Can Environmental Features Explain Variation in Free Ranging Sheep Mortality Exposed to Eurasian Lynx Predation?

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Abstract

The recovery of large carnivores in Europe has led to widespread and chronic conflicts because of their depredation on livestock, which can have important economic implications for farmers. The conflict between Eurasian lynx (*Lynx lynx*) and free-ranging domestic sheep (*Ovis aries*) is widespread in Norway. The grazing system makes it hard to quantify exact losses due to different carnivores, however there is much variation in losses between grazing units. This study aimed to try and explore if landscape features could explain this variation, and to see if this was consistent with what we know about lynx habitat use. Knowledge about the relationship between species and their habitat is potentially important when investigating the lynx – sheep conflict as it could help identify priority areas for the introduction of mitigation measures. Habitat features such as local abundance of wild prey, topographical features, forest cover and distance from human infrastructure have been shown to influence depredation risk in earlier studies. Here, I used 9 years of data on reported losses of sheep, in 104 grazing areas with lynx as the only large carnivore predator, along a gradient of free ranging sheep and wild prey densities in southern Norway. I found that mortality in lambs increased with increasing roe deer- and lynx density within grazing areas. Mortality was positively, and strongly, related to high proportions of forest, in both lambs and ewes, while private road density was negatively associated with lamb mortality. These results were consistent with the hypothesis that lynx depredation was a major cause of lamb mortality, although other mortality factors may also follow the same gradients. The result of this study suggests that there are some areas with predictably high losses where mitigation measures could be concentrated.

Key words: Livestock – carnivore conflict, predation, husbandry, habitat features, *Ovis aries, Lynx lynx*, Norway

Sammendrag

Den økende bestanden av store rovdyr i Europa har ført til omfattende og kroniske konflikter på grunn av sin skade på beitedyr, som kan ha viktige økonomiske konsekvenser for bønder. Konflikten mellom eurasisk gaupe (*Lynx lynx*) og frittgående sau (*Ovis aries)* er utbredt i Norge. Beitesystemet gjør det vanskelig å tallfeste nøyaktig tap på grunn av ulike rovdyr, men det er mye variasjon i tap mellom beiteområder. Denne studien hadde som mål å utforske om landskapsegenskaper kan forklare denne variasjonen, og se om dette var i samsvar med det vi vet om gaupas habitatbruk. Kunnskap om forholdet mellom arter og deres leveområder er potentielt viktig når man skal undersøke konflikten mellom gaupe og sau, da det kan hjelpe å identifisere områder hvor avbøtende tiltak skal prioriteres. Habitategenskaper som lokal bestand av byttedyr, topografiske egenskaper, skog og avstand fra menneskelig infrastruktur har vist seg å påvirke predasjonsrisiko i tidligere studier. Her brukte jeg ni år med data på innrapporterte tap av sau, i 104 beiteområder i Sør-Norge, med varierende saue- og byttedyrtettheter, der gaupe er det eneste store rovdyret. Jeg fant ut at dødeligheten hos lam økte med økende rådyr- og gaupetetthet innenfor beiteområdene. Dødelighet er positivt korrelert til høye andeler av skog, hos både lam og søyer, mens tetthet av privatveier er negativt korrelert med lammedødelighet. Disse resultatene var i samsvar med hypotesen om at predasjon av gaupe var en viktig årsak til dødelighet hos lam, selv om andre dødsårsaker også kan følge de samme mønstrene. Resultatet av denne studien tyder på at det er noen områder med forutsigbart høyere tap hvor avbøtende tiltak burde iverksettes for å redusere tapet av sau.

Contents

Introduction

In recent years, the need to understand habitat-based variation in demography has become important with the increasing fragmentation of habitats and reduction of population sizes of many species (Sanderson et al. 2002). Individuals distribute themselves among habitats, and the variation in reproductive success and survival in those habitats are vital for understanding demographic processes associated with population limitation and regulation (Bowers 1994, Holmes et al. 1996). When choosing a habitat several factors must be taken into consideration like the availability of food, food quality, shelter, and predation risk (Sih 1980). The mixture of these factors may not be optimal in all habitat types, so the resulting habitat choice will be a trade-off between the costs and benefits (Lima and Dill 1990, Mysterud and Ims 1998). In some non-territorial species, the relationship between habitat attributes and fitness at the individual level has been studied (roe deer *Capreolus capreolus* Nilsen et al. 2004) and has shown how individual access to preferred habitat can influence reproductive parameters. Further research on herbivores has underlined the importance of fine-scale spatial heterogeneity and differences in home range features when investigating individual variation in fitness components (Sæther and Heim 1993, Higginbottom 2000, Nilsen et al. 2004).

Such studies of the relationship between habitat and fitness are not only important for wild species. They also have implications for domestic animals that graze freely on rangelands and for the management of their interactions with other conservation objectives. The recovery of large carnivores in Europe has led to a widespread and chronic conflict because of their depredation on livestock, which can have important economic implications for farmers (Kaczensky 1999, Treves et al. 2004, Ripple et al. 2014). Depredation occurs in areas where the distribution of livestock overlaps with that of large carnivores, and are both spatially and temporally variable. This has led to many studies investigating the effect of large carnivores on ungulate prey populations (e.g. Skogland 1991, Baker et al. 2008, Wegge et al. 2009 and references therein). In livestock losses factors such as densities of predators, wild prey and livestock, the size ratio between predator and livestock, landscape characteristics and husbandry practices can all contribute to the observed variation (Linnell et al. 1999, Inskip and

Zimmermann 2009, Zimmermann et al. 2010). Several management approaches have been implemented to mitigate livestock losses, for example through herding, fencing, using livestock guarding dogs, earlier gathering of livestock from summer pastures and translocation or killing of "problem" carnivores (Linnell et al. 1999, Stahl et al. 2001, Ogada et al. 2003, Rigg et al. 2011). However, it is important to understand these dynamics in carnivore-livestock conflicts in order to effectively focus conflict reduction measures.

In addition, compensation schemes exist for farmers living in a carnivore-used landscapes in many countries (Swenson and Andrén 2005). The conflict between carnivores and livestock is high in Norway, and there is a legal requirement that all losses due to carnivores should be compensated through an *ex post facto* compensation system (Swenson and Andrén 2005, Schwerdtner and Gruber 2007). Here, farmers make claims for the number animals they believe is lost due to carnivores, and are compensated based on documented loss (i.e. the number of carcasses found and confirmed by specialists as killed by carnivores). Since grazing pastures are often on extensive rangelands, the number of carcasses found (4-9 %, Odden et al. 2013) is small compared to overall losses, and the actual factors causing losses can consequently be hard to ascertain (Breck et al. 2011). Hence, regional managers base the compensation for carnivore depredation on a qualified guess of estimated losses. Odden et al. (2014) studied compensated losses due to lynx, and found major weaknesses in the calculated losses. There was a general discrepancy when they compared their estimated losses based on extrapolation from research estimates of lynx kill rates with the numbers compensated. The factors causing the discrepancy are undoubtedly complex, for example because some of the losses, which were attributed to lynx, actually could be due to other carnivore species, or due to non-depredation causes.

In Norway, flocks of domestic sheep are released in early summer and graze freely through the coniferous and birch (*Betula sp.*) forests and onto alpine heaths and meadows without being fenced or herded. Therefore, they can be viewed as truly free ranging and are subject to a wide range of non-human induced factors. Sheep are classified as grazers, which prefer graminoids and herb-dominated vegetation types. Alpine land, lee-side and snow-bed communities are used when foraging, and more exposed ridge-habitats while resting (Kausrud et al. 2006, Mobæk et al. 2009, Blix et

al. 2014). About 2 million sheep graze in outlying unenclosed land every summer and around 75 % are mainly using sub-alpine and alpine land (Austrheim 2008). Because of their ability to exploit plant biomass in areas unsuitable for cultivation they are important for agricultural production and rural economies in many parts of Norway (Austrheim 2008, Bye et al. 2014).

Mortality causes in sheep include disease and accidents along with large carnivore depredation (Warren et al. 2001). Eurasian lynx is the primary predator on domestic sheep along with wolverine (*Gulo gulo*), and associated with their recovery there have been an increased depredation on domestic sheep (Kaczensky 1999). Eurasian lynx have seen a dramatic expansion the last two decades and have spread throughout most of Norway, except the west coast. Knowledge about the relationships between species and their habitat is one important component when investigating the lynx – sheep conflict. Habitat features such as local abundance of wild prey, topographical features, cover by trees and area remoteness have been shown to influence the depredation risk (Linnell et al. 1999, Mech et al. 2000, Stahl et al. 2001, 2002, Odden et al. 2008).

This study will broadly examine how environmental features influence ewe and lamb mortality at the grazing area scale, which is a spatially defined area where farmers have legal grazing rights. I will investigate how variation in sheep survival varies between grazing areas, and relate this to environmental-, topographic-, and anthropogenic features, as well as roe deer and lynx density.

Sheep depredation has been hypothesized to be incidental to lynx predation on roe deer, occurring when lynx are in the area in pursuit of their wild prey. Studies of this predator-prey interaction have provided contradictory results, where some studies show that locally high densities of wild prey can increase depredation (Stahl et al. 2001, Treves et al. 2004, Moa et al. 2006, Odden et al. 2008), and others the opposite (Mech et al. 1988, Meriggi and Lovari 1996, Sacks and Neale 2002, Sidorovich et al. 2003, Sacks and Neale 2007). Odden et al. (2013) proposed two models to reconcile these opposing findings, the *attraction model* and the *energetic model*. The *attraction model* proposes that areas with high densities of wild prey will attract carnivores, and induce elevated predation risk for livestock. The opposite, the *energetic model* predicts that in areas with high densities of wild prey, carnivores will reduce their depredation on livestock because the wild prey satisfy their energetic needs. Both models have

support, but differences could also be a matter of scale. The *attraction model* has support on a small scale (Odden et al. 2008), and the *energetic model* on larger scales (Odden et al. 2013). How roe deer density affects depredation of livestock within grazing areas of sheep, have not been investigated. Grazing areas vary in size, but are generally fine scaled from a lynx's point of view. This would imply that the *attraction model* is most likely to explain the relationship between wild prey density and lynx depredation on lambs. My central hypothesis is that lamb losses will be greatest within grazing areas that are most likely to be visited by lynx in pursuit of their wild prey, the roe deer. Accordingly, I predict that (P1) lamb losses will be higher in grazing areas with high roe deer density. A failure to support this prediction, or the finding of an opposing relationship, would then be support of an alternative hypothesis that regards sheep as a deliberately targeted prey for lynx due to a local absence of the preferred wild prey, the roe deer. Lynx have been shown to avoid areas with highest degrees of human modification of the landscape (Basille et al. 2009, 2013). Therefore, I predict that (P2) lamb losses will be lower in the grazing areas with higher degree of human presence, (people, houses, infrastructure, fields). There may be benefits for sheep living in areas where lynx find it harder to hunt, or habitats such as open alpine-tundra that lynx avoid (May et al. 2008). Thus, I predict that (P3) lamb losses will be lower in grazing areas with large proportions above the tree line.

To investigate this I used 9 years of data on reported losses of sheep, in grazing areas with lynx as the only large carnivore predator, along a gradient of different livestock and wild prey densities in southern Norway.

Method

Study area

The study was conducted in a 55 000 km^2 area in southern Norway, between 58°N and 62°N. It encompasses an environmental gradient (north-west– south-east) in Oppland, Buskerud, Telemark and Aust-Agder counties (Figure 1). The area is dominated by coniferous forest, mainly Norwegian spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) below the tree line, and alpine tundra-habitats above the tree line. The valley bottom and lowlands tend to have more deciduous forest fragmented by agriculture lands. Here, the roe deer occur at higher densities (Torres et al. 2011, Bouyer et al. 2015). Agriculture mainly consists of grass- and grain production for animal food purposes.
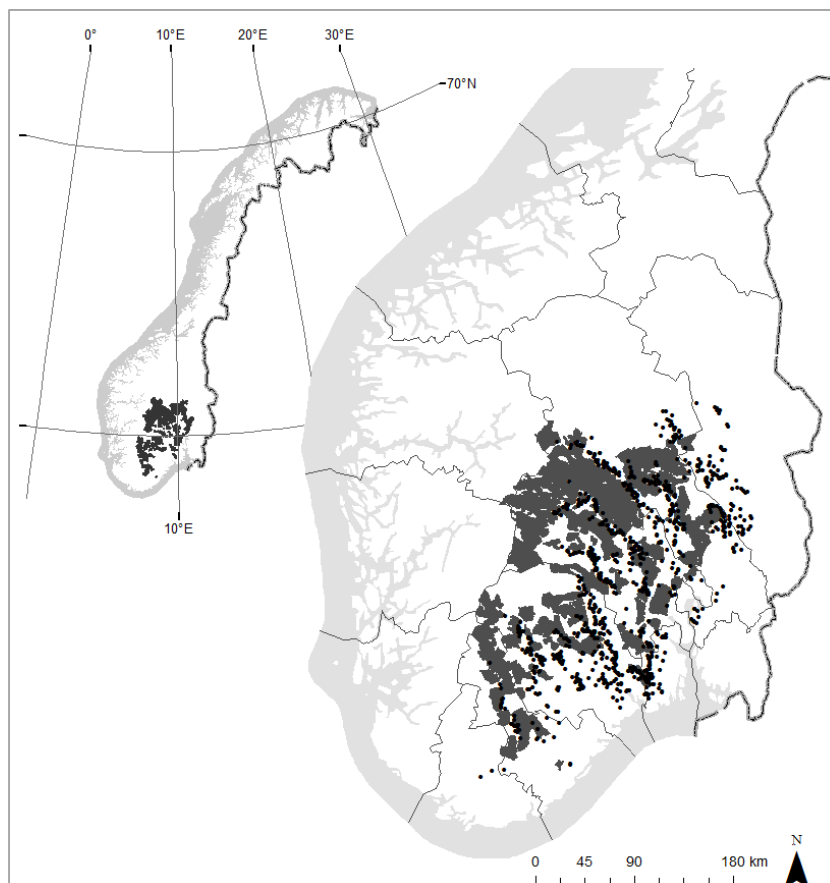
Figure 1. The study area in Oppland, Buskerud, Telemark and Aust-Agder counties, Southern Norway. The grey area represent all the grazing areas studied and black dots represent observation points of lynx family groups within a 30 km buffer, between 2004-2012.

All parts of the study area have free ranging sheep grazing in forest and alpine habitats from early summer (June) to early autumn (September). They move freely with limited supervision or guarding, and have few constraints on their movement. The density and distribution of sheep varies considerably within the study area, where the north and western parts have the broadest distribution of grazing areas and highest densities of sheep. The south and eastern parts can have locally high densities, but grazing areas are more patchily distributed (Gervasi et al. 2014).

Data collection

Sheep

I obtained data on numbers of sheep released and lost in the respective grazing areas from the Norwegian Forest and Landscape Institute based on data from the organized grazing database ("Organisert Beitebruk", OBB). About 80% of the free ranging sheep in Norway belong to farmers that participate in the OBB system. The database holds information about when sheep are released and taken down from summer pastures, claimed loss and spatial data regarding grazing area boundaries (Norwegian Forest and Landscape Institute 2013). Grazing area size ranged from 19.9 – 18 060.0 km^2 (mean= 515.3 km^2).

Roe deer

An index of the spatial variation in roe deer density within the grazing areas was acquired from a predictive density map with a 1 km resolution (Bouyer et al. 2015) extrapolated from pellet count surveys, performed along 346 transects. The density map was deduced from hurdle models (Zuur et al. 2009) applied on variables such as road- and human density, altitude, average snow depth and habitat composition. Using cross-validation and two independent datasets of roe deer density, the models were validated. Using the density map, I could provide an index of roe deer density inside each grazing area. For more information see Bouyer et al. (2015).

Lynx distribution data

In Norway, the national monitoring program for large predators monitors the distribution, size and trend of lynx populations. Two different census methods are used to produce an index of abundance (Brøseth and Tovmo 2014). The first method is based on observations of reproductive units, here termed family groups, and refers to

a mother accompanied by dependent kittens during the winter. As kittens follows their mother until they are 10 months old, tracks in the snow from two or more lynx travelling together during December - February is indicative of a family group (Andrén et al. 2002). The second method uses track counts in snow during one-day censuses, collected along a network of fixed transects before the lynx hunt. Here local people search intensively for lynx tracks 1-2 days after snowfall, and all observations are confirmed by rangers from the Norwegian Nature Inspectorate (SNO). Observations are separated from each other by a set of telemetry-derived distance rules based on home range size and movement rates collected from lynx in Scandinavia.

To estimate lynx density at the grazing area scale I first established 30 km buffers around the observation points of specific family group. The buffer was determined by investigating the distances between confirmed kills by a family group, and was taken as the distance where approximately 75 % of the confirmed kills were found (Mabille et al. 2015). I then added "1 family group" to each grazing area covered by the buffer. This produced a lynx density index for each year (2004-2012) in all grazing areas

Environmental and topographic variables

Habitat type

I used habitat topology based on the AR50 land resource map, which is the Norwegian land resource database for mapping at a scale of 1:50 000. The map describes resources based on land type, site index, tree species and ground conditions based on generalization from AR5 (high resolution database), the national topographic map (N50) and the land cover database for mountain areas (AR-FJELL) (Aune-Lundberg and Strand 2010). I used five habitat classes: urban areas, agricultural areas, forest, bare (treeless) ground and marsh. The proportion of each habitat class was calculated for each grazing area.

Roads

Road density data were obtained from the Norwegian Mapping Authority (www.kartverket.no/). Road density was calculated as total length of roads (km) within each grazing area for public and private roads separately.

Landscape ruggedness

Topographic information was derived from a 25 m digital elevation model. Terrain ruggedness was calculated as the vector ruggedness measure (VRM) proposed by Sappington et al. (2007). This measure is based on a geomorphological method for measuring vector dispersion, and is less correlated with slope than other indices as it takes the aspect into account. I created a layer of VRM values using an ArcView script (available online from the Environmental Systems Research Institute ArcScripts website: www.esri.com/arcscrips). The method works by decomposing each unit vector normal to their grid cell into x, y and z components and running a moving window (5 x 5 pixels in this study) over the digital elevation model. The resultant vector gives a measure of ruggedness with values between 0 (flat) and 1 (highly rugged) (Sappington et al. 2007).

All geographical calculations were processed in ArcGIS v.10.2 (ESRI 2013).

Statistical analyses

The probability of a lamb or ewe dying during a grazing season was modeled as a response variable using environmental-, topographic- and anthropogenic features, lynx density index and roe deer density index as explanatory factors. I used linear mixed models with a logit-link error distribution to analyze the data. Year and grazing area were included as random factors to control for variation between years, because of environmental variations, and repeated measurements per individual grazing area.

Lambs and ewes were analyzed separately, using the same variables and model specification regarding fixed and random factors. To examine the relative importance of environmental vs. lynx related explanatory variables I used a two-step model. First models were fitted with environmental- , topographic and anthropogenic variables into a *'habitat' model*. In the next step, the indices of lynx density and roe deer density were included to the best *'habitat' model* into a *'habitat + lynx' model,* to see if this explained more of the variance in sheep loss. The r-squared (R^2) values were obtained using the method by Nakagawa and Schielzeth (2013). R^2 can be categorized in two types; marginal and conditional (Vonesh et al. 1996). Marginal R^2 is the variance explained by fixed facors, and conditional R^2 is the variance explained by both fixed and random

factors. When a model included an interaction, the main effect of the variables in the interaction were always retained in the model.

I used Akaike Information Criterion (AIC) corrected for small sample sizes (AICc; Burnham and Anderson 2002) in the model selection. If there is a difference in AICc (ΔAICc) of < 2 (or less than two) between alternative models they can be assumed to be equally credible. In the model selection process the models were fitted using maximum likelihood (ML), and when extracting the parameter estimates models were fitted with restricted maximum likelihood (REML) (Zuur et al. 2009).

All statistical analyses were done in R for Windows version 3.1.1 (R Development Core Team 2014) where the mixed models were run through the package lme4 (Bates et al. 2014). All means are given ± SE (standard error), and plots are based on final models from model selection, with alpha-level set to $p < 0.05$.

Results

In the 104 grazing areas under study between 2004 and 2012, 64 569 lambs and 16 794 ewes were lost, which gives a mean of 6.56% (min. = 0, max. = 36.06%) and 2.68% (min. = 0, max. = 14.38%) loss for lambs and ewes, respectively. For a graphical illustration of the distribution of sheep loss, see Figure B1, Appendix B.
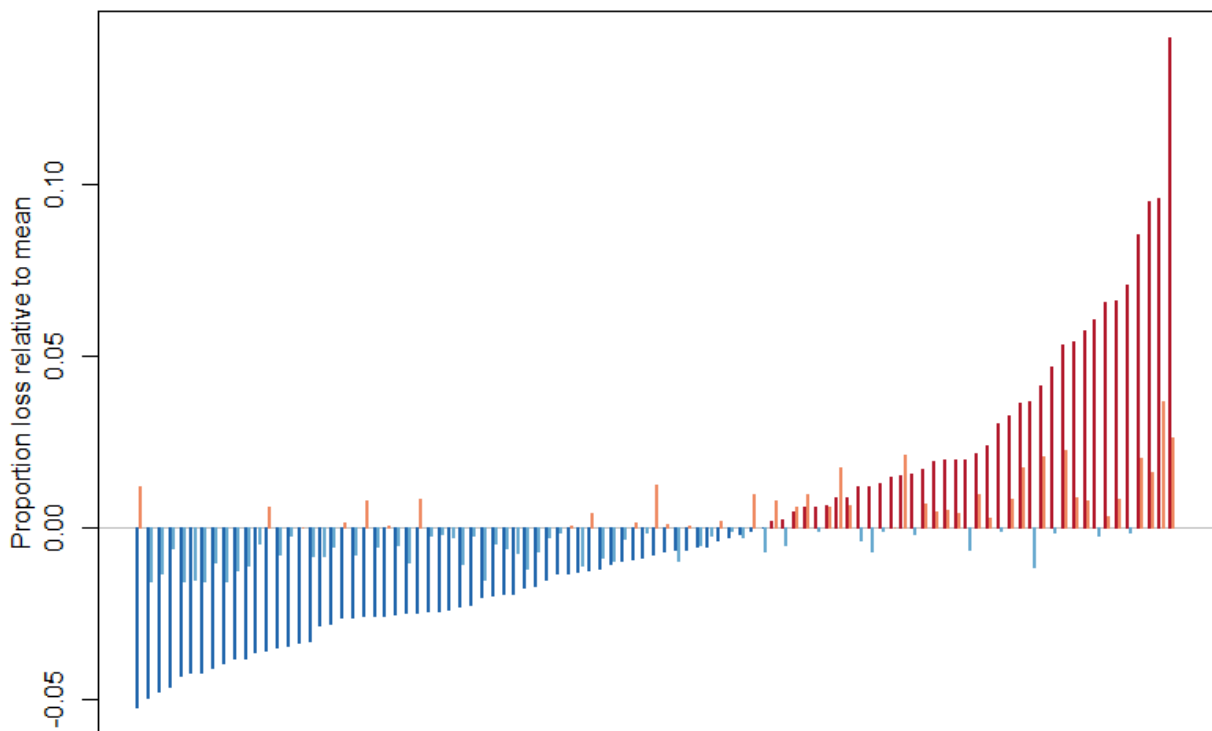

Figure 2. Distribution of the proportion of lamb lost (dark bars) relative to the mean (mean proportion of lamb lost = 0.067) and ewes lost (light bars) relative to the mean sheep lost (mean proportion of ewes lost = 0.027). Each pair of dark and light represents the mean lamb and ewe loss, respectively, over all years for a grazing area. Blue and red colors indicate that the loss is below and above, respectively, the mean of all grazing areas.

The distribution of losses (Figure 2) is uneven among grazing areas. Most of the grazing areas have losses lower than the mean, distributed within 0.05 points. Fewer grazing areas have losses higher than the mean, and distribute within 0.15 points, but here some areas have very high losses compared to the mean. These grazing areas contribute to increase the overall mean loss, especially for lambs. For most grazing

areas the loss of both lambs and ewes are consistent high or low. However, in a few areas, there is a diverging loss pattern, where the grazing area has a high loss of lambs and a low loss of ewes compared to the mean loss, or the opposite relationship.

There is no relationship between annual variation and the loss for the grazing areas. When looking into the coefficient of variation for the grazing areas with very high loss, they do not have more variation than grazing areas with lower loss (Figure 3). This implies that grazing areas with high losses have overall high losses annually, and grazing areas with low losses have overall low losses annually.
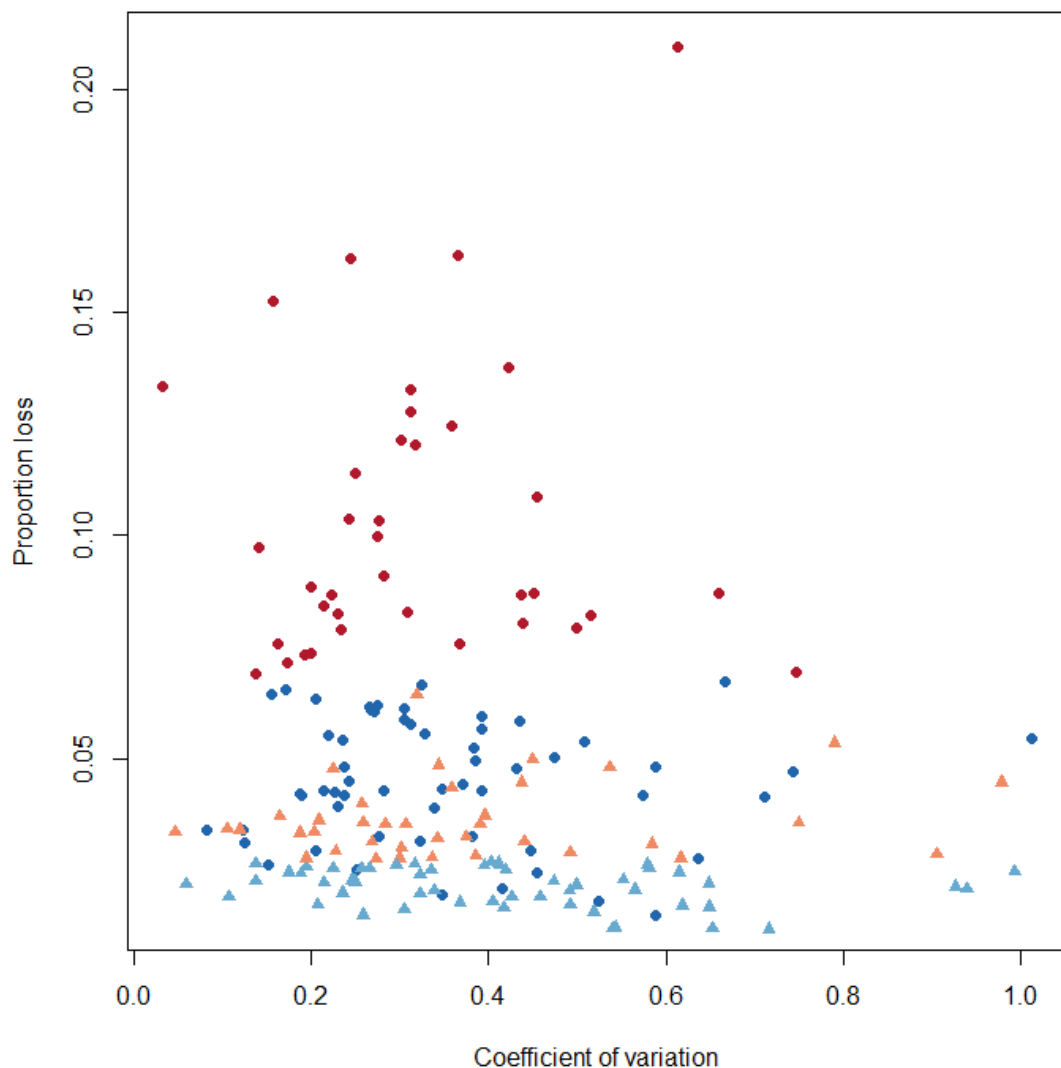
Figure 3. The coefficient of variation of proportion loss for a grazing area in relation to the proportion lost. Circles and triangles represent lambs and ewes, respectively, and blue and red colors are areas with average loss below and above, respectively, the mean of all grazing areas.

The lamb mortality in the *'habitat' model* was best described as a function of proportion of forest and private road density (AICc=1333.30, Appendix A; Table A1). Two alternative models had a ΔAICc < 2, but were rejected since the parameter estimates showed a high degree of uncertainty (-1.96 > t < 1.96). The highest ranked *'habitat + lynx' model* for lambs included proportion of forest, private road density, roe deer density and lynx density index (AICc=1325.64, Appendix; Table A1). No alternative models received considerable support (all ΔAICc > 2). Parameter estimates is given in Table 1.

The ewe mortality in the *'habitat' model* was best described as a function of proportion of forest, terrain ruggedness and an interaction between them (AICc=2407.45, Appendix A; Table A2). However, the effect of the interaction was not significant (β= -190.56±107.71, p=0.06). Eight alternative models had a ΔAICc < 2, but were rejected since the parameter estimates showed a high degree of uncertainty (-1.96 > t < 1.96). When including lynx-variables they showed no significant effect and the highest ranked *'habitat' model* was also the best *'habitat + lynx' model* regarding ewe loss. Ten alternative models had a ΔAICc < 2, but were rejected since the parameter estimates showed a high degree of uncertainty (-1.96 > t < 1.96). Parameter estimates is given in Table 2.

Lamb losses increased with increasing lynx and roe deer density indices (Figure 4a, d). Private road density and lamb mortality was negatively correlated (Figure 4b). Sheep mortality and proportion of forest was positively correlated in all lamb and ewe models (Figure 4c and Figure 5a). However, proportion of forest had a strong positive effect in lamb models, and a weak positive effect in ewe models. Additionally, ewe models had a weak positive effect of terrain ruggedness (VRM) at low proportion of forest, and a weak negative effect at high proportion of forest. There is more or less no effect of terrain ruggedness at mean proportion of forest, and the overall effect has a relative high degree of uncertainty. Lamb models showed no effect of landscape ruggedness.

The '*habitat' model* and *'habitat + lynx' model* for lambs explained 49.01 % and 49.32 % of the variation in mortality, respectively. So when including lynx and roe deer indices in the model, this had just a small increase in explanatory power. For ewes, where the *'habitat' model* and the *'habitat + lynx' model* came out as same model, it explained

22.77 % of the variation in ewe mortality. This suggests that models describing lamb mortality captured the variation better than ewe models.

Table 1. Parameter estimates, standard error, test statistics (t- and P-values) and R^2 values from the linear mixed effects models for lambs. Only the best models for 'habitat' and 'habitat+lynx' are represented. forest = proportion of forest; private = private road density; roe deer = roe deer density index; lynx = lynx density index.

Model	Parameter	Estimate	SE	t-value	P-value	R^2 Marginal	Conditional
'habitat'	(Intercept)	-3.503	0.121	-28.87	<.0001		
	forest	1.843	0.245	7.54	.0001	0.20	0.49
	private	-0.001	0.0003	-3.95	.0004		
'habitat+lynx'	(Intercept)	-3.552	0.119	-29.93	<.0001		
	forest	1.473	0.273	5.40	.0003		
	private	-0.001	0.0003	-4.38	0.001	0.235	0.493
	roe deer	0.541	0.223	2.43	0.02		
	lynx	0.048	0.020	2.43	0.02		

Table 2. Parameter estimates, standard error, test statistics (*t*- and *P*-values) and R^2 values from the linear mixed effects models for ewes. The best 'habitat' model was also the best 'habitat + lynx' model. forest = proportion of forest; VRM = landscape ruggedness.

Model	Parameter	Estimate	SE	t-value	p-value	R^2 Marginal	R^2 Conditional
'habitat'	(Intercept)	-5.129	0.371	-13.82	<.0001		
	forest	1.878	0.572	3.28	.0007	0.042	0.228
	VRM	139.61	68.56	2.04	0.04		
	forest*VRM	-190.56	107.71	-1.769	0.06		
'habitat + lynx'	-	-	-	-	-	-	-
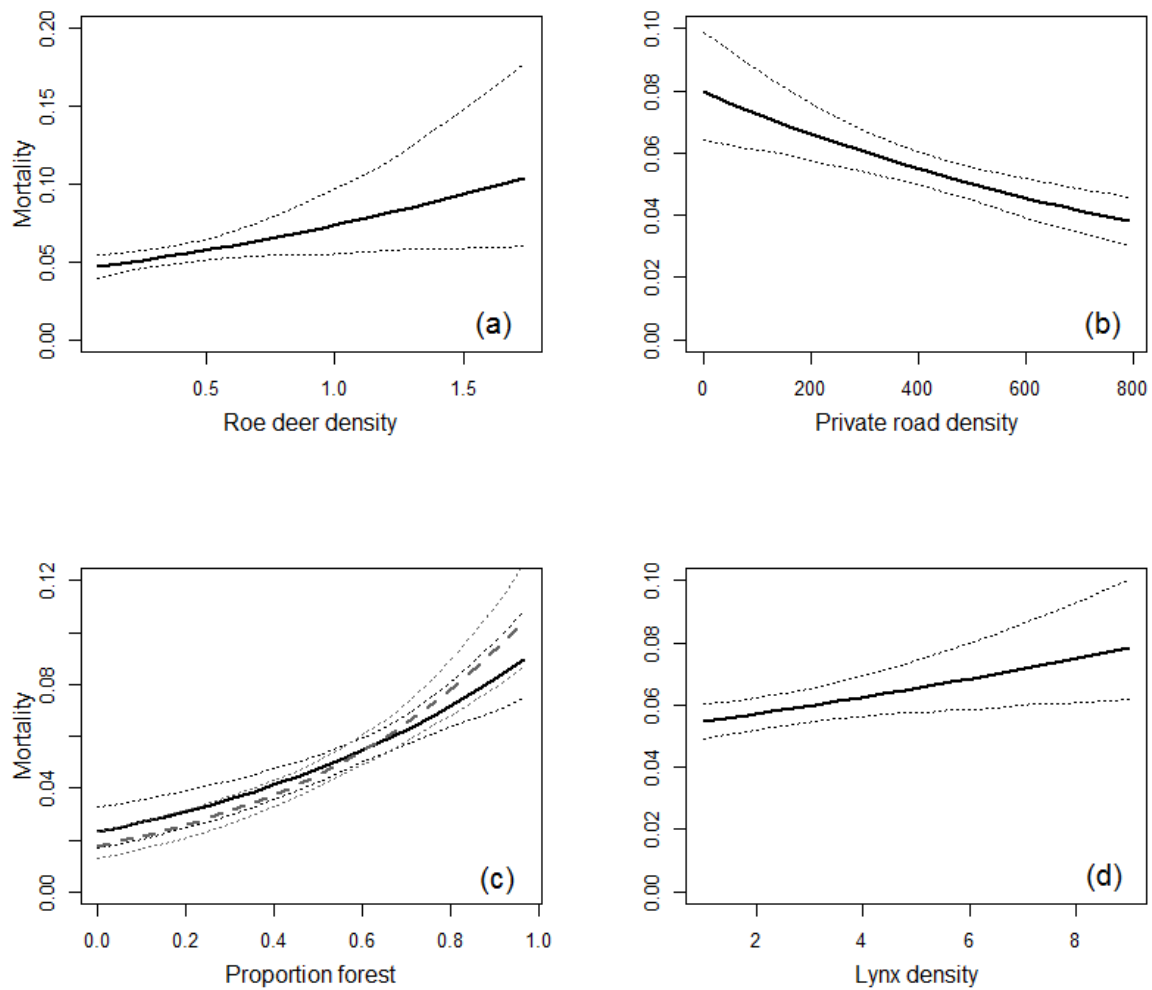
Figure 4. Estimated response of mortality in lambs to proportion of forest (a), private road density (b), roe deer density index (c), and lynx density index (d). Dashed and solid lines represent 'habitat' and 'habitat + lynx' models, respectively. Dotted lines indicate 95% confidence intervals based on a model-based parametric bootstrap for mixed models with 1000 simulations. For each estimated response illustrated in the graphs, all other variables included in the model were kept constant at their mean value.
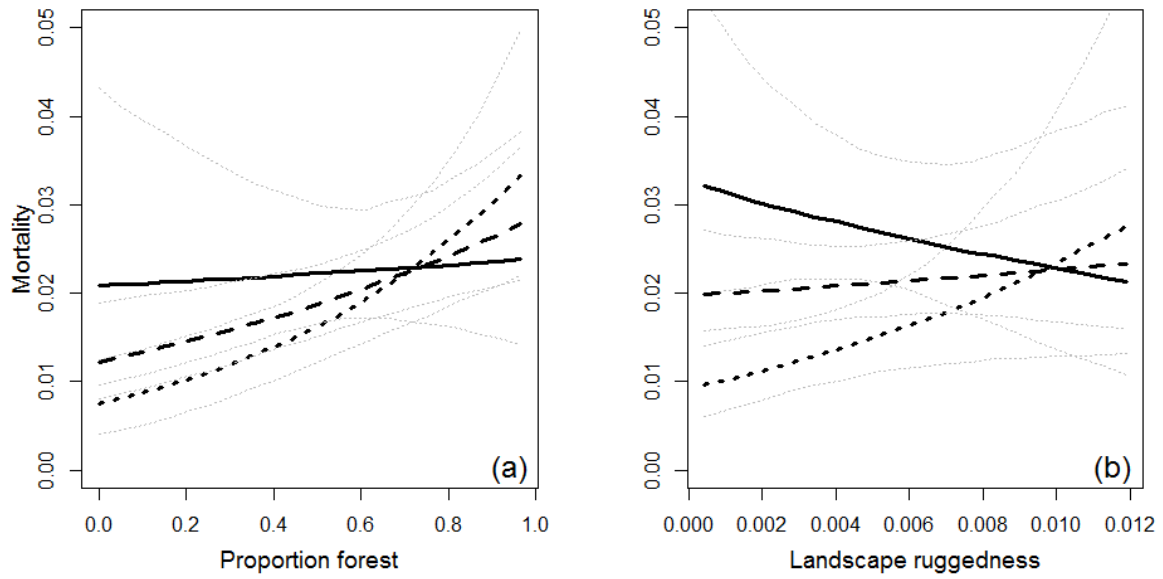
Figure 5. Estimated response of mortality in ewes to proportion of forest (a) and landscape ruggedness (VRM). Dashed, solid and dotted lines represent the effect of forest at mean, high and low landscape ruggedness values in (a), and the effect of landscape ruggedness at mean, high (0.9) and low (0.1) values of proportion of forest in (b). Grey dotted lines indicate 95% confidence intervals based on a model-based parametric bootstrap for mixed models with 1000 simulations.

Discussion

Depredation by large carnivores is an important cause of livestock losses, but several other factors may contribute to increased loss. By using an extensive dataset on sheep losses, environmental-, topographic- and anthropogenic features, this study demonstrates how such features can explain significant amounts of the variation in sheep mortality. I found that variation in grazing area features, road density, roe deer density and lynx density can help to understand the variation in mortality in free ranging sheep exposed to Eurasian lynx depredation.

Lamb mortality and roe deer density were positively related (Figure 4a). This is in agreement with the prediction that lamb losses will be higher within grazing areas that are most likely to be visited by lynx in pursuit of roe deer. The study confirms that the *attraction model* (Odden et al. 2013) explains the relationship between wild prey density and lynx depredation on lambs on the grazing area scale. The attraction model predicts elevated predation risk for livestock in areas where lynx find high densities of their wild prey. My findings support the *attraction model* when using the grazing area scale, and can be comparable with other fine scale studies (Odden et al. 2008). At these small scales one can expect depredation to be associated with patches with high wild prey densities, because carnivores may spend more time in these prey rich patches, leading to more incidental encounters with livestock and more depredation (Stahl et al. 2002, Treves et al. 2004, Moa et al. 2006, Odden et al. 2008). However, this result does not contradict the *energetic model,* since this relationship is a matter of scale. On larger scales, the *energetic model* has also received support (Pearson and Caroline 1981, Meriggi and Lovari 1996, Patterson et al. 2004, Bagchi and Mishra 2006). Studies of lynx in the French Jura mountains by Stahl et al. (2002) found that depredation hot-spots were likely to occur in areas with high roe deer density, similar to the findings in this study. It is likely that the coinciding habitat use between roe deer and lynx is because of their strong predator-prey relationship (Moa et al. 2006). One noticeable source of error is that the roe deer density index was largely calculated from pellet dropped during winter, and lamb loss occurs in summer. Roe deer in southern Norway move to higher elevations during summer (Mysterud 1999, Mysterud et al. 2012), but this should not affect the results of this study significantly.

Lynx generally avoid the most human-disturbed areas (Basille et al. 2009), but sometimes utilize areas with relatively high human accessibility where roe deer occur (Odden et al. 2006). Studies of lynx habitat selection in Norway have shown that lynx can live in relative close proximity to human modified-areas, and often select for areas with medium levels of disturbance (Basille et al. 2009, 2013, Bouyer et al. 2015). Basille et al. (2009) found that lynx avoided areas with highest human and road densities. Moreover, such areas are associated with lower sheep killing rates by lynx in another Norwegian study site (Herfindal 2000). Roads are also used by hunters to locate lynx tracks, and this legal hunt accounts for 43 % of lynx deaths in Scandinavia (Andrén et al. 2006). This avoidance of roads by lynx may explain why lamb losses are lower in areas with high private road density (Figure 4b). Furthermore, higher road density can lead to supervision that is more frequent by owners that may serve to reduce losses to other causes.

The results indicate that grazing areas with a high proportion of forest can have higher sheep mortality rates than grazing areas with low proportions (Figure 4c and Figure 5a). This is in agreement with the prediction that lamb losses will be lower in areas above the tree line, since proportion of forest is highly correlated with bare ground (-0.95). Lynx in southern Norway rarely move above the tree line (May et al. 2008, Bevanger et al. 2013), and Basille et al. (2009) found that lynx habitat was characterized by very low proportions of bare treeless ground and alpine tundra. This avoidance of high elevation areas can be because of the absence of their main prey, roe deer, at higher elevations, which makes it beneficial for sheep grazing in open tundra habitat with respect to avoiding predation. The lynx are stalking predators, and their preferred habitat is forested areas where they can sneak up on their prey (Dunker 1988, Hetherington and Gorman 2007). Rationally, sheep should avoid dense forest, but their generally low anti-predator behavior makes them an easy prey (Squires 1975, Kaczensky 1999). The domestication process of sheep has developed animals that are calmer (easier to handle) and more productive (regarding slaughter weight, lamb numbers and wool weight), and the selection pressure on maintaining an anti-predator behavior has diminished (Hansen et al. 1998) although there are differences in anti-predator behavior between sheep breeds.

Solitary and smaller sized predators are more constrained in their choice of prey than larger predators, leading to prey selection which is a function of predator-prey body

weights (Sinclair et al. 2003). Considering age selection of prey, lambs should be more susceptible to predation than ewes, since a wider range of predator species are able to kill them. Studies on neonatal mortality in ungulates have shown that predation is the main cause of high mortality, when predators are present (Linnell et al. 1995, Kjelvik et al. 2000). Lynx are efficient predators on medium-sized ungulates. Studies have suggested that, as a relatively small predator, lynx should select juveniles over adults when depredating livestock (Stahl et al. 2001, Warren et al. 2001, Mattisson et al. 2011). However, other studies have found that lynx do not have any clear preferences in age composition with their main prey, roe deer (Gervasi et al. 2012, Mejlgaard et al. 2013), but lynx are known to focus their depredation on lambs rather than ewes (Aanes et al. 1996). Lamb losses and the lynx density index were positively correlated (Figure 4d), while the ewe-models showed no significant effect of lynx density.

Recent studies have shown that lynx prefer habitats with a high degree of landscape ruggedness (White et al. in press, Bouyer et al. under revision). There is a growing body of literature that indicates the importance of this feature in predicting carnivore habitat use in human dominated landscapes (Petram et al. 2004, Nellemann et al. 2007). This preference for rugged areas can be related with shelter and avoidance of humans. Steep areas are associated with low human activity, and lynx are known to select steep areas in heavily disturbed landscapes (Basille et al. 2008). Mortality in ewes increased with higher landscape ruggedness at a low proportion of forest, and the opposite relationship with a high proportion of forest. At mean values of proportion of forest, landscape ruggedness showed more or less no relationship. Since mortality in ewes was positively related to landscape ruggedness at low proportions of forest, which accordingly is bare treeless ground, one can expect that it is not due to lynx depredation, but other mortality factors such as accidents.

Lambs are more disposed to diseases than ewes, especially early in the grazing season, and 20 % of the total loss can be attributed to disease in some areas (Warren et al. 2001). As the season progresses lambs become more robust, and disease is a less important mortality factor. This pattern is also found for other ungulates (see review in Linnell et al. 1995). Tick-borne fever is one of the main challenges in Norwegian sheep farming, and is caused by a pathogen (the bacterium *Anaplasma phagocytophilum*) of sheep (Stuen et al. 2002). Increasing temperatures and more

precipitation following climate change is likely to have favored tick (*Ixodes ricinus*) abundance. In addition, the expansion of cervid species during the last two decades has led to an increase in host abundance (Mysterud et al. 2002, Jaenson and Lindgren 2011, Medlock et al. 2013). Another disease in sheep is alveld (literally 'e*lf-fire'*) which is a hepatogen photosensitizing disorder (Flåøyen and Frøslie 1997, Mysterud et al. 2007). Along with accidents, losses from diseases are described as normal losses that are assumed to be constant from year to year and between grazing areas. These normal losses are based on OBB-data from 1970-1980, a period with low or non-existent depredation from large carnivores, and can have uncertain significance for today's husbandry. A structural change in husbandry, climate change, and a rebounding red fox (*Vulpes vulpes*) population (they were largely absent in the 1970's and 1980's due to an outbreak of sarcoptic mange (Lindström et al. 1994)) are factors that could also affect these normal losses.

The fact that ewe mortality (believed to be relatively uninfluenced by lynx) was also effected by proportion of forest implies that non-depredation mortality levels for all sheep are higher in forest areas as compared to the higher elevation, alpine-tundra habitats. Based on our current understanding of distributions it is likely that both tick and red fox densities are higher in low elevation areas, and the quality of grazing in forest habitats is also likely to be lower.

Because of their relative small size, early season depredation of lambs by red foxes and golden eagles (*Aquila chrysaetos*) is common (Warren and Mysterud 1995, Warren et al. 2001). Because my analysis was based on rather rough data (i.e., overall lamb- and ewe losses) such mortality factors can act as a random error in the loss numbers, and contribute to the uncertainty of the analyses. A mixture of factors that point in the same direction makes it hard to disentangle what is due to lynx depredation and other factors that contribute to mortality. Unraveling the mechanisms behind such relationships can be challenging, and needs more in depth studies.

The risk of a sheep farm experiencing a second attack by large carnivores is higher during the year after a depredation event (Karlsson and Johansson 2010). This pattern of repeated depredation has been described for several large carnivores (Linnell et al. 1999, Treves et al. 2004). Such 'hot-spots' for predation can be seen in some of the grazing areas in the study area. These grazing areas have constantly high losses beyond what can be explained by the landscape features. Descriptive investigation of

these grazing areas showed a high proportion of forest (>0.9), little bare treeless ground (<0.01) and a lynx density index above average. Additionally, in some of the grazing areas with high sheep mortality over several years there have been studies conducted at the individual grazing area scale. Using before-after or control-treatment designs, they have shown that lynx depredation was the main reason for lamb losses throughout the grazing season (Hansen 2007, 2009, 2012). Similar studies have shown that birth weight, weight at release to summer pasture, and growth rate from birth to release had a significant effect on lamb mortality (Lynnebakken 1995, Warren and Mysterud 1995, Melting et al. 1998, Warren et al. 1998, Warren et al. 1999, Mysterud et al. 2000, Hansen and Bjøru 2001). The probability of a lamb dying on pasture is higher for a lamb of a young mother (gimmer), than for a lamb of older ewe (Linnell et al. 1995, Warren and Mysterud 1995, Hansen 2007, 2009, 2012). This can be explained by older ewes being more experienced, vigilant and having knowledge of particular predator-prone areas (Hansen 2012). The importance of these factors varies from study to study, and the relationship between them are complex, so there is a need for more research.

In predator – prey theory, habitat heterogeneity can affect the relationship between kill rates and prey density (reviewed in Gorini et al. 2012). Spatial heterogeneity may affect predator – prey dynamics through mechanisms such as altered prey vulnerability or predator hunting success (Luckinbill 1974, Denno et al. 2005, Bergström et al. 2006). For instance, variation in structural features like vegetation and topography in different habitat types can affect the predators search efficiency (Caro 2005). The effect of spatial heterogeneity on predation can either be negative or positive, considering the specific predator strategy. A highly fragmented landscape may increase the searching efficiency of a generalist predator (Storaas et al. 1999), while lack of snow cover may prevent efficiency in a specialist (Oksanen et al. 2001). The effect of spatial heterogeneity on kill rates is sensitive to the scale of observation (Ryall and Fahrig 2006), and the specific predation stage. Stalk-ambush predators, such as many felids, rely on good cover during their hunt for prey (Balme et al. 2007, May et al. 2008, Schaller 2009). Even for fast ambush predators, such as the cheetah (*Acynonix jubatu*) the distance from the prey when the chase starts is central (Purchase and Du Toit 2000). Accordingly, structural complexity of the landscape is associated with the

hunting success for ambush predators, and habitat features can have a high influence on the result of the hunt (Mills et al. 2004).

In conclusion, by investigating how habitat features along with other determinants influence mortality in sheep, I have been able to identify the importance of landscape- and anthropogenic features, along with wild prey densities in explaining the dynamics of lynx – sheep interactions. The fact that the between grazing-area differences in loss were stable over time, and could be explained by the occurrence of environmental covariates, reveals how demographic rates can vary between populations on relatively fine spatial scales. This finding serves as both an illustration of how much spatial variation can exist in demographic rates for a free-ranging herbivore (Gorini et al. 2012), and opens the way for concrete management actions.

Management implications

A prerequisite for reduced losses is that management initiatives are made to reduce the frequency of lynx and sheep encounters. The results of this study suggest management practices where spatial separation between livestock and predator is preferred. Concentrating livestock into patches of less preferred habitat, such as pastures and areas above the tree line could reduce the amount of depredation by lynx. An alternative could be to introduce carnivore-proof electric fencing on smaller, more concentrated pastures. With active protection through fenced pastures one can easily introduce additional protective features, such as electric fence or guarding dogs. However, there is clearly a need to study all mortality causes, especially in forested pastures, to better understand the full range of factors responsible for sheep losses as well as the relative impact of lynx.

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Appendix A

Table A1. The five best models according to AICc and ΔAICc for 'habitat' and 'habitat + lynx' models for lamb. 'X' indicates if a variable was in included in the model. Proportion of forest (forest) was included in all models. Model selection of 'habitat + lynx' takes the best 'habitat' model and includes the mean roe deer density index (roe deer) and lynx density index (lynx) in the full model. private = private road density; public = public road density; VRM = landscape ruggedness.

Model rank	forest	private	public	VRM	roe deer	lynx	forest* VRM	AICc	ΔAICc
'habitat'									
1	X	X						1333.30	0.00
2	X	X	X					1334.27	0.98
3	X	X		X				1334.98	1.68
4	X	X	X	X				1335.98	2.68
5	X	X		X			X	1336.53	3.23
'habitat + lynx'									
1	X	X			X	X		1325.64	0.00
2	X	X			X			1329.40	3.76
3	X	X				X		1329.56	3.91
4	X	X						1333.30	7.66
5	X				X	X		1341.73	16.09

Table A2. The five best models according to AICc and ΔAICc for 'habitat' and 'habitat + lynx' models for ewe. 'X' indicates if a variable was in included in the model. Proportion of forest (forest) was included in all models. Model selection of 'habitat + lynx' takes the best 'habitat' model and includes the mean roe deer density index (roe deer) and lynx density index (lynx) in the full model. private = private road density; public = public road density; VRM = landscape ruggedness.

Model rank	forest	private	public	VRM	roe deer	lynx	forest* VRM	AICc	ΔAICc
Habitat									
1	X			X			X	2407.45	0.00
2	X							2407.65	0.20
3	X		X					2407.65	0.20
4	X		X	X			X	2407.93	0.48
5	X			X				2408.60	1.15
Habitat + Lynx									
1	X			X			X	2407.45	0.00
2	X							2407.65	0.20
3	X		X					2407.65	0.20
4	X		X	X			X	2407.93	0.48
5	X			X				2408.60	1.15

Appendix B
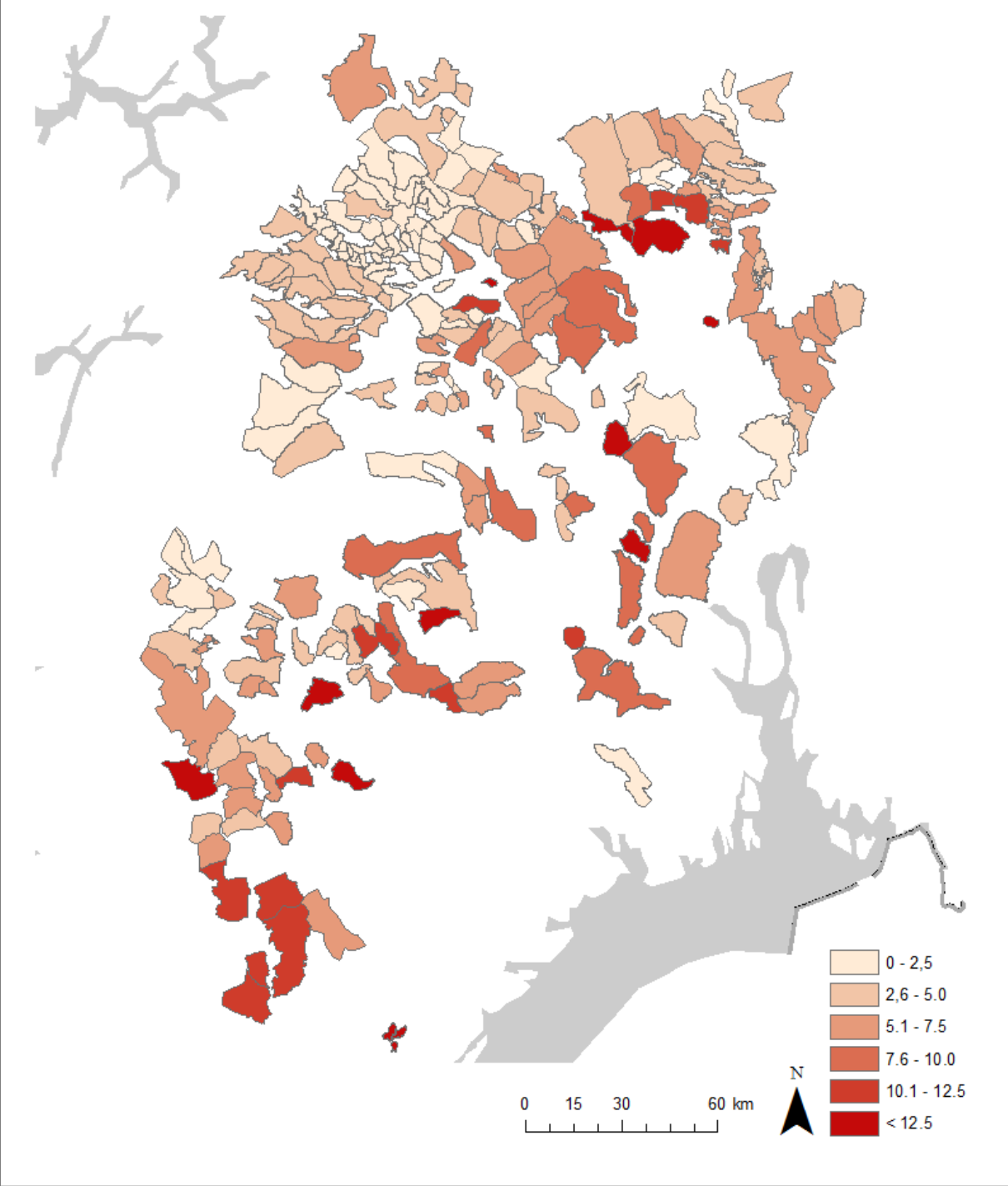
Figure B1. Choropleth-map showing the distribution and extent of mortality in sheep in all grazing areas under study. Legend is based on proportion of loss, and a stronger red color illustrates more loss.