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Calving site selection by moose (*Alces alces*) along a latitudinal gradient in Sweden

Masterarbeit
zur Erlangung des akademischen Grades
Master of Science

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angefertigt am „Department of Wildlife, Fish and Environmental Studies“
an der schwedischen Universität für Agrarwissenschaft (Swedish University of Agricultural Sciences, SLU), Umeå

Januar 2012

Preface

This report is written as the final thesis for my master degree in Wildlife ecology and Wildlife management at the University of Natural Resources and Applied Life Sciences (BOKU), Vienna. I experienced this project as an excellent opportunity to extend my knowledge about ungulate species and to get to know another country as well as culture. My stay in Sweden is supported by the European Union Erasmus scholarship.

I would like to take the opportunity to thank the people who made this project possible.

First of all, I would like to express my gratitude to my friends and family for their patience, encouragements, invaluable support, and faith in me. Not only during the period of my final thesis but throughout my two years master study.

“Tack så mycket“ to my main supervisor Göran Ericsson and my co-supervisor Navinder Singh from the Swedish University of Agricultural Sciences (SLU), Umea.

Göran, I am very grateful for your supervision, guidance and support. Thanks a lot for providing the data and for giving me the opportunity to work on this project.

Navinder, I am very thankful for your guidance, your motivating humour and your useful suggestions. I thank you for your pleasant company in the office and the joyful friendship outside the working hours.

A special thanks to Eric Andersson for sharing your knowledge with me and for organising my two fieldtrips in Sweden. I really enjoyed your company during the stay in the north.

Thanks to Holger Dettki and Anders Kagervall for answering all my questions about ArcGIS, when I knocked on the office door.

I thank Anders Hågeryd for my pleasant stay in Växjö. I loved it to listen to your stories and to join you in the field.

Special thanks to Wiebke Neumann for helping me to get into the data and for all her useful suggestions and comments.

Thanks to Jonas Kindberg for kindly allowing me to use his data.

To all I mentioned here, and those that I did not specifically mention by name, I could not have finished my final thesis without your encouraging support.

Thanks a lot!

Alexandra Haydn

25-10-2011, Vienna

Zusammenfassung

In dieser Studie wurden die Faktoren untersucht, welche die Selektion von Setzplätzen bei Elchen (*Alces alces*) in unterschiedlichen geografischen Gebieten in Schweden beschreiben. Daten von 112 Elchindividuen in den Jahren 2004 bis 2011 wurden genutzt und insgesamt 156 Setzplätze und 800 zufällige Plätze in sechs verschiedenen Studiengebieten (Hemavan, Hällnäs, Nordmaling, Misterhult, Öster Malma and Växjö) wurden für die Analyse verwendet. Die Eigenschaften der genutzten Setzplätze wurden mit denen der verfügbaren Setzplätze verglichen (use versus availability approach), um die Habitatselektion auf zwei Ebenen zu untersuchen: innerhalb Schwedens und pro Gebiet. Die verwendeten Parameter bezogen sich auf die Abwägung zwischen dem Erwerb von ausreichend Nahrung, Wasser und Sicherheit. Das gemischte lineare Regressionsmodell (linear mixed effects model) wurde angewendet, um die genutzten von den zufällig gewählten verfügbaren Setzplätzen zu unterscheiden.

Die Ergebnisse waren unterschiedlich auf Landesebene und Gebietsebene. Innerhalb Schwedens befanden sich die Setzplätze weiter weg von Wasser, höher und näher an Straßen und Häusern im Vergleich zu den zufälligen Plätzen. Die Setzplätze waren häufiger in der Landbedeckungskategorie Laubwald und seltener in einigen anderen Landbedeckungs-kategorien im Vergleich zu den zufälligen Plätzen.

In zwei Studiengebieten lagen die Setzplätze höher im Vergleich zu den zufällig gewählten Plätzen. In einem Gebiet waren sie an steileren Stellen, während in einem anderen die Setzplätze an flacheren Stellen waren. In Nordmaling (63° 34' N, 19° 30' E) waren die Setzplätze weiter entfernt von Straßen, in Misterhult (56° 28' N, 13° 37' E) weiter entfernt von Häusern und in Växjö (56° 52' N, 14° 48' E) weiter entfernt von Wasser. Da unterschiedliche Landbedeckungskategorien genutzt wurden, könnte es sein, daß Elche keine speziellen Landbedeckungskategorien bevorzugen. Allerdings befanden sich die meisten Setzplätze nicht in Sümpfen. Dies könnte darauf hinweisen, dass Elche einen trockenen Untergrund als Setzplatz bevorzugen.

Beide Modelle (Landesebene und Gebietsebene) zeigten, dass die Setzplätze weiter weg von Wasser und in höheren Lagen waren als zufällige Plätze. Elche könnten die Nähe zu Wasser vermeiden, um das Prädationsrisiko zu verringern, da Prädatoren oft an Flüssen entlang gehen, welche als Leitlinien dienen könnten. Somit sind Nahrung und Wasser wohl eher unwichtig und die Sicherheit spielt eine grössere Rolle bei der Wahl des Setzplatzes und

es deutet darauf hin, dass Elche eine Abwägung zwischen Nahrung, Wasser und Sicherheit vornehmen.

Da die Analyse auf Landes- und Gebietsebene widersprüchliche Resultate ergab, wäre es zudem sinnvoll, örtliche und umliegende Habitateigenschaften mit einzubeziehen.

Abstract

In this research I examined the factors determining calving site selection by moose (*Alces alces*) across a latitudinal gradient in Sweden. Data from 112 individual moose between the years 2004 and 2011 was used. In total 156 calving and 800 random sites from six different study areas (Hemavan, Hällnäs, Nordmaling, Misterhult, Öster Malma and Växjö) were used for the analysis. A use versus availability approach was used. Therefore, the characteristics of the calving sites were compared with the characteristics of the random sites to identify habitat selection at a country- and area-scale. The used variables were related to the trade-off between acquiring forage, water and safety. Linear mixed-effects models (LME) were used to distinguish the used from the random sites.

The results of the country-scale (all areas were analysed together) often differed from the results of the area-scale (each area was analysed separately). At the country- scale, calving sites were located further away from water, at higher elevation and closer to roads and houses compared to the random sites. The calving sites were located more often in the land cover class broad leaved forest on mires compared to the random sites. Calving sites were less often located in several other land cover classes. At the area-scale, calving sites were located at higher elevations in two study areas. In one study area, the calving sites were located at steeper slopes, whereas in another study area, calving sites were located at lower slopes. Calving sites were further away from roads in Nordmaling (63° 34' N, 19° 30' E), further away from houses in Misterhult (56° 28' N, 13° 37' E) and further away from water in Växjö (56° 52' N, 14° 48' E) compared with random sites.

As a wide variety of land cover classes were used, moose might not have preferences for some special land cover class. However, most of the calving sites were located not on mires. This could indicate that moose prefer dry ground as calving sites. Both, the among-area and the within-areas models showed that the calving sites were further from water and at higher elevation than random sites. Moose might avoid water to reduce risk of predation, as predators often walk along rivers, which might work as lead lines. As a variety of land cover classes were used, safety seems to play a key role. Altogether, this indicates that moose need to make a trade-off between water, forage and safety, whereof safety seems to be more essential than forage and water.

Additionally, as contradictory results were found, when analyzing the data at the country-scale and at the area-scale, the suggestion will be to include local habitat characteristics as well as the characteristics of the surrounded area.

Contents

1 Introduction

Habitat selection by animals is a multiscale process (Johnson 1980). Animals select habitat to access food, to escape predators and find denning or resting sites (Krausman 1999). These decisions are made to increase the survival (Hilden 1965). Especially during the calving/lambing season habitat selection of animals is crucial, as animals need to find a suitable nest site or birth place to ensure survival of their offspring (Hilden 1965).

To increase the chances of offspring survival, females make trade-offs. These maternal trade-offs may occur between escaping predators and ensuring access to food (Bowyer et al. 1998b, Poole 2007). Females need to find calving sites where the risk of neonatal predation is low and the availability of food and water supply is high enough to fulfill their nutrient requirements during lactation (Bowyer et al. 1998b; Poole 2007). Hence, birth site selection is an important decision in many animal species to maximize their reproductive success.

Predation risk for ungulate neonates is often high during the first days or weeks of life (Bowyer et al. 1998b; Bowyer et al. 1999; Ballard et al. 2001; Carr et al. 2006), hence they may adopt behavioural strategies to minimize risk of predation. These may involve: forming aggregations to give birth or using different maternal-neonate strategies, known as follower or hider strategies (Lent 1974). Species living in wide and open environments form aggregations for giving birth and their neonates adopt the follower strategy (Lent 1974; Kie 1999). While ungulates living in forested areas give birth in solitude, their neonates are classified as hiders (Lent 1974; Kie 1999). Followers actively follow their mother shortly after birth, whereas hiders spend their first few days of life hidden on the ground (Lent 1974). For e.g., Wildebeest (*Connochaetes taurinus*) as well as Saiga antelopes (*Saiga tatarica*), are ungulate species living in open habitats and they form large aggregations to give birth and synchronize their time of birth to the peak of the forage availability (Kie 1999). Beside these strategies, Saiga antelopes for instance, select calving grounds in relation to environmental factors, as well as availability of water and food (Singh et al. 2010). This indicates a trade-off between predation and water requirement (Singh et al. 2010).

Roe deer (*Capreolus capreolus*) as a representative of an ungulate species living in forested habitat use the strategy of giving birth in solitude and their neonates are classified as hiders (Lent 1974). By using the hider strategy, roe deer might reduce the predation risk (Lent 1974). Additional to the hider strategy of the neonates, female roe deer select calving site located in denser habitat that provided cover from predators (Bongi et al. 2008).

Moose (*Alces alces*) is a typical representative of ungulate species living in forests. Moose females give birth in solitude and the neonates follow mostly the hider strategy (Stringham 1974). Especially ungulates with vulnerable neonates and hider strategy spend more time at one place. Moose calves, for instance, are generally less mobile during their first days of life and are sensitive to predation by brown bears up to the first 4 weeks (Swenson et al. 2007). Female moose are also known to make trade-offs between risk of predation and food availability (Boywer et al. 1999).

Since habitat selection is a hierarchical multiscale process, the factors that determine these decisions may differ at scales. At a broad landscape scale factors such as elevation, habitat type, predators and distance to water or infrastructure may determine the calving site selection (Bowyer et al. 1999; Berger 2007; Poole et al. 2007). Factors such as food availability, soil moisture and vegetation cover might be the main predictors at the fine scale (Bowyer et al. 1999; Poole et al. 2007). Bowyer et al. (1999) identified greater forage abundance, a southeasterly aspect and better visibility as being the key parameters at Alaskan moose birth sites. Similarly, Wilton & Garner (1991) found that moose calving sites were most often situated at high points, and on knolls, on islands, and Addison et al. (1990) determined the calving sites were usually within 200 m of water.

In this study, I examine the factors affecting the calving site selection by moose across a large latitudinal gradient in Sweden. The natural predators of moose in Sweden are brown bear (*Ursus arctos*) and wolf (*Canis lupus*). Due to the low numbers of wolves in Sweden, wolves are not the main predators of moose in Sweden. The main predator of moose, especially for the neonates, is the brown bear. In the southern part of Sweden, brown bears are absent; whereas in the northern part of Sweden the brown bear population counts about 3200 individuals in 2008 (Kindberg et al. 2011). Berger (2007) showed that moose cows may give birth next to paved roads, when brown bears are present in the area. As Brown bears tend to avoid human infrastructure (houses and roads) within a distance of at least 500 m in the Yellowstone (Mattson 1990; Mace et al. 1996), this indicates that moose may use human infrastructure as a protection against predation. In Sweden, brown bears prefer habitat further than 10 km away from human settlements, only younger brown bears might come closer (Kindberg 2010). Given that humans are main hunters of moose in Sweden, moose may avoid human disturbance. Humans may be regarded as predators in Sweden, especially in areas with high hunting pressure. Limited data is available on moose calving site selection in Sweden, whereas Sweden has the highest moose population in Europe with a winter population of about 250.000 individuals (Lavsund et al. 2003). Hence, Sweden offers an interesting opportunity to study its moose population. Besides having the largest moose population in Europe, Sweden has a large variation in climate from north to south.

1.1 Aim of the research

In this research I examined the factors determining calving site selection by moose across a latitudinal gradient in Sweden. I compared the characteristics of the calving sites with the random sites to identify habitat selection. The used variables are related to the trade-off between acquiring forage, water and safety.

1.2 Research question

Which factors determine calving site selection by moose across a geographical gradient in Sweden in relation to forage and safety?

1.3 Hypotheses

Hypotheses 1: Availability of forage and water will affect the calving site selection

Prediction 1a) If forage availability is important for moose, the calving sites should be located in land cover classes with much forage (younger forest, broadleaved forest or coniferous forest) compared to random sites.

Prediction 1b) If water availability is important for moose, calving sites should be located closer to water than random sites.

Hypotheses 2: Safety will affect the calving site selection

Prediction 2a) If bears frequent lower elevation, calving sites should be located at higher elevations compared to random sites.

Prediction 2b) If steeper slopes provide cover through offering higher visibility, calving sites should have steeper slope angles compared to random sites.

Prediction 2c) If humans are seen as predators, calving sites should be further away from roads and houses compared to random sites.

Prediction 2d) If humans are used as a shield against predation, calving sites in areas with brown bears should be closer to roads and houses compared to random sites.

2 Materials and method

2.1 Study areas

This research was conducted in six different study areas in Sweden, located in the counties Norrbotten, Västerbotten, Småland and Södermanland (see Figure 1). These study areas were chosen to represent different latitudinal gradients in Sweden. The general differences between these areas are population density, elevation, bear density and climate. In the northern regions of Sweden, there is general lower density in population and infrastructure compared to the southern regions in Sweden. The three northern study areas are Nordmaling (56° 52' N, 14° 48' E), Hällnäs (64° 18' N, 19° 38' E) and Hemavan (65° 48' N, 15° 6' E). They are located in the counties Norrbotten and Västerbotten. The main differences between these areas are elevation, forest types and population density. Hemavan, the northernmost study area is in a mountainous area (higher elevation), lies next to the border with Norway and has the highest bear density of 0,36- 0,95 brown bear observations per 1000 hours as described in Kindberg et al. (2009). Hällnäs is between the coast and the mountains with a medium bear density of 0,043 - 0,36 observations /1000h (Kindberg et al. 2009). Nordmaling is close to the coastline and has a low bear density (0 - 0,043 observations/1000h; Kindberg et al. 2009). The three southern study areas Växjö (56° 52' N, 14° 48' E), Öster Malma (58° 57' N, 17° 9' E) and Misterhult (56° 28' N, 13° 37' E) are located in the counties Småland and Södermanland. No bears are present in these study areas. Misterhult and Öster Malma are close to the coast, whereas Växjö is located more inland. Due to the latitudinal extent of Sweden a wide range of climate can be found between southern and northern Sweden. The sub-arctic climate in the northern regions is characterized by shorter, cooler summers and longer, colder and snowier winters. Above the Arctic Circle, the sun never sets for some weeks in summer and it never rises for some weeks in winter. With temperatures often below freezing from September through May, snow covers the ground for about 6 month each year, but in summer temperatures can rise up to 25 °C. The annual average rainfall of whole Sweden lies between 500 and 800 mm, while the south-western part receives more precipitation than the rest of the country. The climate in the southern part of Sweden is characterized by warm summers and cold winters, with average high temperatures in summer of 20-25 °C and average low temperature of -4 to 2 °C in the winter. Forests cover about half of Sweden and there are numerous lakes and streams.

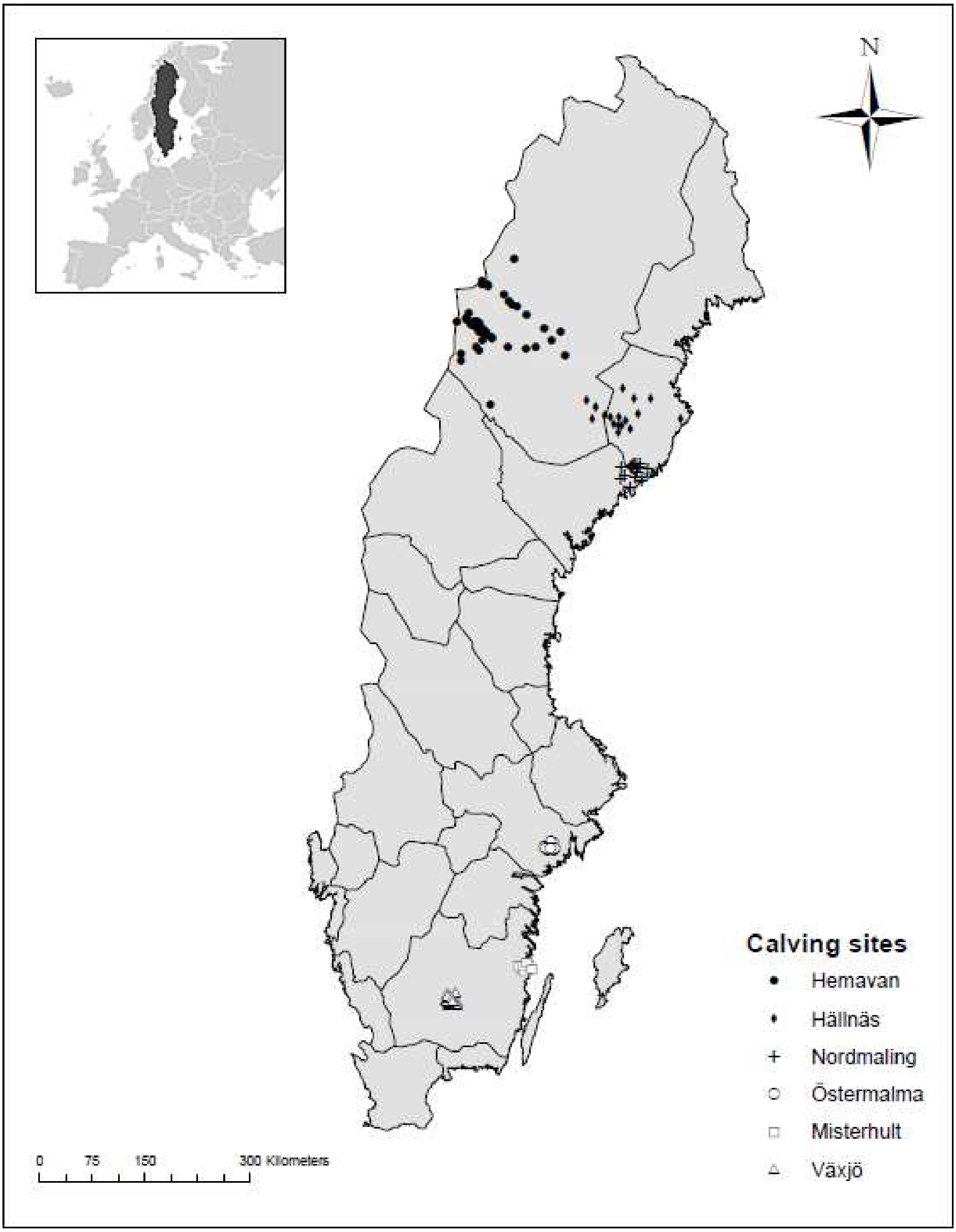

Figure 1. Map of Sweden with calving sites (n=156) for each area.

2.2 Study species

Distribution

Moose are the largest species of the deer family and hence one of the biggest ungulate species in Europe. They are found in the boreal forests of the northern hemisphere. Moose occur in Russia, United States, Scandinavia, Finland, Estonia, Lithuania, Poland, Canada, Czechoslovakia, Manchuria and China (Franzman & Schwartz 2007). Factors that limit their distribution to the north are forage availability and snow depths. Warm climate with temperatures above 27 ˚C for longer periods limit their distribution to the south (Franzman & Schwartz 2007).

Habitat

Moose prefer habitats in the colder northern regions which have seasonal snow cover. They live in taiga and in temperate forests, including the Tundra-subalpine zone. Forest types preferred by moose include boreal, broadleaf and mixed forest. Moose favor patches with early successional stage, which offer abundant forage. In addition to forest, moose also select areas close to water, such as ponds, lakes, rivers and swamps, which have a high concentration of salts. Moose are browsers and they feed on the most digestible plant materials, such as seedlings, buds and tree leaves of e.g. *Betula*, *Fagus* or *Quercus* (Putman 1986; Shipley et al. 1998). Woody species make up > 96 % of moose summer diets (Joyal & Scherrer 1978; Dugan & Wright 2005). The diet is complemented with forbs and aquatic species like *Nitella* sp., *Chara* sp. and *Potomegaton* sp. (Belovsky 1978).

Characteristics

Moose have a massive body with long legs and a short, thick neck. They have long ears, a short tail and their upper lip is longer than the lower lip. Moose are sexually dimorphic. Males are 40 % heavier than females. Their shoulder height is between 180 and 210 cm and the weight ranges for males between 380 and 720 kilograms and for females between 270 and 360 kilograms. The antlers can weigh up to 30 kilograms. The expected life span of moose in the wild is on average 15 years (Novak 1999; Engan 2001; Bubenik 2007).

Behaviour and mating

Moose are solitary animals, with strong bonds between mother and calves. They are not territorial and their activity peaks during sunrise and sunset. Moose spent most of their time feeding, traveling to new feeding sites, ruminating and resting, while lying on the ground.

They mainly stay in the same area, but some populations migrate between winter and summer sites.

The mating season is between September and October. After about 234 days of gestation (Cederlund 1987) females give birth to one or two calves in May or June. Only the females take care of their calves. The calving site is often a secluded area. The calves are very vulnerable during their first few weeks of life and they weigh between 13 to 16 kilograms. The calves begin nursing within the first few hours following birth and take solid food a few days later. Weaning occurs at the age of five months and the calves remain with their mother till shortly before the next offspring are born (Franzmann 1981; Schwartz & Hundertmark 1993; Schwartz 2007).

Moose population and management in Sweden

Sweden has one of the most productive and harvested moose populations in the world. The population size has changed from very low numbers before 1960 to very high numbers in the 1980s with a peak of about 500.000 individuals. The estimated moose population in Sweden during winter 2000/2001 has been 250.000 individuals (Lavsund et al. 2003).

Moose is the most important game species in Sweden. Hunting is a tradition in Sweden and thus a lot of management is done. The most common cause of death of moose in Sweden is hunting (Ericsson & Wallin, 2001). The second most common cause of death is traffic accidents and the lowest impact on moose mortality has the natural predation by brown bears or wolves. However, in core areas of brown bear abundance, up to 26 % of the calves can be killed (Swenson et al. 2007).

With high numbers of moose, conflicts between hunters, forestry and infrastructure agencies occur. Moose have an impact on the forest ecosystem and with higher densities it might get higher (Lavsund et al. 2003). Furthermore, high moose populations increase the chances of traffic collisions in Sweden (Seiler 2005).

2.3 Research design and data collection

In different areas in Sweden, adult moose were immobilized using a dart gun from a helicopter. A mixture of an anaesthetic and a tranquilizer (ethorphine and xylazine) was injected (Sandegren et al. 1987).

Age of the moose was estimated by evaluating tooth wear while moose were tranquilized (Ericsson & Wallin 2001). The used collars are from the company Vectronic Aerospace GmbH (Fielitz 2003). The collars weighed about 1.1 kilograms and have a battery lifetime of about 3 years. The moose were equipped with these collars and additionally with uniquely numbered ear-tags. A picture of a collared and ear tagged moose can be found in Appendix I. The collars included a Global Positioning System (GPS) receiver, Global System for Mobile communication (GSM) modem, and a traditional VHF-beacon (Vectronic Aerospace GmbH, Berlin, Germany). Positions were taken every 30 minutes or every 2 hours and this information was sent to a database server by using the Short Messaging Service (SMS). The GSM cell phone network was used. Data is stored in a Microsoft Access Database on a server of the Swedish university of Agricultural Sciences (SLU) in Umea (Dettki et al. 2004). The GPS-coordinates were automatically displayed as point locations on a map. A figure of the used automatic system can be seen in Appendix II. Each captured moose got a unique number to identify the individual in the database. For this research only females with collars were used. During the calving season, GPS positions of the females were taken in an interval of 30 minutes.

To prevent missing a birth event, the GPS positions of the collared females were monitored on a daily basis during the calving season. The calving site is defined as the place where the females give birth. This site can be identified by looking at the GPS data on the Map. The calving site on the map is characterized by seeing the "calving cluster". A calving cluster is defined as a cluster of points. In the middle of the cluster a cloud of points can be seen which is the point where the offspring is born. Some points (GPS-coordinates) are outside the cloud of points. These points were taken when the mother left its offspring to search for forage. But it can clearly be seen that the female is always coming back to the middle of the cloud. Two examples of calving clusters are shown in Appendix III. After the identification of the calving cluster, the coordinates from the point in the middle of the cluster were used to find the site in the field. With the use of GPS and a VHF antenna, the female moose were tracked to find the calving site. The field check is done when the calves are expected to be not younger than 24 hours to prevent disturbing them too early and to ensure that the mother- offspring bond is strong enough. Fieldwork was done to check the number of calves born and to collect some site characteristics and as well to find out the real calving site location.

The calving date and the location of the calving site were registered and confirmed after the field check. One example of a calving site in the field is shown in Appendix IV. This procedure of fieldwork is done for all study sites.

2.4 Modelling and statistics

2.4.1 Observed parameters

For the spatial modeling I used the software ArcGIS 9.3.1 to combine data from different datasets for each area and the layers of environmental and other variables. All used layerfiles were available on the server of the SLU network.

First, all calving sites had to be extracted from the general moose dataset from the main server of the SLU network. This was done with Microsoft Access. The access file was used to create a new dataset and a new layer with calving sites from moose in ArcGIS. Some calving sites had to be removed, because they were located outside of Sweden and others had to be removed due to missing data. More than 300 calving sites were recorded, but only 156 calving sites were used for the analysis.

Another layerfile was created in ArcGIS with the random sites. The random sites were taken within the surrounding of each study area. The boundaries of the polygon were based on the locations of the calving sites per area. The parameters water, roads and buildings were erased from the buffer areas to prevent taking random sites in non suitable calving habitat. Within these buffer areas, 200 random sites were taken for areas with more than 40 calving sites, and 100 random sites were taken for areas with less than 40 calving sites (see Table 2).
The used parameters were related to safety, water and forage. Distance to water described the availability of water. The land cover classes younger forest, broadleaved forest and coniferous forest represented the available forage. Parameters related to safety were elevation, slope and distance to roads and houses (Table 1).

The response variable was USE i.e. the calving site, with a used versus availability approach (Manly et al. 2002). This parameter is binary with zero for random sites and one for calving sites.
For each calving and random sites the explanatory variables bear density, elevation, slope, distance to roads, water and houses and land cover class were extracted from the GIS layer files in ArcGIS. Examples of GIS layer files can be found in Appendix V.

The used data to calculate the bear density was provided by Jonas Kindberg from Kindberg et al. 2009. The bear density was calculated by using the average observations of brown bears by moose hunters per 1000 hours during 1998–2006 (Kindberg et al. 2009). The remaining layer files were provided by the Swedish Land Survey Agency. The land cover data map was reclassified into 13 more general land cover-classes (shown in Appendix VI) to ensure their relevance for moose. The distance to roads, water and houses was calculated with Arc GIS by using the “Euclidean distance” function in the distance tool of the spatial analysis tools. The layer files of water (rivers and lakes), roads and houses from Sweden were used to calculate the distance layers. The "Euclidean distance" function measures straight-line distance from each cell to the closest source. New shapefiles were created for each parameter (roads, water and houses), where each raster cell of the map described the distance to the closest road, water or house in Sweden.

Finally, all parameters were extracted for random as well as for calving sites, by using spatial analysis, extract values to points or by using the point intersect tool, in the Hawth's Tools extension of ArcGIS 9.3.1 (ESRI). An extraction of the used Data is shown in Appendix VII.

Table 1. Description of digital variables extracted with ArcGIS

Parameters	Description
Bear density	Average bear densities 1998-2006
Elevation	Elevation (m)
Slope	Slope (%)
Road distance	Distance to the nearest road (m)
Water distance	Distance to the nearest water (rivers and lakes; m)
House distance	Distance to the nearest house (m)
Land cover class	Land cover classes of Sweden

2.4.2 Data analysis

The used calving sites were compared with the available random sites close by. In total 156 sites were used and 800 random sites.

The linear mixed-effects models (LME) were used to distinguish the used from the random sites. Use (1= used calving site, 0= random site) was included as the binary response variable and bear density, slope, elevation, distance to roads/water/buildings and land cover class were included as fixed effects. A Correlation Matrix was performed to prevent that used parameters were correlated. LME was chosen because this model accounted for non-independent observations. Multiple calving sites for individual moose and individual differences in behavior were considered by using LME and the moose ID as a random effect.
Bear density was included as a fixed effect only in the three northern study areas, where brown bears occur to see differences in used and random sites.

In the analysis for whole Sweden the parameter area was included as a random effect. For the analysis of each area, moose ID was included as random effect instead of area. In Appendix VIII examples of the R function can be found.

Models were fitted by the LME function with Maximum-Likelihood (ML) in the nlme library of the software R (Crawley 2002). The Dredge function in the MuMIn library in the software R (R project 2.13.0) was used for model selection. Akaike Information Criterion

(AIC) is a method for selecting a model from a set of models (Burnham & Anderson 2002). In this study, AICc was used instead of AIC, as the number of included parameters was rather high in relation to sample size as this method corrects for it (Burnham and Anderson 2002). Model selection was performed by using the model with the highest weighted AICc value. Akaike weights give the probability that a model is the best model, given the data and the set of candidate models (Burnham & Anderson 2002). The results of the three best fitted models per area are shown in Appendix VIII. Statistical analysis was performed with the software R version 2.13.0.

3 Results

The results are split up into two parts. The first part includes the calving site description. The second part describes the results from the data analysis, which are split into country-scale and area-scale. All used parameters are related to the main trade-off between safety, forage and water.

3.1 General results

In total 156 calving sites were selected between the years 2004 and 2011 (see Table 2 and 3). Calving sites from 112 individual moose were found. Table 2 shows the number of calving sites per area. The highest number of used calving sites has the study area Hemavan with 53, followed by Växjö with 41 calving sites. The numbers of calving sites lie between 14 and 17 for the remaining study sites. In total 800 random sites were created (Table 2).

Table 2: Number of individual moose, total calving sites and random sites per area.

AREA	Number of moose	Number of calving sites	Number of random sites
Hemavan	31	53	200
Hällnäs	17	17	100
Nordmaling	16	16	100
Öster Malma	13	14	100
Misterhult	12	15	100
Växjö	23	41	200
Total:	112	156	800

With the existing data, the mean calving date could be calculated. The mean calving date differs between areas and years. Table 3 shows that the calving date for Hemavan varies between the years from 3, 4 or 8 June. For Hällnäs and Nordmaling only one year data exists with a mean calving date in Hällnäs of 31 may 2005 and in Nordmaling of 23 May 2004. In the southern study area Öster Malma, the mean calving date varies between 12, 15 or 20 May for several different years. 17 may or 20 may is the mean calving date in Misterhult and 12, 15 or 16 May in Växjö for different years (Table 3).

Table 3. Mean Calving date per area and year.

Area	2004	2005	2006	2007	2008	2009	2010	2011
Hemavan		8 June	4 June	4 June	3 June	3 June		
Hällnäs		31 May						
Nordmaling	23 May							
Öster Malma					15 May	20 May	12 May	
Misterhult						20 May	17 May	
Växjö						12 May	16 May	15 May

In terms of land cover class as a representative of forage availability, most of the used calving sites lay in broad leaved forests - not on mires (21 %) whereas only 8% of the random sites were located there. 18 % of the calving sites lay in coniferous forest higher than 15 meters, followed by 12 % in mixed forest not on mires and 11% in young forest as shown in Figure 2. A small percentage of used calving sites lay in broad leaved forest on mires (1.3 %), coniferous forest on lichen dominated areas (0.6) and pastures (0.6 %). No calving sites are located in coniferous forest - not on lichen dominated areas and mixed forest on mires. Most of the random sites lay in coniferous forest higher than 15 meters (20%), followed by coniferous forest 5 to 15 meters and younger forest with each 14% as shown in Figure 2. Only a small percentage of random sites are located in these land cover classes (Figure 2).

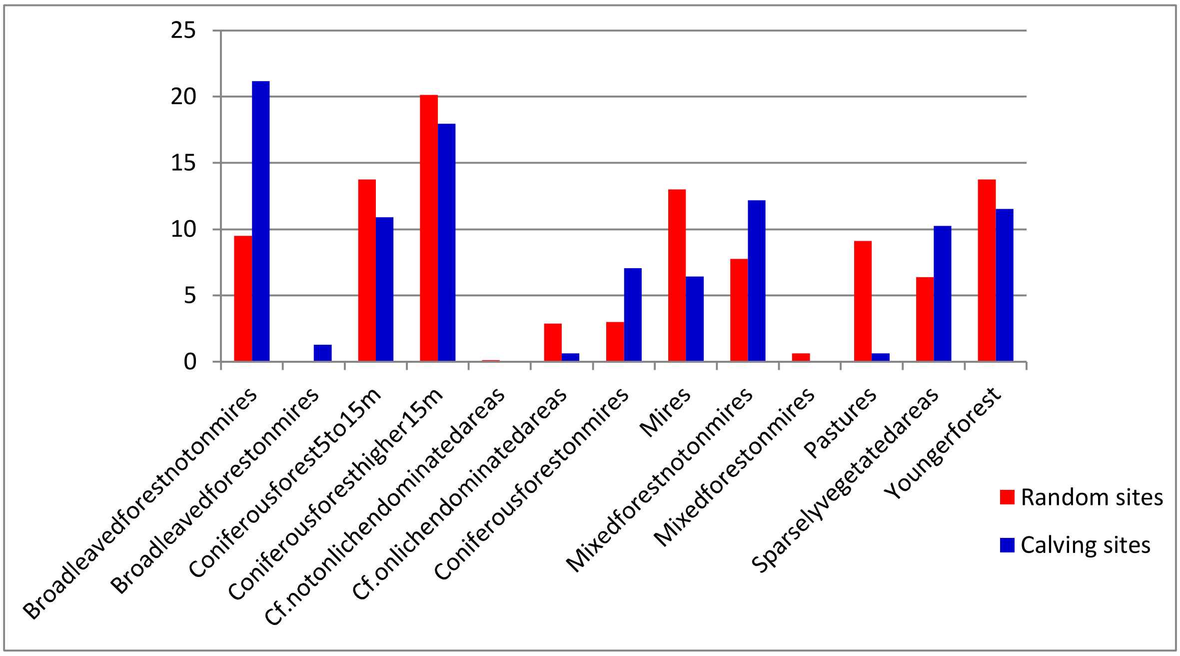

Figure 2. Frequency distribution of land cover classes of calving and random sites

The remaining parameters, which are related to water and safety, vary across the study areas. Table 4 shows the mean and the standard deviation for each parameter per area for random as well as calving sites. For instance, the highest mean elevation of the calving sites exists in Hemavan with 574 m ± 120 m, whereas the lowest mean elevation of the calving sites exists in Misterhult with 34 m ± 13 m (Table 4).

Table 4. Summary statistics for different parameters describing calving and random sites

Parameters	Calving sites		Random sites	
	Mean	SD	Mean	SD
Hemavan				
Bear density	0.53	0.14	0.58	0.19
Elevation	574.60	119.56	639.01	189.12
Housedistance	1560.09	1120.59	2053.58	1215.98
Roaddistance	2822.50	4372.32	4994.18	5950.67
Slope	5.63	3.74	4.78	3.58
Waterdistance	582.83	334.03	546.39	370.22
Hällnäs				
Beardensity	0.12	0.06	0.12	0.05
Elevation	244.41	68.33	239.60	60.37
Housedistance	1148.59	613.49	1327.61	700.61
Roaddistance	351.41	226.48	347.01	251.43
Slope	2.20	1.52	3.08	3.16
Waterdistance	811.14	560.97	681.47	516.64
Nordmaling				
Bear density	0.05	0.05	0.03	0.03
Elevation	134.63	75.99	100.14	51.88
Housedistance	939.31	535.97	927.16	628.65
Roaddistance	442.33	306.61	280.84	228.89
Slope	2.98	4.02	2.55	2.26
Waterdistance	1127.92	897.34	1109.24	784.99
Öster Malma				
Elevation	52.79	9.42	37.58	14.29
Housedistance	458.29	158.99	435.74	231.36
Roaddistance	298.03	147.81	214.28	156.94
Slope	4.10	2.88	3.88	2.65
Waterdistance	536.62	339.94	459.54	369.97
Misterhult				
Elevation	34.27	12.99	33.55	11.66
Housedistance	733.20	247.39	540.04	288.09
Roaddistance	238.54	129.27	204.65	127.86
Slope	2.67	1.60	2.54	2.13
Waterdistance	780.41	606.22	783.07	526.19
Växjö				
Elevation	193.98	28.10	195.35	26.35
Housedistance	399.17	190.96	369.71	286.50
Roaddistance	220.98	136.78	161.76	111.80
Slope	1.31	1.19	2.27	1.96
Waterdistance	933.70	655.18	703.57	542.34

3.2 Modelling results

All areas were combined when analyzing the data for whole Sweden to find a general pattern in calving site selection – termed country scale hereafter. The data was analyzed separately for each area to test for local differences in calving site selection in relation to the trade-off between safety, water and forage.

3.2.1 Country-scale

Elevation, distance to roads, water and houses as representing the factor safety were significant in the general model (Table 5) as well as several land cover classes, which are representing available forage (Table 5). The final model was selected with a weighed AIC value of 0.191 as shown in Appendix IX. When all study areas were combined, the main parameters in the final linear mixed-effects model were elevation (safety), distance to roads (safety), houses (safety) and water (water availability), as well as land cover class (forage availability). The calving sites were located at higher elevation compared to random sites (Value ± SE: < 0.01 ± 0.00008). The calving sites were located closer to roads (< -0.01 ± 0.000005) and houses (< -0.01 ± 0.05) and further away from water (< 0.01 ± 0.26) compared to the random sites. The calving sites were located more often in the land cover class broad leaved forest on mires (0.74 ± 0.05) compared to the random sites (see Table 5). Calving sites were less often located in the land cover class coniferous forest 5 to 15 meters (-0.14 ± 0.36), coniferous forest higher than 15 meters (-0.12 ± 0.08), mires (-0.22 ± 0.16), pastures (-0.27 ± 0.06) and younger forest (-0.13 ± 0.05) compared to random sites as can be seen in Table 5.

Table 5. Results of the general and final linear mixed-effects model for each parameter in Sweden. Empty cells indicate that the parameter is not included in the final model. P-values in bold are significant.

	General model			Final model		
Parameters	**Value**	**SE**	**p-value**	**Value**	**SE**	**p-value**
(Intercept)	0.22	0.05	0.00	0.22	0.05	<0.01
Bear density	0.07	0.08	0.38			
ELEVATION	<0.01	<0.01	**0.02**	<0.01	<0.01	**<0.01**
SLOPE	<-0.01	<0.01	0.65			
ROADDIS	<-0.01	<0.01	**0.06**	<-0.01	<0.01	**0.05**
WATERDIS	<0.01	<0.01	**0.04**	<0.01	0.26	**0.04**
HOUSEDIS	<-0.01	<0.01	**0.01**	<-0.01	0.05	**0.02**
Broadleaved forest on mires	0.74	0.26	**<0.01**	0.74	0.05	**<0.01**
Coniferous forest 5-15m	-0.14	0.05	**0.01**	-0.14	0.36	**0.01**
Coniferous forest >15m	-0.12	0.05	**0.01**	-0.12	0.08	**0.01**
Cf.notonlichendominatedareas	-0.26	0.36	0.47	-0.25	0.07	0.48
Coniferous forest on mires	0.06	0.07	0.40	0.06	0.06	0.42
Mires	-0.22	0.05	**<0.01**	-0.22	0.16	**<0.01**
Mixed forest not on mires	-0.03	0.06	0.61	-0.03	0.06	0.57
Mixed forest on mires	-0.25	0.16	0.14	-0.25	0.16	0.13
Pastures	-0.26	0.06	**<0.01**	-0.27	0.06	<**0.01**
Sparsely vegetated areas	0.01	0.06	0.89	<0.01	0.06	0.96
Younger forest	-0.13	0.05	**0.01**	-0.13	0.05	**0.01**

3.2.2 Area- scale

The results of the general linear mixed-effects models with all parameters included are shown in Table 6. After this, the dredge function in the MuMIn package in R was used to identify the main parameters of calving site selection. The model with the highest weighted AIC value was chosen. The parameters included in the highest weighed AIC model were used to conduct a final linear mixed- effects model for each area. The results of the final models are shown in Table 7.

<u>Hemavan</u>

The general model showed that the parameters slope and distance to houses, related to safety, were significant as well as several land cover classes, which are related to forage availability (see Table 6).

The model with the highest weighed AIC value (0.058) shown in Appendix IX, included elevation, distance to houses, slope and land cover-class as main parameters. The final linear mixed- effects model showed that the calving sites were located at steeper slopes (0.02 ± 0.01) compared to random sites. A trend has been seen that the calving sites were closer to houses (< -0.01 ± 0.00002) than random sites.

The calving sites in Hemavan were less often located in the land cover classes, coniferous forest 5 to 15 m (-0.31 ± 0.09), mires (-0.28 ± 0.07) and younger forest (-0.26 ± 0.10) compared to random sites (Table 7).

Hällnäs

The general model showed that only land cover class (forage availability) was significant (see table 6). The final model with the highest weighed AIC value (0.076) included none of the parameters (see Appendix IX). That means, that none of the used parameters describe the calving site selection in this study area (Table 7).

Nordmaling

None of the used parameters was significant in the general model (Table 6). The main parameters included in the model with the highest weighed AIC value (0.142) were elevation and distance to roads (see Appendix IX), which both are related to safety. In Nordmaling, the calving sites were located at higher elevations (<0.01 ± 0.01) and further away from roads (<0.01 ± <0.01) compared to random sites as can be seen in Table 7.

Öster Malma

The general model showed that the parameters elevation (safety) and broad leaved forest on mires (forage availability) were significant (Table 6). The model with the highest weighed AIC value (0.223) included elevation and distance to roads as parameters as shown in Appendix IX. Calving sites were located at higher elevation (0.01 ± 0.002) compared to random sites. But no significant difference of the distance to roads between calving and random sites was found (Table 7).

Misterhult

Distance to houses (safety) and sparsely vegetated areas (forage availability) were significant in the general model (Table 6). The highest weighed AIC value (0.214) has the model which included only one parameter, namely distance to houses (Appendix IX). Calving sites were further away from houses (<0.01 ± 0.0001) compared to random sites (Table 7).

Växjö

The general model (Table 6) showed, that slope, distance to roads and water as representatives of safety and water availability were significant and pastures as a land cover class representing forage availability was significant. The parameters slope, distance to roads and distance to water were included in the final model with a weighed AIC value of 0.415 as can be seen in Appendix IX. Calving sites were located at lower slope (-0.03 ± 0.01), further away from roads (<0.01 ± 0.0002) and further away from water (<0.01 ± 0.00004) compared to random sites (Table 7).

Parameters	Hemavan Value	Hemavan SE	Hemavan p-value	Hällnäs Value	Hällnäs SE	Hällnäs p-value	Nordmaling Value	Nordmaling SE	Nordmaling p-value	Östermalma Value	Östermalma SE	Östermalma p-value	Misterhult Value	Misterhult SE	Misterhult p-value	Växjö Value	Växjö SE	Växjö p-value
(Intercept)	0.71	0.17	0.00	0.96	0.37	0.01	-0.07	0.33	0.83	-0.29	0.19	0.13	-0.09	0.22	0.68	0.17	0.20	0.39
Bear density	-0.16	0.14	0.26	0.89	0.87	0.31	1.19	1.00	0.24									
ELEVATION	<-0.01	<0.01	0.14	<- 0.01	0.01	0.96	<0.01	<0.01	0.14	0.01	<0.01	**0.01**	<-0.01	<0.01	0.51	<-0.01	<0.01	0.67
SLOPE	0.01	0.01	**0.07**	-0.01	0.01	0.37	<-0.00	0.02	0.87	<-0.01	0.01	0.88	0.01	0.02	0.66	-0.03	0.01	**0.04**
ROADDISTANCE	<-0.01	<0.01	0.82	<0.01	<0.01	0.57	<0.01	<0.01	0.11	<0.01	<0.01	0.14	<0.01	<0.01	0.57	<0.01	<0.01	**0.03**
WATERDISTANCE	<0.01	<0.01	0.39	<0.01	<0.01	0.29	<0.01	<0.01	1.00	<0.01	<0.01	0.92	<-0.01	<0.01	0.73	<0.01	<0.01	**0.02**
HOUSEDISTANCE	<-0.01	<0.01	**0.09**	<-0.01	<0.01	0.24	<-0.01	<0.01	0.85	<-0.01	<0.01	0.47	<0.01	<0.01	**0.08**	<-0.01	<0.01	0.77
Broadleavedforestonmires				-0.06	0.50	0.91				0.94	0.34	**0.01**						
Coniferousforest5to15m	-0.30	0.09	**<0.01**	-0.94	0.36	**0.01**	-0.02	0.35	0.96	0.17	0.17	0.33	0.14	0.16	0.39	-0.01	0.11	0.95
Coniferousforesthigher15m	-0.21	0.11	**0.06**	-0.88	0.36	**0.02**	-0.05	0.34	0.88	-0.03	0.16	0.88	0.08	0.15	0.62	0.01	0.08	0.90
Cf. notonlichendominatedareas	-0.38	0.39	0.33															
Cf. onlichendominatedarea	-0.30	0.17	**0.07**	-1.00	0.38	**0.01**	-0.12	0.37	0.75	-0.07	0.36	0.85	0.04	0.21	0.87			
Coniferousforestonmires				-0.75	0.36	**0.04**	0.25	0.37	0.51	0.22	0.24	0.35				0.11	0.12	0.38
Mires	-0.27	0.07	**<0.01**	-0.92	0.37	**0.01**	-0.11	0.36	0.75	0.11	0.23	0.62	-0.01	0.28	0.97	0.26	0.27	0.32
Mixedforestnotonmires	-0.18	0.17	0.31	-1.03	0.37	**0.01**	0.20	0.34	0.56	0.13	0.19	0.48	<0.01	0.19	0.99	0.09	0.10	0.35
Mixedforestonmires							-0.10	0.41	0.81							-0.12	0.22	0.58
Pastures	-0.33	0.23	0.16	-1.01	0.50	**0.05**	-0.09	0.36	0.81	0.10	0.16	0.56	0.10	0.28	0.73	-0.15	0.09	**0.09**
Sparselyvegetatedareas	-0.15	0.18	0.43				-0.01	0.36	0.98	0.16	0.17	0.33	0.26	0.15	**0.09**	-0.16	0.37	0.67
Youngerforest	-0.27	0.10	**0.01**	-0.82	0.36	**0.02**	-0.08	0.34	0.81	0.06	0.19	0.74	0.12	0.16	0.46	-0.03	0.10	0.80

Table 6. Results of the general linear mixed-effects model for each parameter per area. Empty cells indicate that the parameter does not exist in the study area. P-values in bold are significant.

	Hemavan			Hällnäs			Nordmaling			Östermalma			Misterhult			Växjö		
Parameters	Value	SE	p- value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value	Value	SE	p-value
(Intercept)	0.65	0.14	0.00	-	-	-	-0.07	0.07	0.32	-0.24	0.09	0.01	-0.02	0.07	0.79	0.06	0.06	0.37
Bear density																		
ELEVATION	-<0.01	<0.01	0.11				<0.01	<0.01	**0.04**	0.01	<0.01	**<0.01**						
SLOPE	0.02	0.01	**0.05**													-0.03	0.01	**0.01**
ROADDISTANCE							<0.01	<0.01	**0.02**	<0.01	<0.01	0.10				<0.01	<0.01	**<0.01**
WATERDISTANCE																<0.01	<0.01	**0.01**
HOUSEDISTANCE	-<0.01	<0.01	**0.08**										<0.01	<0.01	**0.02**			
Broadleavedforestonmires																		
Coniferousforest5to15m	-0.31	0.09	**<0.01**															
Coniferousforesthigher15m	-0.20	0.11	**0.06**															
Cf. notonlichendominatedareas	-0.38	0.39	0.32															
Cf. onlichendominatedarea	-0.31	0.17	**0.07**															
Coniferousforestonmires																		
Mires	-0.28	0.07	**<0.01**															
Mixedforestnotonmires	-0.16	0.17	0.36															
Mixedforestonmires																		
Pastures	-0.35	0.23	0.14															
Sparselyvegetatedareas	-0.18	0.18	0.32															
Youngerforest	-0.26	0.10	**0.01**															

Table 6. Results of the final linear mixed-effects model for each parameter per area. Empty cells indicate that the parameter is not included in the final model or does not exist in the study area. P-values in bold are significant.

4 Discussion

This chapter deals with the discussion of the calving site selection. First of all, some general problems will be discussed, followed by the discussion of the description of the calving sites. At the end the hypotheses about safety, water and forage will be discussed.

4.1 Description of calving sites

In total 156 calving sites could be used for the analysis. Due to the lack of some data many calving sites had to be excluded from the analysis. To include more calving sites, it is necessary to include Norway in the analysis, because some moose in the northern study area Hemavan migrated to Norway and gave birth there.

The differences between the calving dates as shown in Table 3 can be clarified by the differences between the areas. It can be seen that across the geographical gradient of Sweden, the mean calving dates vary. In the northern parts the mean annual calving date is later compared to the southern part of Sweden. Hemavan, which lies next to the border of Norway in a mountainous area, has the latest mean annual calving dates, whereas the most southern study area Växjö has the earliest mean annual calving dates.

Sweden has a wide divergence of climate. In the northern part, the winter starts earlier and lasts longer. Hence, the growing season starts later and ends earlier in the northern part compared to the southern part of Sweden.

The calving period is often correlated with the time of most abundant food in the year. Forage quality and availability are influenced by the weather conditions and hence, influencing the time of calving (Bowyer et al. 1998a). Therefore, the mean calving date in the northern study sites is later compared to the southern study sites. The variance of the mean calving date within one study area could be described by the variation of the weather. It might have been a harder winter and hence the mean calving date is later in spring, because calving date is correlated with the weight of the female (Saether et al. 1996). Another reason for the variation in calving dates might be the timing of the rut. The rut might have started later or earlier in autumn (climate change) because it is triggered by day length or temperature (Feldhamer et al. 2003) and consequently, differences occur in calving date within the areas.

Other studies showed that also the nutritional condition of female moose during pregnancy had an effect on gestation length. Saether et al. (1996) indicated that females with poor conditions had later mean calving dates. Keech et al. (2000) showed the same effect as

females with the thickest rump fat gave birth earlier. They concluded that the time of parturition is the result of environmental factors during gestation (Keech et al. 2000).
Most of the calving sites were located in dry land cover classes as a large number of calving sites were not on mires (Figure 2). Broad leaved forest was most commonly selected with 21 % of the total calving sites, followed by coniferous forest higher than 15 meters with 18 %. Especially, coniferous forest has been shown to be important in providing forage and cover for moose in several studies (Markegren 1974; Bergström & Hjeljord 1987; Nikula et al. 2004). This coincides with the used land cover classes in this study. Moose also selected calving sites in young forest (11 %) as found in a previous study of Cederlund & Okarma (1988).

However, land cover class could also be regarded from another point of view. Some land cover classes might offer more ground vegetation and hence, better concealment as others (Bongi et al. 2008). This hiding strategy is used by moose as well (Stringham 1974). Because of the variety of used land cover classes it seems that moose do not have a clear preference for special land cover classes. However, the calving site does not have to lay in a typical land cover class with abundant forage, when at least the surrounded area provides a lot of forage. Female moose often leave their offspring at the calving site and forage up to 50 meters away (Franzman & Schwartz 2007). As long as enough forage is available in the surrounded area of the calving site, the available forage at the calving site itself may not be important.

4.2 Hypotheses

It was not possible to confirm all predictions. One main problem was that not all parameters entered the final model at the country scale, as well as at the area scale. In none of the final models all parameters were included. For each area, different parameters entered the final model. The parameter bear density never entered the final model. One reason could be that at the area-scale, the calving and the random sites were mostly located in areas with the same bear density. So no differences within the areas were found.
The results of the country-scale often differed from the results of the area-scale. This will be discussed in more detail in the next two chapters.

4.2.1 Forage and water

Forage

In relation to forage, different land cover classes were used. Most of the land cover classes entered the final model at the country-scale and at the area-scale. At the country-scale, calving sites were located more often in the land cover class broad leaved forest on mires (0.74 ± 0.05) compared to the random sites (see Table 5). Calving sites were less often located in some other land cover classes as can be seen in Table 5. Broadleaved forest on mires was used 1.3 % (Figure 2), which means that two calving sites out of 156 were located in this land cover class, whereas none of the random sites were located in it. This means, that the results are not useful and the land cover class might be scaled incorrect.

At the area-scale land cover class entered the final model only in Hemavan. Calving sites were less often located in all of the present land cover classes. This indicates that the problem exists for both scales. As already mentioned above, the scale of this parameter is incorrect. Because the number of random sites used in this study is higher compared to the calving sites, the results are biased. Consequentially, most random sites were located more often in the land cover classes compared with the calving sites. No clear results were found and no predictions can be made on available forage.

So for Sweden as well as for the areas, the prediction that moose prefer habitat types with much forage (younger forest, broadleaved forest or coniferous forest) cannot be confirmed. One solution for this problem might be to use the Normalized Difference Vegetation Index (NDVI) as this is often used in other studies about forage availability (Hansen et al. 2009; Singh et al. 2010; Pettorelli et al. 2011).

Water

Another parameter, which is thought to be important for calving site selection, was the presence of water close by. Especially during lactation moose had to fulfill nutritional requirements (Oehlers et al. 2011). Water is suggested to be important for lactating females (Bowyer 1984). Hence, it was expected moose choose calving sites close to water. The parameter distance to water entered the final model of Sweden as well as the final model of the study area Växjö. However, at the country scale and at the area scale, water seems to be not as important as expected, because calving sites were further away from water (Table 5 and Table 7).

At the country-scale, Sweden has different densities of water and it could be that the distance to water is not important. In general, Sweden has a high percentage of water (rivers and lakes). Hence, water might not be the limiting factor in Sweden and moose do not need to select their calving sites related to the distance to water.

Furthermore, moose might avoid water at the country and at the area-scale, because of human disturbance. Especially the southern areas have a higher population density and during summer more people visit these places for recreation. Hence, a lot of disturbance could take place close to water, which might influence the calving site selection by moose. Addison et al. (1990) found that moose calve within 200 meters of water, whereas in another study, Saiga antelopes give birth at an intermediate distance from water (Singh et al. 2010).

The avoidance of giving birth close to water may also be anti-predator behaviour. Water and especially its edges may work as attractants for predators as for instance buffalos avoid water holes in the Hwange National Park in Zimbabwe when the lions (*Panthera leo*) are most active (Valeix et al. 2009). Moose may use the same strategy by avoiding of giving birth close to water as brown bears may also be attracted by rivers when searching for food or rivers may provide lead lines for them when moving in the landscape. As moose calves are vulnerable during the first weeks, brown bears may detect them easier when they were lying close to rivers.

However as moose in Sweden give birth further away from water than random sites, this might indicate that a trade-off between predation or disturbance and water supply exists (Bowyer et al. 1999; Singh et al. 2010) and the prediction that water availability is important for female moose and hence calving sites should be located closer to water than random sites had to be rejected.

4.2.2 Safety

The parameters elevation, slope and distance to roads and houses were regarded as factors representing safety.

Elevation

Elevation entered the final model of Sweden (Table 5) as well as the final model in Nordmaling and in Öster Malma (Table 8). In Nordmaling brown bears are present, whereas in Öster Malma brown bears are absent. At the country-scale and at the area-scale calving sites were located at higher elevation compared to random sites.

Bowyer et al. (1999), Oehler et al. (2011) and Wilton & Garner (1991) found that moose select higher elevation for calving or during calving season. Bowyer et al. (1999) interpreted this as increasing visibility for predators. Moose might use the same strategy. A general pattern might be that moose choose calving sites at higher locations to reduce risk of predation. Moose might feel safer at higher places which provide a better overview and allow moose to react faster in case of danger.

Micro climatic differences may also be a reason for selecting higher elevations. Ground moisture may be reduced in higher elevations as water drains off to lower elevation or the ground cover composition may be more suitable for moose calves in higher elevations. The presence or absence of brown bears as a predator on moose neonates does not seem to influence the calving site selection in terms of elevation, because moose select calving sites at higher elevation in areas with and without brown bears. Hence, the hypotheses that brown bears frequent lower elevation and therefore the calving sites should be located at higher elevations compared to random sites can not be confirmed.

Slope

Slope did not enter the final model at the country-scale (Table 5), whereas an effect at the area-scale could be found (Table 8). Calving sites were located at steeper slope in Hemavan and at flatter areas in Växjö.

Carr et al. (2007) found that female caribou selected nursery sites with greater slope. He suggested that caribou might use this strategy to reduce the risk of predation by detecting potential predators easier (Carr et al. 2007). Oehler et al. (2011) strengthened this theory as female moose used steeper slopes during spring compared with males. Moose in Hemavan might use the same strategy, by selecting calving sites with steeper slope, because this area has the highest bear density in this study. No precautions need to be made in Växjö, because no bears occur in this area and hence the risk of neonatal predation is very low.

The prediction that steeper slopes provide cover through offering higher visibility and hence the calving sites should have steeper slope angles compared to random sites can be confirmed, at least for the study areas with brown bears at the area- scale. In this area it seems that female moose use this strategy.

Distance to roads

Distance to roads entered the final model of Sweden (Table 5) as well as the final model in Nordmaling and in Växjö (Table 8). At the country-scale, calving sites were closer to roads (Table 5), whereas at the area- scale calving sites were further away from roads compared to random sites (Table 8).

A general pattern in Sweden might be that moose tend to give birth close to roads, whereas in two different study areas moose prefer to calve further away from roads. At the country-scale, moose might use humans as a shield against predation as Berger (2007) suggested. This means that the hypotheses that humans are used as a shield against predation, calving sites in areas with brown bears should be closer to the roads compared to random sites has to be rejected, because bear density has no influence on calving site selection.

At the area-scale, the avoidance to calve close to roads could indicate that moose might regard humans as predators or at least as a source of disturbance in specific areas. The avoidance of human infrastructure has often been described in previous studies (Bowyer et al. 1999; Vistnes & Nellemann 2001). Bear density has no influence on distance to roads, as brown bears are present in Nordmaling and absent in Växjö.

The prediction that humans are seen as predators and hence, the calving sites should be further away from roads compared to random sites can be confirmed at least in two study areas.

Distance to houses

Distance to houses entered the final model at the country- and area-scale (Table 5 and 8). At the country-scale calving sites were closer to houses ($-< 0.01 \pm 0.05$) compared to the random sites. The same results were obtained for the study area Hemavan, where the calving sites were also closer to houses. While in Misterhult, the calving sites were further away from houses than random sites. Hemavan is an area with low density of human population and infrastructure, but is the area with the highest brown bear density. Moose might use humans as a shield against predation in this area, which coincided with prediction 2d.

However, in Misterhult moose avoid humans, because calving sites were farther from roads. This indicates that moose do not need to use humans as a shield against predation in this area, because no brown bears occur. Moose might see humans as a kind of predator or disturbance and avoid built up areas. This agreed with prediction 2c. As no natural predators were present in this area, moose might prefer to give birth in undisturbed areas, further away from human infrastructure. The avoidance of areas with humans or human infrastructure by ungulates during calving has often been described (Bowyer et al. 1999; Vistnes & Nellemann 2001). Bowyer et al. (1999) showed that, the calving sites of moose were further away from human developments in Alaska, whereas in the model at the country-scale of Sweden it is vice versa.

4.3 General discussion

To start with, some general problems will be discussed, which had not been taken into account and which might have influenced the results.

Moose individual was included in the model as a random effect. This was done to account for the effect that some moose individuals might have preferences of special habitat types or general differences in behavior. But the moose population in Sweden differs in migration behaviour; some migrate and some not. Especially in Northern Sweden a large part of the moose population migrates between summer and winter home ranges (Ball et al. 2001). They start migrating before calving and some moose might give birth during migration. This might influence the calving site selection. Furthermore, differences exist in home range size and available habitat for the selection of calving sites. In general, moose in the southern areas have smaller home ranges than moose in the northern areas, as moose in the northern areas often migrate. This might influence the availability of calving sites as some moose might have less choice of calving sites compared to others.

As calving sites were verified in the field, this field check might influence the behaviour of the female moose and its offspring. Researchers might be regarded as a disturbance and moose might avoid this calving site the next year or leave the calving site earlier, which might be a disadvantage for the health of the offspring.

One general problem in studies using GPS collars is the accuracy of the coordinates. GPS systems are not always as accurate as expected and might have an error of up to 10 meters (Dettki et al. 2004). Research from collared free-ranging moose indicated that position accuracy varied among months as well as between day and night (Dussault et al. 1999). The GPS-coordinates accuracy might be influenced e.g., when calving sites were located in forest with thick stems or a dense canopy cover (Edenius 1997). Thus, the identified location of the calving site, which often lays in forest, might be incorrect That means that some parameters of the calving sites are incorrect, because the calving sites might have been located, for instance in another land cover class or at higher or lower elevation.
Altogether, it is never sure that the calving site which is checked in the field is also the real calving site. Moose might have given birth a few meters away and have moved a little bit further.

Up to date, a lot of studies use vaginal implant transmitters to locate the real calving site in the field. This might be a solution for the problem of finding the real calving site. Using vaginal implant transmitters is suggested for further studies (Barbknecht et al. 2011; Johnson et al. 2006; Bowman & Jacobson 1998).

Another problem which is not taken into account is the difference in moose density between the areas. In areas with a high density of moose it could be that some females cannot use the most suitable calving site, because it is occupied by another female. Hence, some moose might have to give birth at an alternative place, which is not as perfect as the occupied one.

Next to that, age of the female might also influence the behaviour. Older females might have more experience and might prefer similar calving sites (Schaefer et al. 2000). Therefore, age of the female should be included in the analysis. Survival or loss of offspring might also influence the behavior of the female moose. As an example, moose that lost offspring shift their calving site the previous year (Testa et al. 1998) and hence, they might select it in relation to other criterions.

Hunting pressure could also influence the anti-predator behavior of moose. Especially in areas with a high hunting pressure, moose might tend to avoid humans (Berger et al. 2001). As a consequence, moose might give birth farther from roads or houses in areas with high hunting pressure.

Besides that, the method for selecting random points has to be kept in mind. In this study, random points were selected within one area. The most outer calving sites per area were used as borders. The random points were created within these areas. One problematic could be that moose already prefer some special habitat types and hence the calving sites were not evenly distributed in these areas. So it might be better to create random points within the home range of each individual as other studies have used this method already.

5 Conclusion

A trade-off between forage, water and safety could not be confirmed in all cases. As forage did not give useful results the NVDI index should be used for following analysis. Forage in relation to used land cover classes was very diverse. As a wide variety of land cover classes were used, moose might not have preferences for some special land cover class.

However, most of the calving sites were located not on mires. This could indicate that moose prefer dry ground as calving sites. The parameter water entered the final model of Sweden and once the final model of one area. Both models showed that the calving sites were farther from water than random sites. In general water seems to play another role as expected. Moose might need to make a trade-off between risk of predation and water, as they space them away from water, which might indicate an anti- predator behavior.

As a variety of land cover classes were used, safety seems to be more essential than forage. Especially, elevation seems to play a key role as this analysis gave a clear result. At both scales, moose select calving sites at higher elevation compared to random sites. This assured the assumption that safety is more essential than forage. It indicates that moose need to make trade-offs between forage and safety.

Additionally, as contradictory results were found, when analyzing the data at the country-scale and at the area-scale, the suggestion will be to include local habitat characteristics. One special attention should be given to the microhabitat of a calving site, for instance ground cover and moisture. Besides that, the surrounded area of the calving site should be taken into account, as forage at the calving site is not essential. It might be more important to have good foraging grounds in the surrounded area.

As a lot of contradictory results exist as well in other studies, moose might need a heterogeneous habitat to select a calving site and the selection of a calving site might depend on a variety of factors.

Literature

Addison, E. M., J. D. Smith, R. F. McLaughlin, D. J. H. Fraser and D. G. Loachim, 1990. Calving sites of moose in central Ontario. Alces 26:142-153.

Ball, J. P., C. Nordengren and K. Wallin, 2001. Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden. Wildlife Biology 7:1.

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter and J. C. Devos JR., 2001. Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99-115.

Barbknecht, A. E., W.S. Fairbanks, J.D. Rogerson, E.J. Maichak, B.M. Scurlock and L.L. Meadows, 2011. Elk parturition site selection at local and landscape scales. The Journal of Wildlife Management 75:646–654.

Belovsky, G. E. and P. A. Jordan, 1978. The time-energy budget of a moose. Theoretical Population Biology 14:76/104.

Bergström, R. and O. Hjeljord, 1987. Moose and vegetation interactions in northwestern Europe and Poland. Swedish Wildlife Research Supplement 1:213-228.

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Berger, J., J.E. Swenson and I.L. Persson, 2001. Recolonizing carnivores and naive prey: Conservation lessons from pleistocene extinctions. Science 291:1036-1039.

Bongi, P., S. Ciuti, S. Grignolio, M. Del Frate, S. Simi, D. Gandelli and M. Apollonio, 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology 276:242-251.

Bowman, J. L. and H. A. Jacobson, 1998. An Improved Vaginal-Implant Transmitter for Locating White-Tailed Deer Birth Sites and Fawns. Wildlife Society Bulletin 26(2):295-298.

Bowyer, R. T., V. van Ballenberghe, J. G. Kie, and J. A. K. Maier, 1999. Birth site selection by Alaskan moose: strategies for coping with a risky environment. Journal of Mammalogy 80:1070-1083.

Bowyer, T. B., J. G. Kie, and V. van Ballenberghe, 1998a. Timing and synchrony of parturition in Alaskan moose: long term versus proximal effects of climate. Journal of Mammalogy 79:1332–1344.

Bowyer, R.T., J.G. Kie, V. van Ballenberghe, 1998b. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415–425.

Bowyer, R.T., 1984. Sexual segregation in southern mule deer. Journal of Mammalogy 65:410-417.

Bubenik, A., 2007. Behavior. Pp. 173-221 in A. Franzmann, C. Schwartz, eds. Ecology and Management of the North American Moose. Boulder, Colorado: University Press of Colorado.

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

Carr, N.L., A.R. Rodgers and S.C. Walshe, 2007. Caribou nursery site habitat characteristics in two northern Ontario parks. Rangifer Special Issue No. 17:167-179.

Cederlund, B-M., 1987. Parturition and early development of moose (Alces alces L.) calves. Swedish Wildlife Research (Suppl.) 1:399-422.

Cederlund, G. N. and H. Okarma, 1988. Home Range and Habitat Use of Adult Female Moose. The Journal of Wildlife Management 52(2):336-343.

Crawley, M.J., 2002. Statistical computing an introduction to data analysis using S-Plus. Wiley West Sussex, UK.

Dettki, H., G. Ericsson, L. Edenius, 2004. Real-time moose tracking: an internet based mapping application using GPS/GSM-collars. Alces 40:13-21.
Dugan, J. D., and R.G. Wright, 2005. Summer diet composition of moose in Rocky Mountain National Park, Colorado. Alces 41:139-146.
Dussault, C., R. Courtois, J. P. Ouellet and J. Huot, 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildlife Society Bulletin 27:965-972.
Edenius, L., 1997. Field test of a GPS location system for moose Alces alces under Scandinavian boreal conditions. Wildlife Biology 3:39-43.
Engan, J., 2001. Changes in the relationship between palmate and cervine antlers in moose in southeastern Norway. Alces, 37: 79-88.
Ericsson, G. and K. Wallin, 2001. Age-specific moose (Alces alces) mortality in a predator free environment: evidence for senescence in females. Ecoscience 8:157-163.
Estes, R. D., 1976. The significance of breeding synchrony in the wildebeest. East African Wildlife Journal 14:135-152.
Feldhamer, G. A., B. C. Thompson and J. A. Chapman, 2003. Wild mammals of North America: Biology, management, and conservation. Baltimore, Md: Johns Hopkins University Press.
Fielitz, U., 2003. Remote GPS-data transmission via mobile phone, http://www.environmental-studies.de/products/02/gps-gsm_collars.html. Accessed October 25, 2011.
Franzmann, A., 1981. Alces alces. Mammalian Species 154:1-7.
Franzmann, A. W. and C. C. Schwartz, 2007. Ecology and Management of the North American Moose, Second Edition. The University Press of Colorado. Boulder, USA. ISBN: 978-0-87081-895-0.
Hansen B.B., R. Aanes, I. Herfindal, B.E. Sæther and S. Henriksen. 2009. Winter habitat-space use in a large arctic herbivore facing contrasting forage abundance. Polar Biology 32:971–984
Hilden, O., 1965. Habitat selection in birds. Annales Zoologici Fennici 2:53-75.
Johnson, B. K., T. McCoy, C.O. Kochanny, R.C. Cook, 2006. Evaluation of vaginal implant transmitters in elk (Cervus elaphus nelsoni). Journal of Zoo and Wildlife Medicine 37(3):301-305.
Joyal, R. and B. Scherrer, 1978. Summer movements and feeding by moose in western Québec. Canadian Field-Naturalist 92: 252-258.
Keech, M.A., R.T. Bowyer, J.M. Ver Hoef, R.D. Boertje, B.W. Dale and T.R. Stephenson, 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.
Kie, J.G., 1999. Optimal foraging in a risky environment: lifehistory strategies for ungulates. Journal of Mammalogy, 80:1004–1020.
Kindberg, J., J.E. Swenson, G. Ericsson, E. Bellemain, C. Miquel and P. Taberlet. 2011. Estimating population size and trends of the Swedish brown bear Ursus arctos population Wildlife Biology 17(2):114-123
Kindberg, J., 2010. Monitoring and Management of the Swedish Brown Bear (Ursus arctos) Population. Doctoral thesis. Departement of Wildlife, Fish, and Environmental Studies, SLU.
Kindberg, J., G. Ericsson and J.E. Swenson, 2009. Monitoring rare or elusive large mammals using effort-corrected voluntary observers. Biological Conservation 142:159-165.
Krausman, P. R., 1999. Some basic principles of habitat use. In K. Launchbaugh, K. Saunders and J. Mosley (Eds.): Grazing Behaviour of Livestock and Wildlife, pp. 85-90. Idaho Forest, Wildlife and Range Experiment Station. University of Idaho. Moscow. Idaho.
Lavsund, S., T. Nygren, E.J. Solberg, 2003. Status of moose populations and challenges to

moose management in Fennoscandia. Alces 39:109-130.

Lent, P.C., 1974. Mother–infant relations in ungulates. The behaviour of ungulates and its relation to management.14–55. Walther, F. (Ed.). Morges, Switzerland: IUCN.

Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring, 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains. Montana Journal of Applied Ecology 33:1395-1404.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald and W.P. Erickson, 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, second edition. Kluwer Academic Publishers, Boston, MA, USA, p. 240.

Markegren, G., 1974. The moose in Fennoscandia. Naturaliste Canadien 101:185-194.

Mattson, D. J., 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8:33–56.

Nikula, A., S. Heikkinen and E. Helle. 2004. Habitat selection of adult moose Alces alces at two spatial scales in central Finland. Wildlife Biology 10:121–135.

Novak, R. 1999. Walker's Mammals of the World. Baltimore, MD: The John Hopkins University Press.

Oehlers, S. A., R.T. Bowyer, F. Huettmann, D. K. Person, and W. B. Kessler, 2011. Sex and scale: implications for habitat selection by Alaskan moose Alces alces gigas. Wildlife Biology 17(1):67-84.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima and K. Kausrud. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Poole, K. Serrouya G., R., and K. Stuart-Smith, 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139-150.

Putman, J. R. 1986. Grazing in temperate ecosystems: Large herbivores and the ecology of the new forest. Department of Biology, university of Southampton, Timber Press Pp. 127-128.

Ratikainen, I.I., M. Panzacchi, A. Mysterud, J. Odden,J. Linnell, and R. Andersen, 2007. Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. Journal of Zoology 273:192-199.

Saether, B.-E., R. Andersen, O. Hjeljord, M. Heim, 1996. Ecological correlates of regional variation in life history of the moose Alces alces. Ecology 77(5):1493-1500.

Sandegren, F., L. Pettersson, P. Ahlqvist and B. O. Roken, 1987. Immobilization of moose in Sweden. Swedish Wildlife Research Supplement 1:785-791.

Schaefer, J.S., C.M. Bergman and S.N. Luttich, 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology 15:731–739.

Schwartz, C. and K. Hundertmark, 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57:454-468.

Schwartz, C., 2007. Reproduction, natality, and growth. Pp. 141-171 in A. Franzmann, C. Schwartz, eds. Ecology and Management of the North American Moose. Boulder, CO: University Press of Colorado.

Seiler, A., 2005. Predicting locations of moose–vehicle collisions in Sweden. Journal of Applied Ecology 42:371–382.

Shipley, L.A., S.Blomquist and K. Danell, 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry and morphology. Canadian Journal of Zoology 76:1722–1733.

Singh, N.J., I.A. Grachev, A.B. Bekenov and E.J. Milner-Gulland, 2010. Saiga antelope calving site selection is increasingly driven by human disturbance. Biological Conservation 143:1770-1779.

Stringham, S. F., 1974. Mother-infant relationships in moose. Naturaliste Canadien 101:325-369.

Swenson, J. E., B. Dahle, H. Busk, O. Opseth, T. Johansen, A. Söderberg, K. Wallin and G. Cederlund, 2007. Predation on Moose Calves by European Brown Bears. The Journal of Wildlife Management 71:1993-1997.

Testa, J. W., E.F. Becker and G.R. Lee, 1998. Movements of female moose in relation to birth and death of calves. Alces 36:155-162.

Valeix M, H. Fritz, A.J. Loveridge, Z. Davidson, J.E. Hunt, F. Murindagomo and D.W. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral Ecology and Sociobiology 63:1483–1494.

Vistnes, I. and C. Nellemann, 2001.Avoidance of Cabins, Roads, and Power Lines by Reindeer during Calving. The Journal of Wildlife Management 65(4):915-925.

Wilton, M. L. and D. L. Garner, 1991. Preliminary findings regarding elevation as a major factor in moose calving site selection in South Central Ontario, Canada. Alces 27:111-117.

Appendices

Appendix I - Moose with GPS collar and ear tags

Figure 1. Female moose with GPS collar and ear tags photographed in Växjö (56° 52' N, 14° 48' E).

Appendix II – Automated system

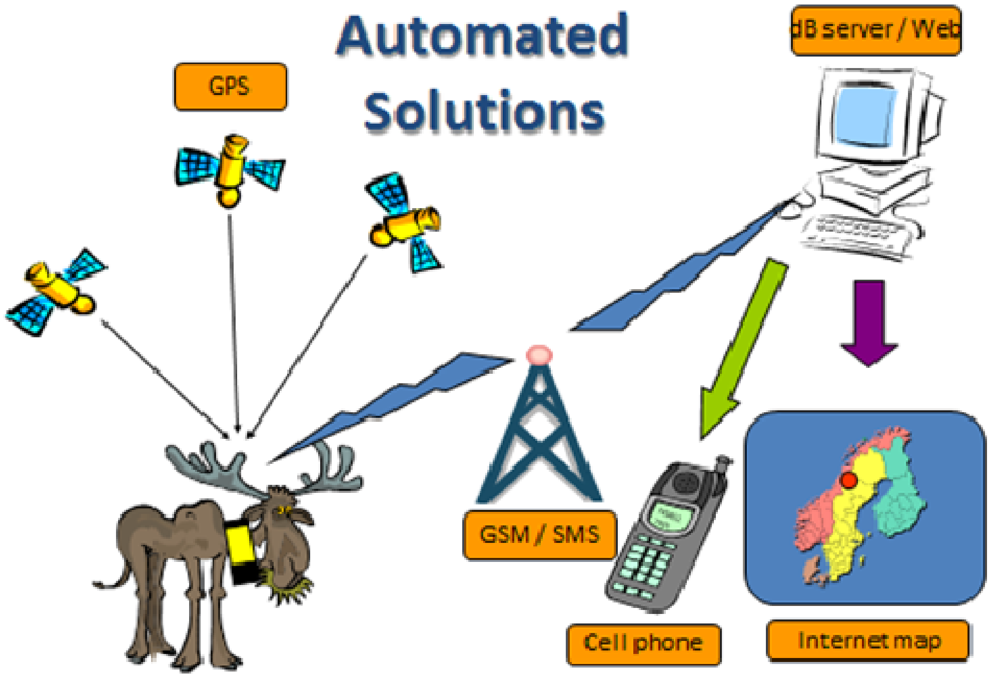

Figure 2. Illustration of the automated solution used at the SLU for collecting GPS-data.

Appendix III - Examples of Calving clusters

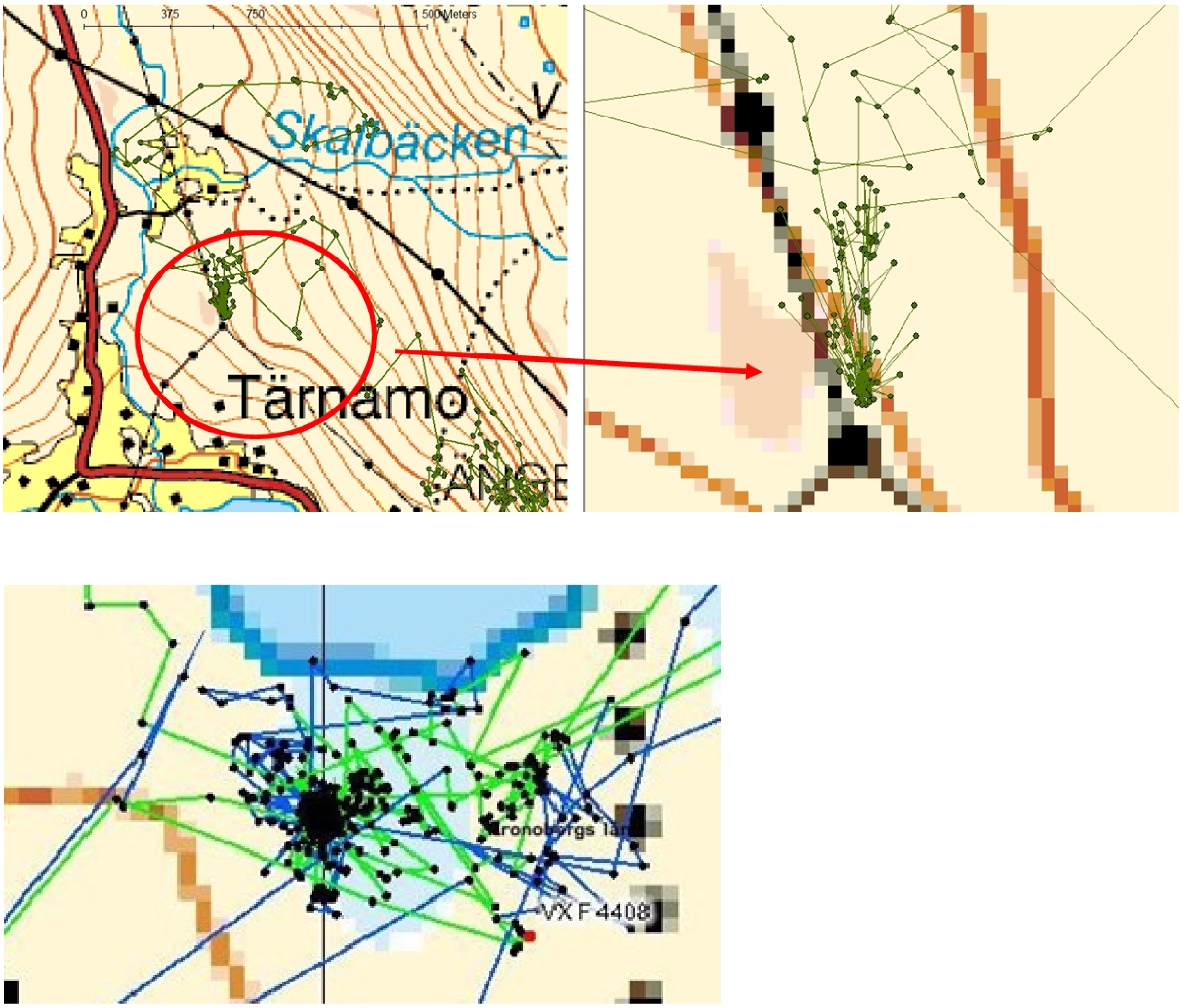

Figure 3. Examples of two different calving clusters shown on the map (First calving cluster in the study area Hemavan (65° 48' N, 15° 6' E); Second calving cluster in the study area Växjö (56° 52' N, 14° 48' E) .

Appendix IV – Calving site

Figure 3. Example of a calving site in the field photographed in Växjö (56° 52' N, 14° 48' E).

Appendix V - ArcGIS layers

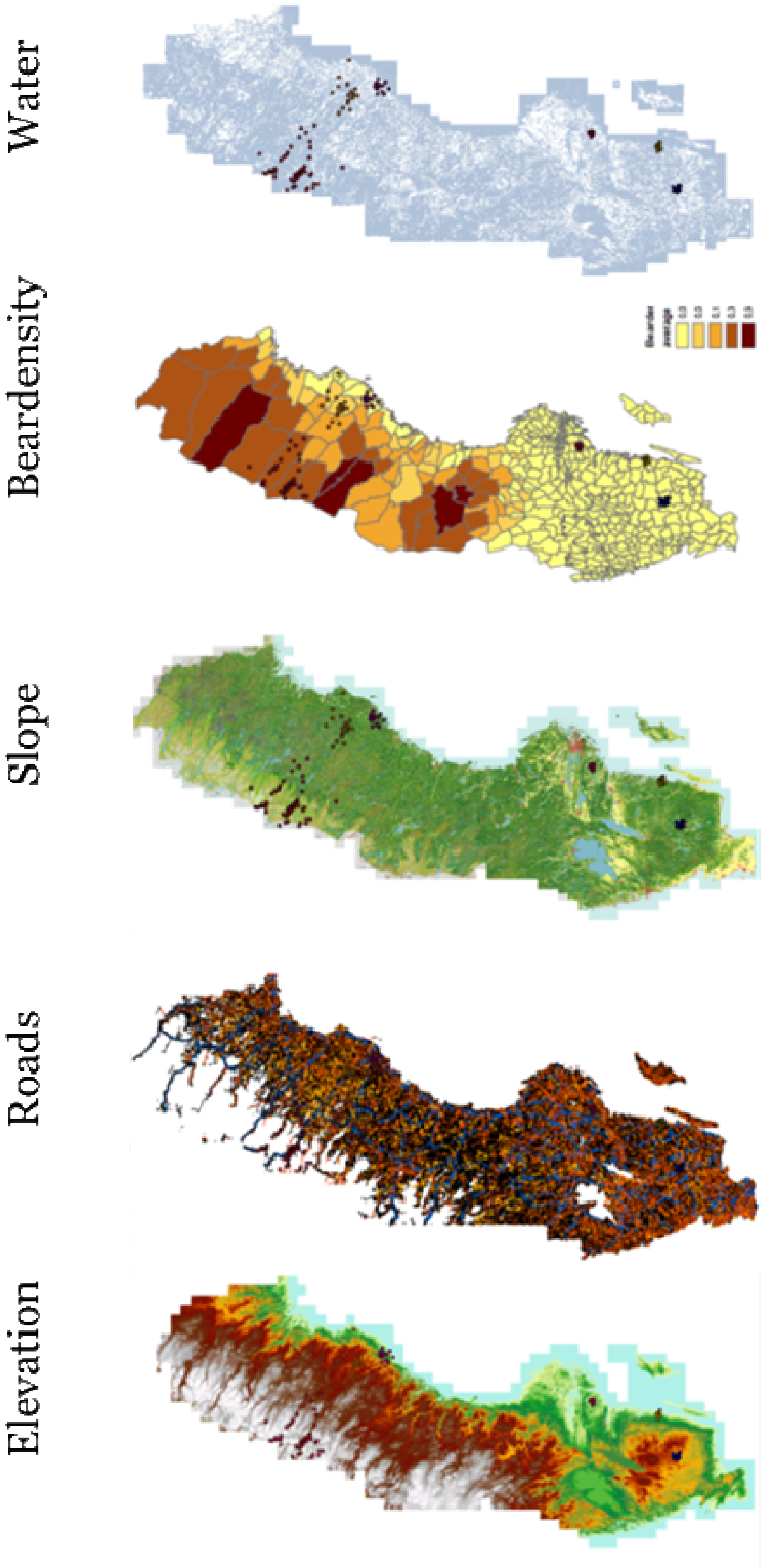

Figure 4. Examples of used GIS layers for collecting different site characteristics.

Appendix VI - Original and reclassification scheme of used land cover classes

Table 1: Original and reclassification scheme of used land cover classes related to moose

Original land cover-class	*Reclassified land cover-class*
Arableland	*Pastures*
Barerock	*Sparselyvegetatedareas*
Broadleavedforestnotonmires	*Broadleavedforestnotonmires*
Broadleavedforestonmires	*Broadleavedforestonmires*
Broadleavedforestonopenbedrock	*Sparselyvegetatedareas*
Clearfelledareas	*Youngforest*
Coniferousforest5to15m	*Coniferousforest5to15m*
Coniferousforesthigher15m	*Coniferousforesthigher15m*
Coniferousforestnotonlichendominatedareas	*Coniferousforestnotonlichendominatedareas*
Coniferousforestonlichendominatedareas	*Coniferousforestonlichendominatedareas*
Coniferousforestonmires	*Coniferousforestonmires*
Coniferousforestonopenbedrock	*Sparselyvegetatedareas*
Grasstundra	*Sparselyvegetatedareas*
Inlandmarshes	*Mires*
Lakesandponds,opensurface	*Mires*
Meadowgrasses	*Pastures*
Mixedforestnotonmires	*Mixedforestnotonmires*
Mixedforestonmires	*Mixedforestonmires*
Mixedforestonopenbedrock	*Sparselyvegetatedareas*
Moorsandheathland	*Mires*
Othermires	*Mires*
Pastures	*Pastures*
Peatextractionsites	*Mires*
Solitaryhouseswithproperty	*Sparselyvegetatedareas*
Sparselyvegetatedareas	*Sparselyvegetatedareas*
Thickets	*Youngforest*
Wetmires	*Mires*
Youngerforest	*Youngforest*

Appendix VII - Extraction of used Data

Beardensity	HOUSEDIS	ROADDIS	WATERDIS	SLOPE	LANDCOVER_CLASS	ELEVATION	USE	MOOSE_ID	YEAR	AREA
0.081885599	838.5255127	742.0410767	2053.807373	12.062	Coniferousforest5to15m	188	0	aa_ac_05_010	2005	Haellnaes
0	357.9455261	412.3105774	25	2.471163	Coniferousforesthigher15m	25	0	aa_d0_09_016	2010	Oestermalma
0.599032998	1343.50293	5400.520996	371.6517334	1.58173	Cf.onlichendominatedareas	591	0	aa_ac_05_119	2007	Hemavan
0	182.0027466	25	261.0076599	1.232002	Pastures	165	0	aa_g0_09_001	2009	Vaexjoe
0	515.3881836	134.6291199	840.0148926	4.542678	Sparselyvegetatedareas	64	0	aa_h0_10_004	2010	Misterhult
0.01514	680.0735474	302.0761414	1188.48645	7.125016	Youngerforest	160	0	aa_ac_04_004	2004	Nordmaling
0.567963004	2211.47583	2183.03125	638.8466187	9.365158	Coniferousforest5to15m	660	0	aa_ac_05_078	2007	Hemavan
0	190.3943329	100	375	3.816451	Coniferousforesthigher15m	35	0	aa_h0_10_013	2010	Misterhult
0.081885599	1955.760742	425.7346497	100	4.36445	Mixedforestnotonmires	292	0	aa_ac_05_022	2005	Haellnaes
0	496.2358398	50	620.9871216	0.20257	Mixedforestnotonmires	168	0	aa_g0_09_002	2009	Vaexjoe
0	353.5534058	90.13877869	406.97052	0	Pastures	21	0	aa_d0_09_003	2010	Oestermalma
0.01514	886.7073975	340.0367737	1450.215454	0.835163	Youngerforest	122	0	aa_ac_04_013	2004	Nordmaling
0	250	176.7767029	2030.394043	0.405136	Broadleavedforestnotonmires	248	0	aa_g0_09_002	2009	Vaexjoe
0.129059002	604.6693115	364.0054932	1134.955933	1.833734	Coniferousforesthigher15m	158	0	aa_ac_04_015	2004	Nordmaling
0.081885599	257.3907471	406.97052	956.8829346	1.280959	Mixedforestnotonmires	125	0	aa_ac_05_003	2005	Haellnaes
0.567963004	254.9509735	648.5560913	195.2562408	4.718376	Youngerforest	393	0	aa_ac_04_047	2007	Hemavan
0	460.9772339	90.13877869	565.6854248	1.866953	Youngerforest	39	0	aa_h0_10_023	2010	Misterhult
0	740.3546143	158.1138763	111.8033981	4.149145	Youngerforest	34	0	aa_d0_09_015	2010	Oestermalma
0.567963004	1195.04187	502.4937744	369.120575	1.432096	Broadleavedforestnotonmires	350	0	aa_ac_05_119	2007	Hemavan
0.01514	1202.601318	300	1439.183838	0.835163	Coniferousforest5to15m	83	0	aa_ac_04_020	2004	Nordmaling
0	304.1381226	215.058136	1380.443726	3.646971	Coniferousforest5to15m	165	0	aa_g0_09_004	2009	Vaexjoe
0	452.7692566	285.0438538	90.13877869	1.417709	Coniferousforesthigher15m	34	0	aa_h0_10_014	2010	Misterhult
0.108874001	602.0797119	430.116272	811.2490234	0.452953	Mires	250	0	aa_ac_05_007	2005	Haellnaes

Figure 5. An extraction of the used data for the analysis.

Appendix VIII - R script

<u>Country- scale:</u>

```
modall<-lme(USE~Beardensity+LANDCOVER_CLASS+ELEVATION+SLOPE+
ROADDIS+WATERDI+HOUSE25+AGE_CLASS,all,random=~1|Area,method="ML")
summary(modhema)
dredge(modhema)
finalmodall<lme(USE~ELEVATION+ROADDIS+WATERDIS+HOUSEDIS+LANDCOVE
R_CLASS,all,random=~1|AREA,method="ML")
```

<u>Area-scale:</u>

```
modhema<-lme(USE~Beardensity+LANDCOVER_CLASS+ELEVATION+SLOPE+
ROADDIS+WATERDI+HOUSE25+AGE_CLASS,hema,random=~1|MOOSE_ID,method="
ML")
summary(modhema)
dredge(modhema)
finalmodhema<lme(USE~ELEVATION+SLOPE+HOUSEDIS+LANDCOVER_CLASS,
hema,random=~1|MOOSE_ID,method="ML")
```

Appendix IX – Model selection

Table 1: Results of the model selection with the dredge function in the R package MuMIn (the third best models are shown for each area)

Model	AICc	weight	k
Sweden			
ELEVATION+HOUSEDIS+LAND COVER_CLASS+ROADDIS+WATERDIS	766.70	0.191	19
Bear density+ ELEVATION+ HOUSEDIS+LAND COVER_CLASS+ROADDIS +WATERDIS	767.90	0.102	20
ELEVATION+HOUSEDIS+LAND COVER_CLASS+WATERDIS	768.50	0.078	18
Hemavan			
ELEVATION+HOUSEDIS+LAND COVER_CLASS+SLOPE	253.80	0.058	15
HOUSEDIS+LAND COVER_CLASS	253.90	0.055	13
Bear density+HOUSEDIS	254.00	0.053	14
Hällnäs			
-	94.19	0.076	3
SLOPE	95.05	0.049	4
HOUSEDIS	95.34	0.043	4
Nordmaling			
ELEVATION+ROADDIS	82.08	0.142	5
Bear density+ELEVATION+ROADDIS	83.18	0.082	6
Bear density+ROADDIS	83.82	0.059	5
Öster Malma			
ELEVATION+ROADDIS	63.00	0.223	5
ELEVATION	63.64	0.161	4
ELEVATION+HOUSEDIS+ROADDIS	64.66	0.097	6
Misterhult			
HOUSEDIS	78.40	0.214	4
HOUSEDIS+SLOPE	79.88	0.102	5
ELEVATION+HOUSEDIS	79.95	0.098	5
Växjö			
ROADDIS+SLOPE+WATERDIS	201.40	0.415	6
ELEVATION+ROADDIS+SLOPE	203.20	0.163	7
HOUSEDIS+ROADDIS+SLOPE	203.50	0.146	7