pm 33.09\%$, and varied between 0 and 100%. Canopy cover at foraging sites were significantly different from canopy cover at random points (Wilcoxon signed rank test, $n = 168$, $p < 0.001$, random point = 30.65 ± 32.22). The most parsimonious linear model (table 3) explained 30% of the variation in canopy cover above foraging sites ($n = 167$).

Roe deer foraged at sites with more canopy cover in strong wind compared to when there were no wind, but especially late in the season (i.e., a significant “date” and “windspeed” interaction; table 3, figs. 1a and b). In strong wind, roe deer used foraging sites with higher (about ten percentage points more) canopy cover at cold temperatures compared to warmer; this was not observed when there was no wind (significant interaction between “windspeed” and “temperature”; figs. 1a and b, table 3), an expected response based on operative temperature (table 1). Contrary to expectation (table 1), there was no support that families foraged in areas with higher canopy cover than single animals (table 3). Early in the season roe deer foraged in areas with denser canopy cover by day compared to at night. This changed towards the end of the winter season, when no obvious difference was observed (nearly significant “night/day” and “date” interaction; table 3). The difference between night and day is small (about one percent difference), and this effect probably has little biological importance.

Canopy cover above sites first increased, and then decreased as the season progressed (sign. effect of date up to 2nd order; table 3). This was a quite strong effect, and even though the effect of date interacted with wind speed and night/day, the overall picture of the seasonal effect was fairly stable (figs. 1 a and b).

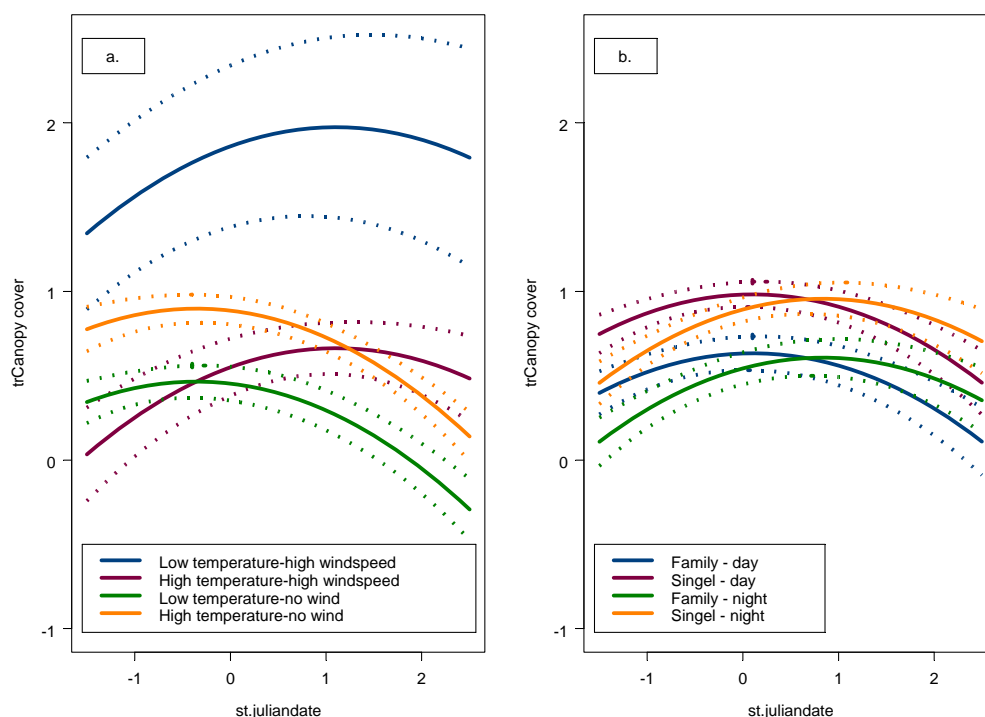


Figure 1 Canopy cover over foraging sites by date, with no wind, and with strong wind.

a. shows that roe deer in Akershus seeks more cover when conditions are harsh, both strong wind and low temperatures.

b. shows that families have marginally lower cover than single animals. In the beginning of the season canopy cover is higher by day compared to night.

Table 3. Parameter estimation using linear models for transformed canopy cover over foraging sites. After model selection with wind as a continuous variable. p-values in **bold** are significant.

		<u>LM</u>			<u>LME</u>
	estimate	Std. Error	T	P	P
Intercept	0.687	0.048	14.297	0.000	<.0001
Time of day (night vs. day)	-0.044	0.031	-1.423	0.157	0.232
St.temperature	0.020	0.039	0.509	0.612	0.908
St.juliandate	-0.008	0.038	-0.215	0.830	0.649
St.juliandate ²	-0.091	0.026	-3.505	0.001	0.005
Group type (family vs. single)	-0.175	0.038	-4.600	0.000	0.002
St.windspeed	0.075	0.042	1.798	0.074	0.075
St.windspeed*st.temperature	-0.132	0.045	-2.925	0.004	0.003
St.juliandate*st.windspeed	0.094	0.035	2.707	0.008	0.009
Time of day*st.juliandate	0.067	0.032	2.082	0.039	0.024

3.1.2 Ground cover

Ground cover at foraging sites was significantly different from ground cover at random points nearby ($n = 168$, $p = 0.0173$ at the distances of 5m from point and $p = 0.0005$ and 30m from point). The mean ground cover was 18.60 ± 29.01 at five meters and 45.95 ± 37.42 in thirty meters from random point. Mean ground cover was 26.81 ± 34.04 in five meters and 55.19 ± 35.43 in thirty meters from foraging sites, and ground cover was classified as “open” in 30.9% of foraging sites.

Only one explaining variable, “family”, was included in the most parsimonious model describing ground cover as measured at 30 meters from the foraging site. Families used sites that were “hidden” more often than single animals (transformed estimate for single animals - 0.393 ± 0.201 , $p = 0.025$; estimate for families 0.798 ± 0.201 , $p < 0.0005$). The final model describing ground cover at 5 m from the foraging sites included only snow depth. Although the effect of snow depth was significant ($p < 0.01$), the model was somewhat overdispersed (residual deviance 208 on 166 degrees of freedom), and the effect biologically negligible (ground cover $\sim 2.16 \pm 0.64 - 0.05 \pm 0.02 * \text{st. snow depth}$). In addition, the null model was nearly as good as the model including snow depth ($\Delta\text{AICc} = 0.063$).

There was no evidence that sighting distances in the direction of the incoming tracks were longer than expected from random (Wilcoxon signed rank test, $n = 125$, $p = 0.0236$, mean = 27.90 ± 45.23 m, opposite direction mean = 68.12 ± 136.59 m).

3.1.3 Use of artificial feeding sites

Fourteen of the 27 animals were observed at an artificial feeding site during the study, but no pattern could be detected in which animals used artificial feeding sites. Among those roe deer using artificial feeding sites, the final model included no climate variable. The only effect found was that females use artificial feeding sites more often than males (females: 0.081 ± 0.224 ; males: -0.425 ± 0.224 , $p = 0.015$).

3.1.4 Distance to human settlements

Mean distance from human settlements to roe deer foraging sites in this study was 151.2 ± 121.7 m, minimum distance was 7 m, and maximum distance was 550 m. The most parsimonious model included only temperature ($\text{Sqrt}[\text{distance to humans}] \sim 11.026 \pm 0.462 - 0.076 \pm 0.062 * \text{st. temperature}$, $p = 0.2228$, $n = 168$) and explained very little of the variation ($R^2 = 0.009$). This may indicate that none of the tested variables can explain any pattern in roe

deer distances from humans when foraging. As support to this, the null model had a better fit than the model including temperature ($\Delta AICc = 0.57$).

3.1.5 Local scale selection

Foraging sites of roe deer in Akershus and Østfold County winter 2004 were placed on upper thirds or microtopographic tops more frequently than expected by chance (fig 2; $\chi^2 = 24.798$, $p < 0.001$). Data from comparisons between foraging sites and random points are presented in table 4. Snowdepth at foraging sites were lower than snowdepths at random points. Temperatures and wind expositions at foraging sites on the other hand were not different from random sites. Roe deer preferred foraging closer to conifers and the closest conifer had larger diameter than conifers at random positions. Foraging sites were placed near a conifer more often than random points ($\chi^2 = 40.1901$, $p < 0.001$) and had closest live branch closer than expected by chance.

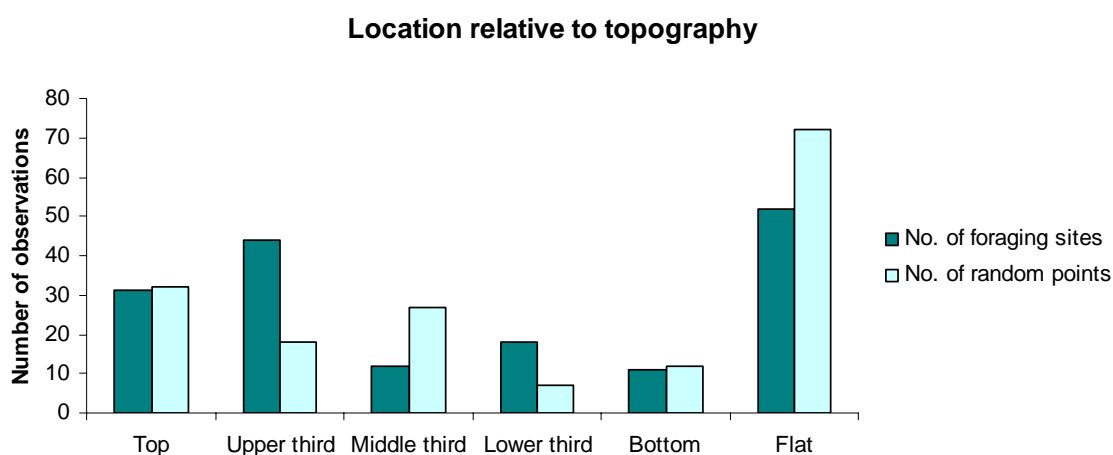


Figure 2 Locations of roe deer foraging sites in relation to microtopography. More foraging sites are found in upper third than expected by chance.

Table 4 Characteristics for foraging sites and data from Wilcoxon signed rank test. p-values in **bold** are significant. Dbh: diameter at breast height.

	Foraging site			Random site
	mean	n	P	mean
Snowdepth (cm)	22.18	124	0.000	31.12
Temperature (°C)	-3.36	114	0.387	-3.56
Wind exposition	78.55	58	0.568	82.39
Distance to conifer (m)	24.57	164	0.000	33.20
Dbh (cm)	27.24	143	0.001	26.18
Closest branch (cm)	1436.31	80	0.000	2427.53

3.2 Bed sites

3.2.1 Canopy cover

Mean canopy cover over roe deer beds were $80.12 \pm 21.12\%$, and varied between 0 and 100%. This was significantly more cover than expected from random choice (Wilcoxon signed rank test, $n = 144$, $p < 0.001$, random site mean = $44.27 \pm 30.70\%$). The final linear model (table 5) explained 8.9 % of the variation in canopy cover above sites ($n=144$).

Roe deer bedded with significantly lower canopy cover when snow was deep, this effect levels off when snowdepth is higher than about 20 cm, and then increases slightly (table 5, fig 3). There is also a trend, although not significant, that roe deer chose beds with more canopy cover when windspeed was high (table 5, fig. 3). Predicted canopy cover is almost five percent higher when wind is strong.

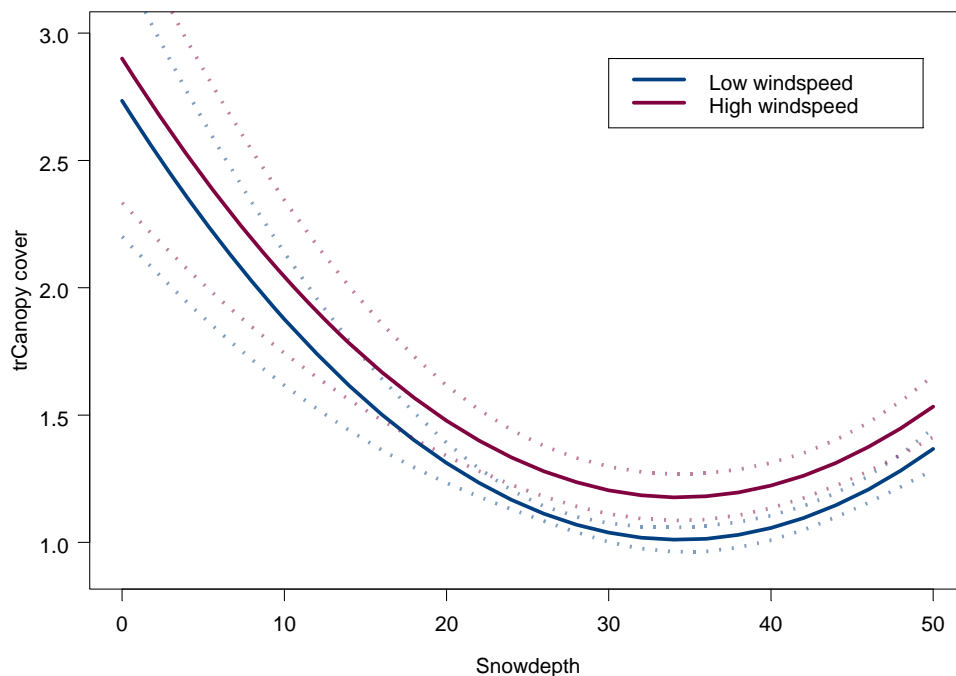


Figure 3. Roe deer in Akershus and Østfold selected habitats with more canopy cover for bed sites as snow depth increased. Higher canopy cover was also selected when windspeed increased, indicating that they compensated for higher rates of heat loss.

Table 5. Parameter estimation using linear models for transformed canopy cover over bed sites. p-values in **bold** are significant.

	<u>LM</u>				<u>LME</u>
	Estimate	Std. Error	T	P	P
Intercept	1.043	0.038	27.829	0.000	<.0001
St.snowdepth	-0.064	0.037	-1.744	0.083	0.078
St.snowdepth ²	0.099	0.030	3.257	0.001	0.001
St.windspeed	0.038	0.024	1.588	0.115	0.109

3.2.2 Ground cover

Ground cover at roe deer beds in Akershus and Østfold was significantly higher than expected by chance (Wilcoxon signed rank test, $n = 144$, $p = 0.0117$, mean = 31.45 ± 31.62 , random site mean = 23.62 ± 30.31 , for measures at 5 meters from bed site, and $p = 0.0038$, mean = 72.47 ± 20.36 , random site mean = 62.64 ± 30.15 , for measures at 30 meters from bed site). In only 9.7% of beds, ground cover was classified as “open”.

The most parsimonious models describing ground cover at bed sites were the null models, and thus variation in ground cover could not be explained by any of the measured variables.

Overall, sighting distances were shorter than expected (Wilcoxon signed rank test, $n = 123$, $p = 0.7586$, mean = 27.30 ± 33.94 , opposite direction, mean = 40.69 ± 72.22). This was the opposite of expected (table 1). If restricting the analysis to include data points with sighting distances no longer than 100 m in any direction, sighting distance was longer in direction of the incoming track than expected from random (Wilcoxon signed rank test, $n = 108$, $p = 0.0279$, mean = 21.53 ± 20.97 m, opposite direction, mean = 17.56 ± 17.19 m).

3.2.3 Distance between bedding and foraging sites

Mean distance between roe deer beds and foraging sites were 47.11 ± 75.37 m, and varied between 0 and 338 m. The final model (table 6) explained 79.40 % of the variation in distances between foraging and bedding sites ($n = 121$).

Roe deer in Akershus and Østfold walked significantly longer distances between bedding and artificial foraging sites than between bedding sites and other foraging sites (table 6, fig. 4). They also walked significantly longer when snowdepth was low (table 6, fig. 4), suggesting a smaller trade-off between energy spent on walking and benefit of moving to a safer habitat for bedding. Early in the season distances between bedding and foraging site were longer than late, this effect was only seen when there was much snow (i.e., a significant “St.juliandate” and “St.snow depth” interaction; table 6, fig. 4). Families tend to walk shorter distances between bedding and foraging sites than single animals (table 6). Although not statistically significant, distances were longer at higher wind speeds (table 6).

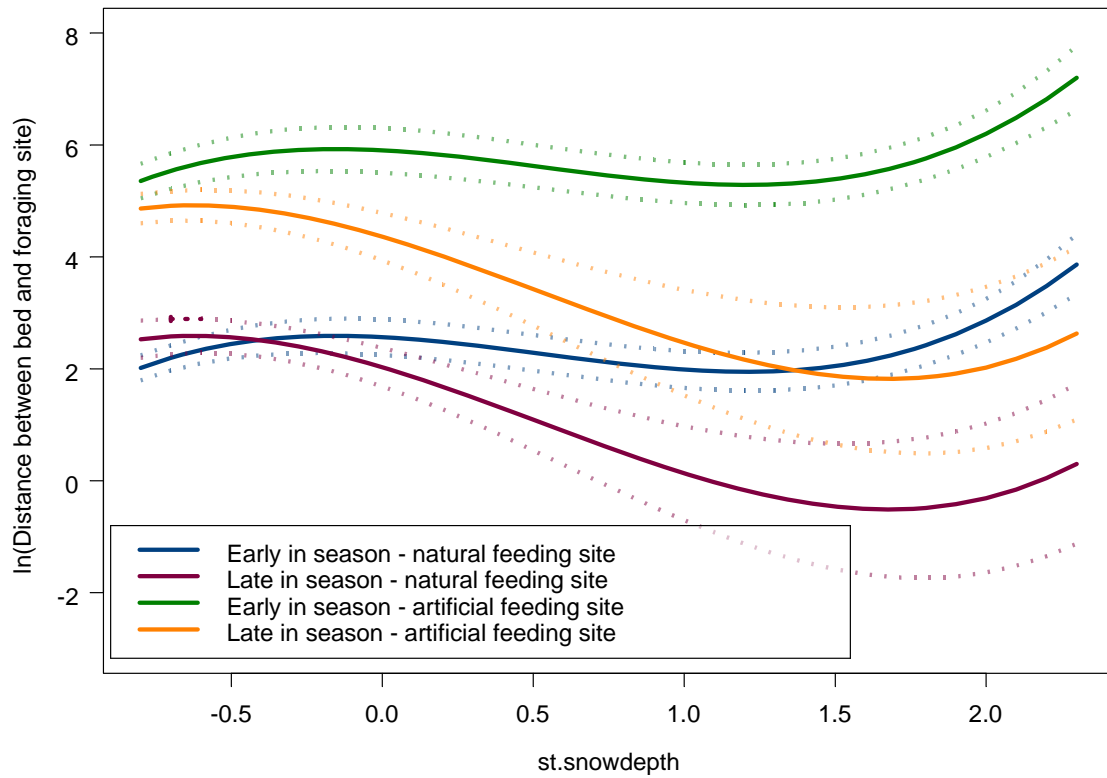


Figure 4. Distances between beds and foraging sites. Roe deer walked longer when there was little snow, except for early in the season when they were foraging at artificial feeding sites. Generally roe deer travelled longer between an artificial feeding site and bed than between a natural feeding site and bed. There is also an indication that they walked longer between bed and foraging site early in the season compared to late in the season, but this difference can only be seen when there is much snow.

Table 6. Parameter estimation using linear models for ln (distances between bedding and foraging sites). p-values in **bold** are significant

	<u>LM</u>			<u>LME</u>	
	Estimate	Std. Error	T	P	P
Intercept	1.868	0.164	11.409	0.000	<.0001
Time of day (night vs. day)	0.257	0.153	1.679	0.096	0.095
St.snow depth	-0.749	0.200	-3.751	0.000	0.001
St.snow depth ²	-0.822	0.284	-2.899	0.005	0.007
St.snow depth ³	0.523	0.141	3.703	0.000	0.001
St.juliandate	-0.190	0.152	-1.248	0.215	0.272
Group type (family vs. single)	0.440	0.196	2.243	0.027	0.056
St.windspeed	0.148	0.084	1.775	0.079	0.060
Artificial feeding site	2.994	0.202	14.850	0.000	<.0001
St.juliandate*st.snowdepth	-0.431	0.199	-2.163	0.033	0.049
St.juliandate*artificial feeding site	-0.309	0.177	-1.749	0.083	0.099

3.2.4 Distance to humans

Mean distance from bedding sites to nearest house was 168.09 ± 98.25 m, and varied from 15 to 500 m. The most parsimonious model (table 7) explained 19.6 % of the variation in distances between beds and nearest house ($n = 144$).

Roe deer stayed further from houses when there were high windspeeds (table 7, fig 5). Females kept longer distances to humans than males (table 7), as predicted if they take less chances (table 1). However, this effect was no longer significant in the mixed model. Distances from humans were longer later in the season (table 7).

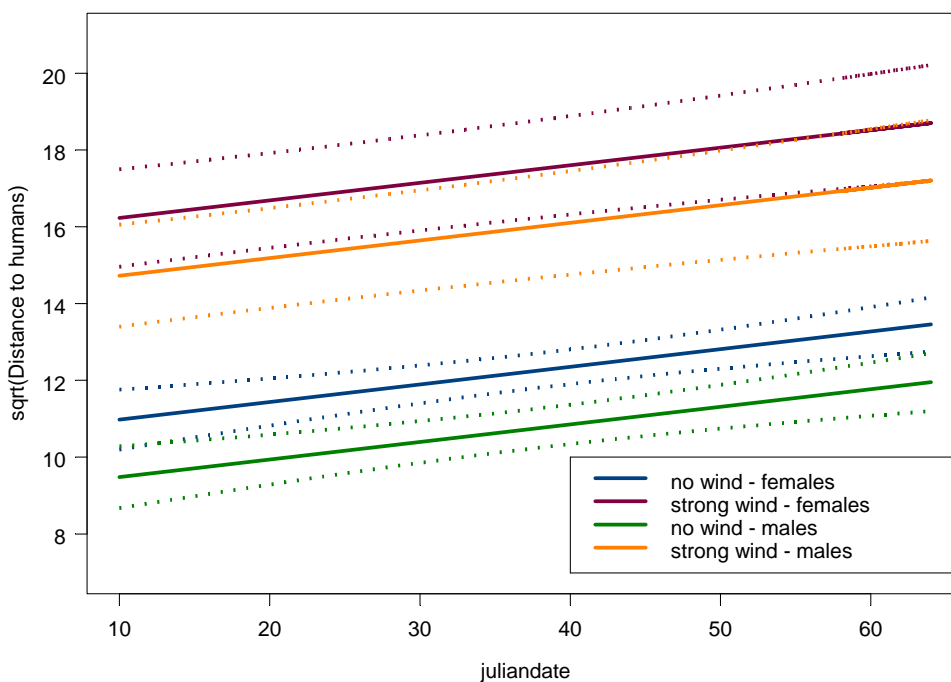


Figure 5. Distance from bed sites to houses. Distances are longer when wind is strong and females keep longer distances to houses than males. There is also an effect of date, as distances to humans increase later in season.

Table 7. Parameter estimation using linear models for sqrt (distances from bed to nearest house). p-values in **bold** are significant

	<u>LM</u>				LME
	Estimate	Std. Error	T	P	P
Intercept	9.554	0.926	10.318	0.000	<.0001
Time of day (night vs. day)	-0.542	0.320	-1.696	0.092	0.086
St.juliandate	0.048	0.022	2.192	0.030	0.018
Sex (male vs. female)	-0.741	0.307	-2.416	0.017	0.222
St.windspeed	0.761	0.213	3.575	0.001	0.012

3.2.5 Local scale selection

Roe deer beds in Akershus were more commonly placed on the upper third of microtopographic tops (fig 6; $\chi^2 = 60.427$, $p < 0.0001$). Beds were closer to a conifer (table 8) and placed below spruce trees more often than expected by random ($\chi^2 = 18.2487$, $p = 0.001$). The chosen tree had larger diameter and lower branches than random trees (table 8). Roe deer also chose bed sites with snowdepths that were significantly smaller than expected by chance (table 8). Temperature in the bed was also lower than in random points, although not significant (table 8). The beds were no less wind exposed than random points, but this is based on merely 18 observations (table 8).

Table 8. Characteristics for roe deer beds and data from Wilcoxon signed rank test. p-values in **bold** are significant. Dbh: diameter at breast height.

	Foraging site			Random site
	mean	n	P	mean
Snowdepth (cm)	12.90	137	0.000	31.46
Temperature (°C)	-3.29	136	0.080	-3.39
Wind exposition	90.74	18	0.528	87.70
Distance to conifer (m)	1.94	133	0.000	8.29
Dbh (cm)	23.34	117	0.001	18.23
Closest branch (cm)	151.09	91	0.054	264.91

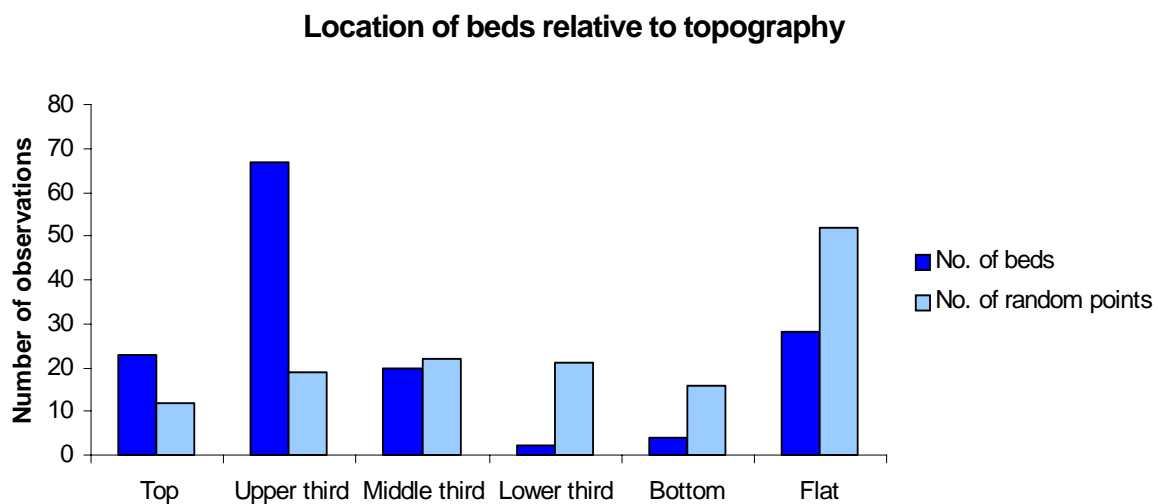


Figure 6 Locations of roe deer beds in relation to microtopography. More beds are found in upper third and top, and rarely in lower third or bottom, compared to random points which are more

4 Discussion

I have analyzed habitat use of roe deer in an area with lynx, which is an important predator of roe deer in this area all year round. Roe deer selected both foraging sites and bed sites with more cover than expected from random. Variation in canopy cover was mostly explained by weather factors, but little variation in ground cover could be explained by any of the measured variables except activity. Roe deer bedded and foraged high in topography. Families walk shorter distances and forage with higher canopy cover than other animals, while males keep shorter distances to humans. Habitat use also changed over the winter season: ground cover increased and canopy cover decreased at daytime while increased at nighttimes. In general, most of the results found in this study do not differ from the results found in areas without lynx. However, some behaviour observed can be interpreted as predator avoidance. Hence, predator avoidance strategies are, in addition to and together with shelter from climatic factors, predicted to be essential for survival in roe deer.

4.1 *Predator avoidance behaviour*

Predators can affect prey populations in two distinct ways, through direct predation or by affecting prey behaviour through fear (Brown *et al.*, 1999). In systems where fear is the driving force in the predator-prey interaction, predators can affect prey fitness more through behavioural adaptations like vigilance and trade-off behaviour (like choice of less productive foraging habitat in change for safety), than through actual killing. Several studies of ungulates have assessed the behavioural differences between adjacent areas with and without predators or in one area, before and after introduction of predators. Results show that predation risk is not only enough to make prey species shift their habitat (Hernandez & Laundre, 2005), but it reduced foraging through increased vigilance (Hunter & Skinner, 1998; Laundre *et al.*, 2001; Wolff & Van Horn, 2003) and reduced forage quality (Hernandez & Laundre, 2005). In the Swiss Alps it took roe deer only ten years to behaviourally readapt to the predation risk from lynx (Breitenmoser & Haller, 1993). The lynx disappeared from Akershus and Østfold by the end of the 19th century but reappeared around 1950, although the constant presence of reproducing lynx was only reestablished in the mid 1990's (Linnell *et al.*, 1998). It is thus likely that roe deer in the study area have had the time to adapt to the lynx.

Another study from the Swiss Alps showed that ruminating (while bedded) is the most dangerous activity, in the sense of predation risk, for roe deer (Molinari-Jobin *et al.*, 2004).

This can be explained by habitat choice because roe deer prefer dense cover when ruminating, which may allow the lynx to approach undetected, or it may be explained by a lowered sense of hearing while ruminating (Molinari-Jobin *et al.*, 2004). The first explanation would, however, involve maladaptive behaviour, which would probably be strongly selected against. In addition, a study from Norway indicates that more deer were killed while foraging than resting and considering that roe deer are active only 35% - 45% of their time during winter (Cederlund, 1981; Jeppesen, 1989), foraging seems to be the most dangerous activity in this area.

Comparisons of the present study with a study of roe deer selection of bed sites (Mysterud & Østbye, 1995) and foraging sites (Mysterud *et al.* 1999) in Lier can give some clues to differences in behaviour in areas with and without lynx, and thus to anti-predator responses. This comparison involves some difficulties though. Available habitat in Lier is not the same as in the present study, and weather was different during the winter it was conducted, leaving the roe deer with a different energy budget. Despite these differences in habitat and winter weather, patterns were remarkably similar; beds are placed closer to conifers and with more canopy cover than expected from random while feeding sites are in more open areas, and distances to humans were less at night compared to day. Qualitative patterns in canopy cover are also the same in Lier and Akershus/Østfold, and seem to be controlled to a large extent by climatic variables.

Both in Lier and in Akershus / Østfold roe deer selected bed sites placed high in the topography. In the present study, however, beds were placed in the upper third in contrast to top placements in Lier and other studies of bed and foraging sites of roe deer (Chen *et al.*, 1999; Markgren, 1966; Mysterud & Østbye, 1995) and other deer (Armstrong *et al.*, 1983; Huot, 1974; Smith *et al.*, 1986). The choice of micro-topographic tops is a way of getting an overview over the surroundings. Not only is the risk of being attacked important for habitat choice, the probability of escape is just as important (Lima, 1992). Roe deer also have an advantage over the predator, the roe deer can escape downhill, but the predator must attack uphill (Mysterud & Østbye, 1995). Compared to the highest point, I propose that it will be more advantageous to stay just below the top where the roe deer is harder to spot because it does not show itself against the sky and is covered in one direction.

4.1.1 Hiding in cover or seeking the open?

Most authors assume it is always good to seek cover to avoid predation (reviewed in Mysterud & Østbye, 1999). However, different predators use different hunting techniques, felid and canid predators for example, use the habitat differently to approach and catch their prey (Murray *et al.*, 1995). Thus, to avoid predation from these different predators, prey should apply different anti-predator strategies.

Ground cover is also termed “hiding cover” from the assumption that it will hide the prey. It is also suggested that ground cover will function as a physical protection against predators, forcing them to go around the obstacle (Smith *et al.*, 1986). However, there are also examples that the opposite strategy, enhancing predator detection by choosing areas with little cover, is also conceivable (e.g. Carey, 1985; LaGory, 1986, 1987; Stahl *et al.*, 2002). Little ground cover can also be more effective for escape (Lima, 1992). Most cover can function as both protective and obstructive cover (Lazarus & Symonds, 1992; Mysterud & Østbye, 1999), but the largest effect will determine whether the cost or benefits are highest, and thus the amount of ground cover chosen. Preference for ground cover is therefore a balance between effective escape and risk of attack (Lima, 1992).

Canopy cover is usually seen as shelter from climatic conditions, with additional benefits through reduced snow depth, but it is also possible that high canopy cover can work as an anti predator strategy; contrasts are broken up, and there is less light for the predator to spot potential prey (Smith *et al.*, 1986). It is also possible that scent is not spread as efficiently in habitats with much cover (Mysterud & Østbye, 1995). Canopy cover will, just as ground cover, also inflict a potential cost by reducing roe deer sight and possibly scent detection of lynx.

The lynx is a stalking predator, and usually attacks from a short distance. Most attacks on roe deer are from less than 20 meters distance, and very few are from longer than 50 meters (Dunker, 1988; Haglund, 1966). The lynx has excellent hearing and they also use sight to locate their prey. When a roe deer is detected, the lynx sneaks slowly towards it until it is close enough for an attack, seldom with the wind in the back (Haglund, 1966). Lynx also prefer to hunt in dense cover which allows them to sneak up on their prey (Dunker, 1988). This probably makes hearing and sight the most important “anti predator senses” for the roe deer. Logically roe deer should avoid dense cover to be able to detect the lynx before it is too late. It is also widely believed by hunters in the area that roe deer have started bedding on open fields more frequently since the recolonisation of lynx.

In the present study, both canopy and ground cover were higher at both foraging and bed sites than expected from random. The amount of canopy cover was mainly explained by climatic factors, but this does not exclude any anti-predator effects it may have. Only date could partly explain variation in amount of ground cover. This lack of correlations between predictor variables and ground cover may have two potentially non-conflicting explanations. Firstly, the winter season when the current study was conducted is harsh. This may force the deer to spend all their energy on avoiding climatic factors, while predator avoidance is ranked second in the priority to survive. If this is correct, one may expect more predator avoidance when climatic conditions are milder, but this was not observed in this study, as none of the climatic variables are correlated to ground cover.

The other possible reason for small effects on ground cover could be an overall similar predation pressure within the study area. One would then only expect differences in ground cover when comparing with an area with lower predation pressure. This is consistent with the findings in this study. Ground cover is higher than expected from random choice, but no systematic differences are found within the area. In addition, the study in Lier reports lower ground cover than expected from random choice (Myrsterud & Østbye, 1995). This may indicate that roe deer under predation risk chose sites in order to hide from predators rather than to enhance predator detection, although the pattern could also have been caused by wind, which was stronger in the present study.

Bed sites with generally low visibility in the present study had higher visibility in the direction of the incoming track, than in the opposite direction. In Lier, roe deer also had good visibility in the direction of incoming tracks. This can be adaptive in two ways: either to discover predators that follow their incoming tracks, or a secondary effect of energy efficient movements in the terrain (Myrsterud & Østbye, 1995).

The roe deer in the present study do not only need to avoid predation by lynx, but also hunting by humans. In many areas there are interactions with more than one predator. If the predators use different hunting techniques, the question is which anti-predator strategy to apply?

4.1.2 Effects of humans versus lynx as a predator

In the Akershus / Østfold area, more roe deer are killed by human hunting than by lynx, but the hunting is confined to the period from mid August to late December, and optimally roe deer should not exhibit anti-predator behaviour towards humans during the remaining part of

the year. However, there may be limits to how optimal roe deer can behave and one cannot expect a perfect response on every occasion. Failing to escape human hunting is fatal, and selection may be stronger in the direction of avoiding humans than exploiting the benefits associated with them. The outcome can then be fear of humans independent of season. Either of two conditions must be satisfied for differences between anti predator behaviour towards humans to be differentiated from anti predator behaviour towards lynx when comparing an area with only human hunting with an area with both humans and lynx. First, selection on deer can act differently in the two areas because of different hunting techniques of humans and lynx. Second, response to predators can be plastic according to hunting technique of the predators present, and difference between areas is therefore a product of different presence of different predators.

Distance to human activities can be seen as an anti predator behaviour. This can have two causal explanations. The roe deer can see humans as a risk and keep their distance as humans are their most important predator. This was observed in roe deer in Lier, where a trade off between food availability and distance to human settlement was found (Myysterud *et al.*, 1999b). However, if lynx are present, roe deer may consider closeness to humans as safety because the lynx tend to keep away from human vicinity (Bunnefeld, 2003; Stahl *et al.*, 2002). Mule deer, vervet monkeys (*Cercopithecus aethiops*) and moose decreased their predation risk by associating near human dwellings where coyotes (*Canis latrans*) and mountain lions (*Felis concolor*), leopards (*Panthera pardus*), and wolves, respectively, are less likely to occur (Geist, 1980; Isbell & Young, 1993; Stephens & Peterson, 1984).

For foraging sites, variation in distances to humans was not explained by any of the tested variables. Bed sites were placed further from humans at day compared to night. This supports the hypothesis that humans are seen as threats, although this would also be expected if predation from lynx is higher at night and humans are seen as safety. These explanations are not mutually excluding and may work together to produce the observed pattern.

Ungulates have been found to utilise open habitats more at night than during day (e.g. Armstrong *et al.*, 1983; Chen *et al.*, 1999; Histøl, 1992; Hjeljord *et al.*, 1990; Selås *et al.*, 1991). This could be expected if visibility is lower at night and hiding cover is not needed, or on the opposite, night is a more risky time and less cover is necessary to discover predators before they can attack. No differences could be found between night and day in the present study, perhaps because predation risk from lynx is largest at dusk and dawn (Sunquist & Sunquist, 2002) and is then equal among day and night. Similar results were found for roe

deer in Lier (Mysterud *et al.*, 1999a). Artificial feeding sites are used more frequently by roe deer during night and distances between foraging sites and beds are larger during night. In addition, distance from beds to humans are shorter during night. This is the exact same pattern as roe deer in Lier exhibited (Mysterud *et al.*, 1999b), and may be explained by a trade-off between avoidance of humans and forage availability or other characteristics, like snow depth.

4.1.3 Time scale of predator avoidance

Between five and ten percent of the roe deer population in Southern Norway is killed by lynx every year (Andersen *et al.*, 2005), and when 66% of lynx attacks are successful (Andersen *et al.*, 2005), it can be estimated that less than 15% of the roe deer population is attacked by a lynx during one year. It is not possible for a roe deer to survive a harsh winter if it used all energy on predator avoidance, and high risks are unavoidable even if mistakes are fatal. This relatively “low” predation risk in combination with harsh weather conditions during the winter season predicts that the trade-off between energy gain (and conservation), and predator avoidance, cannot be expected to be in favour of the latter. It is premature though, to reject any effect of lynx on roe deer behaviour, but such effects, if present, might be more pronounced in less stressed periods.

Roe deer have shown themselves to be a very flexible ungulate, they inhabit areas from the Mediterranean to Northern Norway and thrive in both forest and agricultural areas (Cederlund & Liberg, 1995; Lister *et al.*, 1998). Roe deer are able to learn quickly, and adapt their behaviour according to predation pressure (Observed in moose (*Alces alces*); Berger *et al.*, 2001; roe deer: Breitenmoser & Haller, 1993; african ungulates; Hunter & Skinner, 1998; elk (*Cervus elaphus*) and bison (*Bison bison*); Laundre *et al.*, 2001). It is also possible that they are able to adjust their behaviour to immediate predation pressure. Lynx are a territorial predator with large territories, therefore their density is low. As emphasized above, few roe deer are ever exposed to lynx attacks. If there is a trade-off between predator avoidance and energy optimization, and roe deer are able to asses immediate predation pressure, then it would be adaptive and possible to adjust level of predator avoidance in a temporally fine scale fashion. Berger (1999) tested moose reactions to scavenger sounds. The scavengers can function as signals of predator presence and moose did indeed increase vigilance rates when scavenger sounds were played. Other possible ways of detecting predator presence could be olfactory detection of predators (through e.g. urine or faeces; Berger, 1998; Berger *et al.*, 2001) or direct observation of conspecifics (Caro *et al.*, 2004; Krebs & Davies, 1993), scavengers or

other species with the same predators (Observed in birds; Grønningsæter, 2003; Nuechterlein, 1981).

Perhaps roe deer do seek open habitat when exposed to a lynx, but only for a very short amount of time. Support for this was observed when one of two roe deer in the same area was killed by a lynx and the other changed to a habitat with more cover (M. Panzacchi, personal comm. and personal observations). Similar anecdotal evidence is also reported by others (A. Mysterud, personal comm.). Unfortunately, our data is not sufficient to demonstrate this in a robust manner.

4.2 Differences between bucks and does

Most literature considers two main reasons for differential habitat use between sexes. Because of sexual dimorphism, one sex can have larger predation risk than the other, or one sex can have other energy needs or foraging availabilities (Main, 1998). However, in roe deer there is little sexual dimorphism, and bucks and does have similar fat reserves in late fall (Holand, 1990, 1992). Differences between the sexes or between animals without fawns and females with fawns may also contribute to different risk taking because fawns are generally more prone to predator attacks (Molinari-Jobin *et al.*, 2004; but see Okarma *et al.*, 1997). Roe deer fawns have low reserves in late fall because they prioritize growth (Holand, 1990). Lynx predation is also not selective for age or sex (R. Andersen *et al.* unpublished data). According to this pattern in roe deer, single females and males should have similar energy budgets in winter, while families with fawns will have a tighter energy budget. Such a difference between females with young, and males and females without young, is suggested by Main (1998), and found in e.g. wild bighorn sheep (Berger, 1991). An alternative, but not conflicting, explanation for differences in risk taking between males and females is proposed by Laundré *et al.* (2001). They suggest that males have more to lose by lowering their predation risk at the cost of foraging because their reproductive success is dependent upon body condition while females are assured a chance to mate even in a lowered nutritional state. It is, however, shown that snow depth does affect female fecundity and offspring survival, as fewer white tailed deer fawns and moose calves are found when snow was deep the previous winter (Mech *et al.*, 1987). Female roe deer fitness is also affected by their winter habitat (Nilsen *et al.*, 2004).

This study from an area with lynx shows inconsistent results. Families have higher ground cover at foraging sites than single animals. No difference is observed at beds. The

predicted response was that families would walk longer distances in order to get to safer bed sites if there was a trade-off between qualities of foraging and bed sites. In Akershus / Østfold roe deer families had high ground cover at foraging sites, and walked shorter distances than other deer, as predicted. It is thus possible that all animals are maximizing their ground cover while bedding, but families forage close to protected bed sites to minimize predation risk and have less energy to spend on travel between forage sites and beds. All females use artificial feeding sites more often than males. This pattern together with differences in ground cover and distance between bed and foraging sites best fits the hypothesis of tighter energy budgets for families, which is also consistent with the fact that there is no difference in age or sex in roe deer killed by lynx in South-Eastern Norway (Andersen *et al.*, 2005). Earlier studies actually indicated that females were generally killed more often by lynx than males, while the opposite is observed with mortality due to hunting (reviewed in Aanes *et al.*, 1998). The pattern of lynx predation can usually be explained by the sex structure of the available population (Aanes *et al.*, 1998), but the difference in human hunting between sexes is interesting with respect to the observed differences between females and males in use of artificial feeding sites.

4.3 Effects of weather

It has recently been much focus on large scale climate changes or fluctuations, and there is little doubt that these changes affect ecological systems (reviewed in Stenseth *et al.*, 2002). There are a number of studies showing effects of climate on ungulate populations (e.g. Forchhammer *et al.*, 2001; Forchhammer *et al.*, 2002; Mysterud *et al.*, 2000; Ogutu & Owen-Smith, 2003; Weladji *et al.*, 2003). However, few of these studies have addressed the mechanisms of the climatic effects, which can be revealed in studies of individual responses to climate. This study of roe deer in Akershus and Østfold is a contribution to that missing link.

Many earlier studies have shown that habitat use in ungulates is significantly affected by local climate variables (e.g. Lang & Gates, 1985; Mysterud *et al.*, 1997; Mysterud & Østbye, 1995). Snow depth is arguably the most important climatic factor for a small and short-legged ungulate like the roe deer. Snow depth can increase the costs of moving around to find a covered place to forage or bed (Moen, 1976; Mysterud *et al.*, 1997; Parker *et al.*, 1984), and reduce the availability of forage to deer (Mysterud *et al.*, 1997). As a result, deer tend to bed in areas with less snow (Huot, 1974; Mysterud *et al.*, 1997). As a consequence of

such a strategy, Cervids at northern latitudes preferably use mature forest stands in winter time (Armleder *et al.*, 1994; Armstrong *et al.*, 1983; Mysterud *et al.*, 1997; Pierce & Peek, 1984). In addition to this energetic cost, lynx are more successful in roe deer hunts when there is deep snow (Andersen *et al.*, 2005; Sunkuist & Sunkuist, 2002). Snow depths at foraging sites and bed sites are lower than expected from random choice. The importance of snow depth is also supported from present results showing that increasing snow depth was correlated with decreasing distances between beds and foraging sites, suggesting that roe deer chose habitats to minimize travel costs. In spite of this, canopy cover over bed sites was higher when snow was deep. This can possibly be explained by the fact that snow will also act as cover and thus might make it easier to find places that are more covered. It is also possible that there is an increase in predator avoidance when snow is less favourable for escape.

Temperature can also be important for winter survival, as lower temperatures will increase energy expenditure (Parker & Robbins, 1984). Wind will further increase amount of energy needed to avoid hypothermia (Moen, 1973). Cover might protect against wind or low temperatures, canopy cover can also reduce loss of heat through thermal radiation (particularly during night, while it can hinder heating through solar radiation during day) (Moen, 1968, 1976; Schwab & Pitt, 1991). In earlier studies of roe deer, canopy cover was higher when temperatures were low, both over beds (Chen *et al.*, 1999; Mysterud & Østbye, 1995) and over feeding sites (Mysterud *et al.*, 1999b). The present study supports these findings. In addition, roe deer both forage and bed closer to a conifer with larger diameter than expected from random. There was also an indication that temperature was higher in beds compared to random sites, suggesting roe deer succeeded in choosing beneficial micro habitats. White-tailed deer placed their beds low in the terrain, and with large trees in the direction of incoming wind (Lang & Gates, 1985). In this study, there was no support that beds were placed with more cover in the direction of the incoming wind, neither was ground cover higher when wind was stronger, but beds were often placed just below the top instead of on the top. This could be accounted for if these spots are less wind exposed, and is also observed in an earlier study of roe deer (Zhaowen *et al.*, 1996). In addition, there are indications that roe deer walk longer distances from foraging sites to beds when wind is strong, presumably to seek shelter. This is also supported by the fact that roe deer use bed sites with higher canopy cover when wind is stronger.

4.4 Variation in habitat use over the winter

Ungulates living in northern latitudes undergo an annual cycle in body weight and body fat, and are heavily dependent on their energy reserves (Mautz, 1978). Roe deer in southern Norway similarly undergo an annual fat cycle, and fat deposits are depleted from January to April (Holand, 1992). Even though Norwegian roe deer have fat reserves, those contribute only to approximately 20% of total energy expenditure in winter, and their main source of energy during winter is without doubt their food supply (Holand, 1990). To lower the rate of fat depletion, it is important to feed and save energy (Alonzo, 2002; Brown, 1992; Houston *et al.*, 1993). Depending on available resources and cost of obtaining those resources, animals could either choose to lower their activity to save energy, or to increase their search effort. White-tailed deer change their response to cold weather through the winter season, as fat reserves are depleted (Moen, 1976), and increase their preference for protective cover (Huot, 1974). The present study suggests that, possibly due to diminishing fat reserves, importance of energy saving activities in roe deer increases as season progress. Roe deer in Akershus / Østfold were found with longer distances from beds to humans, later in the season. Distances between bed and foraging sites were longer later in the season especially when snow depths were small, indicating a tighter energy budget later in the season. Ground cover also increased around beds as the season progressed.

There are also other factors contributing to a changing habitat trade-off through season. When winter season progresses, days become longer and heat radiation from the sun increases. This may, together with diminishing fat reserves, explain the strong non-linear relationship between canopy cover over foraging sites and julian date. Canopy cover first increased, possibly due to tighter energy budgets, and then decreased at day sites only, possibly explained by higher solar radiation. In conclusion, although fat reserves are important, gaining energy is essential for survival through winter and habitat choice will be based on this need.

5 Conclusions

The habitat use of roe deer in wintertime is not only a trade-off between forage availability and predator avoidance but also shelter from climatic conditions. In foraging sites I expected habitat use to reflect a selection based on forage availability. Thus, safety and climatic shelter may be traded off. This was generally confirmed, although results still indicated a reasonable degree of climatic shelter. When beds are selected, safety and energy conservation should be maximized. However, there may also be a trade-off between these two, and higher risks may be unavoidable. Severe winters can have large impact on roe deer survival, and can possibly make them more prone to predation (Cederlund & Lindstrom, 1983). To survive, food is strictly necessary and must be the first priority for animals with low fat reserves, like the roe deer. In the present study, weather was quite harsh and results indicate that habitats were chosen mainly with regards to climatic variables. However, there are also indications of predator avoidance behaviour, such as high placement relative to topography and patterns of distance to humans.

I suggest that there is a need for further studies with direct comparisons between an area with and without lynx or other important predators to gain more information on the impact of large predators on the behaviour of roe deer. I also suggest that the behavioural responses of roe deer to immediate predation pressure be investigated to assess the fine-scale plasticity of behavioural response to predation and possible timing of the response.

6 References

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Appendices

Appendices depict model selection procedures for all response variables. x = term included in model. AIC = Akaike Information Criteria; Δ AIC = difference in AIC value between the AIC for the model given in that row and the most parsimonious model (lowest AIC).

Appendix 1 - Model selection on canopy cover at foraging sites

Results from model selection performed on transformed canopy cover for feeding sites. The most parsimonious model (bolded) explained 29.14% of the variation, and was used for parameter estimation (table 3).

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*Temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Family	Juliandate*winds	AICc	Δ AICc
	x	x	x			x			x		x									190.274	15.897
	x	x	x			x				x	x									205.681	31.304
	x	x	x	x		x			x		x									188.421	14.044
	x	x	x	x	x	x			x		x									190.030	15.653
	x	x	x	x		x	x		x		x									183.678	9.301
	x	x	x	x		x	x	x	x		x									183.754	9.377
	x	x	x	x		x	x		x		x	x								185.878	11.502
	x	x	x	x		x	x		x		x		x							180.600	6.223
	x	x	x	x		x	x		x		x		x	x						182.760	8.384
	x	x	x	x		x	x		x		x		x		x					182.529	8.152
	x	x	x	x		x	x		x		x		x		x					178.744	4.367
	x	x	x	x		x	x		x		x		x		x	x				180.885	6.509
	x	x	x	x		x	x		x		x		x		x		x			181.094	6.717
	x	x	x	x		x	x		x		x		x		x			x		176.205	1.828
		x	x	x		x	x		x		x				x					178.269	3.893
	x		x	x		x	x		x		x		x							183.615	9.238
	x	x				x	x		x		x		x		x					174.377	0.000
	x	x	x			x	x		x		x		x		x					176.426	2.050
	x	x				x			x		x		x		x					184.665	10.288
	x	x							x		x				x					194.274	19.897
	x	x				x	x				x		x		x					193.201	18.825
	x	x				x	x		x				x							179.163	4.787
	x	x				x	x		x		x				x					176.631	2.255
	x	x				x	x		x		x		x							180.942	6.565
	x	x				x	x		x		x		x		x					179.699	5.322
	x	x				x	x		x		x	x			x					176.616	2.240
	x	x				x	x		x		x		x	x						176.683	2.306
	x	x				x	x		x		x		x		x					175.871	1.495
	x	x				x	x		x		x		x		x	x				176.518	2.141
	x	x				x	x		x		x		x		x		x	x		176.662	2.285

Appendix 2 - Model selection on ground cover at foraging sites

Results from model selection performed on ground cover as seen 30m from foraging sites. The most parsimonious model (bolded) was used for parameter estimation.

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Family	Juliandate*winds	AICc	ΔAICc
	x	x	x			x			x		x									519.541	11.319
	x	x	x			x				x	x									529.316	21.094
	x	x	x	x		x			x		x									521.862	13.640
	x	x	x	x	x	x			x		x									523.769	15.546
	x	x	x			x	x		x		x									519.522	11.300
	x	x	x			x	x	x	x		x									522.595	14.373
	x	x	x			x	x		x		x	x								521.861	13.639
	x	x	x			x	x		x		x		x							524.131	15.908
	x	x	x			x	x		x		x			x						521.750	13.528
	x	x	x			x	x		x		x				x					521.822	13.599
	x	x	x			x	x		x		x					x				524.521	16.299
	x	x	x			x	x		x		x						x			523.053	14.831
	x	x	x			x	x		x		x							x		520.095	11.873
	x	x	x			x	x		x		x								x	522.107	13.884
		x	x			x	x		x		x									519.475	11.253
			x			x	x		x		x									518.041	9.819
						x	x		x		x									514.818	6.596
						x			x		x									513.724	5.502
									x		x									510.747	2.525
											x									519.168	10.946
									x											508.222	0.000
	x								x											509.470	1.248
		x							x											510.174	1.951
			x						x											512.079	3.856
						x			x											511.629	3.407

Appendix 3 - Model selection on use of artificial feeding sites

Results from model selection performed on use of artificial feeding sites by animals known to use artificial feeding sites. The most parsimonious model (bolded) was used for parameter estimation.

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*Temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Sex	Juliandate*winds	AICc	ΔAICc
	x	x	x			x				x	x									282.209	10.855
	x	x	x			x			x		x									289.162	17.808
	x	x	x	x		x				x	x									285.488	14.134
	x	x	x	x	x	x				x	x									289.584	18.230
	x	x	x			x	x			x	x									283.539	12.185
	x	x	x			x	x	x		x	x									287.110	15.756
	x	x	x			x				x	x	x								285.103	13.749
	x	x	x			x				x	x		x							284.482	13.128
	x	x	x			x				x	x			x						283.529	12.175
	x	x	x			x				x	x				x					282.891	11.537
	x	x	x			x				x	x					x				284.437	13.083
	x	x	x			x				x	x						x			284.580	13.226
	x	x	x			x				x	x							x		284.159	12.805
	x	x	x			x				x	x								x	284.646	13.292
		x	x			x				x	x									279.220	7.866
			x			x				x	x									276.967	5.613
						x				x	x									275.320	3.966
										x	x									273.172	1.818
											x									275.102	3.748
										x										271.354	0.000
	x									x										272.525	1.171
		x								x										273.475	2.121
			x							x										272.785	1.431
						x				x										273.337	1.983

Appendix 4 - Model selection on distance from foraging site to nearest house

Results from model selection performed on distance between foraging site and bed site. The most parsimonious model (bolded) was used for parameter estimation.

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*Temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Sex	Juliandate*winds	AICc	ΔAICc
	x	x	x			x				x	x									1002.481	10.060
	x	x	x			x			x		x									1002.638	10.217
	x	x	x	x		x				x	x									1004.196	11.775
	x	x	x	x	x	x				x	x									1001.257	8.836
	x	x	x	x	x	x	x			x	x									1003.516	11.095
	x	x	x	x	x	x	x	x		x	x									1003.624	11.203
	x	x	x	x	x	x				x	x	x								1001.939	9.518
	x	x	x	x	x	x				x	x		x							1002.824	10.403
	x	x	x	x	x	x				x	x			x						1002.614	10.193
	x	x	x	x	x	x				x	x				x					1003.335	10.914
	x	x	x	x	x	x				x	x					x				1002.703	10.282
	x	x	x	x	x	x				x	x						x			1003.263	10.842
	x	x	x	x	x	x				x	x							x		1002.155	9.734
	x	x	x	x	x	x				x	x							x		1003.351	10.930
		x	x	x	x	x				x	x									999.185	6.763
			x	x	x	x				x	x									998.551	6.130
						x				x	x									997.844	5.423
			x			x				x	x									999.666	7.244
			x	x		x				x	x									1001.571	9.150
			x	x	x					x	x									995.718	3.297
											x									993.869	1.448
	x																			993.611	1.189
	x																			992.4213	0.000
		x																		993.5253	1.104
						x														993.9297	1.508
									x											993.9284	1.507
										x										993.6522	1.231
	x	x																		994.2648	1.844
		x	x																	994.4374	2.016
		x				x														994.4216	2.000
		x							x											994.4995	2.078
		x								x										994.3305	1.909
		x									x									994.4648	2.043

Appendix 5 - Model selection on canopy cover at bed sites

Results from model selection performed on transformed canopy cover for bedding sites. The most parsimonious model (**bolded**) explained 08.89% of the variation, and was used for parameter estimation (table 5).

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Family	Juliandate*winds	AICc	ΔAICc
	x	x	x			x			x		x									49.581	13.084
	x	x	x			x				x	x									49.750	13.254
	x	x	x	x		x			x		x									43.189	6.692
	x	x	x	x	x	x			x		x									45.390	8.894
	x	x	x	x		x	x		x		x									44.625	8.128
	x	x	x	x		x	x	x	x		x									46.483	9.986
	x	x	x	x		x			x		x	x								45.499	9.003
	x	x	x	x		x			x		x		x							45.220	8.723
	x	x	x	x		x			x		x			x						45.488	8.992
	x	x	x	x		x			x		x				x					45.287	8.791
	x	x	x	x		x			x		x					x				45.493	8.997
	x	x	x	x		x			x		x						x			44.131	7.634
	x	x	x	x		x			x		x							x		45.149	8.653
	x	x	x	x		x			x		x								x	44.329	7.832
		x	x	x		x			x		x									41.118	4.622
			x	x		x			x		x									39.049	2.553
						x			x		x									44.603	8.106
			x			x			x		x									45.999	9.503
			x	x					x		x									38.674	2.178
			x	x							x									36.496	0.000
			x	x																36.920	0.423
x			x	x							x									38.558	2.061
		x	x	x							x									38.106	1.610
			x	x		x					x									36.886	0.389
			x	x					x		x									38.674	2.178
			x	x						x	x									38.671	2.175
			x	x							x									37.553	1.056

Appendix 6 - Model selection on ground cover for beds

Results from model selection performed on ground cover as seen 30m from bed sites. The most parsimonious model (bolded) was used for parameter estimation.

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Family	Juliandate*winds	AICc	ΔAICc
	x	x	x			x			x		x									386.493	36.391
	x	x	x			x				x	x									416.283	66.181
	x	x	x	x		x			x		x									413.558	63.456
	x	x	x	x	x	x			x		x									465.711	115.609
	x	x	x			x	x		x		x									390.049	39.947
	x	x	x			x	x	x	x		x									398.296	48.194
	x	x	x			x	x	x	x		x	x								389.036	38.934
	x	x	x			x			x		x		x							391.573	41.471
	x	x	x			x			x		x		x							391.212	41.109
	x	x	x			x			x		x			x						392.694	42.591
	x	x	x			x			x		x				x					389.338	39.236
	x	x	x			x			x		x					x				398.237	48.135
	x	x	x			x			x		x						x			470.146	120.044
	x	x	x			x			x		x							x		389.585	39.483
		x	x			x			x		x									382.497	32.395
			x			x			x		x									378.363	28.261
						x			x		x									372.198	22.096
									x		x									370.094	19.992
											x									353.194	3.092
x																				350.382	0.279
		x																		352.334	2.232
			x																	352.054	1.951
						x														350.102	0.000
									x											365.018	14.916
x						x														352.508	2.406
		x				x														354.451	4.349
			x			x														354.184	4.082
						x			x											366.5079	16.406
						x					x									355.5661	5.464

Appendix 7 - Model selection on distance between foraging and bedding sites

Results from model selection performed on log (distance between foraging and bedding sites). The most parsimonious model (**bolded**) explained 79.40% of the variation, and was used for parameter estimation (table 6).

	NightDay	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Artificial feeding site	Canopyc feeding site	Night/Day*temperature	Night/Day*Juliandate	Night/Day*winds	Night/Day*art	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Snowdepth*art	Juliandate*Family	Juliandate*winds	Juliandate*art	Family*art	Windspeed*art	AICc	ΔAICc
	X	X	X			X			X			X															309.512	12.146
	X	X	X			X			X				X														417.501	120.136
	X	X	X			X				X		X															311.466	14.100
	X	X	X	X		X			X			X															308.563	11.197
	X	X	X	X	X	X			X			X															301.420	4.054
	X	X	X	X	X	X	X		X			X															303.626	6.260
	X	X	X	X	X	X	X	X	X			X															306.100	8.734
	X	X	X	X	X	X		X	X			X		X													303.777	6.411
	X	X	X	X	X	X		X	X			X		X	X												303.582	6.216
	X	X	X	X	X	X		X	X			X		X	X	X											303.383	6.017
	X	X	X	X	X	X		X	X			X		X	X	X											302.707	5.341
	X	X	X	X	X	X		X	X			X		X	X	X											303.162	5.796
	X	X	X	X	X	X		X	X			X		X	X	X					X						302.982	5.616
	X	X	X	X	X	X		X	X			X		X	X	X					X						300.574	3.208
	X	X	X	X	X	X		X	X			X		X	X	X					X	X					301.989	4.623
	X	X	X	X	X	X		X	X			X		X	X	X					X	X					303.069	5.703
	X	X	X	X	X	X		X	X			X		X	X	X					X		X				301.999	4.633
	X	X	X	X	X	X		X	X			X		X	X	X					X		X				299.701	2.335
	X	X	X	X	X	X		X	X			X		X	X	X					X		X	X			302.172	4.806
	X	X	X	X	X	X		X	X			X		X	X	X					X		X		X		300.074	2.709
	X	X	X	X	X	X		X	X			X		X	X	X					X		X		X		300.067	2.701
	X	X	X	X	X	X		X	X			X		X	X	X				X		X		X		297.366	0.000	
	X					X			X			X													X		306.277	8.911
	X		X			X			X			X								X					X		309.466	12.100
	X		X	X		X			X			X								X					X		309.115	11.749
	X		X	X	X				X			X								X							298.287	0.921

X	X	X	X	X		X	X				X		X	300.311	2.945
X	X	X	X	X	X		X				X		X	298.316	0.950
X	X	X	X	X	X	X					X			426.003	128.637
X	X	X	X	X	X	X	X	X			X		X	301.992	4.626
X	X	X	X	X	X	X	X	X	X		X		X	299.435	2.069
X	X	X	X	X	X	X	X	X	X		X		X	299.801	2.435
X	X	X	X	X	X	X	X	X	X	X		X		298.668	1.302
X	X	X	X	X	X	X	X	X	X	X		X		299.364	1.998
X	X	X	X	X	X	X	X	X	X	X	X		X	299.657	2.291
X	X	X	X	X	X	X	X	X	X	X	X		X	299.938	2.572
X	X	X	X	X	X	X	X	X	X	X	X	X		299.868	2.502
X	X	X	X	X	X	X	X	X	X	X	X	X		299.297	1.931
X	X	X	X	X	X	X	X	X	X	X	X	X	X	299.180	1.814
X	X	X	X	X	X	X	X	X	X	X	X	X	X	298.218	0.852
X	X	X	X	X	X	X	X	X	X	X	X	X	X	299.812	2.446
X	X	X	X	X	X	X	X	X	X	X	X	X	X	297.960	0.594

Appendix 8 - Model selection on distance from beds to humans

Results from model selection performed on distance to humans for bedding sites. The most parsimonious model (**bolded**) explained 15.49 % of the variation, and was used for parameter estimation (table 7).

	Night/Day	Temperature	Snowdepth	Snowdepth2	Snowdepth3	Juliandate	Juliandate2	Juliandate3	Family	Sex	Windspeed	Night/Day*temperature	Night/Day*Juliandate	Night/Day*winds	Temperature*Juliandate	Temperature*windspeed	Snowdepth*Juliandate	Juliandate*Sex	Juliandate*winds	AICc	ΔAICc
	x	x	x			x				x	x									787.971	2.588
	x	x	x			x			x		x									793.058	7.675
	x	x	x	x		x				x	x									788.671	3.288
	x	x	x	x	x	x				x	x									790.575	5.192
	x	x	x		x	x	x			x	x									789.309	3.926
	x	x	x			x	x	x		x	x									790.432	5.049
	x	x	x			x				x	x	x								789.538	4.155
	x	x	x			x				x	x		x							788.2062	2.823
	x	x	x			x				x	x			x						787.5876	2.204
	x	x	x			x				x	x			x	x					789.6317	4.249
	x	x	x			x				x	x			x		x				789.8901	4.507
	x	x	x			x				x	x			x			x			789.4226	4.039
	x	x	x			x				x	x			x				x		789.8723	4.489
	x	x	x			x				x	x			x					x	789.6856	4.303
		x	x			x				x	x									788.0955	2.712
	x		x			x				x	x			x						785.8547	0.472
	x					x				x	x			x						785.7127	0.330
	x									x	x			x						789.227	3.844
	x					x					x			x						788.0224	2.639
	x					x				x										795.8723	10.489
	x					x				x	x									785.3831	0.000
						x				x	x									786.1526	0.769
	x	x				x				x	x									787.3585	1.975
	x		x			x				x	x									786.134	0.751
	x		x	x		x				x	x									786.5839	1.201
	x		x	x	x	x				x	x									788.5039	3.121
	x									x	x									788.099	2.716
	x					x	x			x	x									786.3479	0.965
	x					x	x	x		x	x									786.6769	1.294
	x					x			x		x									790.3795	4.996
	x					x					x									789.1282	3.745
	x					x				x										795.8723	10.489
	x					x				x	x		x							785.7439	0.361
	x					x				x	x							x		787.5902	2.207
	x					x				x	x								x	787.0949	1.712