

Disentangling risk in a multi-predator landscape:

Roe deer respond to differing patterns of risk to lynx, wolves and humans through shifts in their habitat selection

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Master's thesis
Grimsö 2015

Independent project/Degree project / SLU, Department of Ecology 2015:10



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Credits: 45 HEC

Level: A2E

Course title: Independent project in biology

Course code: EX0596

Programme/education: Master's Programme in Biology, Uppsala University

Place of publication: Grimsö

Year of publication: 2015

Cover picture: Andrew Lewis

Title of series: Independent project/Degree project / SLU, Department of Ecology

Part number: 2015:10

Online publication: <http://stud.epsilon.slu.se>

Key words: *Canis lupus, Capreolus capreolus, indirect effects, landscape of fear, Lynx lynx, multi-predator systems, predation risk, Scandinavia, spatial risk patterns, ungulates.*

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Abstract

Predation risk is known to evoke behavioural responses in prey animals, and prey are often faced with a trade-off between lowering their risk to predation and acquiring resources. This situation becomes more complex in a multi-predator landscape, especially if those predators employ different hunting strategies, and induce different spatial patterns of risk. In this study, the spatial patterns of predation risk that roe deer face from humans, as well as their natural predators, lynx and wolves, were identified. Using the natural experiment provided by the return of large predators and the coinciding decline in hunting mortality, the behavioural responses of roe deer to shifting patterns of predation risk were examined. Using predation and hunting mortality locations, combined with used locations from the same 149 roe deer, predation risk to each predator was related to habitat and infrastructure attributes. Mostly in line with predictions, agricultural lands were found to present the highest risk to human hunting, while old forest provided a safe habitat from lynx predation, and no strong pattern was found for wolf predation. Habitat selection in relation to the most important risk factors was then compared between the period before and after lynx recolonized the area, using location data from 231 roe deer individuals. All analyses were conducted at the within home-range scale. I found that in general, agricultural lands were selected for, although less intensively during the hunting season both before and after lynx recolonisation. Moreover, there was a tendency for weaker differences between hunting and non-hunting seasons in the period after the return of lynx, potentially reflecting the lower hunting intensity in that period, and the added risk to lynx in that habitat throughout the year. An increased use of old forest was found after the recolonisation of lynx, potentially due to the relative safety from lynx attack that this habitat provides. Hence, this study demonstrates that different predators can generate different spatial patterns of predation risk, and roe deer seem to respond to these differential patterns through spatial and temporal habitat selection shifts.

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Popular science summary

Many of us have heard about what happened in Yellowstone national park in the USA when wolves were reintroduced there after over 50 years of absence. Their main prey, elk started spending less time in confined stream and river valleys where they were at most risk to wolf attack. Supposedly as a result of this, tree species in those areas started to bounce back from heavy browsing, and wolves were accredited with the recovery of these river-side ecosystems. The story has become a classic example of how predators can control natural ecosystems both directly and indirectly through “trophic cascades”, although recent studies have questioned whether wolves are solely responsible.

In south-central Sweden, wolves had been absent for over 100 years, due to persecution by humans, but have naturally recolonized the area during the last decade. Likewise, Lynx had been absent for around 30 years, but started to recolonize the southern half of Sweden during the mid-1990s. This situation posed the question of whether the return of these top predators could lead to an ecological cascade similar to Yellowstone’s.

At the Grimsö Wildlife Research Area, Roe deer have been monitored using VHF and GPS collars since the 1970s. This provided the opportunity to study the changing patterns of predation risk that these deer have been exposed to with the return of their natural predators. By comparing the death site characteristics of roe deer with locations that they had used during their life-times, I was able to identify which habitats presented the most risk from each predator, as well as from human hunting. I found that older forest stands (> 60 years old) provided a relatively safe habitat to roe deer from lynx predation, while wolf predation didn’t show any strong patterns, and as expected, agricultural lands presented the most risk to hunting by humans.

Using this information, I set out to determine whether roe deer have responded to these changing spatial patterns of risk by selecting for safer habitats. To do this I compared location data from roe deer before and after the return of lynx and wolves. I found that during the hunting season, roe deer use agricultural lands considerably less. Furthermore, after the return of lynx, they have used old forest more than they did before. Hence, it seems that roe deer respond to the different spatial patterns of predation risk induced by their top predators, by avoiding the most risky habitats, and using safer habitats more often.

The consequences of these indirect predator effects to the ecosystem itself however, are unknown. Conversely, other studies have found that the direct effects of lethal predation by lynx are likely responsible for the strong reduction in roe deer population growth rate and density after the return of this predator. It may be that in these types of human dominated ecosystems which are common throughout Europe, the potential for indirect predator effects to cause phenomenon such as trophic cascades, is limited. Nevertheless, this study may be one of the first to show that roe deer in Europe are responding to the return of their natural predators through shifts in their habitat selection.

Introduction

It is a well-known phenomenon that prey species make behavioural decisions to reduce their risk of predation (Lima and Dill, 1990). These behaviours include reducing time spent foraging (Hughes and Ward, 1993; Brown and Kotler, 2004), increasing vigilance (Elgar, 1989), reduced activity (Sih and McCarthy, 2002), group size changes (Creel and Winnie Jr., 2005) and shifts in habitat selection (Creel et al., 2005). These indirect effects induced upon prey species by their predators are known to be of high importance and in some cases are thought to be more significant than the actual direct effects of lethal predation (Creel and Christianson, 2008; Kuijper et al., 2013). The reason for this is that shifts from optimal habitats and reductions in feeding, can have greater net costs to the prey population than predator induced mortality itself (Lima and Dill, 1990; Lima, 1998; White et al., 2011; Middleton et al., 2013).

Habitat selection is the process by which individual animals choose between the habitats available to them in order to, at least theoretically, maximize their fitness (Johnson, 1980; Manly et al., 2002). Many studies have found that habitat structure is important in determining predator success, and that this effect is usually tied to the hunting capabilities or tactics of the predator (Lewis and Eby, 2002; Brown and Kotler, 2004; Laundré et al., 2010). For example, pumas (*Puma concolor*) have a much higher success rate at killing Mule deer (*Odocoileus hemionus*) along forest edges, than in open areas (Laundré and Hernández, 2003). This is due to the hunting tactics of pumas which are stalking predators and therefore need cover in order to get close to their prey. In contrast, open areas presented moose (*Alces alces*) with higher risk to predation from wolves (*Canis lupus*), which are coursing predators (Gervasi et al., 2013). Thus, different habitats can present varying levels of predation risk from different predators. The spatial and temporal variation in the activity and efficiency of predators may result in a “landscape of fear” due to the resulting effect on the prey’s predator avoidance behavior and decision making (Laundré et al., 2001). The concept of a “landscape of fear” essentially implies that animals express fear from anticipated attack from predators, and not only from immediate or imminent threats (Laundré et al., 2010), and select for habitats where predation risk is deemed to be lower. However, this behavioural response can come at a cost, as prey animals are often faced with a trade-off between avoiding predators and acquiring resources.

Understanding these interactions between predators and their prey is vital to understanding the way that ecosystems work because the behavioural and population responses by a prey species to a predator have the potential to impact the ecosystem through processes such as trophic cascades (Drossel et al., 2001). The return of large predators to many parts of their former ranges in North America and Europe has provided the opportunity to study these processes in detail. The reintroduction of wolves into Yellowstone National Park has become a classic example of how the indirect effects of predation and the landscape of fear can potentially produce cascading effects in the ecosystem. In response to the return of their major predator, elk (*Cervus elaphus canadensis*) shifted their habitat use from high risk open areas towards forest edges which acted as a refuge (Creel et al., 2005; Hernández and Laundré, 2005). A consequence of this shift was that elk had fewer foraging opportunities and a significant reduction in their diet quality (Hernández and Laundré, 2005). Other studies also found changes in the patchiness and composition of vegetation and a recovery of North

American beaver (*Castor Canadensis*) due to the resurgence of their woody food supply (Ripple and Beschta, 2003, 2004a, 2004b, 2006, 2007). However, in recent years, these claimed ecosystem effects of wolves in Yellowstone have been contested and a number of studies have suggested that the reintroduction of those predators alone cannot explain the trophic dynamics and changes in vegetation patterns observed (Kauffman et al., 2010; Winnie, 2012; Marshall et al., 2013, 2014).

Studies on the indirect effects of predators are less common in Europe despite it also experiencing large-scale recoveries of native large carnivores (Chapron et al., 2014). Moreover, many North American studies have been conducted in national parks such as Yellowstone or other relatively intact ecosystems. Europe poses some interesting differences, in that many predator-prey communities are located in rural parts with relatively high human population densities and not a lot of protected land. Gervasi et al. (2013), in a study looking into the effect of recolonising wolves in Scandinavia, found strong evidence for spatial variation in predation risk for moose and roe deer (*Capreolus capreolus*), but no evidence of a behavioural response to that. Gervasi et al. (2013) suggests that the apparent naivety of certain Scandinavian prey species and the largely human-dominated landscape in Scandinavia restricts the possibility of wolves to have large indirect effects on the ecosystem. This may be because reducing risk to human related mortalities is the best strategy for ungulates in these landscapes, even if it means increasing their risk to wolf predation (Gervasi et al., 2013). This notion is supported by Nicholson et al. (2014) who also found limited evidence that moose habitat use was influenced by recolonizing wolves in south-central Sweden. It should be noted that both of these studies looked into the response of ungulates to a returning coursing predator, and that the hunting strategy of the predator in question may influence the potential to have important ecosystem effects. It is suggested that anti-predator behaviour should be stronger when exposed to stalking or ambushing predators than to coursing predators (Preisser et al., 2007). A study by Wikenros et al. (2015) found that both roe deer and red deer (*Cervus elaphus*) reduced their visitation durations to sites with a lynx (*Lynx lynx*) olfactory cue, in contrast to a similar study that instead used wolf olfactory cues in the same study area (Kuijper et al., 2014). This suggests that ungulates are able to recognize different threats from different predators and adjust their anti-predator response accordingly (Wikenros et al., 2015). To date, the majority of work on this subject has concentrated on the response to a single predator species (Thaker et al., 2011). In reality this is often not the case, and so studies on predation risk across the landscape should reflect this. In Europe, human hunting pressure can be quite high, even in areas that also accommodate large predators, and therefore, the influence of human hunting on prey behaviour should also be taken into account. Lone et al. (2014) demonstrated that roe deer in south-central Norway are faced with areas of contrasting risk to predation by lynx and humans, as well as areas of risk overlap. This is potentially a situation that many ungulates now face with the return of multiple predators to their former ranges.

In south-central Sweden, over the last few decades, roe deer have been faced with an increasingly complex predator community. Since the beginning of the study period humans have been hunting roe deer in the area through regulated annual harvest, although the intensity of this has changed over time. Since around 1996 roe deer have additionally been faced with lynx after about 30 years of absence, and in 2003, wolves also returned after >100 years of absence. This system therefore provides an ideal

natural experiment to study the indirect effects of multiple predators on a common prey species. Previous work in the area found no evidence of a habitat selection response by roe deer to lynx recolonisation (Samelius et al., 2013), although that study, based on smaller sample sizes, did not consider multiple sources of predation risk and excluded agricultural areas from analysis. For those reasons, and with a few years of extra data, it was deemed justifiable to partially repeat this study, and attempt to disentangle all of the major causes of predation risk to roe deer.

The aim of this study therefore was to determine whether three predators; humans, lynx and wolves, each with their own unique hunting strategy, present different spatial patterns of risk to roe deer. The risk of hunting mortality is expected to be higher in open areas due to the requirement for a long line of sight. Lynx risk is expected to be higher in areas with dense understory vegetation (Lone et al., 2014) due to their stalking and ambushing tactics, while wolf risk is not expected to show a clear pattern as their hunting of roe deer is thought to be mainly opportunistic (Gervasi et al., 2013). A further objective was to determine whether roe deer habitat selection has shifted in response to the return of lynx and wolves. Since humans and lynx are their two main predators, it was expected that roe deer will avoid or select less intensively for areas of high risk to those predators and select more strongly for low risk areas, and in the process, potentially trade forage quality for lower predation risk.

Methods

Study Area

Grimsö Wildlife Research Area (GWRA hereafter) ($59^{\circ} 60' N, 15^{\circ} 16' E$) is located within Örebro County in south-central Sweden. The research area encompasses 137 km^2 of the southern boreal zone and is covered mainly by forests (73 %) and large boggy areas (19 %). Lakes and rivers make up 6% of the area, while agricultural lands cover 2% (Samelius et al., 2013). The topography of the area is fairly regular with altitudes varying between 75m and 180m above sea level. Average temperatures vary between 20°C in summer and -10°C in winter, with snow typically covering the ground from December until March (Samelius et al., 2013).

Commercial forestry is conducted in the research area and surroundings where the forest is owned and managed by the Swedish National Forest Enterprise (Sveaskog) for timber and pulp. Owing to this management, the research area is largely made up of a patchwork of even aged stands with a clear-cutting rotation of about 100 years. The forest is predominantly coniferous with Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) being the main tree species. Deciduous species such as birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), and willow (*Salix* spp.) also occur. Beneath the trees, the understory consists of bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), heather (*Calluna vulgaris*), and common hair grass (*Deschampsia flexuosa*) (Samelius et al., 2013).

The first known lynx-killed roe deer in GWRA was found in 1994, although functional recolonisation occurred between 1995 and 1996, with the first documented reproduction occurring in 1996 (Samelius et al., 2013). Within one year, there was approximately $>1 \text{ lynx}/100\text{km}^2$ (Liberg and Andrén, 2006). The area was then

recolonized by wolves in 2003, with the first reproductive event occurring in 2004. Since 2009, one or more wolf territories have encompassed the entire GRWA (Viltskadecenter, online annual reports). Red fox (*Vulpes vulpes*) have always been present, although the population experienced a significant decline due to sarcoptic mange between 1982 and 1990 (Lindström et al., 1994), but has since recovered. In addition, moose, wild boar (*Sus scrofa*), mountain hare (*Lepus timidus*), European hare (*Lepus europaeus*), Eurasian beaver (*Castor fiber*), black grouse (*Tetrao tetrix*), and capercaillie (*Tetrao urogallus*) all reside within the research area.

Study Species

The European roe deer is a relatively small ungulate (adults: 20-30 kg) that is distributed across most of Europe, and is the most widespread of the continents ungulates (Sempéré et al., 1996). The species is found across the whole of Sweden, apart from its most northerly reaches and at high altitudes (>1000m) (P. Kjellander, Grimsö Wildlife Research Station, pers. comm.). In Sweden, roe deer are seen as an important resource to hunters and so the population has long been heavily harvested. Though, within the GWRA, the annual roe deer harvest has dropped considerably since the mid-1990s, due in part to the return of natural predators (P. Kjellander and G. Rauset, Grimsö Wildlife Research Station, pers. comm.).

The main natural predator of roe deer is the Eurasian lynx (Melis et al., 2013), while the red fox can take a large number of roe deer fawns during their first two months of life (Kjellander and Nordström, 2003; Kjellander et al., 2004a; Jarnemo and Liberg, 2005; Panzacchi et al., 2009). The wolf also occasionally predaes upon roe deer but it is usually regarded as a secondary prey species, especially when moose are present (Gervasi et al., 2013).

Roe deer capture and monitoring

The roe deer population has been monitored since the establishment of the GRWA, and the first animal was fitted with a VHF collar in 1974. Roe deer are captured during the winter using box traps baited with livestock feed, and fitted with radio-collars (70-350g) (Televilt Int., Lindesberg, Sweden and Telonics Inc., Mesa, Arizona). Since 2011, some (13 in this study) individuals have been fitted with GPS collars (Vectronic Aerospace Systems, Berlin, Germany). At the time of writing, > 1000 individuals had been marked in this way, and their movements tracked. Deceased individuals and any tracks surrounding them were examined in the field to determine the likely cause of death and to note the location of the mortality site. An autopsy on the carcass or remains was also carried out in the lab for this purpose. Since lynx are short range attackers, and most attacks occur from < 50 m away (Haglund, 1966) and carcasses are rarely moved > 20 m away from the kill site (Samelius et al., 2013), the locations of lynx-killed roe deer were deemed to be good estimates of the actual attack and kill location. Triangulations were performed to locate individuals with VHF collars from a tracking bus at least once or twice per week, although the tracking schedule differs widely across the study period and some animals were located daily. Most locations were made between 08:00 and 18:00, although the few GPS collared individuals included in the study were located during both day and night. Samelius et al. (2013) found no difference in habitat use between day and night in roe deer in the same study area, and so these locations were not separated. Telemetry error was estimated to be < 150 m (Cederlund et al., 1979;

Samelius et al., 2013).

Data management

In order to achieve better correspondence between VHF and GPS fix rates, the GPS data was resampled to a maximum of 2 locations per day. To account for potential long term and seasonal variation in patterns of mortality and habitat selection, the telemetry and mortality data was classified by three temporal processes. Following a before-after design, the location data was divided into two time groups representing before and after lynx recolonisation. The Pre-lynx period was defined as from 1984 until December 1994, while the Post-lynx period was defined as from January 1997 until 2014. In order to avoid the effect of any lag in roe deer response to lynx, individual and location data falling between those periods was not included. A second, three time-period parameter was created including a post-wolf period from January 2004 until 2014. For the risk analysis, the 15th of November until the 31st of March was defined as "Winter" to capture the period with the highest chance of snow on the ground. The "Hunting season" was defined as from the 16th of August until the 31st of January.

Environmental data

A digital map of the GWRA and areas immediately surrounding it was procured from the forestry company Sveaskog, and used to prepare a habitat map in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California). The exact or approximate clear cut year of each stand within the study area was calculated and used to determine the age of the stand at the time of death or use by an individual. The stand age was used to classify the habitat into clear cuts (0-10 years old), young forest (10-25 years old), middle aged forest (25-60 years old), and old forest (> 60 years old), following Samelius et al. (2013).

The Swedish CORINE Land Cover map (SMD) with 25x25m resolution was used to define areas not covered by the forestry map. In all, 18 habitats were identified in the study area, but to increase generality and statistical power, these were grouped into six final broad habitat classes (Appendix 7); agricultural lands, clear-cuts, mires, young forest, middle aged forest and old forest. Habitats of extremely low probability of roe deer use such as lakes, rivers and gravel pits were removed using the snip tool in ArcGIS. Human infrastructure features, roads and buildings were obtained from a vector map of Sweden (GSD-Översiktskartan, Lantmäteriet, Sweden). At GWRA, trap sites for roe deer capture are also actively provided with livestock feed during the snow season to attract roe deer, which could potentially influence both mortality and habitat selection patterns. A map of these feeding sites was obtained from digitalized trap site point locations. Using these maps, the habitat class and distance to infrastructure features were calculated for each mortality site, telemetry location or randomly generated availability location (see below) included in the risk and habitat selection analyses. Average habitat patch size was calculated to be >0.057 km² (Range: 10⁻⁴ - 4.4 km²) and therefore no attempt to correct for telemetry error (< 150 m) was made.

Analysis

Risk Analysis

Logistic regression was used to model the spatial variation in the probability of predation by the three different predators as well as spatial variation in the probability

of starvation. Mixed effects models were built in R (R Core Team, 2014) with the package lme4 (Douglas et al., 2014) to compare the habitat and infrastructure characteristics of known mortality sites with a set of randomly selected locations of use by each individual. The number of used locations was limited to max 30. However, not all individuals had that many observations before mortality, and so only individuals with ≥ 20 locations were included in analysis (i.e. range: 20-30 locations). These random locations were assumed to represent the proportional use of the habitats available to individual deer. To account for individual variation in habitat availability and uneven sampling of used locations, individual ID was included as random intersects in the models. Risk model analysis was carried out separately for roe deer killed by *human*, *lynx*, and *wolf*. Spatial patterns of *starvation* were also examined in an attempt to check for any background patterns of mortality.

Before model selection commenced, habitat and infrastructure variables were checked for collinearity and multi-collinearity. If variables were highly correlated ($r > 0.7$), only the variable with the lowest AIC (Akaike information criterion) (Burnham and Anderson, 2002) in a univariate regression was kept. Due to collinearity between the covariates, *Roads* and *Buildings*, the latter was excluded from further analysis. Model ranking was performed using the dredge function of the package MuMIn (Bartoń, 2012) which performs automatic model ranking based on AIC_c (AIC with small sample adjustment). Model averaging (using the MuMIn package) was used to achieve robust parameter estimates while accounting for model selection uncertainty, as recommended by Grueber et al. (2011). Only models $\Delta AIC_c < 4$ were selected to delineate the top model set used in model averaging (Burnham and Anderson, 2002; Grueber et al., 2011).

To evaluate potential confounding effects from feeding sites, the effect of these on lynx, wolf and starvation risk was specifically checked within a season specific risk analysis (i.e. including only data during the winter season, when feeding sites were active). The distance to feeding sites did not significantly affect lynx, wolf or starvation risk, and the identification of year round effects commenced. It must however be noted that this season specific risk analysis was limited by small sample sizes for the wolf and starvation caused mortalities. For the hunting risk models, all mortalities occurred within the hunting season, and adding a seasonal effect was thus redundant.

Based on the model averaged parameters, spatial maps of the predicted probability of being killed by each predator or starvation were created in ArcGIS, by interpolating model point predictions (one per 25x25m grid) using the inbuilt Kriging function (max 9 neighbouring locations). The maps assist the visualisation of the relative risk between habitat types.

Habitat Selection Analysis

Habitat selection was analysed at the within-home-range scale. Thus the spatial extent of habitats available to individuals was defined by their home range. The home-range therefore approximates the area over which a roe deer would likely travel between VHF or GPS locations. In order to define reasonable home ranges, only individuals with at least 20 locations were included (Kjellander et al., 2004b), and 95 % minimum convex polygons (MCPs) were generated from these locations using the program Geospatial Modeling Environment (Beyer, 2012). Deer locations falling far outside of their usual home ranges or falling between their summer and winter ranges if they were migrators, were manually excluded. Random points were generated within each home range at a 1

random point to 1 used location ratio. These random points thus represented the locations available to each roe deer individual.

In order to evaluate the hypothesis that roe deer select habitats spatially and temporally to reduce the risk of encountering and being killed by their most important predators, a before-after predator recolonisation design was used, and a priori models were built to specifically target those habitat or infrastructure characteristics that showed significance in the risk analysis. Thus, the risk-associated habitat covariates were tested for interactions with time period (before/after recolonisation); for hunting mortality, the interactions with seasonal variation was also included (hunting/non-hunting season), and finally the three-way interaction between habitat, period, and hunting season was included. Habitat selection models were created by comparing used and available habitats to obtain Resource Selection Functions (Manly et al., 2002). Generalized linear mixed effects models were fitted in R package lme4, with binomial error distributions, and with collar type (GPS or VHF) and individuals (animal ID) as random intersects to correct for uneven sampling and individual variation in habitat availability. Suites of competing models were ranked and models $\Delta AIC_c < 4$ were used for model averaging in the MuMIn package (Burnham and Anderson, 2002; Grueber et al., 2011).

Results

Changing mortality patterns in the GWRA

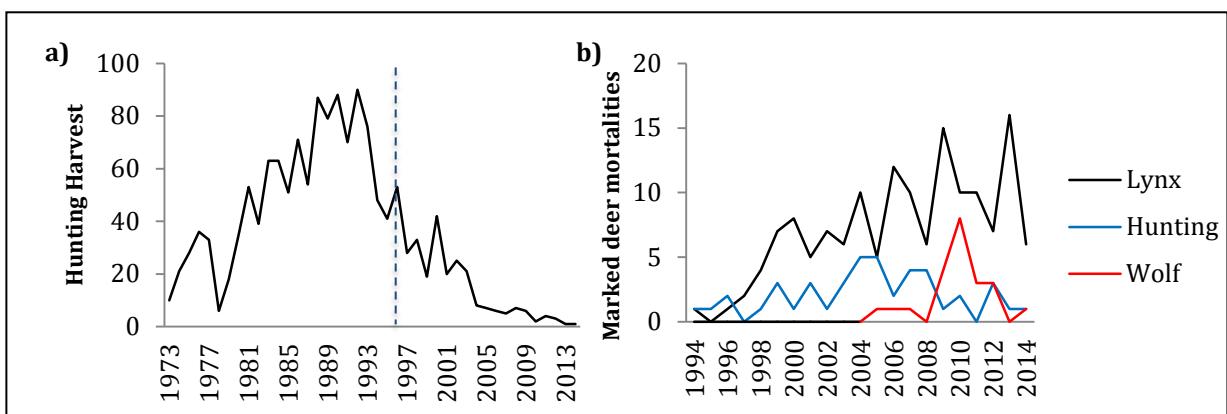


Figure 1. Time series showing annual roe deer hunting harvest figures (both marked and un-marked) between 1973 and 2014 (a) in and around the Grimsö Wildlife Research Area, and the number of roe deer (marked) killed by lynx, hunting and wolf since recolonisation (b) in and around GWRA between 1994 and 2014. The dashed lines represent the recolonisation of lynx.

The time series of roe deer hunting statistics and predation from GWRA (Figure 1) highlights the changes in the relative importance of each predator to roe deer during the past couple of decades. The hunting harvest of roe deer (both marked and un-marked) inside and within the vicinity of the GRWA peaked during the mid-1980s until the mid-1990s when hunting intensity started to be relaxed (Figure 1a). The decline in hunting coincided with the return of lynx, and later on with the return of wolves to the GWRA. Lynx predation commenced in 1994, gradually increasing and peaking at about 15 monitored/marketed roe deer per year (Figure 1b). The first known wolf-killed roe deer occurred in 2005, and the number taken has gradually increased in the ensuing years

(Figure 1b). Since the return of lynx, no more than 5 marked roe deer have been hunted per year (Figure 1b).

Risk Models

After imposed restrictions on the data, a total of 88 monitored individuals were lynx-killed and included in the analysis of habitat specific risk of lynx predation. Twenty-eight individuals were included in hunting risk analysis, 16 in wolf risk analysis and 17 in starvation analysis. All individuals included in risk analysis were at least 1 year old at the time of their death.

The best model predicting hunting risk included only the factor *Agriculture* which had a positive correlation with risk (Appendix 1; $\beta = 1.689$, SE = 0.442, P < 0.001). The second best model included *Young Forest* which was also positively correlated with risk ($\beta = 0.386$, SE = 0.525, P = 0.462), along with *Agriculture* ($\beta = 1.773$, SE = 0.46, P < 0.001), and had an increase in AIC_c of 1.51. The third best model included the parameter *Roads* which was negatively correlated with hunting risk ($\beta = -0.123$, SE = 0.403, P = 0.761), again with *Agriculture* ($\beta = 1.672$, SE = 0.445, P < 0.001), and had an increase in AIC_c of 1.93 (I.e. *Roads* was close to an uninformative parameter). After model averaging, *Agriculture* still came out as the only significant hunting risk factor to roe deer (Appendix 1; $\beta = 1.701$, SE = 0.464, P < 0.001). *Agriculture* was included in all models $\Delta\text{AIC}_c < 4$ of the best model (Relative variable importance (RVI) = 1.00). Evidently, agricultural lands seem to be the only habitat significantly important in terms of hunting risk when taking into account the proportional use of each habitat (Figure 2b).

The best model predicting lynx predation risk included only the parameter *Old Forest* which had a negative correlation with risk (Appendix 2; $\beta = -0.776$, SE = 0.355, P = 0.029). The second best model included *Agriculture* which was positively associated with risk ($\beta = 0.51$, SE = 0.384, P = 0.184) along with *Old forest* ($\beta = -0.735$, SE = 0.357, P = 0.04), and had an increase in AIC_c of 0.44. The third best model included *Roads* which was negatively associated with lynx risk ($\beta = -0.258$, SE = 0.218, P = 0.237), again with *Old forest* ($\beta = -0.771$, SE = 0.355, P = 0.03), and increased AIC_c by 0.68. These models were not much worse than the top model in terms of model fit, although when model averaging was conducted on models $\Delta\text{AIC}_c < 4$, *Old forest* was still the only parameter that was significant (Appendix 2; $\beta = -0.744$, SE = 0.378, P = 0.049) and was included in almost the entire top model set (RVI = 0.86). Old forest seems to be a relatively safe habitat for roe deer from lynx predation (Figure 2c).

In modeling predation risk to wolves, *Agriculture* had to be excluded from analysis in order to achieve model convergence, due to the dearth of kill data, and absence of kills in that habitat. The best model predicting wolf predation risk did not include any of the remaining habitat or distance parameters (i.e. the null model performed the best). The second best model included *Roads* which was positively correlated with risk (Appendix 3; $\beta = 0.43$, SE = 0.561, P = 0.443) and had an increase in AIC_c of 1.38. In the model average of those $\Delta\text{AIC}_c < 4$ of the best model, *Roads* was still the strongest factor influencing predation risk to wolves, although it was far from significant (Appendix 3; $\beta = 0.113$, SE = 0.346, P = 0.744). *Roads* was included in only a quarter of the top model set (RVI = 0.25).

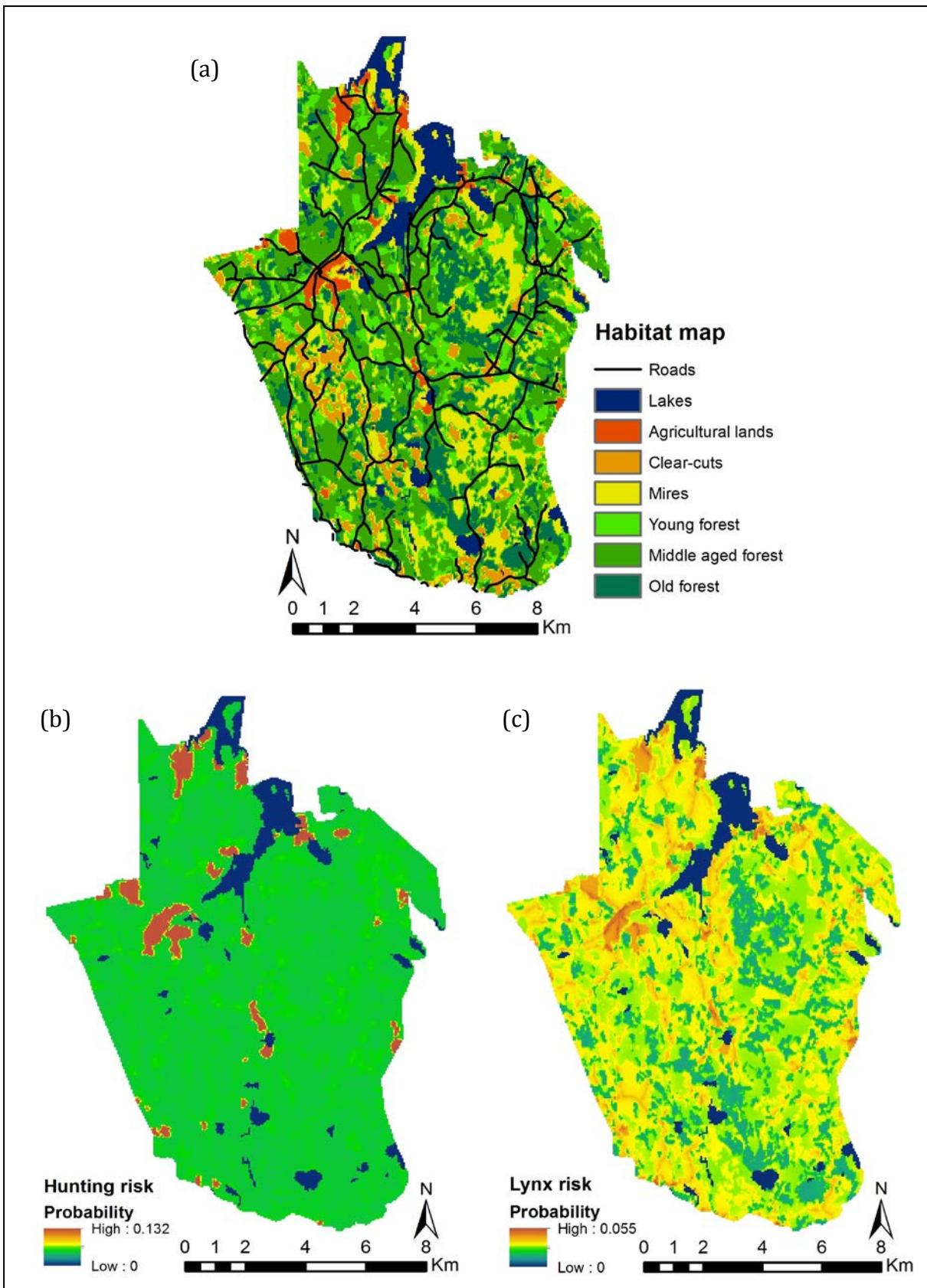


Figure 2. Maps of the GWRA, showing (a) the spatial structure of the 6 habitat classes during the year 2013 (Road data © Lantmäteriet, i2014/764.), and the predicted probability for a roe deer to be killed by (b) hunting and (c) lynx in the different habitat classes. These predictions were generated from the model averages for each predator. The spatial risk maps depict high risk to hunting in agricultural lands (b), and low risk of lynx predation in old forest (c).

The best model predicting risk of starvation also did not include any parameters in the top model. The second best model included *Young forest* which was positively associated with starvation risk, although not significantly (Appendix 4; $\beta = 0.69$, SE = 0.546, P = 0.206), and increased AIC_c by 0.56. Model averaging was again conducted on those $\Delta\text{AIC}_c < 4$, and *Young forest* was still the strongest factor in terms of starvation risk (Appendix 4; $\beta = 0.828$, SE = 0.653, P = 0.206). *Young forest* was included in 42% of the top model set (RVI).

Habitat Selection Models

A total of 231 individuals were included in the habitat selection analysis with a mean of 238 locations per animal (st.dev = 270, range = 20 - 1785). The pre lynx period (February 1984 to December 1994) included 67 individuals, while 164 individuals were included in the post lynx period (January 1997 to April 2014). Individuals and locations falling between those time periods were not included in analysis in order to avoid the effects of any lag in roe deer response to predators.

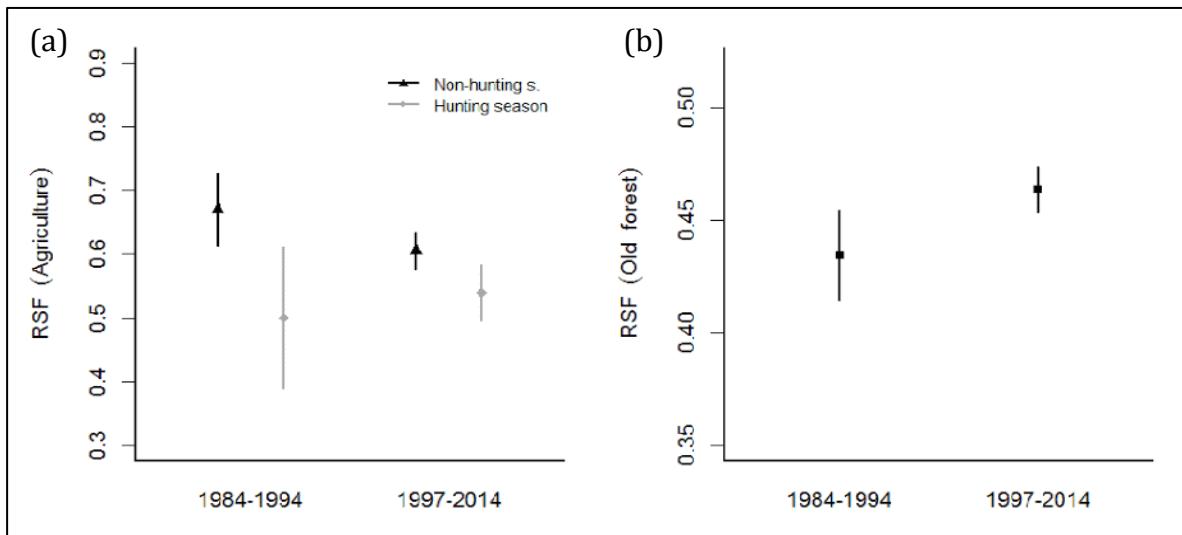


Figure 3. Relative probability of habitat use by Roe deer in GWRA (with 95% confidence intervals) for the model-averaged parameters, (a) Agriculture during the hunting and non-hunting seasons, both before and after the return of lynx, and (b) Old forest before and after the return of lynx.

From the prior analysis, it was clear that *Agriculture* and *Old Forest* were the only parameters significantly important in terms of risk. A priori habitat selection models were constructed specifically addressing those two habitat categories and potential interactions with time period (before-after) and hunting season. The best model included an interaction between *Agriculture* and *Hunting season*, along with an interaction between *Old forest* and *Time period* (weight = 0.396) (Appendix 5 and 6). The next best model additionally included an interaction between *Agriculture* and *Time period* (weight = 0.227) and increased AIC_c by 1.11. Model-averaging was then conducted on the 5 best models that were $\Delta\text{AIC}_c < 4$ of the best model (Appendix 5). The model averaged parameters showed a general selection for agricultural lands and an avoidance of old forest. They also included an interaction between *Agriculture* and *Hunting season*, as well as an interaction between *Old forest* and *Time period*, indicating less intensive selection for agricultural lands during the hunting season and increased use of old forest after the recolonisation of large predators (Figure 3). There was also a tendency for a three-way interaction between *Agriculture*, *Hunting season* and *Time*.

period; after the recolonisation of large predators, seasonal differences in selection for agricultural lands were weaker (Figure 3).

Discussion

With the return of large carnivores to many parts of North America and Europe, ungulates are faced with multiple angles of predation risk. These multi-predator systems have only recently been explored in detail (Atwood et al., 2007, 2009; Thaker et al., 2011), and to a very limited extent in European ecosystems (Lone et al., 2014). This study found that changes in the major causes of roe deer mortality, with the return of lynx and wolves, led to alterations in the spatial patterns of predation risk that roe deer in south-central Sweden are faced with. Roe deer then responded to these changes in predation risk by reducing their risk exposure through shifts in their habitat selection. The two main predators of roe deer in the area, humans and lynx imposed the clearest patterns of risk. These patterns were not distinctly contrasting with human hunting risk highest in agricultural lands, while that habitat was not associated with lower risk to lynx, and old forest was significantly safer from lynx predation. No clear pattern of risk was found in a non-predation related mortality cause (starvation).

Though not significant, higher risk to lynx predation in open areas like agricultural lands was somewhat unexpected as it differs from the findings of other studies on lynx (Lone et al., 2014), and cougars which employ a similar hunting strategy (Atwood et al., 2007), and justifies the inclusion of these areas in the analysis of lynx risk. The common perception is that open agricultural lands provide areas of safety for roe deer from lynx attack, and perhaps this is not completely true. The pattern is possibly due to the penchant for lynx to use the cover of forest edges to attack prey in open areas (Laundré and Hernández, 2003). Agricultural areas within GWRA are generally small, meaning that a large proportion of them are close to forest edges, potentially adding to this effect. Furthermore, the pattern may be influenced by the landscape composition of the GWRA. Very few agricultural fields interspersed amongst the dominant forest habitats may make roe deer utilization of agricultural lands spatially predictable to lynx (Panzacchi et al., 2009), and the pattern may be less pronounced in more heterogeneous landscapes with higher proportions of agricultural fields. Old forest in the GWRA is predominantly managed and is generally characterized by tall conifers with limited structural complexity beneath the canopy. The scarcity of adequate undergrowth cover may be a reason for old forest providing relative safety to roe deer from lynx attack.

No clear pattern of risk was found for wolf predation, which may simply be explained by the as yet limited number of known wolf-killed roe deer in the GWRA. Still, the result is supported by Gervasi et al. (2013) who found that wolf predation on roe deer did not differ markedly from a random process, and suggested that wolves kill roe deer opportunistically. Wikenros et al. (2009) found that the average chase distance for wolf attacks on roe deer in Scandinavia was 237m, which may also play a part in cancelling out any patterns if they do exist. Wolf predation of roe deer tended to occur far from roads and never in agricultural lands. Likewise, Gervasi et al. (2013) that wolf predation on roe deer usually occurred far from agricultural fields, and these findings perhaps indicate that fear of humans is an important factor in wolf habitat selection. Therefore, the concentration of roe deer on and near agricultural lands, although putting them at

increased risk to humans and lynx, may inadvertently lower their risk to wolves. The failure to find a strong spatial risk pattern for wolf predation provides some support to conclusions by Preisser et al. (2007) that stalking and ambushing predators such as lynx evoke stronger indirect effects on prey than coursing predators like wolves. No clear pattern of starvation mortalities may also be due to limited observations, but supports the assumption that no background patterns of mortality were at play.

Roe deer exhibited clear patterns of spatial and temporal habitat selection at the home range scale, potentially in response to these differing patterns of predation risk. In order to lower their risk to hunting, roe deer selected less strongly for agricultural land during the hunting season. This is not totally surprising, as red deer (*Cervus elaphus*) too have been shown to respond behaviorally to the onset of the hunting season (Jarnemo and Wikenros, 2013). There was also a tendency for a smaller difference in the use of agricultural lands between the hunting and non-hunting season in the years after 1996 compared to before. This may be a reflection of the corresponding decline in the annual hunting harvest and the risk of lynx predation in agricultural lands also outside of the hunting season, and roe deer adjusting as such. After the return of lynx in 1996, roe deer also used old forest significantly more than before. Since old forest is generally not a quality habitat in terms of resources, except for bilberry patches, it seems likely that this increase in use is due to old forest providing relative safety from lynx attack.

In the recent two decades, suggestions have been made that large carnivores can create a landscape of fear for their prey (Laundré et al., 2001). Roe deer in south-central Sweden do seem to face such a situation, as certain parts of their home ranges present varying levels of risk to their predators. It has also been argued by some that the indirect effects of these situations can cause trophic cascades in the ecosystem (Laundré et al., 2001; Ripple et al., 2001, 2014). The potential for this largely depends on the strength of the anti-predator responses that prey employ in relation to other fitness related behaviours. In the present study system, roe deer seem to be faced with at least two trade-off situations; a high-risk, high-reward compromise in productive agricultural areas, and a low-risk, low-reward compromise in low quality old forest. Furthermore, and in contrast to the findings of Lone et al. (2014), roe deer in the GWRA do not seem to be faced with a strong trade-off in avoiding lynx and human predation. In other words, selection of habitats in order to avoid one predator does not seem to distinctly increase their risk to the other predator. Cresswell and Quinn (2013) proposed that contrasting spatial patterns of risk from two or more predators should buffer the potential for large indirect effects on the ecosystem. Likewise, Lone et al. (2014) highlights the possibility that when prey can avoid both predators through one strategy or habitat shift, the potential for indirect effects to cause trophic cascades should be greater. In our case, this may be particularly true as the habitat with the highest risk to both predators also contains important resources, and therefore the cost of reduced use is high.

Despite finding clear shifts in habitat use in response to the return of lynx, the ecological importance of these shifts is difficult to infer. It does seem that roe deer may be responding to added lynx risk by using agricultural lands less. Therefore one can speculate that it is possible that these predators can both directly, through limiting prey densities, and indirectly, through habitat shifts, reduce crop damage by ungulates. If true, this would give weight to the assertion by Ripple et al. (2014) that large predators can have unexpected benefits to human agriculture and pastoralism. An obvious

consequence of this and roe deer's heightened use of old forest after the return of large predators may be a decrease in their time spent foraging. However, the consequences of this to plant communities and to the roe deer population as a whole are unknown. From this evidence only, it is difficult to categorically state that the return of lynx has contributed substantially to the maintenance of ecosystem functions in this system, through risk mediated indirect effects. Contrary to this, a recent study in the same study system, found that the population growth rate of roe deer was strongly affected by the recolonisation of lynx (Arbieu, 2012; Andrén and Liberg, 2015). This was likely due to the non-selective nature of lynx predation on roe deer (Andersen et al., 2007; Andrén and Liberg, 2015), and their killing of prime reproductive females. Annual pellet counts also show a large decline in roe deer density corresponding with the return of lynx, and despite the declining hunting harvest (Andrén and Liberg, 2015). Therefore, this indicates that in this system, the direct effects of the return of large predators are more important to the roe deer population than risk mediated indirect effects. In addition, other levels of control that lynx (or wolves) can assert must be taken into account, for example removing old and sickly prey animals, and controlling the abundance of mesopredators. In Finland for example, the return of lynx was accompanied with a decline in the red fox population and an increase in forest grouse (*Tetrao tetrix* and *T. urogallus*) and mountain hare (Elmhagen et al., 2010; Ritchie et al., 2012).

Notwithstanding the widespread return of large carnivores throughout Europe, few studies have demonstrated strong indirect effects in ecosystems as a result. As previously suggested (Gervasi et al., 2013; Lone et al., 2014), this may not come as much of a surprise when accounting for the high human population densities and human dominated landscapes on the continent. For example, in Sweden, the intensive forestry industry alone may hinder indirect processes from strongly affecting forest ecosystems. Another possibility is that the long time interval that Scandinavian ungulates have lived, reproduced, and died in without exposure to top predators may mean that costly predator avoidance traits have largely been lost from ungulate populations (Blumstein and Daniel, 2005), resulting in naïve prey (Sand et al., 2006). Moreover, the seemingly stronger response to the hunting season than to natural predators may be due to the higher temporal predictability of the hunt. Natural predation is a continuous process throughout the year, while the hunting season occurs during a defined period of the year, perhaps making it both easier and more cost efficient to respond to compared to natural predation (Proffitt et al., 2009). As Sönnichsen et al. (2013) surmised, the lower selection of agricultural lands during the hunting season indicates that roe deer are able to assess temporal distributions of risk and adjust accordingly. It must however be taken into account that the hunting season does extend into winter, and reduced use of agricultural fields during the hunting season may also be due in part to scarcer food in those areas during winter.

Research into the indirect effects of the recolonisation of large predators on ungulates in Europe is limited, and this study may be one of the first to show habitat selection shifts potentially as a response. Nonetheless, it is apparent that there are still a lot of questions surrounding the potential for indirect ecosystem effects of returning large carnivores in human dominated landscapes such as those found throughout Europe. This study therefore furthers our understanding of the indirect effects of predators in these types of ecosystems. Studies on the indirect effects of multiple predators on prey are also

limited, and this study gives further evidence into how different predators can evoke differential spatial risk patterns and behavioural responses in prey.

Acknowledgements

I would like to express my gratitude to Petter Kjellander for his guidance and for providing me the opportunity to conduct this study, and to Geir Rune Rauset for his insights, for answering endless questions and for all his help with the modeling. Thanks also go to all the people who took part in the data collection, particularly Lasse Jäderberg who has been capturing roe deer in the GWRA since 1974, and to Linda Höglund for her data compiling. Without them, this study would never have been possible.

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Appendices

Appendix 1. Summary statistics for the best model explaining risk to hunting, along with model averaged parameters of models $\Delta AIC_c < 4$. Significant effects ($P < 0.05$) are in bold.

Best model	Estimate	SE	P
(intercept)	-3.599	0.237	<0.001
Agriculture	1.689	0.441	<0.001
Model Averaging	Estimate	SE	P
(intercept)	-3.555	0.499	<0.001
Agriculture	1.701	0.464	<0.001
Young Forest	0.394	0.538	0.465
Log Roads	-0.124	0.404	0.759
Middle Aged Forest	-0.129	0.512	0.802
Old Forest	0.061	0.542	0.91
Clear-cuts	-0.018	0.763	0.981

Appendix 2. Summary statistics for the best model explaining lynx risk, along with model averaged parameters of models $\Delta AIC_c < 4$. Significant effects ($P < 0.05$) are in bold.

Best model	Estimate	SE	P
(intercept)	-3.257	0.115	<0.001
Old Forest	-0.777	0.355	0.029
Model Averaging	Estimate	SE	P
(intercept)	-3.175	0.423	<0.001
Old Forest	-0.744	0.378	0.049
Agriculture	0.62	0.431	0.15
Log Roads	-0.247	0.22	0.261
Middle Aged Forest	0.328	0.279	0.241
Young Forest	-0.227	0.359	0.529
Mires	-0.144	0.398	0.718
Clear-cuts	-0.184	0.433	0.671

Appendix3. Summary statistics for the best model explaining wolf risk, along with model averaged parameters of models $\Delta AIC_c < 4$. Significant effects ($P < 0.05$) are in bold.

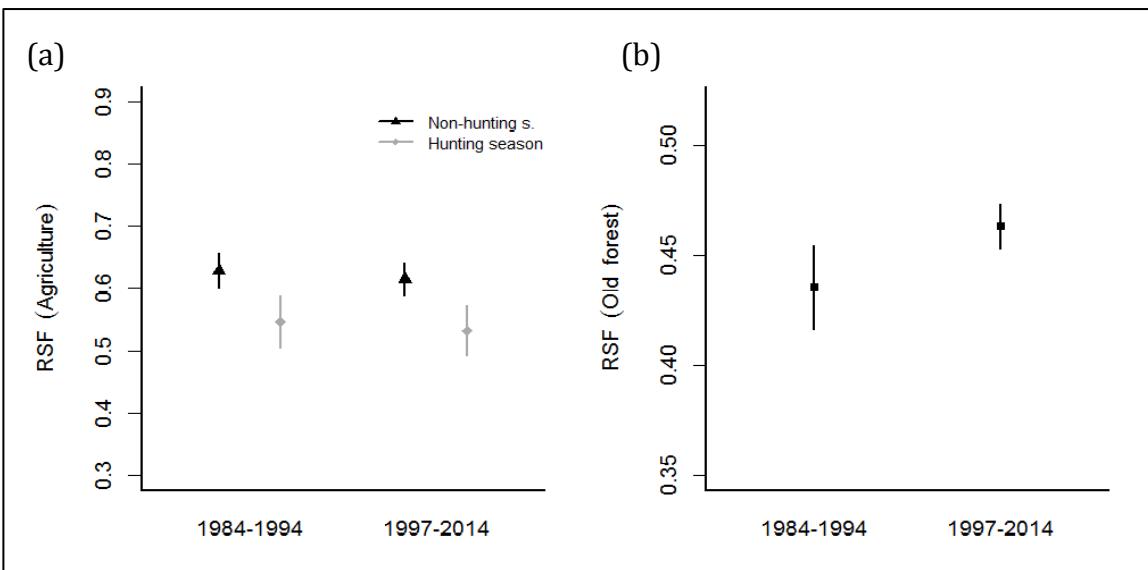
Best model	Estimate	SE	P
(intercept)	-4.278	1.268	<0.001
Log Roads	0.43	0.561	0.443
Model Averaging	Estimate	SE	P
(intercept)	-3.608	0.819	<0.001
Log Roads	0.113	0.346	0.744
Mires	-0.094	0.404	0.817
Middle Aged Forest	0.065	0.279	0.815
Old Forest	-0.074	0.38	0.846
Young Forest	0.066	0.331	0.843
Clear-cuts	0.044	0.355	0.902

Appendix 4. Summary statistics for the best model explaining starvation risk, along with model averaging of models $\Delta AIC_c < 4$. Significant effects ($P < 0.05$) are in bold.

Best model	Estimate	SE	P
(intercept)	-3.512	0.293	<0.001
Young Forest	0.69	0.546	0.206
Model Averaging	Estimate	SE	P
(intercept)	-3.502	0.659	<0.001
Young Forest	0.828	0.653	0.206
Old Forest	-0.711	0.8	0.375
Middle Aged Forest	0.514	0.638	0.421
Clear-cuts	-0.683	1.073	0.526
Log Roads	0.16	0.544	0.769
Mires	0.184	0.859	0.831

Appendix 5. Summary statistics of the best model and the model average of those $\Delta AIC_c < 4$ describing variation in habitat selection by roe deer at the spatial and temporal scale of home ranges and years in the GWRA between 1984 and 2014. Significant effects ($P < 0.05$) are in bold.

Best Model	Estimate	SE	P
(intercept)	0.083	0.023	0.001
Agricultural	0.443	0.055	<0.001
Hunting	0.015	0.019	0.432
Old Forest	-0.343	0.046	<0.001
Time Period	-0.058	0.027	0.032
Agricultural*Hunting	-0.354	0.099	<0.001
Old Forest*Time Period	0.171	0.051	<0.001
Model Averaging	Estimate	SE	P
(intercept)	0.081	0.027	0.003
Agricultural	0.496	0.111	<0.001
Hunting	0.016	0.031	0.618
Old Forest	-0.341	0.046	<0.001
Time Period	-0.055	0.029	0.06
Agricultural*Hunting	-0.397	0.179	0.026
Old Forest*Time Period	0.168	0.051	<0.001
Agricultural*Time Period	-0.148	0.14	0.291
Hunting*Time Period	-0.004	0.05	0.943
Agricultural*Hunting*Time Period	0.454	0.282	0.107



Appendix 6. RSF scores (with 95% confidence intervals) for the best model parameters, (a) Agriculture during the hunting and non-hunting seasons, both before and after the return of lynx, and (b) Old forest before and after the return of lynx. The RSF score represents the probability of use of a habitat by a roe deer. The best model did not include a 3 way interaction between Agriculture, Hunting season and Time period.

Appendix 7. All habitats found using the SMD map and forest stand map, along with the final 6 habitat groups that they were assigned to. Habitats were assigned to groups based on biological similarities such as openness and resource availability.

Final Habitat Groups	All habitats
Agricultural lands	Arable land
Clear-cuts	Clearcut Clear-felled area
Mires	Mire Wet Mires Inland marshes
Young Forest	Coniferous forest 5-15m Younger forest Young forest
Middle Aged Forest	Broad-leaved forest not on mires Coniferous forest >15m Coniferous forest on open bedrock Coniferous forest on lichen dominated areas Middle Age Forest Mixed forest not on mires
Old Forest	Broad leafed forest on mires Coniferous forest on mires Old Forest