

**Risk of lynx (*Lynx lynx*) predation in roe deer
(*Capreolus capreolus*) depends on habitat structure**

**Faren for predasjon fra gaupe (*Lynx lynx*) på rådyr
(*Capreolus capreolus*) avhenger av habitat struktur**

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Preface

This thesis is written at the department of Ecology and Natural Resource Management (INA) at the Norwegian University of Life Sciences (UMB). The thesis provides 60 credits for my Master of Science degree in Natural Resource Management. Financial support during fieldwork was from both Scandlynx (<http://scandlynx.nina.no>) and UMB.

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Abstract

Large carnivores are recolonizing Scandinavia with possible wide reaching consequences for prey populations and ecosystems. Impacts beyond numerical effects on prey populations such as behavioral effects are still poorly understood. The idea that predators can affect their prey by just being present and inducing habitat specific fear responses is widely supported in the ecological literature; a phenomenon termed “the landscape of fear”. Habitat selection by prey animals will often result from trade-offs, in particular between food and predation risk. To understand if the concept of landscape of fear may be applied to roe deer (*Capreolus capreolus*) I here evaluate how the risk of being killed by lynx (*Lynx lynx*) differs among habitats relative to level of cover. To investigate this I compare habitat types on sites where roe deer had been killed by GPS-collared lynx with the habitat found on locations visited by GPS-collared roe deer in Hallingdal, Norway. Because the lynx is a stalking predator, I predicted that the risk for roe deer would increase with vegetation density. Accordingly, I found that roe deer in Hallingdal had a higher relative probability of getting killed by lynx in dense forest habitat. My study demonstrates that the habitat specific distribution of mortality caused by the lynx was not random and may create a landscape of fear on its main prey in Hallingdal. Dense forest structures, such as spruce seems to be riskier habitat for the roe deer to occupy, when the lynx are present, than open habitats such as clear cuts and infield. I suggest that the possible reasons for why roe deer do not avoid cover to a higher extent is most likely caused by the low chance of actually meeting a lynx at any time and associated trade-offs with access to food, avoiding human hunting and thermoregulation being given greater weight.

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1. Introduction

Large carnivores are recolonizing Scandinavia. It has been demonstrated in other sites, for example in North America, that recovery of predators can affect at least their main prey, and potentially impact the whole ecosystem through trophic cascading effects. Predation is well known to be a major proximate cause of mortality in many systems (Crête & Manseau 1996; Cresswell et al. 2010). Increased predation risk may change the distribution of prey populations on a landscape scale (Fortin et al. 2005). Yet the impact of predation beyond numerical effects on prey populations has largely been ignored.

There are at least five factors that impact the suitability of habitat for prey animals. These factors are physical and climatic factors, food availability, competitive interactions and finally safety from predators (Brown & Kotler 2004; Merwe & Brown 2008).

The “landscape of fear” concept was first presented by Laundré et al.(2001) when studying elk (*Cervus elaphus*) and bison (*Bison bison*) after the reestablishment of grey wolves (*Canis lupus*) in Yellowstone National Park. It predicts a negative relationship between the spatial distribution of a predator and its behaviorally active prey, also known as “the behavioral response race” (Brown et al. 1999; Laundré 2010). In ecological studies the prediction that predators can affect their prey’s foraging behavior by their sheer presence has broad support (Laundré et al. 2010). Thus habitat selection often will be guided by trade-offs, in particular between food availability and predation risk (Godvik et al. 2009). The consequences of a perceived landscape of fear will thus depend strongly on the strength of the trade-off between shelter and food, i.e., to which extent predator refuges also contains adequate food (Brown & Kotler 2004; Merwe & Brown 2008). Fear is caused by anticipation or awareness of potential danger (Laundré et al. 2001). When prey animals flee from approaching predators, the underlying emotion driving these responses to imminent danger can be expressed as fear of being killed by a carnivore. Yet, prey should not only express fear from the true attacks of their predators, but also from the anticipation or risk of possible attacks (Laundré et al. 2010).

Even though canid and felid predators typically occur in the same habitats in the Palearctic region north of 60°N (May et al. 2008) they usually have different approaches to hunting (Kleiman & Eisenberg 1973). Canids usually exhaust larger prey by chasing them over longer distances, and typically don’t use vegetation as concealment (Wells & Bekoff 1982). Felids

typically uses vegetation as concealment while stalking their prey and then uses a short distance to chase before they make contact and kill (Elliott et al. 1977). Felids are also often solitary hunters and more specialized feeders than canids (Elliott et al. 1977). The Eurasian lynx (*Lynx lynx*), hereafter called lynx, is mostly a stalking predator (Nilsen et al. 2009). It rarely succeeds in catching prey on distances over one hundred meters, or in open terrain where the prey can easily detect it. However, in forests and steep terrain it is regarded as an exceptionally efficient predator (Haglund 1964; Odden et al. 2006). The lynx is known to mainly prey on medium sized ungulates, like roe deer (*Capreolus capreolus*), wherever they coexist (Jedrzejewski et al. 1993; Odden et al. 2006).

The roe deer is the smallest of Norway's ungulate species, it is usually associated with cultural landscapes (mixed forest – farmland matrices), and can locally be found in high numbers. It usually inhabits habitats such as rich deciduous woodlands and anthropogenous grasslands (Selås et al. 1991). The best habitat for most of the year is relatively closed habitat (Selås et al. 1991), but roe deer often uses areas with a mixture of habitats for different purposes (Mysterud et al. 1999). Several hypotheses suggest that dense forest habitat provides shelter to its main predator (May et al. 2008). In the absence of predators, roe deer have been shown to prefer habitats with high lateral cover during summer, which could be because of the amount of food, cover, or both (Tufto et al. 1996; Nilsen et al. 2004). During winter, food are often in more open habitat, while dense habitat are used for resting especially during cold (Mysterud & Østbye 1995), and may create strong trade-offs in roe deer habitat selection. Roe deer is the only ungulate in Norway who's population can be strongly limited by predation from red fox (*Vulpes vulpes*) and lynx (Melis et al. 2010; Gervasi et al. 2012). However, it is not understood how the relative risk of predation from lynx is distributed between habitats, which is important for understanding how roe deer might respond in behavior, habitat selection or distribution to lynx recovery.

As a first step towards understanding how the landscape of fear concept may relate to roe deer-lynx systems, I here evaluate how the risk of being killed by a lynx differ among habitats for roe deer. To investigate this, I compared the habitat on lynx kill sites with the habitat use patterns of roe deer as determined from locations retrieved by aid of GPS and feces counts. Because the lynx is a stalking predator, I predict that the risk of being killed will increase with increasing vegetation density.

2. Material and methods

2.1 Study area

The study area covers the valley of Hallingdal in Buskerud County, Norway (Figure 1). Hallingdal consists of the municipalities Flå, Nes, Gol, Hemsedal, Ål and Hol (60°21' - 60°52' N; 8°15' - 9°37'E). The total study area covers approximately 5 830 km². The main part of the area is located > 900 m above sea level (70 %), productive forest covers nearly 21 % and farmland covers roughly 2 % of the area (Thorsnæs 2009). The main valley has a distinctive change in direction, from southwest – northeast in the flat landscape west of Gol, to northwest – southeast in the steep hills south of Gol. Especially on the north side of the valley west of Gol the farms are relatively dense because of much lateral moraine settlements (Thorsnæs 2009). The duration of the winter varies from year to year, but the mean snow cover the last six years has been from early November until the end of April. In Hemsedal the snow cover lasts longer than in Flå, which is situated in the south of Hallingdal valley. The mean temperature varies along the valley. In Nesbyen (Nes), which is roughly in the middle of Hallingdal valley the mean temperature has been approximately - 5°C during the last six winters, while the mean temperature during the summers has been 10.5°C (NVE et al. 2012).

2.1.1 The study species

According to the hunting statistics on roe deer in Hallingdal, the population is low, but stable. Since 2006, on average 36 roe deer have been shot annually in Hallingdal (Naturdata as 2012). In winter, artificial feeding sites are established for roe deer but also for moose (*Alces alces*) and red deer (*Cervus elaphus*) to avoid traffic-accidents. These sites are also frequently used by roe deer (Bunnefeld et al. 2006). The lynx population is registered as family groups (lynx reproduction) per carnivore management region. Hallingdal belongs to Region 2, consisting of Buskerud, Telemark, Vestfold and Aust-Agder Counties. In Region 2 it has been registered a mean of approximately 15 family groups of lynx between 2006 and 2011. Of these family groups between 1 and 4 has been registered in Hallingdal (Rovdata 2011). Though roe deer are the main prey for the lynx, two other ungulate species, red deer and moose, are also represented in the study area. Red deer have increased in the hunting statistics since 2006, and has an average of 60 felled deer per year in Hallingdal, whereas the moose is stable with over 700 felled moose per year (Naturdata as 2012). Lynx regularly kill red deer

and rarely moose calves. During the summer also high densities of sheep are available as prey (Swenson & Andrén 2005; Odden et al. 2012).

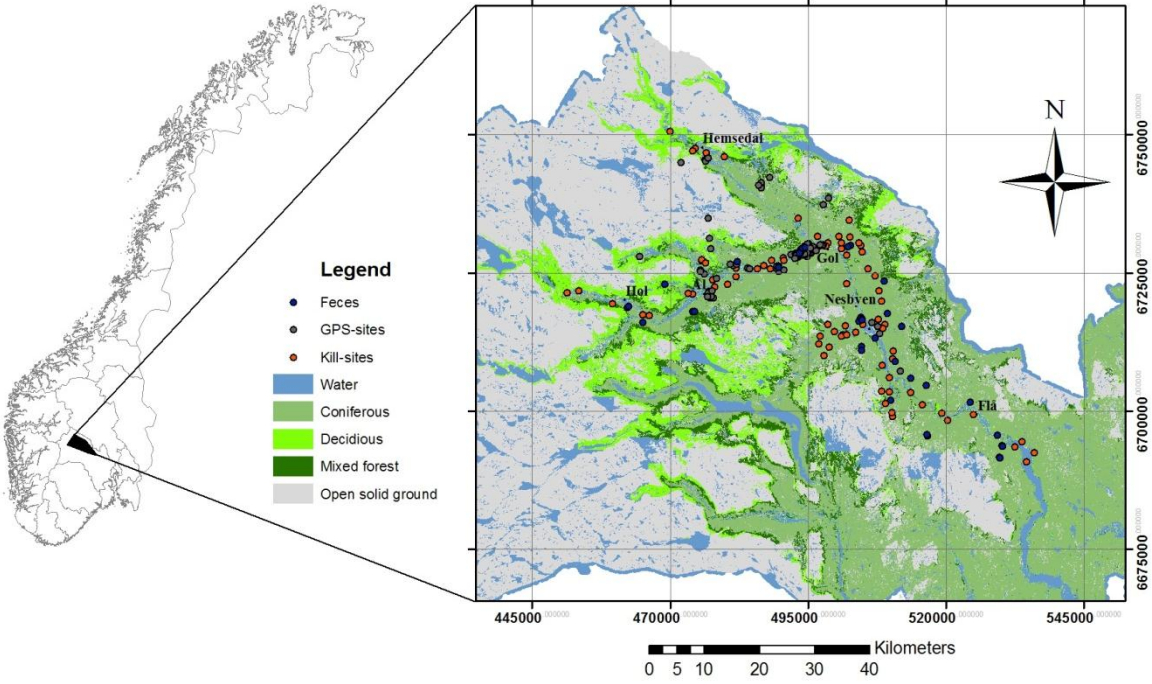


Figure 1: Hallingdal valley (study area) is a valley in Buskerud County. It includes the municipalities of Flå, Nes, Gol, Hemsedal, Ål and Hol. GPS-sites = plots from live radio collared roe deer, kill-sites = sites where lynx have killed roe deer. UTM zone = 32 W.

2.2 Data

The study was conducted in cooperation with the Scandinavian lynx project (Scandlynx) which has captured both lynx and roe deer and fitted them with GPS collars from 2006 – 2011 (Odden et al. 2012). All of the sites in Hallingdal where a roe deer has been killed by lynx (n=81) (kill-sites) and positions of GPS-marked roe deer (n=150) within the same study area enabled a comparison of vegetation and forest structure on both kill-sites and sites used by live roe deer.

Most of the GPS-marked roe deer were captured and radio collared on supplementary feeding sites in and nearby the town of Gol. This could potentially have generated a bias during winter when the roe deer gathers around more anthropogenous areas. To compensate for this, data from Scandlynx on pellet group counts of any roe deer (n=39) were used to balance the distribution of roe deer in the landscape during winter. Feces registrations were carried out towards the end of the winter and were at a scale more equal to the distribution of winter kill-sites than the GPS-data from the winter. Feces were sampled as pellet group counts along triangular transects with a total length of 3.24 km per transect, and with plots approximately every 100 meters (Hoel & Hermansen 2008).

The kill-sites are derived from four female lynx (F189, F218, F228 and F237) and four male lynx (M187, M209, M263 and M273). Roe deer have been killed in various numbers from 2006 – 2010 (range: 7 to 24 kills per year), while the feces were sampled in 2007 (n=24) and 2008 (n=17). Plots from collared roe deer are from 2008 – 2010, and consist of 16 male roe deer and 22 female roe deer.

All of the preliminary data processing was done in ArcGIS 9.3.(ESRI 2009) with the extension program “Hawth’s Analysis Tools” (Hawthorne 2010).

2.3 Fieldwork

On each kill site, GPS-roe deer site, and roe deer feces site, a suite of forest- and vegetation structure measurements were registered. Each site was considered as the area with a 50 m radius around the point location, divided into four sectors linked to each of the cardinal directions (North, East, South and West). Measurements were made separately for each sector. In the statistical analyses the sectors is combined to express the dominating or mean value of each site.

The following variables were measured or registered:

Habitat type

Habitat were classified into nine classes, coniferous, mountain birch, high- and low alpine, alpine zone, deciduous forest, mixed forest, bog and infield.

Ground vegetation

Vegetation at the ground level was registered as dominating species in each sector. As many species as possible were registered to obtain an easy classification later in the process. The vegetation were then classified in one of the main vegetation types; Lichen / bryophyte and dwarf-shrub woodland (A), tall-fern and tall-herb woodland (C), anthropogenous grassland (G) and freshwater shore (O) (Fremstad 1997). Infields were also registered as a separate class. The class bilberry woodland (A4) was retained from the original classification because a lot of sites were consisted of this type. The remaining vegetation types were grouped into the class “other” (9% of the total sample).

Cutting class

Registration of the different cutting classes follows the standard national forest evaluation of Norway (Fitje 1989), clear cuts (cc1), young plantations (cc2), pole size stands (cc3), medium-aged stands (cc4) and older mature stands (cc5). If there were no trees at the site, it was recorded as “none” (cc0). This was typically infield.

Measurement of tree species

Tree species were classified as: spruce (*Picea abies*), pine (*Pinus sylvestris*), birch (*Betula pubescens*), other deciduous tree species such as rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and goat willow (*Salix caprea*), called RAG from now on, and other coniferous tree species. Density of each species of trees were measured using a relascope, by counting

numbers of trees that had a diameter bigger than the factor opening of 0.5 mm, 1 mm or 2 mm. The relascope value gives a number for tree density by estimating the base amount in a forest stand, expressed in square meters per hectare (Fitje 1996).

Mean tree height

Mean tree height was measured using a Vertex hypsometer (Haglöf Sweden AB 2007). The sensor was placed 1.3 meters above ground, and the tree height is calculated by looking through the receiver from the sensor to the tree top in one movement.

Hiding cover

The method described in Mysterud (1996) was used to measure hiding cover. Two cover-boards measuring 30 x 40 cm placed on top of each other to mimic both a resting roe deer and a standing roe deer. Each cover board had 40 grid cells (5 x 6 cm) each representing 2.5% cover. I recorded the minimum distance required for the board to be completely hidden inside the 50 m radius. If topography blocked visibility, this was also noted.

Canopy cover

Canopy cover were measured using a spherical densiometer (model A) (Lemmon 1956; Lemmon 1957). It was held at breast height (1.3 meters), and estimates density of forest canopy on permanent sample plots. It contains a concave mirror that is divided into 24 squares. Each of these squares is divided into four, and the number of small squares open was counted. By multiplying the value for each sector with 1.04, an estimate of percentage open canopy was obtained in each sector.

2.4 Statistical analyses

All statistical analyses were performed in R 2.12.2 (R Development Core Team 2011) for Windows using the TinnR 2.3.7.1 (Tinn-R Team 2011) code editor. A set of different packages have been used during the analysis.

2.4.1 Correlation between variables

The first step in my analyses was to investigate if the habitat variables are correlated. Correlation measures the strength positively or negatively of the linear relationship between two quantitative variables (Moore et al. 2009). Because habitat measurements consist of both

numerical and factor variables a heterogeneous correlation matrix (Table 1) was calculated. I used the function “hetcor” in the “polycor” package in R (Fox 2010) to calculate this matrix. The package calculates Pearson product-moment correlations between numeric variables, polyserial correlations between numeric and factor variables, and polychoric correlations between factor variables.

2.4.2 Principal component analysis

Secondly, principal component analysis (PCA) was run to check if the many correlated variables described one or a few general ecological gradients. The PCA only takes as input, continuous variables, while the dataset contains both measurements of continuous and factor variables. To be able to incorporate factor variables the “dudi.mix”-function in the “ade4” package in R (Dray & Dufour 2007) was used. This process generalized the method described in Hill and Smith (1976), but excludes NA-values. Approximately 25 % of the sites had one or more NA-values and was therefore removed. The data was standardized (mean=0, SD=1) to be able to use the “dudi.mix”-function. Thus all the variables were transformed into similar numeric classes. A biplot of the first two principal components was produced to visualize the results of the PCA (Johnson & Wichern 2007).

2.4.3 Logistic regression analyses and model selection

Logistic regression analyses (Hosmer & Lemeshow 1989) were run to determine the main habitat characteristics affecting a roe deer’s probability of getting killed by a lynx, using the GLM (generalized linear model) function in R. In all analyses the kill-sites were defined with response 1. Roe deer feces and roe deer GPS-plots were grouped and defined with response 0. Habitat specific predation risk could potentially vary with season. To test for this an interaction term between the various habitat variables and season was added to the model. Season was included as a factor variable with the two levels summer (May – October) and winter (November – April). Errors were assumed to be binomially distributed.

The effect of the wide range of habitat variables was analyzed as follows. I first performed a regression analysis with the first two orthogonal axes created through the PCA as predictor variables. This was to determine if probability of getting killed varied along one or two ecological gradients as defined in the PCA.

Thereafter the focus was returned to the models that included the original field measurements (density of tree species, habitat types etc.) as predictor variables. To establish which habitat variables to include in the best models, Akaike's information criterion (AIC) were used. The aim of using AIC is to identify models that explains the most of the variation in the data with as few variables as possible (Burnham & Anderson 2002). The best AIC model is the one with the lowest value (Anderson et al. 2000). Because of a relatively low sample size an AIC with modified criterion (AICc) was performed to establish which model was the best, as selection based on regular AIC is inadequate for low sample sizes.

First a full model including all uncorrelated variables and the interactions with "season" was fitted. The AICc of this model as well as all simpler models nested within the full model was calculated and thereafter ranked based on AICc value. In accordance with the principle of parsimony the model with the lowest $\Delta\text{AICc} < 2$ value and fewest variables were chosen (Burnham & Anderson 2002). Overdispersion was tested for the full model. There was no overdispersion (acceptable data fit) if $p > 0.05$ (Agresti 2002). The final model (as defined by the AICc) provides the basis for the parameter estimates presented in figures and tables in the thesis.

3. Results

3.1 Forest- and vegetation structure

The habitat variables proportion of spruce, pine, birch, RAG and other, dominating cutting class and ground vegetation, mean canopy cover and coverboard gone, and relascope birch did not correlate with each other to a large extent (values between -0.5 and $+0.5$ (Zuur et al. 2009), Table 1). I therefore continued with these as independent predictor variables in the analyses.

Table 1: The correlation matrix, by using the “hetcor” function in the “polycor” package in R, both numeric and categorical variables could be tested against each other. Pearson = correlation between numeric variables, polyserial = correlation between numeric and ordinal variables and polychoric = correlation between ordinal variables. Spruce, pine, birch, RAG (rowan, aspen and goat willow) and other (other coniferous trees) are all a mean proportion of that type of forest at each site. **Bold** indicate values seen as correlated (positive correlated ≥ 0.5 or negative correlated ≤ -0.5) (Zuur et al. 2009).

	Spruce	Pine	Birch	RAG	Other	Cutting class	Ground-vegetation	Dominating habitat	Vegetation height	Mean tree height	Canopy cover	Relascope pine	Relascope spruce	Relascope birch	Relascope RAG	Coverboard gone	
Spruce	1	Pearson	Pearson	Pearson	Pearson	Polyserial	Polyserial	Polyserial	Polyserial	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
Pine	-0.25	1	Pearson	Pearson	Pearson	Polyserial	Polyserial	Polyserial	Polyserial	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
Birch	-0.55	-0.44	1	Pearson	Pearson	Polyserial	Polyserial	Polyserial	Polyserial	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
RAG	-0.45	-0.44	0.22	1	Pearson	Polyserial	Polyserial	Polyserial	Polyserial	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
Other	-0.17	-0.13	0.06	0.10	1	Polyserial	Polyserial	Polyserial	Polyserial	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
Cutting class	0.39	0.04	-0.28	-0.25	-0.03	1	Polychoric	Polychoric	Polychoric	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	
Ground-vegetation	-0.32	-0.28	0.30	0.46	0.14	-0.23	1	Polychoric	Polychoric	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	
Dominating habitat	-0.71	-0.48	0.80	0.70	0.25	-0.46	0.45	1	Polychoric	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	
Vegetation height	0.48	0.36	-0.47	-0.58	-0.18	0.45	-0.45	-0.62	1	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	Polyserial	
Mean tree height	0.37	0.07	-0.33	-0.21	-0.06	0.71	-0.26	-0.43	0.42	1	Pearson	Pearson	Pearson	Pearson	Pearson	Pearson	
Canopy cover	-0.27	-0.02	0.28	0.09	0.06	-0.47	0.28	0.23	-0.31	-0.49	1	Pearson	Pearson	Pearson	Pearson	Pearson	
Relascope	0.39	0.11	-0.38	-0.22	-0.19	0.53	-0.31	-0.44	0.54	0.59	-0.72	1	Pearson	Pearson	Pearson	Pearson	
Relascope pine	-0.16	0.72	-0.32	-0.31	-0.10	0.17	-0.24	-0.36	0.36	0.23	-0.30	0.46	1	Pearson	Pearson	Pearson	
Relascope spruce	0.74	-0.24	-0.40	-0.27	-0.14	0.44	-0.23	-0.50	0.45	0.50	-0.46	0.72	-0.12	1	Pearson	Pearson	
Relascope birch	-0.13	-0.29	0.42	0.11	0.02	0.18	-0.07	0.29	0.05	0.13	-0.29	0.28	-0.18	0.03	1	Pearson	
Relascope RAG	-0.23	-0.28	0.07	0.66	-0.05	0.02	0.24	0.41	-0.32	-0.02	-0.17	0.10	-0.19	-0.09	0.14	1	
Coverboard gone	0.36	0.30	-0.41	-0.41	-0.10	0.30	-0.29	-0.53	0.81	0.35	-0.16	0.40	0.27	0.37	-0.04	-0.27	1

3.2 Ecological gradients

The biplot (Figure 2) of the principal component analysis (PCA) illustrates that typical closed habitats with spruce in coniferous forest and medium-aged stand forest are close to the x axis and at the negative side of the axis (for example proportion of spruce, “m-sp” and medium aged stands, “cc4” in Figure 2). Typical open habitats such as infield, clear cuts and young plantations are all somewhat at the positive side of the x axis (“h-inf”, “cc1” and “cc2” in Figure 2).

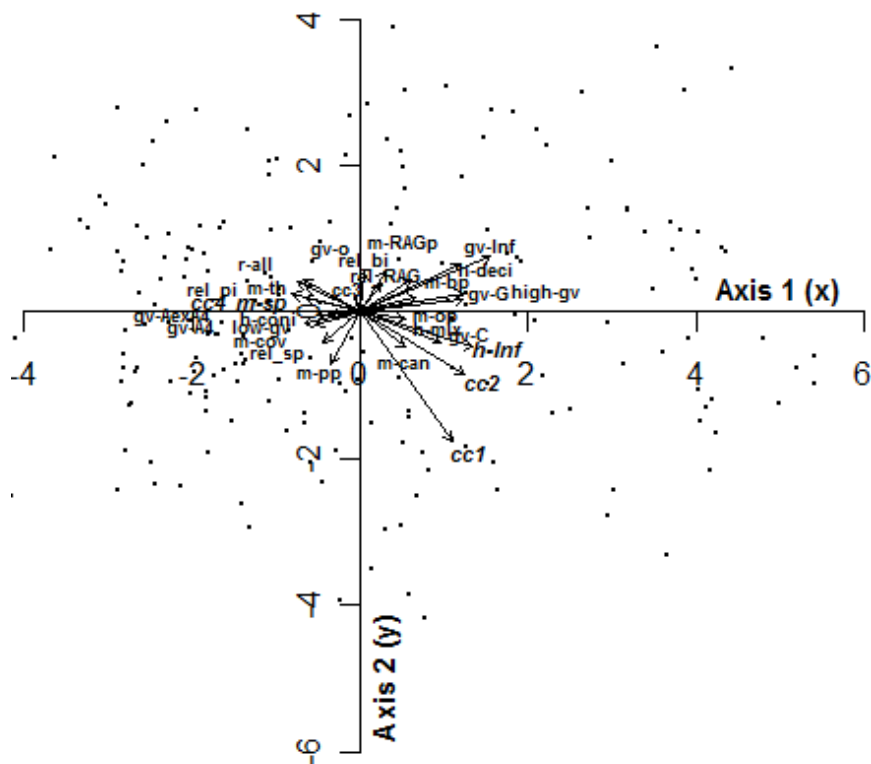


Figure 2: A biplot of the vegetation data, extracted from a principal component analysis (PCA) - The different vegetation variables are drawn in different directions on either axis 1 (x-axis) or axis 2 (y-axis). Typical open habitat is located close to and at the positive side of the x-axis, while typical closed habitat is located at the negative side of the x-axis, but still on or close to it. It looks like axis 2 (y) contributes in less degree to explain the ecological aspect.

The vegetation variables are indicated as follows:

m-sp (mean spruce proportion of forest), **r-all** (mean relascope density), **m-cov** (mean distance coverboard disappears at), **m-can** (mean canopy cover density), **m-op** (mean other coniferous trees proportion of forest), **m-RAGp** (mean RAG, other deciduous tree species, proportion of forest), **m-th** (mean tree mid height), **m-bp** (mean birch proportion of forest), **m-pp** (mean pine proportion of forest), **m-th** (mean tree mid height), **h-coni** (dominating coniferous habitat per site), **h-mix** (dominating mixed forest habitat per site), **h-Inf** (dominating infield habitat per site), **h-deci** (dominating deciduous habitat per site), **cc1** (dominating cutting class per site, clear cut), **cc2** (dominating cutting class per site, young plantations), **cc3** (dominating cutting class per site, pole size stands), **cc4** (dominating cutting class per site, medium-aged stands), **gv-AexA4** (dominating ground vegetation per site, lichen/bryophyte and dwarf-shrub woodland minus bilberry woodland), **gv-A4** (dominating ground vegetation per site, bilberry woodland), **gv-C** (dominating ground vegetation per site, tall-fern and tall-herb woodland), **gv-Inf** (dominating ground vegetation per site, infield), **gv-G** (dominating ground vegetation per site, anthropogenous grassland), **gv-O** (dominating ground vegetation per site, freshwater shore), **high-gv** (dominating height on ground vegetation, high), **low-gv** (dominating height on ground vegetation, low), **rel_sp** (mean spruce density, relascope), **rel_pi** (mean pine density, relascope), **rel_bi** (mean birch density, relascope) and **rel_RAG** (mean RAG, other deciduous tree species, density, relascope). Due to none tolerance of NA-values, the variable **cc0** (no cutting class, typically infield) has been excluded from the analysis.

By doing a logistic regression analysis of the x axis (PCA axis 1) in the PCA (Figure 3), I found a tendency that the further to the positive side you get on the x axis (more open habitat) the lower the relatively probability of getting killed by lynx (Figure 3; Estimate=-0.113, SE=0.0065, p=0.083). This provides some support to my prediction that the risk will increase with vegetation density. The y axis (PCA axis 2) does not contribute much to the prediction and the parameter estimate for the y axis in the fitted GLM was not significant.

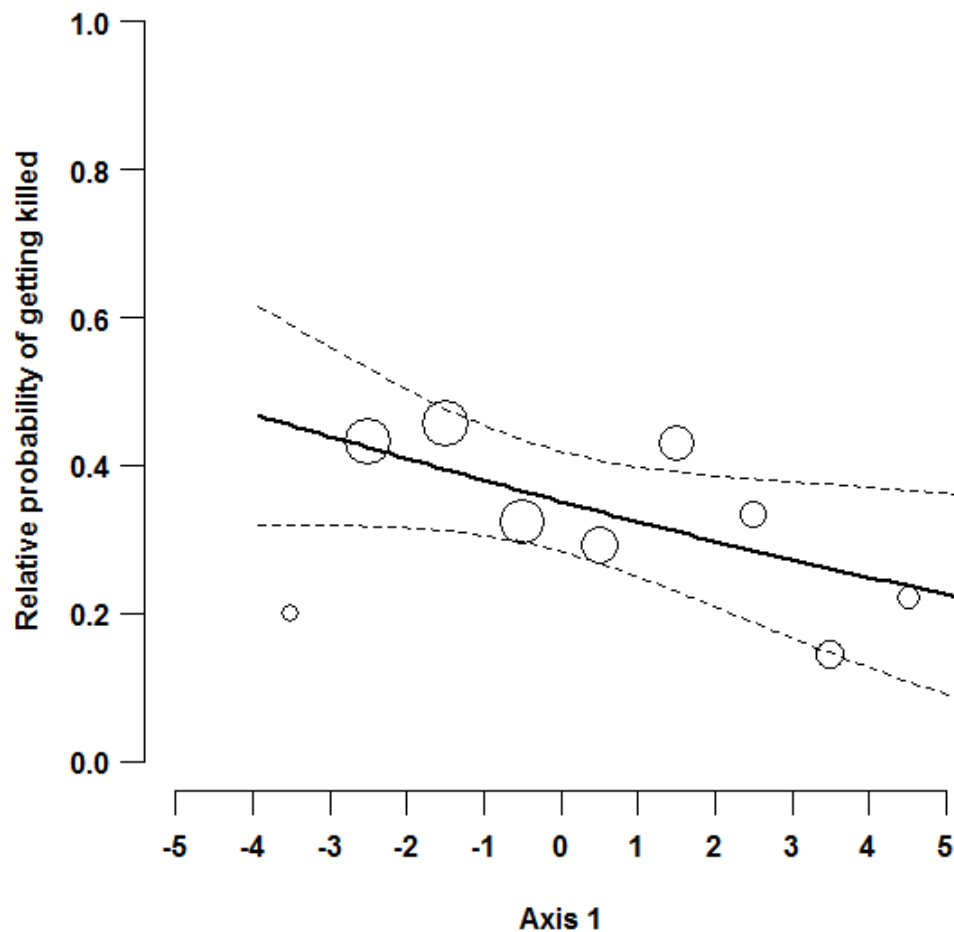


Figure 3: Logistic regression analysis of the x axis (Axis 1) created through the PCA. There is a trend that the further you'll get at the positive side of the axis (more open habitat types), the relative probability of getting killed decreases. The areas of the circles are proportional of the sample size.

3.3 Increased amount of spruce increases mortality

Regression models were compared by the use of the AICc test (top 15 models shown in Table 2) to provide the best model to explain the variation in where roe deers were killed. The best model (on the simplest model within $\Delta\text{AICc} < 2$), included only the proportion of spruce in forest (Figure 4). The number of roe deer killed in each spruce density class is fairly even up to 80 % spruce cover. However roe deer spent most of their time in open habitat, and progressively less time in denser spruce habitat (Table 3). Due to this the probability of getting killed by a lynx increased with the proportion of spruce in the forest (Estimate=0.020, SE=0.00512, p=0.000104). Spruce is a typically dense habitat type so this is also in line with my prediction. There were no differences between seasons (Table 2, see appendix for adaption to seasonal effects).

Table 2: Model selection by the Akaike Information Criterion adjusted for small sample sizes (AICc). The model with the lowest $\Delta\text{AICc} < 2$ is chosen to represent the best compromise between explaining as much variance as possible while using the smallest numbers of variables possible (parsimonious principle) (the grey line), top 15 models.

n variables	Model	AICc value	ΔAICc
3	season + mean spruce (%) + mean RAG (%)	261.0403	0
2	season + mean spruce (%)	261.5329	0.4926031
4	season + mean spruce (%) + mean RAG (%) + dominating ground vegetation	261.7114	0.671128
3	mean spruce (%) + mean RAG (%) + dominating ground vegetation	261.7601	0.7198499
2	mean spruce (%) + mean RAG (%)	261.9451	0.9048258
1	mean spruce (%)	261.9995	0.9592588
4	season + mean spruce (%) + mean RAG (%) + mean relaskop birch	262.1302	1.0899855
3	season + mean spruce (%) + mean relaskop birch	262.3344	1.2941187
4	season + mean spruce (%) + mean RAG (%) + season : mean spruce (%)	262.3681	1.3278479
4	season + mean spruce (%) + mean relaskop birch (%) + season : mean relaskop birch	262.7103	1.6700687
5	season + mean spruce (%) + mean RAG (%) + mean relaskop birch + season : mean relaskop birch	262.7737	1.7334128
4	season + mean spruce (%) + mean birch (%) + mean RAG (%)	262.7784	1.7381499
2	mean spruce (%) + mean relaskop birch	262.8896	1.849336
3	mean spruce (%) + mean RAG (%) + mean relaskop birch	263.0664	2.0261588
4	season + mean spruce (%) + mean RAG (%) + season : mean RAG (%)	263.0677	2.027471

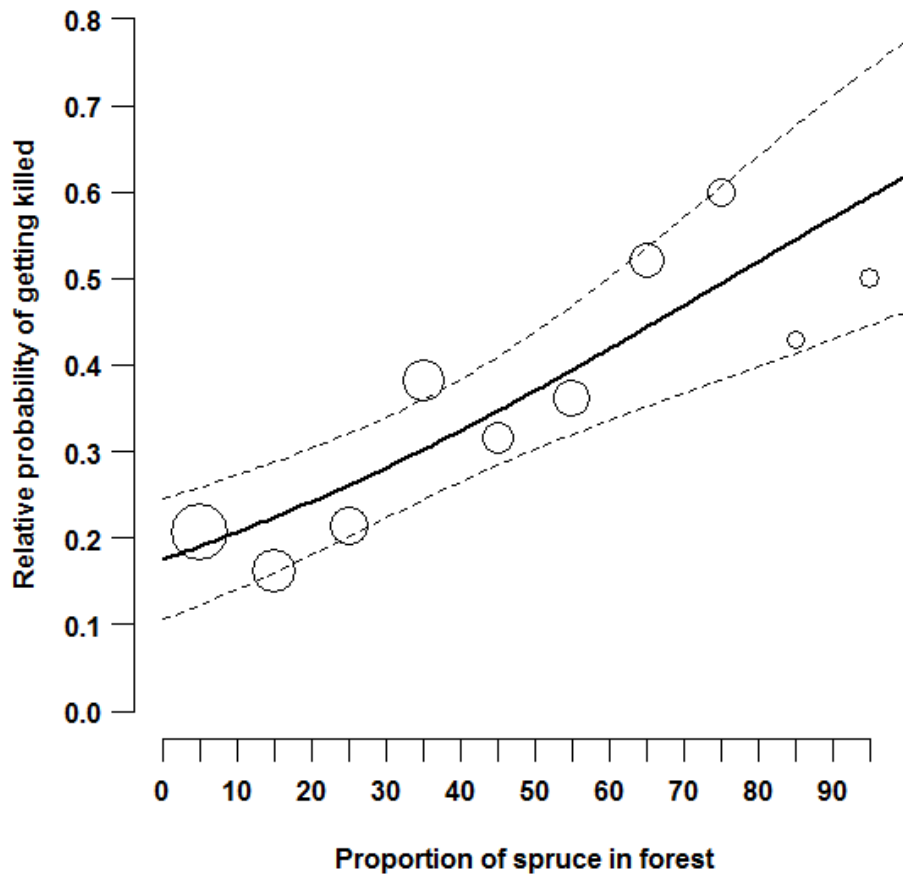


Figure 4: The logistic regression analysis of the best model, proportion of spruce in forest, based on the $\Delta AICc$ value < 2 and the principle of parsimony. When the proportion of spruce in forest increases the relative probability for roe deer of getting killed by lynx also increases. The areas of the circles are proportional of the sample size.

Table 3: The amount of time spent (%) by roe deer and the proportion of roe deer kills in forest with different proportion of spruce.

Proportion of spruce	0-20	21-40	41-60	61-80	81-100
Feces+GPS-sites	86 (46%)	44 (24%)	29 (16%)	18 (10%)	8 (4%)
Kill-sites	19 (23%)	19 (23%)	15 (19%)	21 (26%)	7 (9%)

4. Discussion

In this study I report that roe deer in Hallingdal have a higher relative probability of being killed by lynx in dense forest habitat, in particular spruce forest. Spatial variation in the risk of being killed by a predator is consistent with the idea of a landscape of fear. The main reason for this pattern is probably related to the habitat choice and hunting method of its main predator, the lynx, a stalking predator. The result indicates that typical dense forest- and vegetation-structures, especially forest containing a high proportion of spruce, is a riskier habitat choice for roe deer than open meadows and infield. This suggests that roe deer either ignores risk effects and suffer high predation rates or make a trade-off in their habitat selection which may yield nonlethal effects of predation in terms of potentially reduced forage intake rates.

4.1 Increased risk of predation in denser habitat

I found an increased risk of predation from lynx on roe deer in habitat with a denser vegetation structure. The lynx is a stalking predator, depending on cover to sneak up on its prey before initiating attack (Nilsen et al. 2009). It has been shown that Canadian lynx (*Lynx canadensis*) changed hunting technique depending on what vegetation they occupied, in sparse cover they stalked their prey, while they ambushed it in dense canopy (Murray et al. 1995). In Europe several studies consider forests as the main habitat for Eurasian lynx (Zimmermann & Breitenmoser 2002; Niedzialkowska et al. 2006; Basille et al. 2009).

Laundré (2010) found a negative relationship in the spatial distribution of mule deer (*Odocoileus hemionus*) and puma (*Puma concolor*), supporting the prediction of the “landscape of fear” hypothesis. Several other studies have indicated that the possible presence of predators could increase anti-predator behavior of ungulate populations, not only limiting them - supporting the “landscape of fear” hypothesis (Laundré et al. 2001; Fischhoff et al. 2007; Wirsing et al. 2008; Valeix et al. 2009; Wegge et al. 2009; Laundré 2010; Thaker et al. 2011). Laundré (2010) also found an indication that the puma incorporated the prey’s limited information about its presence. Especially in large patches puma had an advantage over mule deer. The mule deer used longer time to detect the puma, and the puma had more time to hunt before it was detected. This might indicate a behavioral complexity in a landscape, which

could have extensive impacts on interaction between a predator and its prey. Extending this to the interaction between lynx and roe deer one might expect that the lynx would in some way forage in areas where the roe deer has incomplete information about its presence, so that the lynx could remain undiscovered for a longer period of time. This can to some extent be seen from my results (Table 3), where the proportion of the roe deer killed in areas with > 60% spruce was much higher than expected from the time spent in dense spruce forest. In these dense habitat areas roe deer could have limited information about the lynx's presence, and whereabouts. This could have been used to the lynx's advantage leading up to a successful kill.

Prey would possibly win the response race in low-risk patches (Laundré 2010). High- and low-risk patches were specified according to mutual variations in risk of predation, fear-response of prey, and the hunting success and lethality of the predator (Laundré 2010). The prey's predicted strategy is then simply to concentrate their activity in these relatively safe habitats. Due to this, the predators' strategy would then simply be to avoid these patches, because of their low predation success (Hopcraft et al. 2005; Laundré 2010). However, this may not apply for roe deer, due to the possible lack of relatively safe habitats. Ratikainen et al. (2007) observed that roe deer did not change their habitat choice after the re-colonization of the lynx in Scandinavia. This could explain the high predation-rate lynx can have on roe deer. If so, this could be seen as an indication against the landscape of fear hypothesis, and rather point to some other constraint than predation in habitat selection. I do not have data on the availability of habitat types within the study area. However, my results could indicate a possible preference for other habitats than spruce forest. Thus, in areas where there is less spruce, more live roe deer-sites were found in relation to the proportion of roe deer killed. The study period in Ratikainen et al. (2007) was a severe winter, and this could have impacted the findings. It was suggested that high risk of predation could have been inevitable because roe deer are more prone to predation by lynx during severe winters (Andersen et al. 2005). My data is from a longer period of time (four years) and include data from all seasons. However, there was no marked evidence of seasonal effects in my data, as the season term or its interaction with habitat did not enter the best model. Nevertheless, the findings of my study would probably not be affected by one severe winter in the same way as Ratikainen et al. (2007).

4.2 Why do not roe deer move out of risky habitats?

It has been found that roe deer prefer dense forest (Tufto et al. 1996; Nilsen et al. 2004), most likely as a source of both food and cover (Tufto et al. 1996; Mysterud & Østbye 1999; Ratikainen et al. 2007; Torres et al. 2010). However, vegetation in dense spruce forest is not preferred in the roe deer diet, such as vegetation in deciduous forest. But in terms of thermoregulation they both work as a decent cover source (Mysterud 1996). The overall low risk of encountering a lynx may not lead to a lasting landscape of fear because of other constraints in habitat choice; food, human hunting and thermoregulation may limit the roe deer's choice of staying more in the open habitats. Roe deer's staying in the open when lynx is present has been observed both by hunters and researchers (Ratikainen et al. 2007) and can be interpreted as a temporary landscape of fear. However, roe deer can often also be found in open habitats such as meadows and pastures because they also serve as a good source of food, in addition to deciduous forest (Mysterud 1999).

Prey in landscapes with both open and closed vegetation could use two strategies to avoid or minimize predation from carnivores. Hiding in forest to lower rates of predation encounter, or seek open terrain to spot predators from a distance (Kie 1999). The lynx is territorial and has large home ranges (Herfindal et al. 2005), and the probability for each roe deer to encounter a lynx is small. Along with lynx and hunters, predation from the red fox influences the roe deer population in Norway, especially where the population of roe deer is high. Because of its small size, the red fox rarely kill fawns older than six weeks because they become more difficult to catch (Aanes & Andersen 1996; Solberg et al. 2003; Linnell et al. 2008). The roe deer could probably respond to lynx presence by scent, and then choose a flexible strategy to stay out in the open (Ratikainen et al. 2007). Elk started using safer forest and reduced the use of open meadows after the reintroduction of wolves in Yellowstone National Park, whereas bison did not (Hernández & Laundré 2005). This was probably because wolf had higher success rate of killing elk than bison, and that the population of elk was higher (Smith et al. 2000). The strategy of seeking open areas is influenced both by the probability of a prey animal spotting a predator and by the likelihood of the prey escaping if attacked (Ripple & Beschta 2004).

A couple of recent studies (Theuerkauf & Rouys 2008; Crosmarj et al. 2012) has studied human hunters as predators in addition to natural predators and their impact on habitat selection. In Poland they concluded that hunting from humans influenced the distribution of

ungulates more than the predation risk by their natural predator, grey wolf (Theuerkauf & Rouys 2008). This could also be the case in my study, because of the relatively low density of lynx compared to the high amount of hunters in the area, the roe deer could fear open habitats more than dense. Human hunters are dependent on more open habitats, such as open forests, clear cuts, infields, meadows and pastures to hunt roe deer because they need clear sight (Farmer et al. 2006). At the same time the roe deer would probably escape, or not be discovered by hunters in dense forest (Benhaiem et al. 2008).

4.3 Conclusion

My results demonstrate an increased risk for roe deer of being killed by a lynx with increasing habitat density (Figure 3), and in particular in spruce forest than in more typical open habitats. My study indicates that the lynx might superimpose a landscape of fear on its main prey, the roe deer. Spruce forest and other denser forest types seems to be riskier habitat for the roe deer to occupy, when lynx are present, than open habitats such as clear cuts and infield. However, the study also raises the question of why roe deer do not to a larger extent move out of areas of dense vegetation, suggesting that there might be other constraints to habitat selection. The low density of lynx in the area may potentially be insufficient to create a lasting landscape of fear. This may be because safety from lynx predation is traded off against more important factors for roe deer habitat selection, such as food availability, safety from human hunting, and thermoregulatory benefits of cover.

5. References

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Appendix

Appendix 1: Proportion of spruce increases mortality unequally throughout the year

Proportion of spruce adapted to seasonal effects, the winter period stretches from 1.11 – 30. 4 while summer is defined from 1.5 – 31.10. The interaction is almost significant, and that is why I chose to show it in the appendix. It's a negative relationship between increasing density proportion of spruce in forest for the roe deer's relative probability to survive. The relative probability for the roe deer of getting killed increases more rapidly during summer than winter, but has an higher relative probability of survival in other habitats without any or small amounts of spruce.

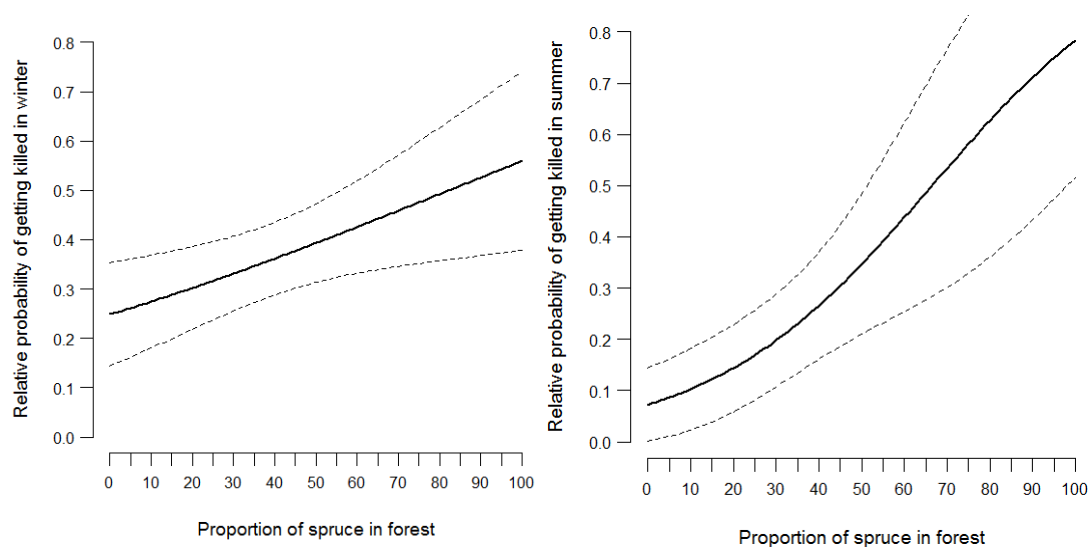


Figure 5: Proportion of spruce in forest adapted to seasonal effects.

Table 4: Estimated values for the adaption of proportion of spruce in forest to seasonal effects.

	Estimate	Std.Error	z value	p-value
Intercept	-2.55357	0.5435	-4.698	2.62E-06
Mean proportion of spruce	0.03842	0.0123	3.123	0.00179
Winter	1.44715	0.61412	2.356	0.01845
Mean proportion of spruce*Winter	-0.02497	0.01357	-1.84	0.06571