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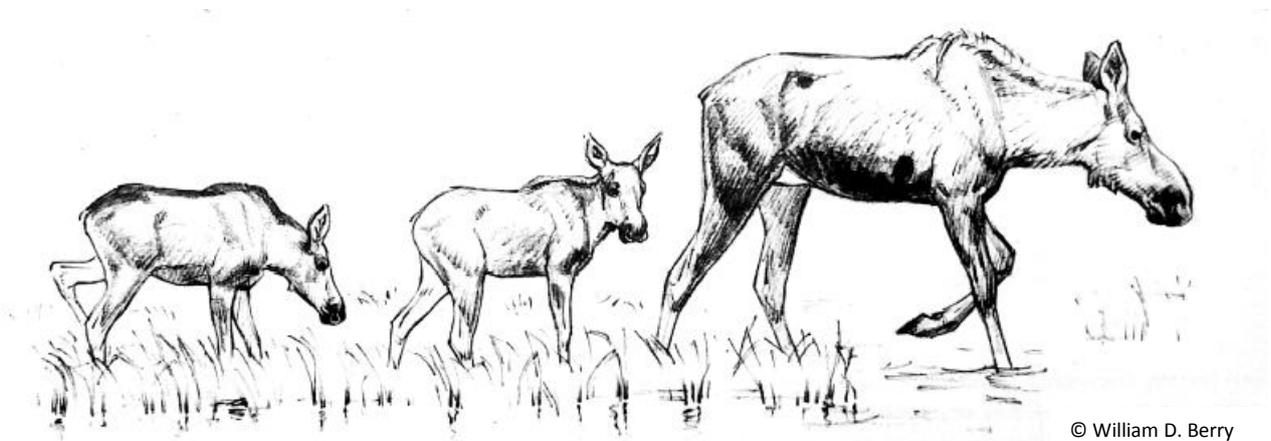


Master's Degree "Biodiversity and Sustainable Development"
Perpignan Via Domitia University

Grimso Wildlife Research Station
Department of Ecology, SLU

Moose calving strategies in response to wolf re-colonization in Sweden

Camille Rostan



Supervisors: Håkan Sand & Kerry Nicholson

Master Thesis 2014

Acknowledgments

First of all, I would like to thank Håkan Sand for giving me the opportunity to do my master's thesis in the small and isolated research station which is Grimsö. Even if there was no field work included for this project, I am really grateful and I feel proud to have been a part of your team.

I would like to warmly thank Kerry Nicholson for her help and the precious advises that she gave me throughout my internship. Thank you for your time, patience and for being available when I needed it. It wouldn't have been possible for me to go through my analysis without you and without all the small, beautiful and explanatory drawings that you made (of course you are an artist)!

I am also thankful to people working for the Roe Deer Project who allowed me to do some field work and for their kindness.

Thank you to Barbara Zimmermann for giving me the opportunity to follow her course on Resource Selection Function in Norway, it was really interesting and it helped me a lot for my analysis.

Thank you to Cyril Milleret for answering my questions about Grismö, the dataset and for hosting me during my stay in Evenstad.

Last but not least, I would like to thank all the students from the Bunker who made my day during those 6 months. MK, thank you for being such a great roommate and thank you for always being so joyful. Thank you Françoise for your chocolate cakes, for your kindness; also, I will never forget our special dance on "Atchi batchi combo ékalé chikichikichikitaaa" (you know what I mean)! Thank you Irène for the walks around the station, watching birds ("les pouics-pouiiiics") and cuddling mini and normal horses. And thank you Fanny for your enthusiasm and interesting talks about Game of Thrones!

Finally, I would like to thank Arthur for always supporting me and for cheering me up when I needed it. Thank you for always being there for me!

And thank you to my parents and sisters for their encouragements and faith in me!

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Introduction

In predator-prey systems, prey have to find a balance between the need to gain energy and other nutritional requirements for maintenance, growth and reproduction at the same time as decreasing the probability of encounter with predators (Lima & Dill, 1990; Kie, 1999). Thus, selecting habitat to meet these requirements is critical for population persistence. Increased familiarity with an area is beneficial, because prior knowledge of local conditions (resources quality, refuge from predators) may allow selecting habitat of higher quality (Howery et al., 1999), increase foraging effectiveness and reduce predation risk, and thus enhance survival (Hinde, 1956; Stamps, 1995). Thus, the repeated use of the same location can be considered as a strategy to maximize fitness: fidelity can reduce the cost associated with the search of a new unknown area that can turn out to be unfavorable (Greenwood, 1980; Switzer, 1993). Selecting habitat that optimizes survival and reproduction can be more important during certain life history events, such as mating periods or parturition, as these are critical for reproductive success (Switzer, 1997).

Calving site selection

For female ungulates, the trade-offs in birth site selection are between supporting nutritional needs for lactation and gestation recovery, and reducing the risk for neonates to be killed by predators (Bowyer et al., 1999; Barten et al., 2001; Hebblewhite & Merrill, 2009). Optimal birth sites might provide adequate cover for young to hide from predators as they are often more vulnerable during parturition and the first weeks after birth (Carl & Robbins, 1988). Sites should preferably also supply sufficient forage to support the increased energetic demands of females (Gasaway & Coady, 1974). Nevertheless, there is commonly a positive relationship between forage availability and predation risk, which is habitats with high forage abundance and quality are also sometimes more risky (Bowyer, Kie, et al., 1998). For instance, caribou (*Rangifer tarandus*) in British Columbia selected birth sites at higher elevation with lower forage quality and abundance, but increased the distance to predation threat and reduced the risk for young to be killed (Bergerud et al., 1984; Bergerud & Page, 1987) Elk (*Cervus elaphus*) in the Rocky Mountains returned to areas of higher quality, i.e. higher forage availability and lower predation risk (Wolf et al., 2009).

In North America, moose (*Alces alces*) calving site selection in areas has been widely studied and several anti-predator strategies have been suggested. In British Columbia, Poole et al., (2007) reported that part of females selected areas higher in elevation with reduced forage and increased distance from water whereas the other part of females favored sites with exactly opposite characteristics. Females which selected sites at higher elevation or further away from water were also farther from potential predators (Chekchak et al., 1998; Bowyer et al., 1999).

These areas are potentially more risky because some predators use rivers as travel routes and remain in valleys at the lower elevation to search for prey (Mech & Boitani, 2010). On Isle Royale, in Michigan, some females select birth sites on more remote islands which reduce the risk of encounter with wolves (Stephens & Peterson, 1984; Addison et al., 1993). Contradictory results have been found concerning vegetation cover, which provides shelter and cover for calves, but at the same time it can reduce visibility and impede detection of approaching predators (Bowyer et al., 1999; Poole et al., 2007). Large carnivores generally avoid contact with humans, which in some areas has led to a behavioral adaptation of prey by using humans as protection against predation (Berger, 2007). Therefore in some areas, moose selected birthing sites situated closer to human development (Stephens & Peterson, 1984) and roads (Berger, 2007). Contrary to what has been observed, Bowyer et al., (1999) found that females selected calving locations situated further away from human developments in Alaska. Increasing distances from humans was also observed in areas where hunting pressure was high (Lykkja et al., 2009). Calving site characteristics are sometimes difficult to describe because of the high variability in environmental variables (e.g. forest structure and composition, distance from shorelines or visibility, Addison et al., (1990). Moose without distinct calving site preferences may be a behavioral strategy to thwart predators by minimizing the predators prior knowledge of where to detect newborn calves (Bowyer et al., 1999; Testa et al., 2000).

Moose habitat selection has been the subject of several studies in Scandinavia, regarding age, sex or reproductive status of individuals. Females with young select most of the time young or coniferous forests and usually avoid open cultivated areas during summer (Cederlund & Okarma, 1988; Bjørneraas et al., 2011, 2012; Olsson et al., 2011; Nicholson et al., 2014). However, most studies were focused on habitat types selected by females with calves at heel with few studies focusing on the selection of the actual calving sites.

Fidelity

Birth site fidelity is the tendency to return to the same location or area for giving birth in successive years (Greenwood, 1980; Waser & Jones, 1983). It has been observed for several species (Greenwood, 1980) with a scale varying from general area to the specific birth location, depending on which species was studied (Switzer, 1993). Fidelity is usually reported to be related to predator avoidance and influenced by previous recruitment success (Greenwood, 1980; Switzer, 1997).

According to recruitment success of the previous years, birth site fidelity is an important strategy for maximizing fitness, especially for species for which offspring is subject to high selective pressure just after birth (Danchin et al., 2001). It has been demonstrated that fidelity to site increases with age for several species (wild turkey (*Meleagris gallopavo*): Badyaev & Faust, 1996; caribou: Schaefer et al., 2000; willow flycatcher (*Empidonax traillii*): Sedgwick, 2004;

Weddell seal (*Leptonychotes weddellii*): Cameron et al., 2007) although this was not established for moose (Tremblay et al., 2007).

Calving site fidelity by moose has been studied repeatedly over the years (Addison et al., 1993; Chekchak et al., 1998; Bowyer et al., 1999; Welch et al., 2000; Testa et al., 2000; Tremblay et al., 2007; McGraw et al., 2012), and quantifying the level or strength of fidelity often comes into question. This is particularly important when defining the distances between successive calving sites. Females which have successfully raised their offspring the previous year might be predisposed to return to the same area; conversely, if a calf was lost because of predation, the birth site may be avoided during subsequent years (Testa et al., 2000; Tremblay et al., 2007).

The aim of my study was to analyze the effect of the re-colonization of wolves (*Canis lupus*) and test if the predation risk they pose to female moose will affect their selection of calving sites. In Scandinavia, the wolf was persecuted and nearly exterminated during the nineteenth and twentieth century (Cederlund & Markgren, 1987), leaving humans as the main source of mortality for moose for decades (Lavsund et al., 2003). However, expansion and recovery started in the 1980s for wolves (Wabakken et al., 2001). Worldwide, wolves are a main predator of moose and show a strong selection for calves; juveniles accounting for 90% of all moose killed by wolves during summer in Scandinavia (Sand et al., 2008).

I studied calving site selection in a resource selection framework within moose home ranges, i.e., calving site selection at the third order scale (Johnson, 1980) in relation to wolf predation risk and various habitat characteristics. I investigated the effect of human-related objects on calving site selection like distance to secondary roads, but also distance to human dominated landscapes and open areas. I tested the hypothesis that (1) moose would select sites with relatively lower predation risk and (2) providing relatively more shelter for calves like established forest. Eriksen et al., (2009) reported that moose distance themselves from roads as an anti-predator strategy in Scandinavia, because wolves use them to travel. Thus, I expected (3) birth sites to be further from secondary roads, but closer to human houses and settlements because predators would avoid these areas. Finally, I expected (4) calving sites to be further away from open landscapes like clear-cuts or pastures because they are considered riskier areas (Gervasi et al., 2013).

In addition to calving site selection, I examined calving site fidelity of female moose. I predicted that (1) for each female, successive calving sites would be situated closer to each other than to sites used by other females. Regarding previous reproductive success, I expected (2) an increased in distance or a change between calving sites in successive years if the cow lost its offspring, especially if it occurred before weaning when the bond between mother-infant is most important (Stringham, 1974; Tremblay et al., 2007). Finally, I expected (3) fidelity to increase with age.

Material & Methods

Study area

This study was conducted within Grimsö wildlife research area (140 km²) and nearby areas totaling 730 km², located in the boreal zone in south-central Sweden (59°-60° N, 15°-16° E, Appendix I). Elevation ranges between 100 and 150 m. Climate is typical of inland south-central Sweden climate, where temperatures in winter are usually down to -20°C and up to 25°C in summer (Vedin, 1995). Mean annual precipitation is 600-700 mm, of which 30% falls as snow and the ground is generally covered by snow from December to late March (Alexandersson & Andersson, 1995). The area consists of 71% forests, 14% bogs, 8% pastures and 6% lakes and rivers. Established forest stands are dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pubescens* and *Betula pendula*) (Rönnegård et al., 2008). Bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), dwarf birch (*Betula nana*) and heather (*Calluna vulgaris*) are the main species which constitute the understory (Rönnegård et al., 2008).

Moose favorite browsing species are rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), and willows (*Salix spp*), even if these species are often absent of mature stands and are quite sparse in study area (Månsson et al., 2007; Rönnegård et al., 2008). Forest management is intensive within the area by clear-cutting; old forest is replaced by planting or natural regeneration. After logging, early successional stages are constituted mainly of birch, willow and aspen, with field layers of wavy hair grass (*Deschampsia flexuosa*), ligonberry, bilberry, and heather (Cederlund & Okarma, 1988). Houses density is low, reaching a maximum of 39 houses per km². Areas where house density is more than 10 houses per km² represent less than 4% of the study area and settlements surface represents less than 1%. Main roads consist of paved roads more than 7 m in width, their density reaches a maximum of 0.75 per km². Secondary roads are all other roads, paved or unpaved, less than 7 m wide including forest service roads, private roads or trails; their density is 1.95 per km² in the study area.

Moose and wolf populations

Moose density was estimated 1.2 moose per km² in 2002 and 0.8 moose per km² in 2006 by aerial counts (Rönnegård et al., 2008). Moose in the area showed strong fidelity to the established home ranges and were considered non-migratory (Cederlund & Okarma, 1988). Hunting was allowed in the study area, and appeared to be the main source of mortality for moose until 2003 (Rönnegård et al., 2008). Since 2003, wolves have naturally re-colonized in and around the Grimsö research area. From 2003 to 2005, wolf packs were monitored by snow tracking, and by Global Positioning System (GPS) collars from 2005 to 2011 (for description of census techniques and population development see (Liberg et al., 2010, 2011).

First, the Uttersberg pack established during the winter of 2003 – 2004 (Wabakken et al., 2004). A new scent-marking pair, named Hedbyn, established during the winter of 2009 – 2010 (Wabakken et al., 2010) and extended the previous Uttersberg pack home range (Wabakken et al., 2010).

Moose and wolf capture

Adult female moose were captured in March 2007 (n=20) and 2010 (n=10). They were immobilized by darts from helicopters (Arnemo et al., 2003) and fitted with GPS/Global System for Mobile Communications (GSM) collars (GPS/GSM Plus 4D; Vectronic Aeospace GmbH, Berlin, Germany) set to acquire locations every two hours. For the analysis, I used GPS locations of parturient females only. Their reproductive status was assessed by experienced field technician and observations were performed in spring (12 May – 04 July) until the presence of calves was verified. Surveys were also performed by field technician in late summer (26 Aug. – 09 Sep.) to determine summer survival of calves and at the end of winter the following year (01 Apr. – 29 Apr.) to determine winter survival.

Wolves were immobilized in winter by darting from helicopter (see Sand et al., (2006b) for more detailed procedure of capture). They were equipped with GPS collars (GPS/GSM Plus 1D; Vectronic Aeospace GmbH, Berlin, Germany) which acquired location every 12 hours. GPS locations were recorded for at least one of the alpha wolves from March 2005 to February 2011, except for a 3 month period between a collar failure and the recapturing event which took place in 2009 – 2010.

GPS data screening

The dataset of moose GPS locations was screened for positioning errors following the method described in Bjørneraas et al., (2010) in program R (R Core Team, 2014). The screening consisted in removing all unlikely movements, defined by travel speed, travel distances and turning angles. The first step was to remove all locations that were further away than 100 km from the surrounding locations, based on the assumption that moose could not have moved and returned that distance in a 2 hour interval. Then, the distance was refined to 10 km, a distance that moose could travel in 2 hours. In the third step, locations forming a spike (locations forming a back and forth with a high speed) were identified and removed when the speed limit exceeded 1.5 km/h and the cosine of the turning angle was less than 0.97. Those criteria were based on the assumption that moose are unlikely to move so fast toward a point further away and immediately turn back suddenly toward the location where they came from (Bjørneraas et al., 2010).

Wolf risk

I used a predator-specific landscape of predation risk created for a parallel study (see Nicholson et al., (2014) for calculation details). Essentially, for each moose, the relative wolf density was estimated on a 25m x 25m grid using kernel density estimator (Worton, 1989). Then, a utilization distribution (UD) was calculated for each year to estimate the probability that wolves were located within a given pixel relative to other pixels. As no GPS data were available after February 2011 to calculate wolf utilization for all of 2011, the utilization data from 2010 was used for 2011. This assumed that wolf presence did not vary significantly among years for the same pack. Thus, I used a calculated mean utilization distribution of wolf within the moose home range as a value of predation risk.

Moose home ranges and random sites

I calculated both spring and yearly home ranges for each female. Similar to Singh et al., (2010), I set spring date range from 1 April to 31 May of the current year and annual home ranges from 1 May of the prior year until 30 April of the current year. For females that were collared in 2007 or 2010 with no prior data, I used the same date range but of the following year. I estimated home ranges using the 95% fixed Kernels (Worton, 1989) using the least squares cross validation technique to estimate the bandwidth using Geospatial Modelling Environment (GME) software (Beyer, 2011).

Moose calving site selection was assessed using a resource selection function approach which consists in comparing resources used by animals and resources available for them in their environment (Manly et al., 2002). Forage quality and density as well as moose metabolic needs change through seasons, therefore seasonal variations in home ranges size are expected (Cederlund & Okarma, 1988). Accordingly, I generated random points within the spring home ranges instead of the yearly home ranges (i.e. third-order scale of selection; Johnson, 1980). I used the Create Random Points tool in ArcGIS 10.2.1TM (© 2014 ESRI Inc.) to generate random points within each spring home range. The random locations represent what is available in the landscape for moose; therefore I did not allowed random points to occur within a 100 meter-buffer around used calving sites, as this could confound results. They were also constrained to not occur in lakes, rivers or in the middle of roads as these are obviously non-suitable calving areas. All random points were buffered by 100 m, as done for observed calving sites.

Estimation of calving location

Without direct observations, obtaining the specific parturition date and time of any animal is a difficult task. Therefore, I used several steps to ensure unbiased and accurate estimation of the calving date and subsequently determined the calving location for each moose during the study.

Basic moose biology indicates that peak calving period occurs from mid-May to early June (Bowyer, Ballenberghe, et al., 1998; Schwartz, 2007). Also, females may modify their movements one month before giving birth (Ciuti et al., 2006), therefore I concentrated my analysis window to mid-April to early July to detect calving locations. For calves born in 2007 and 2008, I used the data collected by field observations in which the technicians monitored moose for calves on average two times a week. Upon observing calves, field personnel would visually estimate calf age. The estimated parturition date was then calculated as:

$$\text{Day of 1}^{\text{st}} \text{ calf observation} - \text{Visually estimated age of calf.}$$

However, there are uncertainties when visually estimating the age of a calf, even with highly trained personnel. Additionally, field protocols changed after 2008 on how the estimation of parturition dates was conducted. Therefore, I used this information as a general guidance and investigated other methods for this assessment.

The first method I used was the Tracking Analyst® (TA) extension on ArcGIS. Tracking Analyst allows for visualizing and mapping spatial patterns or movements through time. By animating the movement paths of the GPS collared females, I could visually identify localization patterns. Localization is when a female has very short movements between locations for several consecutive days and can be used as a method to detect potential calving location (Welch et al., 2000; Poole et al., 2007). It has been reported previously that females reduce their movements just after parturition (Poole et al., 2007; Rolandsen et al., 2010; Wattles & DeStefano, 2013) and stay sedentary during several days (Stringham, 1974; Cederlund et al., 1987; Chekchak et al., 1998; Bowyer et al., 1999; Testa et al., 2000). For example, Poole et al., (2007) observed moose moving more before (95 m/h) than after calving (15 m/h) and Wattles & DeStefano, (2013) found similar result as females reduced their daily movement from 3000 m/day prior to calving, to 500 m/day during the calving period. Additionally, Chekchak et al., (1998) reported that cows stayed in average four days at a birth site after parturition. Bowyer et al., (1999) reported that Alaskan moose females remained near birth sites for three-four weeks after parturition if they were undisturbed by predators, which is consistent with what has been found by Stringham, (1974). Therefore, for this study I assumed that calving was indicated by a sequence of locations confined to an area of less than 100 m² for a period of at least two-three days during mid-May to early June, corresponding to a period of reduced mobility following birth of a calf.

As Tracking Analyst may still be considered as a subjective measure, I then used Behavioral Change Point Analysis (BCPA, Gurarie et al., (2009)). This method identifies structural changes in the underlying movement parameters of time series data, to which I have applied to the moose GPS data. The analysis can be realized on multiple metrics associated with movements, for example step lengths (or distance), turning angles, or velocity.

In addition to these basic metrics, Gurarie et al., (2009) proposed a movement metric of persistence velocity which captures the tendency and magnitude of animal movement to persist in a given direction during a given time interval. Thus, it combines multiple descriptive features of movement like speed, directional persistence and the variability within these measures. The analysis was based on the identification of “most likely change points” in a time series where movements may change, by comparing which of the parameters i.e. mean $\mu(t)$, variance $\sigma^2(t)$ and autocorrelation $\rho(t)$, if any, had changed within a specified analysis window in a time series. The BCPA was expected to identify where changes in the movement metric were abrupt before calving, given that female movements change considerably before parturition (Testa et al., 2000; Poole et al., 2007; Wattles & DeStefano, 2013).

To estimate the start of parturition, i.e. the date and time when a change point occurred, I evaluated several parameters: distance, velocity and persistence velocity. I performed the BCPA analysis using a script provided by the author (Gurarie, 2011) in R. For each moose, I reduced the input GPS data to a period of two weeks before and after the calving date estimated by the field technician. I set the analysis window to 24 hours, corresponding to 12 GPS locations and I used a window step of 1, which allowed detecting more accurately behavioral changes.

Once the calving date was identified, I pooled the GPS locations of 24 hours following that date and time and identified this period as the calving site. I calculated the spatial mean center of the selected locations and I buffered this by 100m to account for the uncertainty in knowing the precise calving site. A 100m-buffer likely included the major part of the post-parturition area used by the cows and calves (Welch et al., 2000). Because moose contractions can start nine hours before parturition (Cederlund, 1987), I chose to use locations of the very first day of the birth period instead of the unique location corresponding to date and time given by the change point.

Environmental variables

According to the literature, I chose environmental variables which were judged as potentially important factors influencing calving site selection.

Habitat classifications were obtained from a 25m x 25m vegetation map classified by satellite imagery (Swedish CORINE Land Cover; SMD, National Land Survey of Sweden). The study area is constituted of thirty eight different vegetation classes which were reclassified into four more general land cover classes (Table 1). Forest management is intense in the study area, but vegetation maps from SMD were constructed from satellite images taken in 2002, therefore new maps were created and updated with clear-cuts from 2002 to 2007 obtained at the Swedish Forestry Agency. Vegetation maps were also updated each year during the study period (2007-2011) to take succession vegetation into account. I assigned one habitat class to each calving site, based on the majority class within the 100m buffer.

I calculated Euclidean distance to secondary roads, houses and settlements (“human structures”) in meters with ArcGIS, derived into raster data (25m x 25m). Pastures and clear-cuts have been reported as risky habitats for moose (Gervasi et al., 2013), therefore I also calculated distance to the nearest clear-cuts or pastures, named hereafter as distance to “modified landscapes”. Elevation can be a factor influencing female birth site selection (Chekchak et al., 1998; Barten et al., 2001; Poole et al., 2007), but was not taken into account for my analysis because the research area lacks variation as elevation ranges between 100 to 150 m.

Table 1: Proportion or range of environmental variables used to describe moose calving site selection in south-central Sweden, 2007-2011. For habitat characteristics, percentage of area covered represents the proportion of a given habitat in the study area. For continuous variables, it is expressed as the range of minimum and maximum values of the observed variable in the study area.

Variables	Description	% Area covered or Range
Habitat types		
Bogs	Wet mires, inland marshes	14 %
	Coniferous, broad-leaved and mixed forests on mires, thickets	
Established forests	Coniferous forests 5 - 15 m or > 15 m	54 %
	Coniferous forests on open bed rock or lichen dominated areas	
	Broad-leaved forests not on mires or on open bedrock	
	Mixed forests not on mires or on open bedrock	
Modified landscapes	Clear-cuts < 5 years old	11 %
	Pastures (grassland or arable land)	
Young forests	Young forests or clear-cuts > 5 years old	17 %
Wolf risk		
	Probability of wolf to be present in a given area	0 – 1.14
Distances		
to secondary roads	Euclidian distance from secondary roads (non-paved roads)	0 – 1546 m
to humans	Euclidian distance from human activity (houses and settlements)	0 – 4802 m
to modified landscapes	Euclidian distance from pastures and clear-cuts	0 – 3537 m

Fidelity to site

I followed the same method described by Tremblay et al., (2007) to study moose calving site fidelity. First, I merged all annual home ranges of each individual in order to obtain one composite home range per female. Then, I calculated the average linear distances between all possible pairs of calving sites from year to year for a given female, but also between all possible pairs of random points. I also measured average linear distances between calving sites of a given cow and calving sites of other females situated within the composite home range of the cow in question (Tremblay et al., 2007).

The effect of past reproductive success on fidelity was assessed by modeling distances between successive calving sites according to the survival of calves before and after weaning (Tremblay et al., 2007), which usually occurs in mid-September (Bubenik, 2007).

I estimated calf survival based on surveys performed by field technicians in early autumn and late winter of the following year. During those controls, the presence of calves was assessed and calf mortality was defined as the absence of a calf that was previously recorded with a female (Testa et al., 2000; Tremblay et al., 2007). Therefore, recruitment was considered successful when the presence of at least one of the female's offspring was detected (Welch et al., 2000; Testa et al., 2000; Tremblay et al., 2007). Recruitment success before weaning was defined when a calf survived to the first survival check in autumn (August) whereas recruitment success after weaning corresponded to calf survival in late winter to the following spring check in April.

Statistical analysis

Calving site selection

I used generalized linear mixed models to study moose calving site selection. Use was defined as a binary response variable, with calving sites scored 1 and random sites scored 0. Explanatory variables, showed in Table 1, were included as fixed factors whereas moose ID was included as a random factor. Prior to model building, I tested for multicollinearity among variables to avoid including highly correlated variables in the same model using a cut of correlation of 0.7 (Hosmer & Lemeshow, 2000). I used Akaike's Information Criterion (AIC) values corrected for small sample sizes (AIC_c) to perform model selection (Burnham & Anderson, 2002). I also checked for linear or quadratic relationships for each continuous explanatory variable and chose the model with the lowest AIC_c value. Finally, I generated a set of candidate models, which were ranked according to their AIC_c value. I used AIC weights as evidence of a model with the most support, and models showing a $\Delta AIC_c < 2$ were considered as equally supported. To evaluate model performance, I used k-fold cross-validation for studies for which data are collected during a single intensive period and across only one region (Boyce et al., 2002). I divided the data set into ten equal bins, fitted the models using 80% of the data and used the remaining 20% to evaluate their performance. Goodness of fit was assessed with Spearman's correlation and selected when $r_s > 0.8$ (Boyce et al., 2002).

I conducted all statistical analysis in R, but specifically used the package lme4 (Bates et al., 2014) for mixed-effects modelling and MuMIn (Bartoń, 2014) for model selection with AIC_c .

Fidelity to site

I used a Wilcoxon signed-rank test to test for differences in means of average linear distances between observed calving sites and random sites of each female whereas the difference in means of successive calving sites of each female and calving sites of other females within its home range were tested using a paired t-test.

Similarly to the calving site selection, I used mixed effects linear models to study the effect of past reproductive success on fidelity. Distance between successive calving locations was the response variable; successful recruitment before and after weaning was included as fixed factor.

I also added age of cows if it improved models. I divided age into three categories: “young” when females were three to five years-old, “medium” when they were six to ten years-old and “old” when cows were more than ten years-old. Moose ID was included as a random factor. Again, I used model inference procedures to select the best model that explained calving site fidelity. Results are presented as means \pm SD and the significance threshold is $\alpha = 0.05$.

Results

Fifty calving sites were recorded for twenty-two females, with one to five successive calving sites per female from 2007 to 2011. Thus, I generated 5 random sites per observed calving site to define what was available for females within their home ranges.

Calving date estimation

Comparing Tracking Analyst and BCPA methods to estimate calving dates, I obtained nearly identical results, which was different from comparing the date estimations between field observations and Tracking Analyst or between field observations and BCPA (Figure 1). As BCPA is the least subjective method and possibly more accurate than Tracking Analyst, I used the BCPA calculated dates for subsequent analysis.

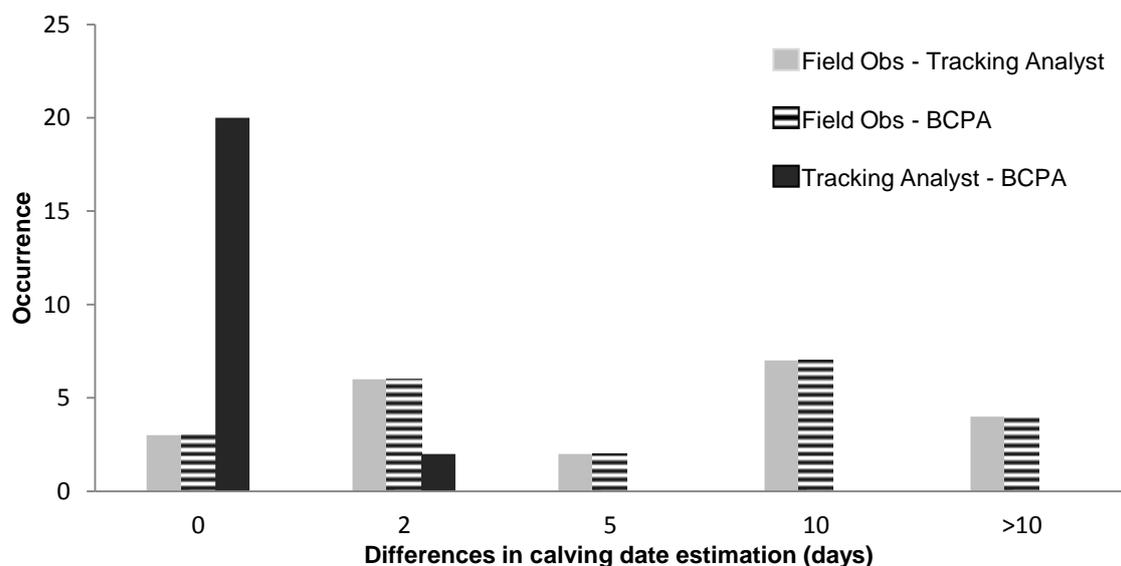


Figure 1: Count of the differences of calving date estimation (in days) between field observation (Field Obs), Tracking Analyst and behavioral change point analysis (BCPA) methods for moose in south-central Sweden, 2007 and 2008.

Among the parameters that I evaluated for the BCPA analysis, persistence velocity allowed me to detect more accurately changes in females’ movement compared to distance or velocity.

Successfully identifying one distinct starting parturition breakpoint varied among individuals. Nevertheless, for all females there was a common pattern in which the change points were followed by a period with very little movement (Appendix II). Hence, I assumed that these dates corresponded to the beginning of the calving period.

Identification of the end of the calving period was not as distinct for all females, which was expected because of the progressive increase in the mobility of a calf with age (van Beest et al., 2011). Therefore, some females increased their movement gradually, in which the mean change was not as abrupt and therefore was not always detected. Mean calving date for females varied from 14 May to 20 May among years (Appendix III).

Calving site selection

Habitat types and distance to secondary roads appeared to be important factors driving calving site selection for moose because they were included in each of the four best models (Table 2). Model including wolf predation risk was equally supported with models which did not include this parameter ($\Delta AIC_c < 2$).

Table 2: Model selection results of *a priori* candidate model list for the analysis of moose calving site selection in south-central Sweden, 2007-2011. Only models with $\Delta AIC_c < 2$ are presented, full list of models is shown in Appendix IV. k = number of model parameters; AIC_c = corrected Akaike's Information Criterion; ΔAIC_c = difference between AIC_c values; w_i = Akaike weight.

Models	k	AIC_c	ΔAIC_c	w_i
Habitat + Dist2ndroads	6	252.72	0	0.288
Habitat + Dist2ndroads + Wolf risk	7	253.66	0.94	0.180
Habitat + Dist2ndroads + DistModLand	7	254.11	1.39	0.144
Habitat + Dist2ndroads + DistHumans	7	254.69	1.97	0.108

Variable definitions: Habitat: habitat classes, Dist2ndroads: Euclidean distance (m) to secondary roads, DistModLand: Euclidean distance (m) to modified landscapes (clear-cuts or pastures), DistHumans: Euclidean distance (m) to houses or settlements, Wolf risk: Utilization density of wolves.

Females selected areas to give birth where wolf predation risk was lower and which were closer to houses and settlements (Table 3, Figure 2). They avoided areas which were closer to secondary roads or modified landscapes (Table 3, Figure 2).

For habitat types, values of beta estimates shown in Table 3 are expressed according to the reference category which is "Bogs". Therefore, bogs were more likely to be selected by females to give birth than established forests, young forests or modified landscapes (Table 3).

For example, females were 0.07 times less likely to select established stands than bogs and 0.12 times less likely to select modified landscapes (Figure 3).

Table 3: Averaged parameters estimates and standard errors from top four competitive models of moose calving site selection in central Sweden, 2007-2011. For habitat variables, values are expressed according to the reference category which is "Bogs".

Parameters	β	SE
Established forests	-1.29350	0.38220
Modified landscpaes	-0.73661	0.71962
Young forests	-1.61028	0.48998
Distance to secondary roads	0.00257	0.00083
Wolf risk	-1.66679	1.57849
Distance to modified land.	0.00042	0.00049
Distance to humans	-0.00006	0.00016

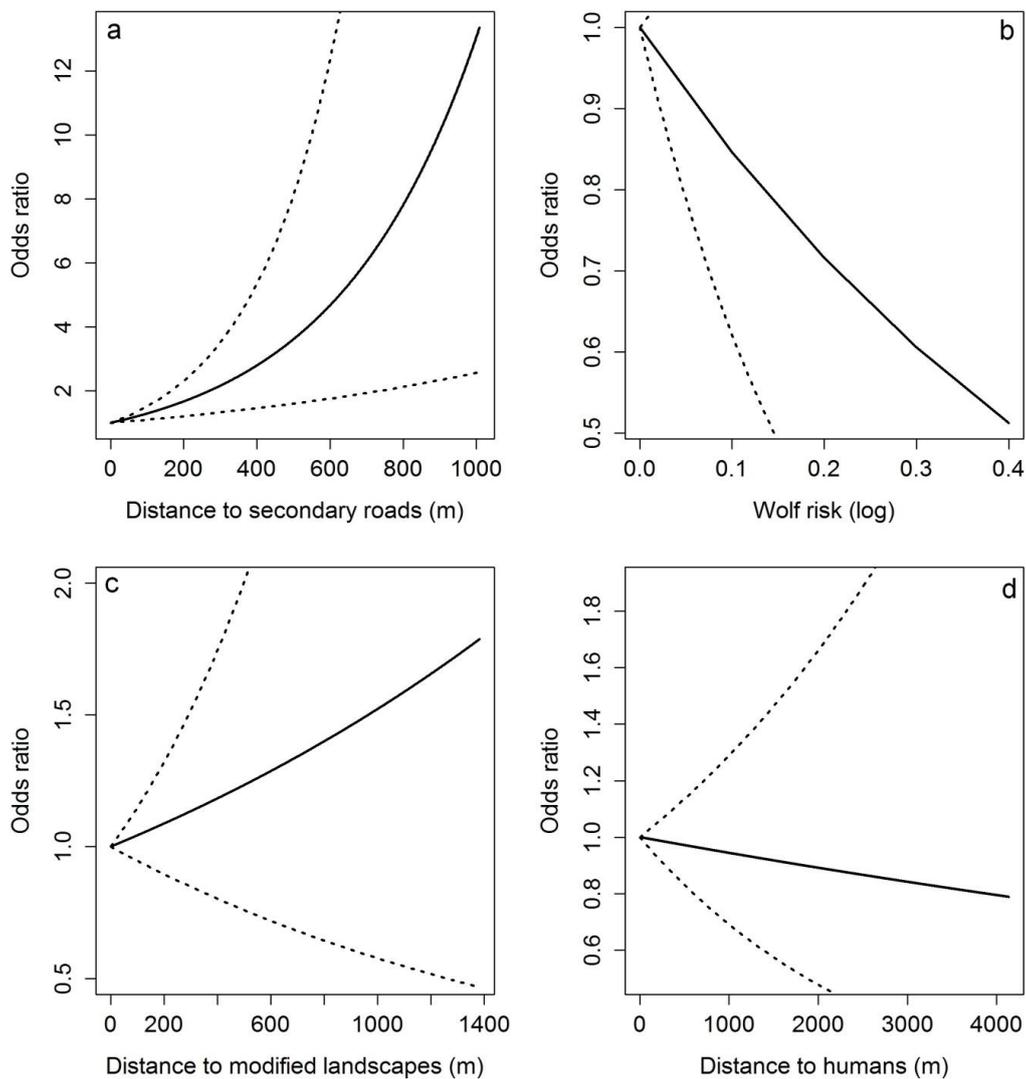


Figure 2: Odds ratios of moose calving site selection in relation to distance to secondary roads (a), wolf risk (b), distance to modified landscapes (c) and distance to humans (d) in south-central Sweden, 2007-2011. Dotted lines represent 95% confidence interval of the parameters estimates. Coefficients from the four best models were averaged in order to represent calving site selection in relation to distance to secondary roads.

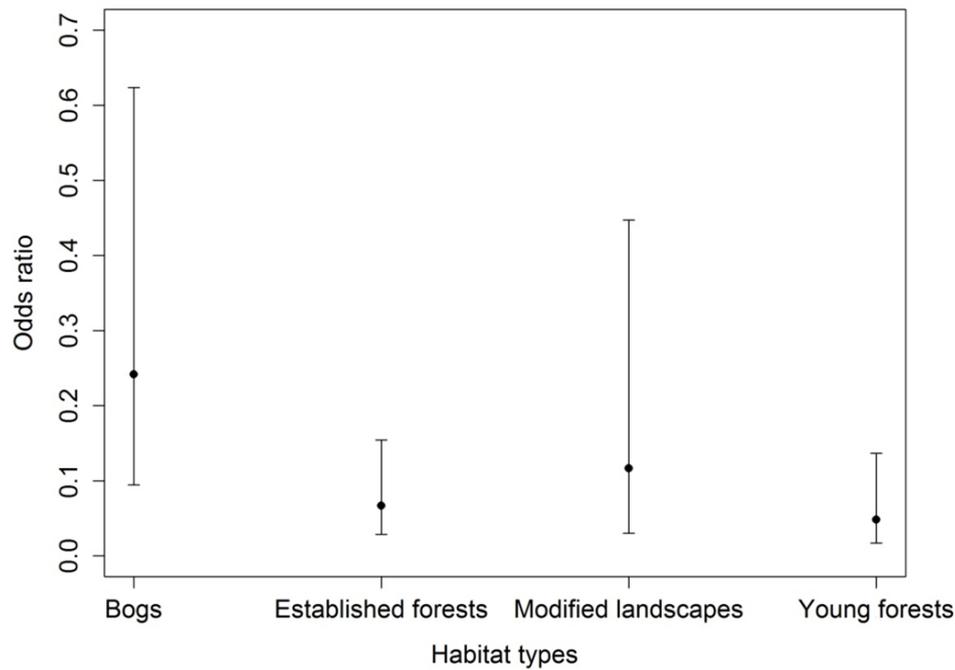


Figure 3: Odds ratios of moose calving site selection in relation to habitat classes in south-central Sweden, 2007-2011. Bars represent 95% confidence interval of the parameters estimates. Values of parameters estimates were averaged from top four competitive models.

Nevertheless, the four best models were not very robust to k-fold cross validation (averaged $r_s = 0.45$, Table 5) and were not considered as good predictive models (Boyce et al., 2002).

Table 4: Cross validated Spearman-rank correlations (r_s) for top four competitive models and average of moose calving site selection in south-central Sweden, 2007-2011.

Models	r_s
Habitat + Distance to secondary roads	0.44
Habitat + Distance to secondary roads + Wolf risk	0.51
Habitat + Distance to secondary roads + Dist to modified landscapes	0.47
Habitat + Distance to secondary roads + Dist to humans	0.41
Average	0.45

Fidelity to site

Successive calving sites used by females were situated closer (1293 ± 920 m) than random sites (1847 ± 606 m, $V=15$, $p < 0.05$) or than calving sites of other females within their home range (3234 ± 1189 m, $t = -4.8877$, $df = 27$, $p < 0.05$).

The best model describing fidelity was the full model incorporating age and past reproductive success both before and after weaning ($\Delta AIC_c > 10$, Table 6).

Table 5: Model selection results for the analysis of moose calving site fidelity in south-central Sweden, 2007-2011. k = number of model parameters; AIC_c = corrected Akaike's Information Criterion; ΔAIC_c = difference between AIC_c values w_i = Akaike weight.

Models	k	AIC_c	ΔAIC_c	w_i
Before + After + Age	7	413.52	0.00	0.996
Before + Age	6	425.21	11.69	0.003
After + Age	6	426.42	12.90	0.002
Before + After	5	437.13	23.61	0
Age	5	437.55	24.03	0
Before	4	449.48	35.96	0
After	4	450.69	37.17	0

Variable definitions: Before: Past reproductive success before weaning, After: Past reproductive success after weaning, Age: age of females (divided in 3 categories: Young, Medium and Old).

Fidelity increased with age of females: distance between successive calving sites was longer when females were younger than were they were older (Table 7). Distance between successive calving sites decreased when females lost their offspring before weaning during the previous year (no success: 783 ± 1090 m; success: 1346 ± 1053 m; Table 7) whereas distance between consecutive birth sites decreased when calves survived after weaning (no success: 1511 ± 1125 m; success: 1209 ± 1023 ; Table 7).

Table 6: Parameters estimates and standard errors from the best model of moose calving site fidelity in central Sweden, 2007-2011. For age variables, values are expressed according to the reference category which is "Medium".

Model Before + After + Age		
Parameters	β	SE
(Intercept)	437.54	791.34
Success before weaning	937.78	837.11
Success after weaning	-497.30	435.42
AgeClass : Old	52.88	718.97
AgeClass : Young	850.74	456.84

Discussion

Calving site selection

My results do not clearly suggest that wolf presence affected moose calving site selection. Females seemed to show a tendency to avoid areas where wolf density was high. However, wolf risk did not appear to be a strongly influential factor in females' selection of calving locations. Female moose seemed to select habitat characteristics that might have allowed them to minimize predation risk, but in some cases they showed a different behavior from what was expected.

Calving sites were more likely to be situated in bogs than in other habitat types, contrary to my predictions. This behavior has rarely been observed for moose during birthing period and bogs are not often reported to be feeding habitats (Renecker & Schwartz, 2007).

In the study area, bogs are habitats where forage is less abundant and of poorer quality compared to other habitats like forests (Månsson, 2009), but offer good visibility of the surrounding landscapes. Moose usually select habitat that provides shelter for calves to hide and still allows visibility of the surrounding landscape to detect predators before they approach (Bowyer et al., 1999). Even if forage is more abundant in young than in mature forest stands, the high tree density in some young forest stands potentially hampers ability to spot predators from great distances, and have been documented as risky environment for moose during winter (Gervasi et al., 2013). Therefore, females might not select bogs for their nutritional value but their choice might rather be influenced by minimization of predation risk. Indeed, wolves commonly spend less time in bogs, because of the absence of prey (Mech & Boitani, 2010). My findings are similar to what was described in British Columbia, where moose which gave birth in lower elevation (less than 100 m) selected bogs, as a strategy because these areas were less accessible for predators (Poole et al., 2007). In the study area, elevation was not assessed to be relevant because of the low variability. Consequently, preference for bogs to give birth could be a strategy by females to avoid predators. Selection of bogs has been suggested to be an anti-predator behavior by caribous during calving period (James et al., 2004; Latham et al., 2011). Those habitats seem to provide refuge and allow them to distance themselves from predators and from other prey species like moose (James et al., 2004). Even if it has rarely been demonstrated for moose so far, selecting bogs to reduce the risk of predation is not uncommon for other ungulates species. In my study, the habitat type “bog” included both wet mires and forests on mires which sometimes form small forested islands within mires. These “islands” might be more likely to be the places where females gave birth. They may have the ground dry and they may provide cover for newborn calf, but still good visibility of the surrounding landscape. However, it was not possible for me to discriminate more forested areas within bogs in my analysis, which could explain why those habitats were more selected than other habitat types by moose in the study area to give birth.

Confirming my predictions, moose distanced themselves from modified landscapes. Open cultivated areas like pastures are often avoided in summer (Cederlund & Okarma, 1988; Bjørneraas et al., 2011, 2012; Olsson et al., 2011; Nicholson et al., 2014) likely because they increase the risk of being detected by predators and do not provide shelter for calves to hide. The risk of wolf predation seems to be higher in areas like open cultivated fields than in more closed types of vegetation (Creel et al., 2005; Winnie & Creel, 2007). Concerning clear-cuts, Gervasi et al., (2013) recently reported that moose have higher probability of being killed in those areas compared to others during winter. Although there were three of the fifty birth sites situated in clear-cuts, which can be attributed to inter-individual variability or the scale of GIS digital layer, I observed a general tendency of females to prefer areas situated further away from modified landscapes.

Although it has been suggested as a strategy to protect themselves from predators (Berger, 2007), in my study moose avoided secondary roads during calving period. Berger, (2007) demonstrated that distance between birth sites of moose and roads decreased across years as the number of brown bears increased. Similar behavior has been suggested through the world in prey-predator systems, where prey selected protected areas or humans presence as a protection from predation (Isbell, 1990; Foley et al., 2001; Sunquist & Sunquist, 2002). Even though additional evidence is sometimes necessary to confirm those patterns, it provides support that mammals may use human-related objects to buffer against predation. In my study, moose did not reveal such a behavior concerning secondary roads. Wolves may use non-paved roads for travelling, because it increases their travel efficiency (Trombulak & Frissell, 2000; Whittington et al., 2005) and can nearly double their travel speed (Zimmermann, 2014). Wolves also use roads for scent-marking (Barja et al., 2004), territory patrolling and searching for moose (Eriksen et al., 2009). Roads can also increase encounter rates between wolves and their prey, and therefore increase kill rates (Hebblewhite et al., 2005; Whittington et al., 2011). Eriksen et al., (2009) found that moose in Scandinavia clearly avoided gravel roads, contrary to wolves which showed a preference for them. Thus, my results support previous findings in Scandinavia suggesting that moose females distance themselves from roads as an anti-predator strategy towards wolves.

On the other hand, calving sites were situated closer to houses or settlements. Moose in Scandinavia might use human presence as a shield against predation rather than using gravel roads. Selecting birth sites closer to humans has been suggested for Isle Royale, Michigan as a strategy to buffer against predation (Stephens & Peterson, 1984) but has received little evidence since then for moose (Langley & Pletscher, 1994; Bowyer et al., 1999). Lykkja et al., (2009) reported that human disturbance has a negative effect on habitat use by moose which moved further away from houses, especially cows with calves. They suggested that the costs associated with human disturbance were similar to those related to perceived predation risk by animals. However, avoidance of areas where human activity is high has been demonstrated for wolves (Whittington et al., 2005; Hebblewhite & Merrill, 2008, 2009), resulting in the use of such areas by elk (*Cervus elaphus*) as predation refuge (Hebblewhite & Merrill, 2009). In the study area, moose females might consider risk to be higher for their offspring to be killed by wolves than by humans. Nevertheless, I used houses and settlements as a representation of human presence and activity, without having the possibility to determine whether or not houses are inhabited during calving period, which might have lead to an overestimation of human activity. Therefore, further investigations might be necessary to better understand wildlife-humans relationships and how human presence affects calving site selection of moose.

Wolf re-colonization did not seem to strongly affect moose behavior during calving period in the study area. Previous studies conducted in Scandinavia also reported that wolf presence did not clearly influence changes in moose behavior (Sand et al., 2006a; Eriksen et al., 2011; Nicholson et al., 2014). Sand et al., (2006a) suggested the lack of response was likely to be due to wolf absence for long time period, and that moose might still be “naive” towards wolves in Scandinavia, compared to other areas in North America where moose have been exposed to wolf presence continuously (Ballard & Ballenberghe, 2007). Moose may also have lost their anti-predator behavior because of the insufficient period of wolf exposure since wolf re-establishment (Sand et al., 2006a). This is in contrast to other studies where authors reported that behavioral adjustments are made faster when predation is directed to offspring (Laundré et al., 2001; Berger et al., 2001; Mao et al., 2005). However, Nicholson et al., (2014) found that moose habitat use in the study area was weakly, if at all, affected by wolf predation risk, but that it differed according to the reproductive status of individuals and season. They suggested that moose response to wolf presence might be stronger and more obvious during a short but important period of time like calving. Consequently, it is possible that moose have started to respond behaviorally to wolf re-colonization for calving site selection rather than for their general habitat use. Wolf avoidance and minimization of predation risk might occur during birthing period by developing strategies in order to ensure survival of the offspring.

I chose to use environmental variables which seemed to be relevant regarding moose biology to evaluate calving site selection; however it could be interesting to consider additive parameters at a finer scale. Indeed, visibility of the surrounding landscapes, tree density or vegetation cover seem to be important factors affecting calving site selection (Chekchak et al., 1998; Bowyer et al., 1999; Poole et al., 2007). Including those parameters in further studies might be useful to understand better the mechanisms of calving site selection in a risky environment.

Fidelity to site

Moose in the study area appeared to show fidelity to their calving sites. As expected, successive sites were situated closer together than random sites or calving sites used by other females. Distances between successive calving sites in this study are analogous or closer to distances reported in other papers (Chekchak et al., 1998; Welch et al., 2000; Testa et al., 2000; Tremblay et al., 2007; McGraw et al., 2012). My results also revealed that the distance between calving sites of conspecifics was almost three times longer than the distance between an individual’s own calving sites, suggesting that females might purposefully increase their distance from each others during the calving period. This too is an anti-predator behavior (Bergerud, 1992) that has been observed in Sweden (Cederlund et al., 1987).

Surprisingly, females which lost a calf before weaning had shorter distances between their successive calving sites than females which successfully weaned a calf. Nevertheless, high calf pre-weaning survival was recorded in the study area, with only two cases where calves did not survive to the autumn which may affect the analysis and decrease statistical power and therefore might not allow firm conclusions to be drawn. Post-weaning mortality usually has an impact on birth site fidelity, because females tend to avoid birth site during subsequent years if they lose a calf (Welch et al., 2000; Testa et al., 2000). My findings are consistent because female moose were more faithful to their calving sites when they had successfully raised their offspring.

Fidelity increased with age: the older the female was, the closer its successive calving sites were. This is not surprising, because old females might benefit from their past experience and accumulated knowledge of site characteristics to select specific site rather than others (Cameron et al., 2007). Older moose females in the study area might have chosen calving sites of higher quality according to their past experience and knowledge of the area, which may explain why they were more faithful to their birth sites than younger females.

Conclusion

My results did not suggest that wolf presence had a strong effect on moose calving site selection in Scandinavia. The lack of moose response might be due to recent wolf re-colonization, contrary to moose in North America which have been exposed to wolf presence continuously. However, female moose might have used anti-predator strategies which allowed them to reduce predation risk. They seemed to ensure survival of newborn calves by selecting calving sites with characteristics that allowed them to distance themselves from wolves. They also used repeatedly areas which were safer from predators, according to their previous recruitment success. To my knowledge, few studies in Scandinavia focused on moose calving site selection. However, my findings suggest that the strategies used by females in Sweden sometimes differ from those which have been observed in North America. Consequently, further investigations might be necessary to enhance knowledge about moose behavior in response to wolf presence during birthing period in Scandinavia.

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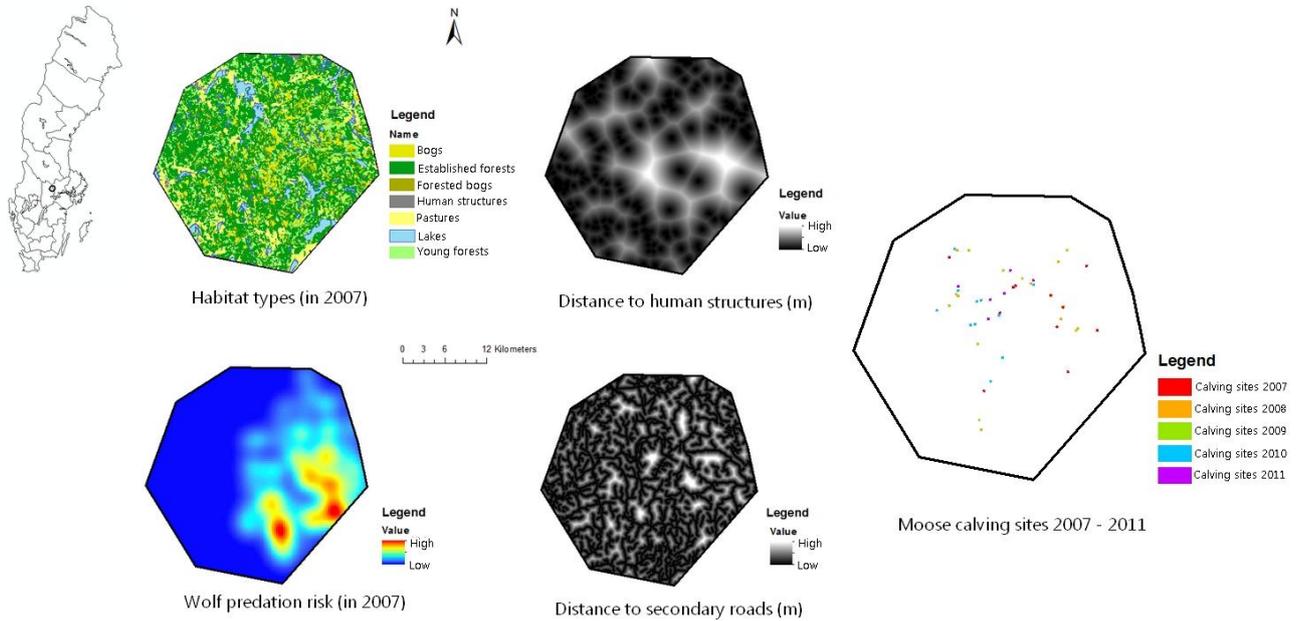
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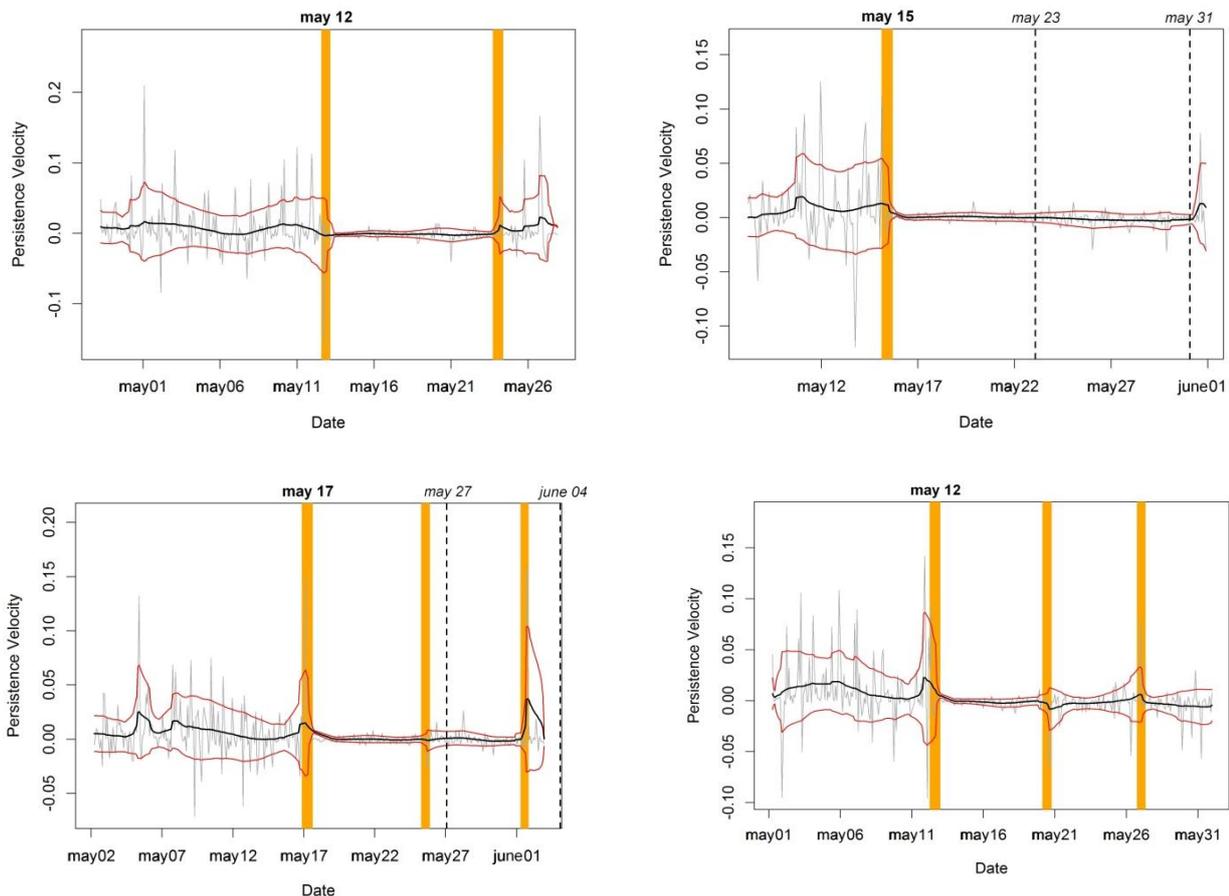
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Appendix

Appendix I: Grimsö Wildlife Research Area and nearby areas with habitat types, distance to human structures, wolf predation risk, secondary roads and moose calving locations from 2007-2011.



Appendix II: Example graphs from the Behavioral Change Point Analysis of persistence velocity for calving date estimation of four female moose in south-central Sweden, 2007-2011. The black horizontal line is the estimate for mean μ ; red lines are the standard deviation σ around the mean. Vertical orange lines indicate a significant change in persistence velocity. Above the first vertical orange line is the date when change points occurred and which was identified as the calving date. The first vertical dashed line from left to right correspond to estimated calving date according to field surveys from 2007 to 2008 and was calculated as *day of 1st calf observation – Visually estimated age of calf*. The second dashed line from left to right is the day of 1st calf observation. Some graphs do not have dashed lines because they correspond to calving date estimation after 2008.



Appendix III: Mean calving date and standard deviation (in days) per year of female moose in south-central Sweden, 2007-2011.

<u>2007</u>		<u>2008</u>		<u>2009</u>		<u>2010</u>		<u>2011</u>	
Mean	SD								
May 18	5	May 20	8	May 14	5	May 18	7	May 19	7

Appendix IV: Model selection results for the analysis of moose calving site selection in south-central Sweden, 2007-2011. k = number of model parameters; AIC_c = corrected Akaike's Information Criterion; ΔAIC_c = difference between AIC_c values; w_i = Akaike weight.

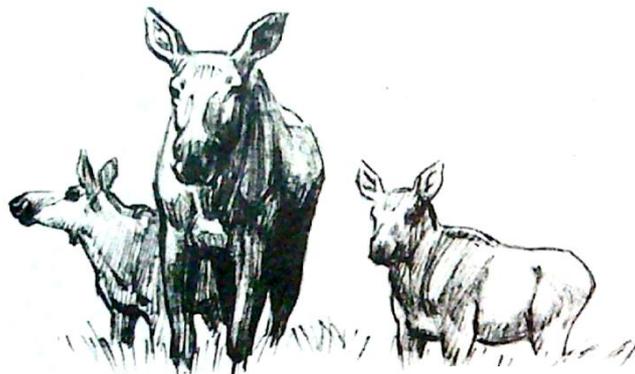
Models	k	AIC _c	ΔAIC _c	w _i
Habitat + Dist2ndroads	6	252.72	0	0.288
Habitat + Dist2ndroads + Wolf risk	7	253.66	0.94	0.180
Habitat + Dist2ndroads + DistModLand	7	254.11	1.39	0.144
Habitat + Dist2ndroads + DistHumans	7	254.69	1.97	0.108
Habitat + Dist2ndroads + DistModLand + Wolf risk	8	254.85	2.13	0.099
Habitat + Dist2ndroads + DistHumans + Wolf risk	8	255.74	3.02	0.064
Habitat + Dist2ndroads + DistHumans + DistModLand	8	256.03	3.31	0.055
Habitat + Dist2ndroads + DistHumans + DistModLand + Wolf risk	9	256.95	4.23	0.035
Habitat	5	260.24	7.52	0.007
Habitat + Wolf risk	6	261.00	8.28	0.005
Habitat + DistModLand	6	261.44	8.72	0.004
Habitat + DistModLand + Wolf risk	7	261.90	9.18	0.003
Dist2ndroads	3	262.06	9.34	0.003
Habitat + DistHumans	6	262.29	9.57	0.002
Habitat + DistHumans + Wolf risk	7	262.92	10.20	0.002
Dist2ndroads + Wolf risk	4	263.63	10.91	0.001
Dist2ndroads + DistHumans	4	264.05	11.33	0.001
Dist2ndroads + DistHumans + DistModLand	5	264.90	12.18	0.001
Dist2ndroads + DistHumans + Wolf risk	5	265.19	12.47	0.001
Dist2ndroads + DistHumans + DistModLand + Wolf risk	6	265.85	13.13	0
DistModLand	3	274.46	21.74	0
DistModLand + Wolf risk	4	275.52	22.80	0
Wolf risk	3	275.89	23.17	0
DistHumans	3	276.17	23.45	0
DistHumans + DistModLand	4	276.41	23.69	0
DistHumans + DistModLand + Wolf risk	5	276.79	24.07	0
DistHumans + Wolf risk	4	276.98	24.26	0

Variable definitions: Habitat: habitat classes, Dist2ndroads: Euclidean distance (m) to secondary roads, DistModLand: Euclidean distance (m) to modified landscapes (clear-cuts or pastures), DistHumans: Euclidean distance (m) to houses or settlements, Wolf risk: Utilization density of wolves.

Abstract

The risk of predation is a strong motivating factor in which prey have to balance avoidance of predators and still be able to obtain the resources they need to survive and reproduce. Calving site selection by moose is associated with trade-offs between meeting certain nutritional needs for lactation and calf rearing, and at the same time, reducing predation risk. Thus females utilize anti-predator strategies such as site fidelity. Fidelity to birth site can maximize reproductive success by using repeatedly sites which have a history of being safe from predators. I evaluated the strategies used by 22 GPS-collared parturient moose (*Alces alces*) to avoid their main predator, gray wolf (*Canis lupus*) in south-central Sweden during the calving period. I examined calving site selection in relation to wolf predation risk, and habitat characteristics such as vegetation, distance to human dominated landscapes, secondary roads and open areas. Additionally, I studied calving site fidelity regarding past reproductive success and age of the cow. Calving locations were situated more often in areas where the threat from wolf presence was low. Cows selected bogs more than other habitats to give birth and were situated further away from pastures and clear-cuts. They avoided secondary roads but they gave birth close to human settlements. Also, fidelity to calving sites increased with age of female and successful recruitment of a calf after weaning. My results did not clearly suggest that female moose may have modified their behavior in response to wolf presence.

Key words: Anti-predator behavior, *Alces alces*, birth site, *Canis lupus*, fidelity



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