A lynx in a sheep's pasture

– Environmental factors and hunting affecting lynx depredation on domestic sheep in Sweden

Marc Velling

MSc thesis • 60 credits
Swedish University of Agricultural Sciences, SLU
Faculty of Natural Resources and Agricultural Sciences • Department of Ecology
Independent Project • Master thesis in Biology
Grimsö Wildlife Research Station 2021

A lynx in a sheep's pasture – Environmental factors and hunting affecting lynx depredation on domestic sheep in Sweden

Marc Velling

Supervisor:	**Henrik Andrén, SLU, Department of Ecology**
Assistant supervisor:	Jens Persson, SLU, Department of Ecology
Examiner:	Johan Månsson, SLU, Department of Ecology

Credits:	60 HEC
Level:	A2E
Course title:	Master Thesis in Biology
Course code:	EX0900
Course coordinating dept:	Department of Aquatic Sciences and Assessment
Place of publication:	**Grimsö**
Year of publication:	**2021**
Cover picture:	Rick Heeres

Keywords: *Lynx lynx*, Scandinavia, conservation, human-wildlife conflict, depredation, spatial analysis, survival analysis, protective hunting, carnivore, lethal control

Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Grimsö Wildlife Research Station

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file.

If you are more than one author you all need to agree on a decision. Read about SLU's publishing agreement here: https://www.slu.se/en/subweb/library/publish-and-analyse/register-and-publish/agreement-for-publishing/.

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.

Preface

MSc Thesis Report regarding the Master Thesis for Marc Velling with the supervisors: Henrik Andrén (Department of Ecology, SLU) and Jens Persson (Department of Ecology, SLU)

During this Thesis I was interested in the dynamics of lynx depredation on domestic sheep and the effectiveness of lethal control to prevent repeated depredation effects.

Marc Velling

MSc thesis SLU

E-mail: marc.velling@gmail.com

Tel: +46 76 1060840

Grimsö, January 2021

Content

Abstract

Large predators have made a return in Europe in the past decades. In Scandinavia, the Eurasian Lynx (*Lynx lynx*) has expanded its distribution further south and recolonized past areas. Due to the recolonization, lynx management has become part of the public discourse in Sweden. One factor of this discourse is depredation on domestic sheep. My thesis focuses on the environmental factors affecting lynx depredation on domestic sheep as well as the effectiveness of lethal control to prevent secondary attacks on sheep in Sweden from 2009-2019. I used logistic regression to investigate the effect of environmental factors on the risk of depredation. Furthermore, I used Survival Analysis to estimate the effect of lethal control on repeated attacks. Between 2009 and 2019 there were a total of 760 depredation events of which 20.7 percent experienced a secondary event within one year. Most attacks occurred during October, while the least attacks occurred during March and April. On average 1.67 sheep were killed during an attack. Depredation events are linked to lynx density, roe deer density distance to settlement, artificial night-time brightness, ruggedness and proximity to water, indicating a “site” effect rather than “problem individuals”. My results support previous literature which suggests that lynx do not actively search for sheep farms, but rather encounter them by chance. The risk of a secondary depredation increased significantly with lynx density, roe deer density and distance to water. Hunting of lynx significantly decreased the probability of a repeated attack within one year by 60 percent. I conclude that mitigation measures should be focused on pastures which are far away from urban structure with rugged terrain and that lethal control is an effective measure for preventing future attacks in the short term, but its long-term effectiveness remains unknown. I encourage future research to investigate the connection between lynx depredation events and water proximity.

Keywords: Lynx lynx, Scandinavia, conservation, human-wildlife conflict, depredation, Spatial analysis, Survival analysis, protective hunting, carnivore, lethal control

Introduction

Wildlife conflicts are a serious concern and have negatively affected large predators in many different parts of the world (Ripple *et al*., 2014). After near extinction on the local scale, large predators have made a recovery in Scandinavia and will expand their current range even further (Chapron *et al*., 2014). With this recovery, past conflicts have re-emerged and have caused public discourse over the management of predators in the past decade (Widman *et al*. 2019). One important point of contention is depredation on domestic animals which shapes part of the public opinion about predator management (Woodroffe *et al*., 2005; Treves & Naughton-Treves, 2005; Gangaas *et al*., 2013; Suryawanshi *et al*., 2013).

The Eurasian Lynx

The Eurasian Lynx (*Lynx lynx*) is the largest of the four lynx species in the world. In Europe, its range spans from northern Scandinavia throughout the Alps all the way down to the northern border of Greece in Europe (Chapron *et al*., 2014). The Eurasian Lynx (lynx hereafter) is generally regarded as a specialist predator. In Scandinavia, its diet consists of roe deer (*Capreolus capreolus*), reindeer (*Rangifer tarandus*), smaller animal species (hares, grouse, etc.) while predation on domestic sheep (*Ovis aries*) can occur (Odden *et al*., 2013). Both males and females are solitary and keep territories (Aronsson *et al., 2016*). Male territories are larger, often overlapping several female territories (Zimmermann *et al*., 2005; Aronsson *et al*., 2016). Northern Scandinavian populations predominately prey on reindeer whereas southern Scandinavian populations have specialized on roe deer (Mattisson *et al., 2011;* Odden *et al*., 2013).

Until the 20th century, lynx had been hunted to near extinction in Norway and Sweden with only two small populations in Norway and less than 100 individuals in Sweden remaining (Hellborg et al., 2002; Basille et al., 2009; Chapron et al., 2014). Through legal protections as well as regulated hunting, the lynx has recovered as well as expanded its range throughout Sweden and Norway. Today, the lynx population is monitored through snow tracking by a joint programme between Sweden and Norway, focusing on family groups, i.e. adult females with her kittens. In the monitoring year 2019-2020, 189.5 family groups were observed in Sweden, which corresponds to about a total of 1100 individuals (Andrén *et al*., 2002; Mattisson & Frank, 2020). Lynx seem to avoid landscapes heavily modified by humans, but do not seem to avoid areas with medium disturbance (for example fields for livestock grazing), prioritizing areas with high roe deer density (Basille *et al*., 2009). In areas that are heavily modified by humans, lynx use areas with high ruggedness (Bouyer *et al*., 2015a)

Sheep depredation in Sweden

The focus of my study was on lynx depredation in Sweden, one of the Scandinavian countries. While exploring sheep farming and depredation in Scandinavia it is important to separate between Norway and Sweden since they differ in both their sheep farming practices as well as their carnivore management strategies (Swenson & Andrén, 2005). In Norway, sheep usually graze freely in the open, specifically in mountain and forest habitat. Sheep farming in Sweden is generally on a smaller scale and sheep are mostly kept within fenced pastures on farmsteads in the centre and south of the country (Figure 1) (Swenson & Andrén, 2005; Linnell *et al*., 2020). In 2019 there was a total of 550,000 sheep in Sweden, of which up to 500 were attacked by lynx each year (Elofsson *et al*., 2015; Swedish board of Agriculture and Statistics Sweden, 2020).

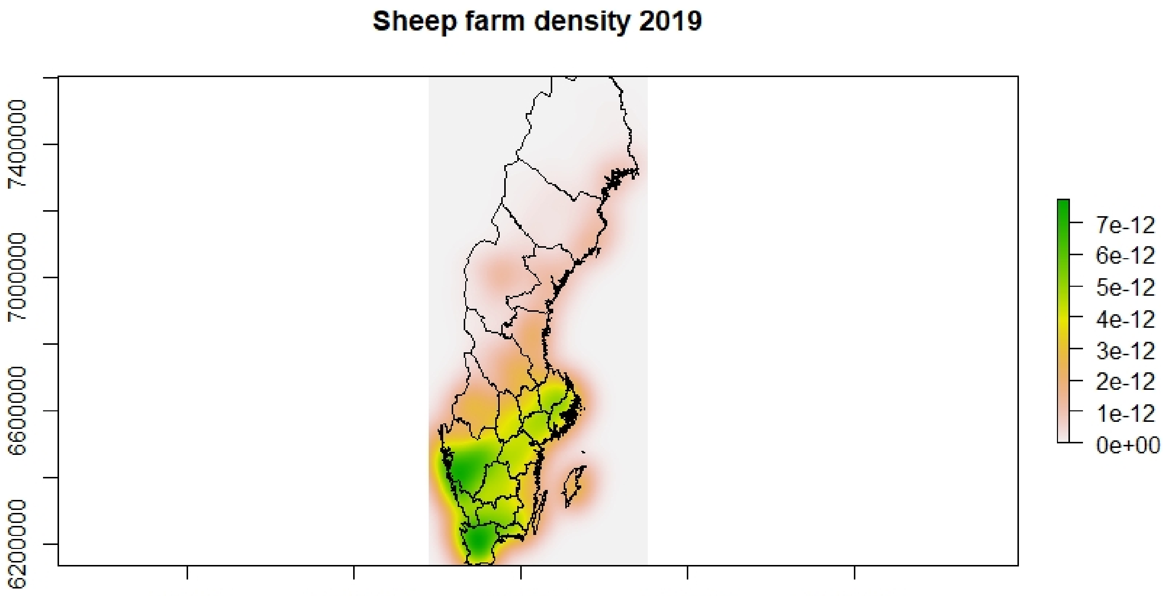

Figure 1 Density of sheep farms registered through Jordbruksverket in 2019. The figure shows the Kernel Density Estimation of sheep farms (Worton; 1989). The X and Y axis show coordinates within the RT90 coordinate system. The Legend shows the Utilization distribution, which is the probability that a sheep farm is found within a 500 m² area. Areas with a high probability have higher farm densities, whereas areas with lower probability have lower farm densities. Density estimations were done in R, using the "adehabitatHR" package (R Core Team;2019, Calenge ; 2006)

Depredation of livestock in Sweden is caused mainly by four large predators: brown bear (*Ursus arctos*), wolf (*Canis lupus*), lynx and golden eagle (*Aquila chrysaetos*). Out of those four, lynx are responsible for most attacks in most years, although other species like the wolf and brown bear tend to kill more individuals per attack (Frank *et al.,* 2020). If a domestic animal is suspected to have been killed by a predator a trained wildlife ranger for the county administrative board will visit the site, examine the surroundings as well as the carcass. Based on expert judgement the cause of death is determined, which has been identified as a reliable approach of determining the cause of death of domestic animals killed by large predators (López-Bao *et al*., 2017). Sheep killed by protected large predators are eligible for compensation. The amount of compensation is suggested by the Wildlife Damage Centre (Swedish University of Agriculture Sciences) and determined by the County Administrative Board (Widman & Elofsson, 2018). On average, total annual compensation (not including reindeer) for livestock killed or injured by large predators in Sweden amounts to 150,000 EUR total (Widman *et al*., 2019). Aside from direct losses from depredation, attacks by predators can have a secondary impact on livestock owners. For example, attacks by wolves on cattle can reduce the mass of calves by about 3.5% resulting in further losses for livestock owners (Ramler *et al*., 2014). Widman *et al*. (2019) estimated that the killing of a single sheep within a fenced area resulted in an additional cost of about 71 EUR, which are not being compensated.

Lynx depredation on domestic sheep has been intensively studied in Norway and other parts of their range. In Norway, free ranging sheep are not a selected prey for by lynx, as the proportion of sheep in lynx diet does not seem to be proportional to their relative abundance (Moa *et al*., 2006). Attacks on sheep seem to be chance encounters rather than selection by lynx, since these events most likely occur due to random encounters during other activities (e.g. maintaining of territories, searching wild prey) (Moa *et al*., 2006). Lynx in Norway select for patches with high roe deer density, but even in areas with low density, roe deer continue to be the most important prey (Sunde *et al*., 2000; Odden *et al*., 2006). Males tend to kill sheep more frequently than females, but studies have found no evidence of "problem individuals" (Linnell *et al.* 1999, Stahl *et al.* 2001; Odden *et al*., 2002). The sex difference in kill frequency might be explained by summer habitat selection, where females select for areas with higher roe deer density (Odden *et al*., 2008). Studies in the Alps also show that domestic sheep encompass a non-significant proportion in lynx diet (Molinari-Jobin *et al*., 2002). Nevertheless, due to the large difference in sheep farming practices between Sweden and Norway, it is unclear if studies from Norway apply to the dynamics of lynx depredation on sheep in Sweden. Thus, a study of the environmental factors affecting lynx depredation in Sweden is needed.

Studies on other large predators suggest that several environmental factors can contribute significantly towards risk of depredation. Kaartinen *et al.*, 2009 show that wolf density and human density significantly contribute towards wolf depredation on domestic sheep. Moreover, Milanesi *et al*., 2019 found that environmental predictors, such as land cover, ruggedness of the terrain and light pollution as well as livestock density can significantly affect the probability of wolf depredation, dependent on the attacked livestock species.

Reduction of lynx populations by harvest is common way to deal with depredation events (Stahl *et al*., 2001; Woodroffe *et al*., 2005; Herfindal *et al.,* 2005). Nowadays, other mitigation measures are also being employed, such as electric fencing. In most parts of Europe, including Sweden, subsidies are available for preventive measures to reduce depredation (Karlsson & Johansson, 2010).

1.1. Aim of the study

The aim of my thesis was to investigate the spatial and temporal dynamics of lynx depredation on domestic sheep within Sweden. The thesis was split into two separate parts.

First, I wanted to investigate what environmental factors may affect lynx depredation. I built a model to identify environmental contributors, like land cover, human density, distance to forest edge, etc. which increase the probability of depredation events occurring on sheep farms. In the future this can be used to identify sheep farms that are especially vulnerable to depredation events. Identifying those farms can help stakeholders and decision makers to focus mitigation efforts on especially vulnerable areas to mitigate further human-wildlife conflicts. For this first part, my research question was: *"What environmental factors influence the probability of a lynx depredation event on domestic sheep?"*

Second, I wanted to focus on temporal dynamics in lynx depredation on sheep, especially on the effect of lethal control on probability of repeated attacks. Protective hunts can be permitted when a certain number of depredation events have occurred in an area within a certain timespan. I was interested in how these hunts affect depredation events and possibly decrease the probability of a second depredation event. For this second part, my research question was: *"What factors affect the probability of a repeated attack on domestic sheep by lynx and does hunting decrease the risk of a second event?"*

1.1.1. Hypothesis

I formulated four hypotheses for this study:

1) Wolf density as well as human density are important factors of sheep depredation (Kaartinen *et al*., 2009). I expect to see the same for lynx, i.e., higher risks of depredation by lynx at areas with high lynx density, high lynx habitat suitability as well as low human density.
2) As lynx have been shown to avoid areas with high levels of human modification (Bouyer *et al*., 2015a). I expect that proximity to human settlements and an increase in artificial night-time brightness decrease the risk of depredation.
3) Lynx utilize forest edges frequently. Consequently, I expect that depredation events tend occur to fields that are close to forests or the forest edge. I expect fields, which are close and at least partially surrounded by forests to be particularly vulnerable to attacks as well as repeated attacks.
4) Lethal control is a recommended short-term mitigation measure to avoid repeated depredation events (Karlsson & Johansson, 2010). Since lynx are territorial and recolonization of territories is not instant, I expect hunting of lynx which have access to a sheep field to be an effective measure of mitigating depredation events on that field for at least one year.

2. Methods

2.1. Study area

Lynx depredation events occurred throughout Sweden, excluding the very north and south as well as the islands of Gotland and Öland. The southernmost part of Sweden is mainly covered by agricultural land, which, together with the two islands, has been excluded from the study, since it is outside of the range of lynx. Therefore, sheep farms which were located in those areas were excluded from the study (Figure 2). Most of the area is covered by boreal forest with Norway spruce (*Picea abies*), Scots pine (*Pinus silvestris*), birch (*Betula pubescens*, *Betula pendula*) and aspen (*Populus tremula*). Most of those forests are subject to intensive silviculture. Generally, we can see a north-south gradient, where agricultural land, human density and roe deer density increases towards the south (López-Bao *et al*., 2019).

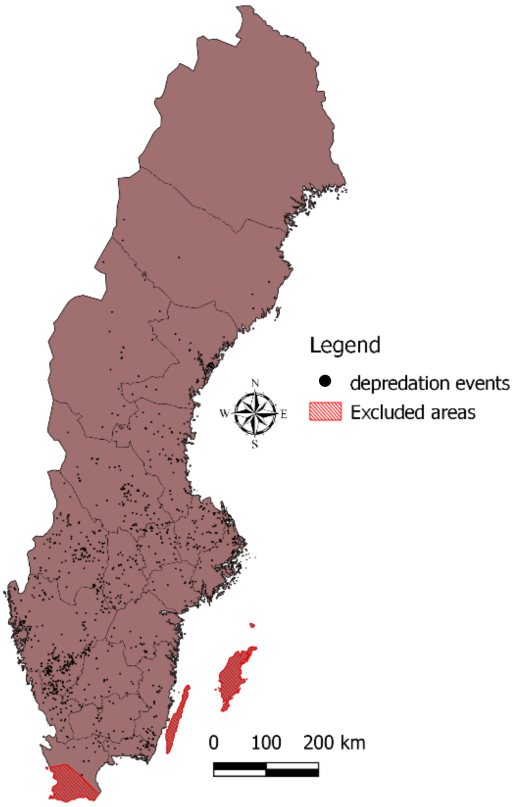

Figure 2 Study area. Sheep farms from areas in red were not included in the study. Points shown on the map are all recorded depredation events by lynx on domestic sheep that took place between 1995 and early 2020. The figure was created in QGIS utilizing depredation data from Rovbase ((QGIS Development team, 2020; www.rovbase30.miljodirektoratet.no)

2.2. Datasets used

For this thesis the main part of the work consisted of gathering data from various resources and managing them to build one cohesive dataset.

Sheep farm locations
Information on sheep farms were provided by The Swedish Board of Agriculture (Jordbruksverket, www.jordbruksverket.se). GPS locations of individual fields, their respective utilization and flock size were provided. The data was transformed into a unified coordinate system (SWEREF99). Fields with the associated use of breeding, ecological breeding, breeding herds and pasture were considered representative of typical fields utilized by sheep flocks which encompassed about 95% of the dataset. Other uses, such as Wildlife Parks were excluded from the data set. It is important to note that this data set is by no means a complete dataset of all sheep fields in Sweden, since only fields registered by The Swedish Board of Agriculture are included. I assumed that these fields were representative of sheep fields in Sweden. The entire dataset consisted of about 18,300 individual fields from 2009 until 2019 after controlling for inaccurate data.

Lynx depredation data
Lynx depredation data was obtained from the database Rovbase (www.rovbase30.miljodirektoratet.no). This dataset included all recorded attacks of lynx on domestic sheep from 1995 until 2020. Cause of death, in this case by a lynx, was determined by the trained ranger on sight. This evaluation has proven to be very accurate (López-Bao *et al*., 2017). Depredation events were considered separate if the attacks occurred 12 hours apart. The entire dataset consisted of 1,276 depredation events between 1995 and 2019 after controlling for inaccurate data, although only data from 2009 to 2019 was used.

Roe deer density
The index for density of roe deer in Sweden was kindly supplied by the Swedish Association for Hunting and Wildlife Management (Svenska Jägareförbundet). Hunting statistics for the different hunting areas were gathered by year and served as an index for roe deer density (number of roe deer harvested per 1000 hectare). Data was available from hunting seasons 1997-1998 until 2018-2019. To account for stochastic variation (weather etc), a five year running average was calculated for roe deer density.

Artificial night-time brightness
The Artificial night-time brightness dataset from The Earth Observation Group (EOG) served as data for measuring artificial lights throughout Sweden. Average Annual night-time brightness was measured by night imaging of the Visible Infrared Imaging Radiometer Suite (VIIRS) from the Suomi NPP (National Polar-Orbiting Partnership) Satellite. VIIRS collects data on light pollution and averages them over the course of a year, removing outliers from cloud cover. Outliers from fires and other ephemeral lights have also been removed (NOOA, 2019).

Land cover
Land cover was extracted from the Swedish Land Cover (SMD, National Lands Survey of Sweden) and reclassified into broader categories. The raster was categorized into cropland, coniferous forest, deciduous forest, mixed forest, grassland, shrubland, water, clear-cut, wetland, urban areas and other. For the Swedish Land cover, two rasters were available, both of which were recategorized. The ungeneralized raster portrayed all land cover on a 10 x 10 m scale while the generalized raster changes very small patches of cover (> 0.25 ha) to the surrounding cover. This is done to give a more general overview of the area while sacrificing some accuracy. Both rasters were utilized in the analysis at different points. The ungeneralized raster was defined as "small forest" and the generalized was defined as "large forest" dataset, providing information on presence and distance to small forest and larger forest patches.

Terrain Data
Data on Elevation was taken from the Copernicus Land Monitoring Service (EU-DEM). The digital surface model cut to the study area and transformed into target coordinate system. From this raster, the Terrain Ruggedness index was calculated (Riley *et al*., 1999).

Sheep density
The index of sheep density was calculated from the provided sheep farm data. Every farm also reported the flock size of a given field. Since multiple fields were used by the same flock, only one field per farm was chosen. From this, livestock density was calculated at a number of sheep per km^2 level and rasterized over Sweden at a resolution of one km^2. It is important to note that this density merely serves as a proxy for actual sheep density, since only sheep farms that were registered at the Swedish Board of Agriculture were included.

Lynx family groups
Lynx presence was estimated from lynx family groups in the area. This annual survey of lynx family groups (adult female lynx with kittens) is based on observations of tracks in the snow, sightings, pictures, and dead kittens has occurred since December 2002 (www.rovbase30.miljodirektoratet.no). Lynx family groups are used to estimate the local lynx population in Scandinavia and thus was used as a proxy of lynx density (Andrén *et al*., 2002).

Lynx harvest data
Data on lynx harvested in Sweden during the study period was taken from the common database Rovbase (www.rovbase30.miljodirektoratet.no). This information included the data, time, and coordinate of shot lynx in Sweden from 1987 until early 2020. Both licensed hunting (legal hunting of lynx with a license) as well as protective hunting (legal hunting of lynx issued to prevent depredation events) were included in the dataset. Illegal killings were not considered.

Human density
Population density was extracted from the Gridded Population of the World 2020 (GPWv4) dataset. The dataset was created by NASA to estimate population density utilizing an algorithm estimating population density at a one-km^2 resolution. The data was converted into a matching Coordinate system (SWEREF99).

2.3. Spatial Analysis via logistic regression

In order to gain an understanding of the environmental predictors that could contribute to lynx depredation events, I utilized logistic regression with 1 as a depredation event and 0 as a sheep field that has not experience a depredation event.

2.3.1. Extracting data

For data extraction a combination of R (R Core Deveolpment Team, 2020), utilizing packages *raster, sp and rgdal* (Hijmans 2020; Pebesma & Bivand, 2005; Bivand *et al*., 2020), QGIS (QGIS Devolopment team, 2020) and ArcGIS (ArcMap 10.7.1, ESRI).
Since there were an about 183,800 registered field locations and only 760 depredation event during the study period, I took a random sample of 1000 registered field locations to balance between "presence" (depredation) and "absence" (no depredation). Points were only considered to be eligible if they were within the study area (Sweden excluding Öland, Gotland and southernmost part of Sweden; Figure 2) and did not have a depredation event within a one-km radius, to exclude fields which associated with depredation events.

Estimating land cover was done by calculating the percentage of different land cover types around the depredation or field point in a 100 m radius by using the *raster* package in R. A 100 m radius was chosen to reflect the immediate surroundings of the field, in which the event did or did not occur. Elevation, ruggedness and artificial night-time brightness were extracted at the specific point, while sheep density was extracted the same way, utilizing density from separate rasters dependent on the year the field or depredation event was recorded. Roe deer density was extracted from the specific hunting region in which the point was found.

Distances to roads, water and human settlements were calculated using ArcGIS. Raster fields with these specific attributes were transformed into points and the closest distance from depredation events and farms to those points was calculated. All distances were log(x+1) transformed, since some of the data was long-tailed to the right. The log(x+1) transformation, where log(x) denotes the natural logarithm, whose base value is e, was useful to put more focus on the differences in short distances, putting less emphasis on differences in long distances. Furthermore, roe deer and sheep density were log(x+1) transformed for the same reason. The (x+1) was used since the data included zeros . For the distance to forest, both the distance to small, forested patches as well as distance to larger patches were used using the ungeneralized and generalized land cover raster.

Lynx density was calculated as the number of family groups within a 22-km radius. The radius of 22 km was chosen since it is used as a threshold to separate between neighbouring lynx family groups and therefore reflects the expected maximum straight-line distance traveled by female lynx in southern/central Sweden (Gervasi *et al*., 2013). The time frame chosen was from 2009 until 2019 since all data was available for this time period.

2.3.2. Analysis Approach

Analysis of the environmental predictors of depredation events was done in R, utilizing the *car, MuMIn* and *lme4* packages (Bates *et al*., 2015; Fox & Weisberg, 2019; Barton, 2020).

First, the data was split into a training set (80% of the data), to build the model, and a test dataset (20% of data), to later test whether the model could be utilized to predict independent data. Then a full model was created, which was a mixed effects model, utilizing the binomial distribution. The response variable was depredation event (0 for no depredation and 1 for depredation) while all predictor variables were included with year as a random effect. I checked for multicollinearity using the Variance Inflation Factor (VIF), which is common practice for looking at multicollinearity in regression (Fox & Weisberg, 2018). Although there were some slight correlations amongst predictor variables only elevation had to be removed due to multicollinearity (all other predictor variables had a VIF score below 5, thus not influencing the predictive power of the model). I prioritized ruggedness over elevation, since it was included in previous studies about lynx habitat selection (Bouyer *et al*., 2015a). Using the dredge function from the *lme4* package, models of all combinations of predictor variables were created and ranked according to their respective Akaike Information Criterion (AIC) (Akaike, 1973).

Model performance was evaluated by its AUC value. AUC (Area under ROC Curve) measures the area under a ROC (receiver operator characteristic graph). This graph depicts the models sensitivity, which is the percentage of points correctly classified (for example depredation events that were classified as depredation), over its specificity, which shows the percentage of falsely classified points (for example depredation events that were classified as non-depredation events, see appendix for figure). Thus, the AUC value measures the average percentage of correctly classified points by the model. An AUC value of one would show that the model predicted all points correctly while an AUC value of 0.5 would show that half of cases were correctly identified (thus the model having no predictive power) (Fawcett, 2006).

2.4. Temporal analysis via survival analysis

2.4.1. Defining Repeated attacks

To define, whether an attack was considered to be repeated or not I followed categorized attacks according to previous literature. I used the definition of a repeated attack used in Karlsson & Johansson (2010), which used the same database, with depredation events until 2009. Karlsson & Johansson defined a repeated attack as: "… the occurrence of two or more predation events within a year on the land of the same farm within 1 km of each other." Furthermore, I assumed that within a 1 km radius all attacks belonged to the same farm. This definition was met as I was able to find the same number of repeated attacks with my method as Karlsson & Johansson (2010) for the years of their study. To determine time between events I calculated the time between the first event and the earliest second event. Depredation events that were a second event re-entered the dataset to become a new first event.

2.4.2. Extracting Data

The dataset encompassed all depredation events from 2009-2019. This timeframe was chosen since all data for all variables were available. Then the dataset was built to be used within Cox proportional hazards analysis. In addition to the previously discussed variables I added the following:

Date of entry: Points entered the survival analysis at t = 0 for points without successful hunts and t = time from first depredation event to hunt for points with successful hunt. This staggered entry was done as to not overestimate the effect of hunting, since the occurrence of a hunt can only have an effect on survival after the hunt has occurred.

Date of exit: Points which did not experience a second depredation event exited the analysis after one year (365 days). All points that experienced a second depredation event left the analysis after the second event had occurred. For example, a point with a hunting event 30 days and a second depredation event 45 days after the first attack would enter the analysis at t = 30 and exit the analysis at t = 45.

Hunting: To check if a hunting event occurred after the initial attack I checked for hunting events around the initial point of depredation. I checked for hunting events within a 22-km radius, since I considered the farm to be accessible by lynx found in this radius (see 2.3.1; Gervasi et al. 2013). The occurrence of hunting was binary with 0 for no hunting and 1 for the occurrence hunting. For this analysis, I included both licensed as well as protective hunting events since I assumed, they would have a similar effect.

Lynx family group presence: Similarly to lynx density in the spatial analysis, this variable described the amount of family groups in the area. The categories were ”absence”, ”1-2 family groups” and “> 2 family groups”. Family group presence had to be categorized from number of family groups in the area as to not violate the proportional hazards assumption of the model.

2.4.3. Analysis Approach

For the analysis of repeated attacks, I used survival analysis (Cox, 1972; Andersen & Gill, 1982), which has been used to investigate repeated depredation events in Sweden in the past (Karlsson & Johansson, 2010).

The Cox proportional hazard model is particularly useful, since it allowed me to create a model that can estimate the impact of both constant factors over time as well as the impact of a specific event that occurred during the time studied. Survival models describe probabilities of an event occurring after a certain amount of time. Specifically, Cox proportional hazards estimate hazard rates which can easily be converted into survival rates (Bradburn *et al*., 2003). The survival probability describes the probability of survival (in this case not experiencing a repeated attack) until the specified amount of time, while hazard rate describes the risk (of a repeated attack occurring) at a specific time (Clark *et al*., 2003). All analysis was done in R, mainly using the *survival* package (Therneau, 2020). First, I investigated all predictor variables in a univariate analysis and included all significant variables in a final model. For the variable of hunting I used staggered entry (see 2.4.3). The full model was first checked for assumptions, most importantly the proportional hazards assumption, which assumes that the baseline hazard is constant over time. Consequently, the variable of lynx density was transformed into lynx presence as to not violate this assumption (see 3.4.2). Then, I selected the best model through the sample adjusted Akaike Information Criterion (Akaike, 1973; Burnham & Anderson ,2002). Then results were visualized using the *survminer, smoothHR* and *Greg* package (Kassambra *et al*., 2019; Gandrud, 2015; Gordon & Seifert, 2020).

3. Results

During the study period from 2009 until 2019 there were a total of 760 depredation events and about of 183,800 of registered field locations. On average there were 53 attacks per year with most attacks (137 attacks) occurring in 2016. Depredation events varied throughout the year, with most attacks occurring in October and least in March and April. On average, 1.67 sheep were killed during an attack (Median of 1).

3.1. Spatial Analysis via Logistic Regression

Since eleven models were below delta 2 in their AIC values, I utilized model averaging to create an average model of the twelve best models (Table 1). The average model used full averaging compared to conditional averaging. Full averaging differs to conditional averaging by decreasing the effect size of predictor variables not included in all models (Burnham & Anderson, 2002). Since some predictor variables (especially those that were statistically significant) were included in all models I decided to use full averaging.
Then, the models respective AUC value was calculated using the pROC package (Robin *et al.*, 2011) and the average model was used on the test dataset to estimate predictive power over independent datasets.

Table 1 AIC values of the best models of logistic regression which were used for model averaging.

Model	AIC	ΔAIC	AIC weight
Included in all models: roe-deer density + settlement distance + night-time brightness + ruggedness			
…+ livestock + water distance	1290.368	0.000	0.134
…+ distance large forest + livestock + water distance	1290.651	0.283	0.117
…+ water distance	1290.694	0.326	0.114
…+ distance large forest + water distance	1290.822	0.454	0.107
…+ forest cover + livestock + water distance	1291.657	1.288	0.071
…+ livestock	1291.662	1.294	0.070
…+ distance large forest + livestock	1291.688	1.320	0.069
…+ distance small forest + livestock + water distance	1291.742	1.374	0.068
…+ distance large forest	1291.775	1.407	0.067
…	1291.914	1.546	0.062
…+forest cover + water distance	1291.951	1.582	0.061
…+ distance small forest + water distance	1291.983	1.615	0.060

Out of the 24 initial variables investigated a total of eleven variables were included in the final model. Specifically, out of all types of land cover only water and forest cover around the points were included in the final model. Furthermore, distance to larger forested areas, distance to roads as well as human density were also not included. The final model showed six significant predictor variables and four non-significant ones. Significant predictor variables of depredation events were the number of lynx family groups in the area, roe deer density, distance to nearest settlement, artificial night-time brightness, ruggedness and percentage of water around the point (Table 2).

Table 2 Model averaging output following the full average method.

Variable	**Estimate**	**SE**	**P value**
Intercept	-4.583	±0.591	**<0.001**
Number of lynx family groups	0.697	±0.075	**<0.001**
Log(roe deer density+1)	0.341	±0.078	**<0.001**
Log(distance to settlement+1)	0.967	±0.06	**<0.001**
Night-time brightness	-0.094	±0.0467	**0.045**
Ruggedness	0.034	±0.014	**0.006**
Water percent	2.296	±1.07	**0.032**
Log(distance to water+1)	-0.084	±0.076	0.27
Log(livestock density+1)	0.063	±0.083	0.45
Forest percent	0.039	±0.161	0.81
Log(distance to small forests+1)	-0.005	±0.023	0.82
Log(distance to large forests+1)	-0.022	±0.039	0.581

My model showed an AUC value of 0.869 giving the model a relatively strong predictive power (Figure 9, see appendix).

Furthermore, validity of the model was tested by determining the accuracy of the model on the test dataset. The model correctly identified 80 percent of the points in the test dataset. Due to the large number of predictor variables no single predictor variable serves as a perfect measure of determining depredation probability. Nevertheless, distance to settlement, number of lynx family groups, ruggedness as well as percentage of water seemed to have a significant positive while night-time brightness seemed to have a significant negative impact on the probability of depredation (Figure 3 and Figure 4 as example).

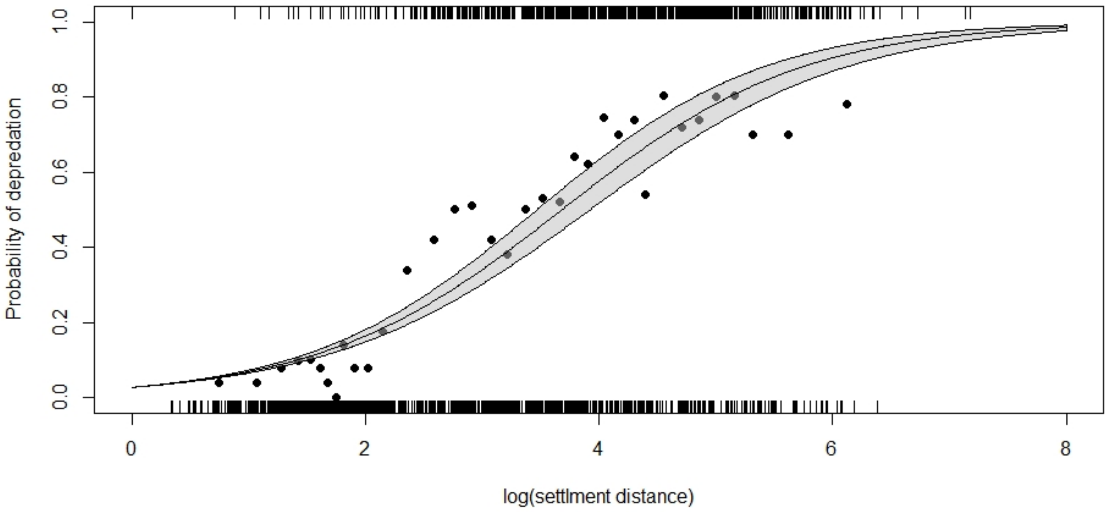

Figure 3 Effect of Distance to nearest settlement on the relative probability of depredation. An increase of 1 in log(distance+1) results in an increase of the log(odds) by 0.97 while all other predictor variables are constant at average. The points show the percentage of depredation events compared to non-depredation events at specific distances, based on binned data (n=50). Stutter along the x axis show the actual data.

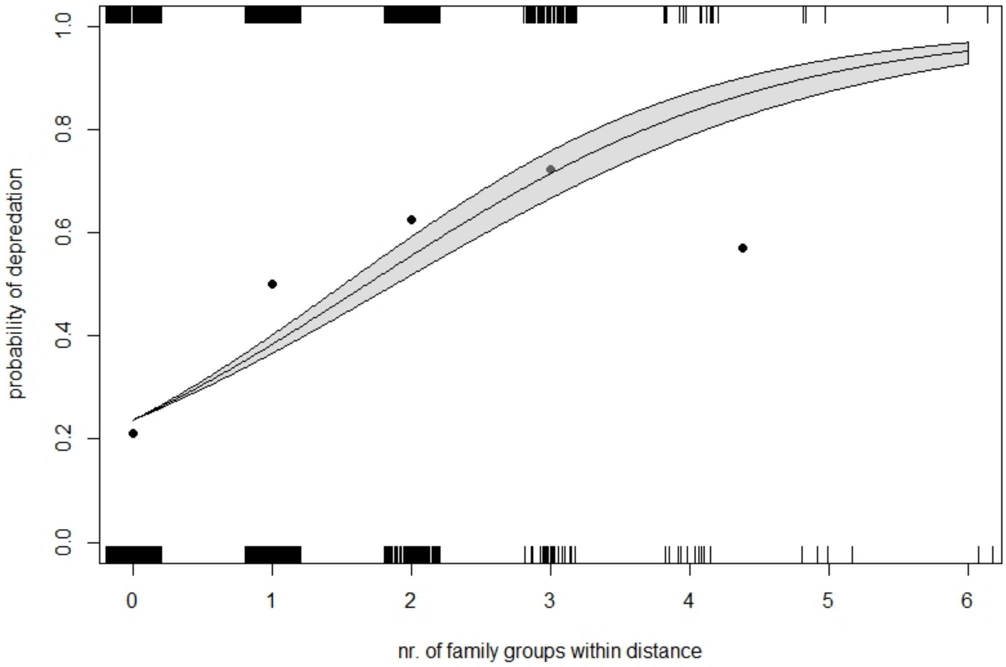

Figure 4 Predicted relative probability of a depredation event based on the number of lynx family groups with 22 km, while all other predictor variables are constant at average. The points show the percentage of depredation events compared to non-depredation events at specific distances, based on binned data (n=50). Stutter along the x axis show the actual data

3.2. Temporal Analysis via Survival Analysis

During the study period (2009-2019), 20.66 percent of recorded events (157 out of 760 total) were repeated attacks in the study area. Out of the 157 repeated attacks, 13 had a hunting event between the two attacks whereas out of the 603 attacks with no repeated attack 206 had a hunting event. Repeated attacks varied greatly throughout the study period with an average of 14.27 repeated attacks per year. The most repeated attacks occurred in 2016 with a total of 40 repeated attacks, while the lowest years were 2011 and 2019 with four repeated attacks.
The full model, only including the significant predictor variables included hunt, lynx family presence, roe deer density as well as distance to water (Table 3). Model selection through AICc revealed that the best fit model was the model including all significant predictor variables, with all subsequent models showing an AICc value greater than Δ2.

Table 3 AICc values of the best models of survival analysis.

Variable	AICc	ΔAICc	AICc weight
Hunt + family group presence + roe-deer density + water distance	1925	0	0.88
Hunt + family group presence + roe-deer density	1929.5	4.49	0.093
Hunt + family group presence + water distance	1932.8	7.84	0.017
Family group presence + roe-deer density + water distance	1934.6	9.61	0.007
Family group presence + roe-deer density	1938.8	13.84	0.001
Hunt + family group presence	1939.7	14.73	0.001
Family group presence + water distance	1940.8	15.80	<0.001
Family group presence	1947	22.03	<0.001
Hunt + roe-deer density + water distance	1957.5	32.48	<0.001
Hunt + roe-deer density	1959.4	34.43	<0.001
Roe-deer density + water distance	1962.7	37.7	<0.001
Roe-deer density	1964.7	39.73	<0.001
Hunt + water distance	1970.4	45.40	<0.001
Water distance	1973.7	48.72	<0.001
Hunt	1974.3	49.35	<0.001

Table 4 Best model output for Repeated attacks, showing the coefficient, exponential coefficient (Estimate), Standard error, confidence intervals as well as p value (Pr(>|z|).

Variable	Coefficient	Estimate	SE	Lower 95 %	Upper 95%	P value
Hunt	-0.931	0.394	0.302	0.218	0.712	**0.002**
Family group presence “1-2”	1.48	4.395	0.331	2.299	8.401	**<0.001**
Family group presence “more than 2”	1.84	6.293	0.372	3.038	13.03	**<0.001**
Roe deer density	-0.001	1.055	0.0169	1.021	1.090	**0.001**
Distance to water	0.054	0.999	0.0002	0.999	0.9999	**0.015**

A hunting event occurring within the area after a depredation event decreased the probability of a repeated attack by about 60 % on average (estimate = 0.39) compared to no hunting event occurring. For lynx family groups in the area, probability of a depredation event increased by 440 % when having one to two and by 630 % when having more than two family groups in the area compared to having no family groups in the area. Roe deer density had a positive impact on the probability of attack with an increase of 5% per increase of an average of one roe deer harvested per 1000 hectare in the past five years. Distance to water affected the probability of depredation negatively. Per ten-meter distance to water the probability of a repeated attack decreased by 1%.

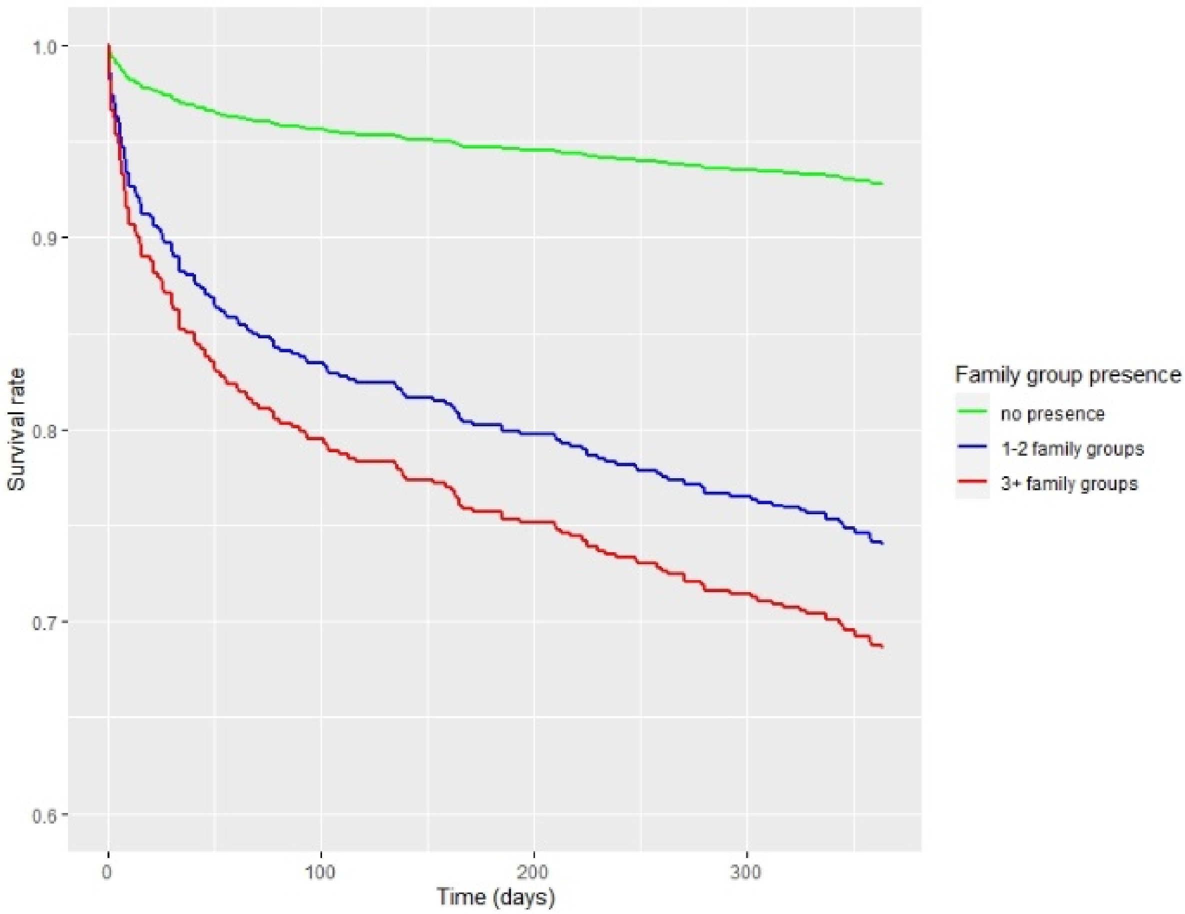

Figure 5 Survival Curve of repeated attacks for different lynx densities. The X axis shows time since first depredation event, while the y axis shows the survival rate (percentage of depredation events that have not encountered a second attack)

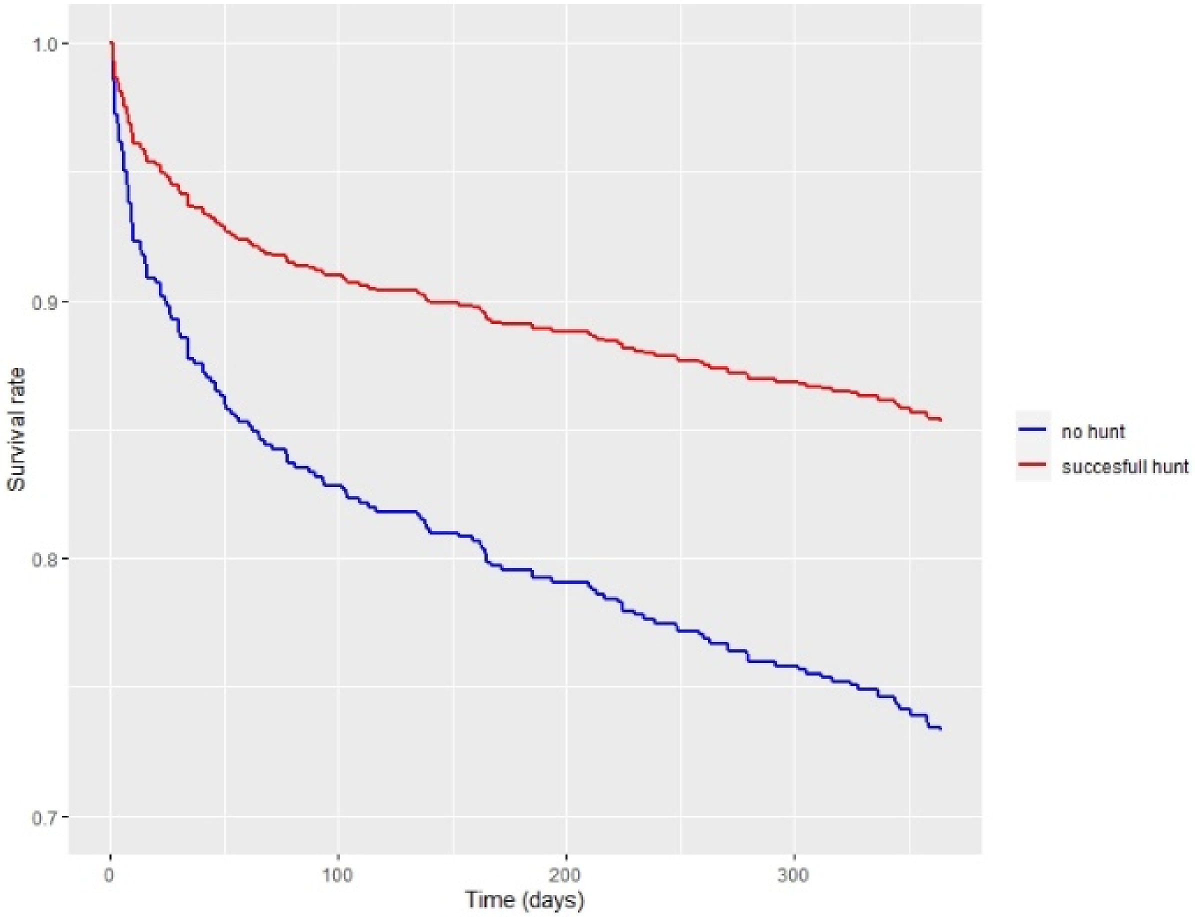

Figure 6 Survival Curve of the impact of hunting on repeated attacks. The X axis shows time since first event, while the y axis shows the survival rate (percentage of depredation events that have not encountered a second attack)

4. Discussion

The dynamics of depredation are complex and many different factors can affect locations of depredation events. Overall, the occurrence of depredation events is linked to lynx density, roe deer density, distance to settlement, night-time brightness, ruggedness as well as water presence. Other factors that might contribute to the risk of depredation might be livestock density and proportion of land covered by forest as well as the proximity to forest edges.

Dynamics of depredation events

As previous studies also showed, density of the predator has a large effect on depredation risk (Herfindal *et al.*, 2005; Kaartinen *et al.*, 2009). In my study, lynx density showed to be a significant factor at determining depredation locations. This, in combination with the significance of other environmental variables (distance to settlement, artificial night-time brightness, ruggedness and water proximity) suggests that the specific “site” of the sheep field significantly influences probability of depredation. This finding is supported by studies in Norway and France, which also found no evidence of ”problem individuals” but rather a ”site” effect (Stahl *et al.*, 2001; Odden *et al.*, 2002; Herfindal *et al.*, 2005). My model described the effect lynx density well, although became inaccurate when reaching high lynx densities (Figure 4). I suggest that after a certain density is reached, other factors become more important for predicting the probability of depredation events. Thus, my results were mostly in line with my first hypothesis that risk of depredation increases as lynx density increases. However, it is important to consider that I used a proxy for lynx density. Lynx density was only estimated using family groups within an area, thus not considering densities of females without cubs and males. Although study has shown that most sheep (in Norway) are killed by male lynx, I still consider my proxy to be valid (Odden *et al.*, 2002). We know that male territory size is strongly dependent on number of female territories, which is strongly linked to roe deer density (Aronsson *et al.*, 2016). Males only seem to prey more upon domestic sheep in Norway since they select less for patches with high roe deer densities while hunting (Odden *et al.*, 2002, Odden *et al.*, 2008;). My study cannot account for this patch selection, since the proxy for roe-deer density measures on larger scale (hunting districts) than is needed. Sheep density had no significant effect on depredation, which was at a finer scale (1-km^2) than roe deer density.

Human density was not identified as an important factor influencing the probability of lynx depredation on sheep, which rejects part of my first hypothesis. In Central Europe, we know that lynx habitat selection is mostly influenced by avoidance of humans during the day, but positively influenced by prey availability at night (Filla *et al.*, 2017). Since depredation events generally occur during the night and lynx tend to select against areas that are heavily modified, human density in areas where lynx and sheep both occur does not seem to be an important factor (Bouyer *et al.*, 2015b).

One of the best predictors of depredation events was distance to human settlement, since it had the largest effect size (Figure 3). Milanesi *et al.* (2019) also showed the importance of distance to human settlement as well as ruggedness as predictors of wolf depredation events. Lynx tend to avoid areas with high human modification (settlements etc.) and tend to utilize areas with medium human habitat modifications, for example fields (Bouyer *et al.*, 2015a; Bouyer *et al.*, 2015b). Furthermore, within heavily modified areas, lynx select stronger for rugged terrain (Bouyer *et al.*, 2015a), which is also included within my model. These results were in line with my second hypothesis, that lynx, as human disturbance and artificial night-time brightness increases, risk of depredation decreases.

My results could also explain why fewer attacks occurred in March and April. During this time, sheep herds are brought to closer, better fenced areas, where lambing can occur at close proximity to the livestock owner. Furthermore, license hunting of lynx occurs during this time, possibly pushing lynx away from human settlements. A study, which focused on wolf depredation in Italy also identified artificial night-time brightness as a significant factor of depredation (Milanesi *et al.* 2019). I found similar results, as artificial night-time brightness also showed to be a significant factor for lynx depredation. This predictor measures the total light pollution and could also serve as a proxy for human disturbance. These results show that fields which are very close to human settlements do not seem to be targets of lynx depredation. These results show that depredation events generally occur within areas lynx utilize independently to the presence of livestock, supporting the hypothesis that attacks tend to occur due to chance encounters rather than individuals specifically seeking out farms (Moa *et al.*, 2006).

While lynx density and roe deer density are factors that are very difficult to control through non-lethal measures, my other results could help mitigating future depredation events. Moving sheep closer to human settlements as well as putting up lights, especially in rugged terrain where lynx occur, might prove to be an effective mitigation tool. Future studies could focus on examining these measures for preventing lynx attacks in Sweden.

Surprisingly, forest presence did not seem to be a significant predictor of depredation events. Lynx tend to utilize forest edges to search for prey, thus I assumed distance to forest would influence the probability depredation as well. Contrary to my third hypothesis, distance to forest and forest presence did not influence the risk of depredation. There are two possible explanations for this: first, fields are treated as points within my analysis and points can occur at any location within the field. Since these points could strongly influence the effective distance to the nearest forest and the percentage of forest cover in a 100 meter radius my method might have failed to detect these trends. Second, the forest variable included all types of forest (coniferous, deciduous, within wetlands or not, all ages and height of trees), simplifying the forested landscape. These kinds of differences could influence lynx movement and possibly hindered my model at detecting trends. Milanesi *et al.* (2019) utilized percent forest cover on a 1-km^2 grid. Looking at the forested landscape on a larger scale would be interesting to include in the future.

Although not included within my hypotheses, water presence seemed to have an effect on depredation. Non-lethal mitigation measures, such as electric fencing, are very difficult to maintain at fields bordering water (Kaartinen *et al.,* 2009). Nevertheless, electric fences are considered an effective mitigation tool against depredation from other large predators, but less effective for lynx (Bruns *et al.,* 2020; Viltskadecenter 2004). Since previous research suggests that lynx do not actively search for sheep fields, but rather encounter them randomly (Moa *et al.,* 2006), water presence might be linked to probability of encounter. As lynx move through the landscape water pose barriers for their movement. Consequently, they have to move alongside those barriers to move through their territory, increasing the probability of encountering a sheep field at random. Furthermore, not water, but rather correlated factors could be responsible for the increase in probability of depredation. Water could be correlated to certain vegetation, or vegetation edges. Also, water could attract prey such as roe-deer. Further research is needed to understand this dynamic.

Dynamics of repeated attacks

The dynamics of repeated attacks seem to be tied to the occurrence of attacks in the first place as many of the factors from the initial analysis influence repeated attacks as well. We can see that density of both lynx and roe deer significantly increases the risk of a second attack. Specifically, we can see that secondary depredation events seem to be heavily tied to the presence of lynx, only slightly increasing at higher densities (Figure 5). Thus, sole presence of lynx family groups seems to be more important than their actual density. Distance to water also significantly affected the probability of a repeated attack. This strengthens the hypothesis, that barriers in the landscape like water increase the probability of a lynx encountering a sheep field (see above).

Hunting also had significant impact on repeated attacks and could be used to prevent further attacks in the short term. My study found that hunting events decreased the probability of a repeated attack within the next year by 60% which is in line with my fourth hypothesis (Figure 6). Similarly, a study a study in France showed that the removal of lynx decreased risk of depredation in the short, but not in the long term (Stahl *et al.,* 2001). For other species, lethal control has proven to be effective as well, with effectiveness ranging between 67 and 83 percent (Miller *et al.*, 2016).

We know that farmers increase their mitigation efforts following an attack (Widman *et al.*,2019). Nevertheless, risk of a lynx attack is 55 times higher on farms that had experienced a depredation event in the past year (Karlsson & Johansson, 2010). In my study, about 20 % of the sheep farms experienced a second depredation event within one year. Karlson & Johansson (2010) suggested that the main reason for this second event was the result of a predator returning to the kill site to either feed or search for new prey, so protective hunt within the area of the event might be warranted. I did not explore the effect of hunting on depredation after one year. Stahl *et al.* (2001) showed that territories where removal of lynx had occurred were recolonized and attacks reoccurred within a few years. Thus, lethal control may only be an effective mitigation measure for the short term. I did not explore the time-delay between initial depredation and hunting event. Since most depredation events occur within the first few days of the first event, effectiveness of hunting could be increased if done immediately after a depredation event (Karlsson & Johansson, 2010). Furthermore, impact on neighbouring farms could be considered as well. Santiago-Avila *et al.* (2018) show that lethal control of wolves in Michigan at a farm can result in an increased risk of depredation on neighbouring farms. Lynx are solitary, thus I do not expect the same result as when using lethal control in wolves.

Future research could also focus on the recent range expansion of lynx in Sweden and investigate its impact on depredation. For other large carnivores, impact levels of depredation were lower in areas where they never experienced local extinction compared to newly recolonized areas (Gervasi *et al.*, 2020). Investigating whether this trend is also seen for lynx in Sweden and, possibly what factors influence it could prove to be valuable to mitigate future depredation.

5. Conclusion

This thesis gives insight into the dynamics of lynx depredation on domestic sheep. Depredation risk seems to be connected to lynx density as well as the density of roe deer, their main prey. Furthermore, distance to human settlements, artificial night-time brightness, terrain ruggedness and water presence influence the risk of lynx depredation on sheep.

I was able to create a relatively strong model for predicting depredation events on farms, which might indicate that a ”site” effect is more likely than the existence of ”problem individuals”. This study could serve as a tool to examine fields and their relative risk of lynx depredation. Mitigation measures should be focused on fields which are further away from human settlements within rugged terrain and on fields in close proximity to water.

Risk of a repeated attack increased with density of lynx, roe deer as well as proximity to water. Especially the presence of lynx family groups seems to have a strong effect on the risk repeated attacks. Lynx hunting within the area after an attack decreases the probability of a second attack by 60 % within the next year. This emphasizes the effectiveness of lethal control at least in the short term. Nevertheless, depredation events are still relatively rare and need to be approached on a case by case basis. Also, I need to acknowledge that there are different ethical and value-based factors that need to be taken into consideration when developing a management plan for lynx. For a sound management strategy, it is crucial to consider values held by all stakeholders involved.

Future research should focus on understanding the dynamic of water presence and distance to lynx depredation events. This dynamic is clear for other large predators but the cause of this effect remains unknown for lynx. Also, the effect of forest on lynx depredation events in Sweden remain unknown and should be investigated. Furthermore, the effectiveness of the non-lethal mitigation measures proposed here could be tested and evaluated.

I hope that this thesis has led to a better understanding of lynx depredation on sheep in Sweden. Understanding these dynamics is crucial for an informed debate about the role of large predators, especially lynx, in Sweden.

References

Akaike, H. (1973). Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, *60*(2), 255-265.

Andrén, H., Linnell, J. D., Liberg, O., Ahlqvist, P., Andersen, R., Danell, A., ... & Segerström, P. (2002). Estimating total lynx Lynx lynx population size from censuses of family groups. *Wildlife biology*, *8*(1), 299-306.

Aronsson, M., Low, M., López-Bao, J.V., Persson, J., Odden, J., Linnell, J.D.C. and Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecology and Evolution* 6(9), 2957-2967, Doi: 10.1002/ece3.2032

Barton, K., & Barton, M. K. (2020). Package 'MuMIn'in R, Version 1.43. 17.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J. D., Odden, J., Andersen, R., ... & Gaillard, J. M. (2009). What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people?. *Ecography*, *32*(4), 683-691.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bivand, R.,Keitt, T.,Rowlingson, B., (2020). rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.5-18. https://CRAN.R-project.org/package=rgdal

Bouyer, Y., San Martin, G., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. (2015a). Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biological Conservation*, *191*, 291-299.

Bouyer, Y., Gervasi, V., Poncin, P., Beudels-Jamar, R. C., Odden, J., & Linnell, J. D. C. (2015b). Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal conservation*, *18*(3), 271-278.

Bradburn, M. J., Clark, T. G., Love, S. B. and Altman, D. G. (2003a). Survival Analysis Part II: Multivariate data analysis- An introduction to concepts and methods. *British Journal of Cancer*, 89: 431–436.

Bruns, A., Waltert, M., & Khorozyan, I. (2020). The effectiveness of livestock protection measures against wolves (Canis lupus) and implications for their co-existence with humans. *Global Ecology and Conservation*, *21*, e00868.

Burnham, K. P. and Anderson, D. R. (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York, *Springer-Verlag*

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197,516-519

Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., ... & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*(6216), 1517-1519.

Clark, T. G., Bradburn, M. J., Love, S. B. and Altman, D. G. (2003). Survival Analysis Part I: Basic concepts and first analyses. *British Journal of Cancer*, 89: 232–238.

Elofsson, K., M. Widman, T. Häggmark-Svensson, Steen, M. (2015).Påverkan från rovdjursangrepp pålandsbygdsföretagens ekonomi. Report167. Department of Economics, Swedish University of AgriculturalSciences, Uppsala, Sweden. [In Swedish.]

ESRI (2020). ArcGIS Desktop 10.7.1. Redlands, CA, USA. Environmental Systems Research.

Fawcett, T. (2006). An introduction to ROC analysis. *Pattern recognition letters*, *27*(8), 861-874.

Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., ... & Heurich, M. (2017). Habitat selection by Eurasian lynx (Lynx lynx) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecology and evolution*, *7*(16), 6367-6381.

J. Fox and S. Weisberg. An R Companion to Applied Regression. Sage, Thousand Oaks CA, 3rd edition, 2019. URL http://z.umn.edu/carbook.

Frank, J., Månsson, J., Levin, M. & Höglund, L. (2020). Viltskadestatistik 2019 Skador av fredat vilt på tamdjur, hundar och gröda *Viltskadecenter, SLU 2020-2* URL www.slu.se/viltskadecenter

Gandrud, C. (2015). SimPH: An R Package for Illustrating Estimates from the Cox Proportional Hazard Models Including for Interactive and Nonlinear Effects. *Journal of Statistical Software*, 65: 1–20.

Gangaas, K. E., Kaltenborn, B. P., & Andreassen, H. P. (2013). Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. *PloS one*, *8*(7), e68849.

Gervasi, V., Linnell, J., Berce, T., Boitani, L., Cretois, B., Ciucci, P., ... & Gimenez, O. (2020). Ecological and anthropogenic drivers of large carnivore depredation on sheep in Europe. *bioRxiv*.

Gervasi, V., Odden, J., Linnell, J. D., Persson, J., Andrén, H., & Brøseth, H. (2013). Re-evaluation of distance criteria for classification of lynx family groups in Scandinavia.

Gordon, M. and Seifert, R. (2020). Greg: Regression Helper Functions. R package version 1.3.3.

Hellborg, L., Walker, C. W., Rueness, E. K., Stacy, J. E., Kojola, I., Valdmann, H., ... & Ellegren, H. (2002). Differentiation and levels of genetic variation in northern European lynx (Lynx lynx) populations revealed by microsatellites and mitochondrial DNA analysis. *Conservation Genetics*, *3*(2), 97-111.

Herfindal, I., Linnell, J. D., Moa, P. F., Odden, J., Austmo, L. B., & Andersen, R. (2005). Does recreational hunting of lynx reduce depredation losses of domestic sheep?. *The Journal of Wildlife Management*, *69*(3), 1034-1042.

Hijmans, R. J., (2020). raster: Geographic Data Analysis and Modeling. R package version 3.3-13. https://CRAN.R-project.org/package=raster

Kaartinen, S., Luoto, M., & Kojola, I. (2009). Carnivore-livestock conflicts: determinants of wolf (Canis lupus) depredation on sheep farms in Finland. *Biodiversity and Conservation*, *18*(13), 3503.

Karlsson, J., & Johansson, Ö. (2010). Predictability of repeated carnivore attacks on livestock favours reactive use of mitigation measures. *Journal of Applied Ecology*, *47*(1), 166-171.

Kassambara, A., Kosinski, M. and Biecek, P. (2019). Survminer: Drawing Survival Curves using 'ggplot2'. R package version 0.4.6.

Linnell, J. D., Cretois, B., Nilsen, E. B., Rolandsen, C. M., Solberg, E. J., Veiberg, V., ... & Kaltenborn, B. (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biological Conservation*, *244*, 108500.

Linnell, J. D., Odden, J., Smith, M. E., Aanes, R., & Swenson, J. E. (1999). Large carnivores that kill livestock: do" problem individuals" really exist?. *Wildlife Society Bulletin*, 698-705.

López-Bao, J. V., Frank, J., Svensson, L., Åkesson, M., & Langefors, Å. (2017). Building public trust in compensation programs through accuracy assessments of damage verification protocols. *Biological Conservation*, *213*, 36-41.

Mattisson, J., & Frank, J. (2020). Bestandsovervåking av gaupe i 2020.

Mattisson, J., Odden, J., Nilsen, E. B., Linnell, J. D., Persson, J., & Andrén, H. (2011). Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: Can ecological research contribute to the development of a fair compensation system?. *Biological conservation*, *144*(12), 3009-3017.

Milanesi, P., Puopolo, F., Fabbri, E., Gambini, I., Dotti, F., Sergiacomi, U., ... & Caniglia, R. (2019). Improving predation risk modelling: prey-specific models matter. *Hystrix, the Italian Journal of Mammalogy*, *30*(2).

Miller, J. R., Stoner, K. J., Cejtin, M. R., Meyer, T. K., Middleton, A. D., & Schmitz, O. J. (2016). Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. *Wildlife Society Bulletin*, *40*(4), 806-815.

Moa, P. F., Herfindal, I., Linnell, J. D., Overskaug, K., Kvam, T., & Andersen, R. (2006). Does the spatiotemporal distribution of livestock influence forage patch selection in Eurasian lynx Lynx lynx?. *Wildlife Biology*, *12*(1), 63-70.

Molinari-Jobin, A., Molinari, P., Breitenmoser-Würsten, C., & Breitenmoser, U. (2002). Significance of lynx Lynx lynx predation for roe deer Capreolus capreolus and chamois Rupicapra rupicapra mortality in the Swiss Jura Mountains. *Wildlife Biology*, *8*(1), 109-115.

NOAA's National Geophysical Data Center (2019). VIIRS Day/Night Band Nighttime Lights. https://ngdc.noaa.gov/eog/viirs/download_dnb_composites.html

Odden, J., Nilsen, E. B., & Linnell, J. D. (2013). Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. *PloS one*, *8*(11), e79261.

Odden, J., Herfindal, I., Linnell, J. D., & Andersen, R. (2008). Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *The journal of wildlife management*, *72*(1), 276-282.

Odden, J., Linnell, J. D., & Andersen, R. (2006). Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *European Journal of Wildlife Research*, *52*(4), 237-244.

Odden, J., Linnell, J. D., Moa, P. F., Herfindal, I., Kvam, T., & Andersen, R. (2002). Lynx depredation on domestic sheep in Norway. *The Journal of wildlife management*, 98-105.

QGIS Development Team. (2020). *QGIS geographic information system*. Beaverton

Pebesma, E.J., R.S. Bivand, (2005). Classes and methods for spatial data in R. R News 5 (2), https://cran.r-project.org/doc/Rnews/

Ramler, J. P., Hebblewhite, M., Kellenberg, D., & Sime, C. (2014). Crying wolf? A spatial analysis of wolf location and depredations on calf weight. *American Journal of Agricultural Economics*, *96*(3), 631-656.

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). Index that quantifies topographic heterogeneity. *intermountain Journal of sciences*, *5*(1-4), 23-27.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167).

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J. C., & Müller, M. (2011). pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC bioinformatics*, *12*(1), 1-8.

Stahl, P., Vandel, J. M., Herrenschmidt, V., & Migot, P. (2001). Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *Journal of Applied Ecology*, *38*(3), 674-687.

Sunde, P., Kvam, T., Bolstad, J. P., & Bronndal, M. (2000). Foraging of lynxes in a managed boreal-alpine environment. *Ecography*, *23*(3), 291-298.

Suryawanshi, K. R., Bhatnagar, Y. V., Redpath, S., & Mishra, C. (2013). People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. *Journal of Applied Ecology*, *50*(3), 550-560.

Swenson, J.E. & Andrén, H. (2005) A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. *People and Wildlife, Conflict or Coexistence?* (eds Woodroffe, R., Thirgood, S. & Rabinowitz, A.), pp. 323–339. Cambridge University Press, Cambridge, UK.

Therneau, T. (2020). A Package for Survival Analysis in R. : R package version 3.1-11.

Treves, A. & Naughton-Treves, L. (2005) Evaluating lethal control in the management of human-wildlife conflict. *People and Wildlife. Conflict or Coexistence?*(eds Woodroffe, R., Thirgood, S. & Rabinowitz, A), pp. 86–106. Cambridge University Press, Cambridge, UK

Widman, M., Steen, M., & Elofsson, K. (2019). Indirect costs of sheep depredation by large carnivores in Sweden. *Wildlife Society Bulletin*, *43*(1), 53-61.

Widman, M., & Elofsson, K. (2018). Costs of livestock depredation by large carnivores in Sweden 2001 to 2013. *Ecological Economics*, *143*, 188-198.

Woodroffe, R., Thirgood, S., & Rabinowitz, A. (Eds.). (2005). *People and wildlife, conflict or co-existence?* (No. 9). Cambridge University Press.

Viltskadecenter (2004). Tamdjursstängsel och lodjur – försök i djurparker. Faktablad Viltskadecenter.

Zimmermann, F., Breitenmoser-Würsten, C., & Breitenmoser, U. (2005). Natal dispersal of Eurasian lynx (Lynx lynx) in Switzerland. *Journal of Zoology*, *267*(4), 381-395.

Acknowledgements

I would like to thank my supervisors for supporting and guiding me through this thesis. Especially, I would like to thank Henrik for helping with his statistical knowledge and guiding me through the analysis. I would like to thank Jens for providing me with his great ecological knowledge as well as reminding me to not only look at numbers but at the ecological connections as well.

Furthermore, I would like to thank Göran Bergqvist from the Swedish Association for Hunting and Wildlife Management (Svenska Jägareförbundet) for providing me with data on hunting districts as well as Swedish Board of Agriculture (Jordbruksverket) for providing me with GPS locations of sheep farms.

I am very thankful for my companions in the "Bunker" at Grimsö Wildlife Research station. Rick Heeres and Roberto Lo Monaco, I am thankful for all the input, statistical discussions and the occasional "Research Meetings" in the late evenings over a beer.

Special thanks to my family and friends who supported me throughout the entire time, even when we were apart due to distance or corona.

Appendix I Additional plots

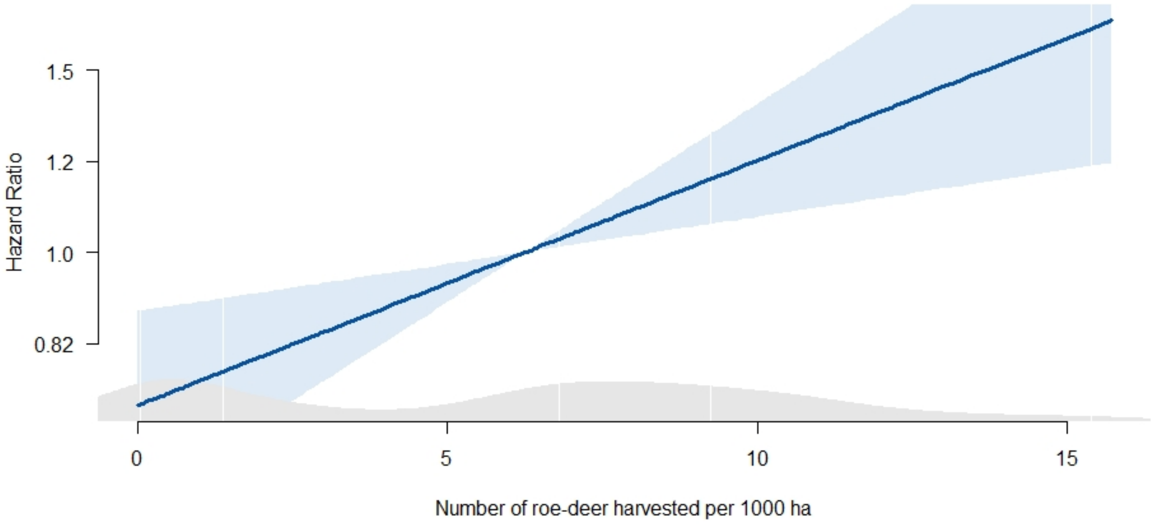

Figure 7 Hazard ratio estimations for roe deer density on repeated attacks (light blue = 95% confidence interval; grey = amount of data).

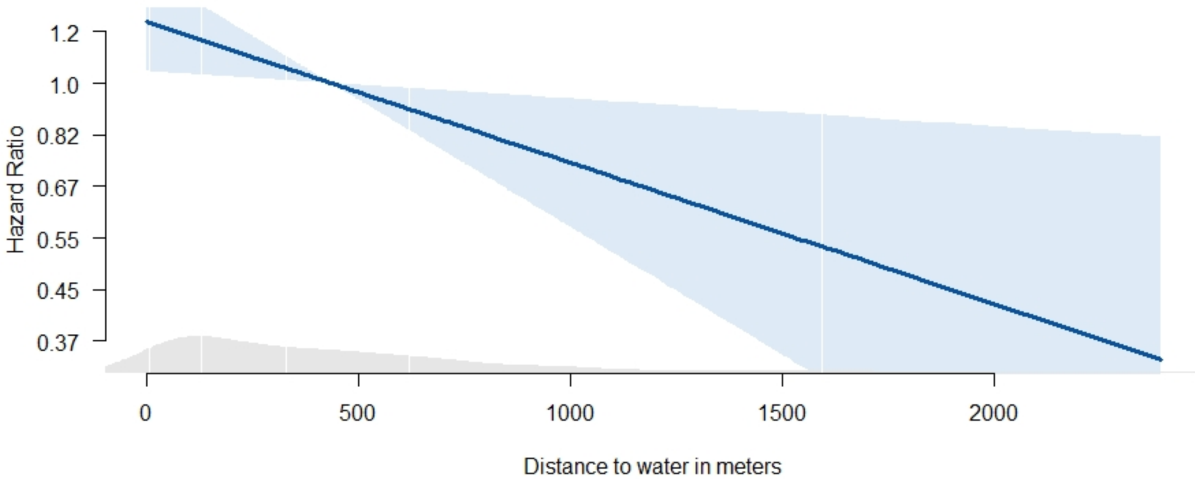

Figure 8 Hazard ratio estimations for distance to water on repeated attacks (light blue = 95% confidence interval; grey = amount of data).

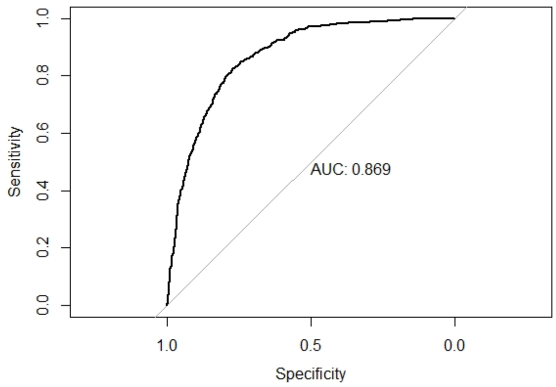

Figure 9 Receiver operator characteristic graph based on the train dataset. AUC value also corresponds to the average model utilizing the train dataset