



Den shifting behaviour of female wolverines (*Gulo gulo*) in Northern Sweden

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Preface

MSc Thesis Report regarding my MSc thesis for the Swedish Wolverine Project with supervisors; Jens Persson (Department of Ecology, SLU), Malin Aronsson (Department of Ecology, SLU and Department of Zoology, Stockholm University), Henrik Andrén (Department of Ecology, SLU) and Andrew Ladle (Environmental Sciences, University of Victoria).

During this thesis I aimed to gain more insight into the denning behaviour of the wolverine (*Gulo gulo*) in and around Sarek National Park (Northern-Sweden). I was particularly interested in the reason for shifting between den sites, using both GPS-collar and den site data from 2004 – 2014 for the analysis.

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Key terms

This section is used to clarify key terms and definitions used in wolverine related research. All terms will be explained and concluded by the specific use in this thesis when relevant.

Den site: In this study “den site” refers to reproductive den sites. Female wolverines make use of specific structures and conditions to create reproductive den sites, used to keep her offspring safe. Depending on the habitat and environmental conditions, den sites may for example be a tunnel or tunnels in deep snow or a cavity under boulders or fallen tree. Within wolverine denning research, a separation has been made between a natal den, maternal (secondary) den and rendezvous site to be able to distinguish use and importance of different den sites. In this thesis the term “den site” was used for natal dens and maternal (secondary) dens, not for rendezvous sites:

- *Natal den site:* Den site in which the female wolverine gives birth to her offspring.
- *Maternal den site:* All den sites where the female kept her offspring after leaving the natal den site. Sometimes referred to as secondary den sites in other literature.

Denning behaviour: Behaviour regarding the use of reproductive dens by female wolverines. Here, this refers to general information about the number of den sites used during the denning period and length of stay at each den site.

Den shift: The moment when a female wolverine moves her offspring to a new den site. The shifts can be from the natal den site to maternal den site or from maternal to maternal. Den shifts are the main topic of this thesis. The term “den abandonment” has been used in other studies regarding shifting between den sites (Magoun & Copeland, 1998). As said before, the term used in this thesis will be den shift.

Denning period: Most wolverines give birth during mid-February. The average birth date is the 15th of February, but birth dates range from end of January until begin of March (Inman *et al.*, 2012; Aronsson, 2017). The period from birth of the offspring to the end of May is the main period when wolverine females make use of den sites to care for their offspring.

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ABSTRACT

Many species of mammals make use of “den sites” for multiple purposes. Wolverine (*Gulo gulo*) females give birth to and rear their cubs in den sites during the denning season (February to June, hereafter denning season). Previous studies have focused on studying the den site habitat, den site characteristics and impact of reproduction on the condition of female wolverines. My thesis focusses on how many den sites are used, for how long the den sites are used and why wolverines shift den sites, which has not received much attention yet. I used GPS-collar data collected during 11 years (2004-2014), from 18 adult wolverine females that were intensively followed during a total of 33 denning seasons in and around Sarek National Park in the north of Sweden. Then the use of den sites was defined during this period and a total of 271 den sites were found. On average a female used 12 den sites during one denning season. The natal den site (i.e. where the cubs were born) was on average used for 43 days, but the variation was high ranging from 10 to 83 days. I used a survival analysis approach to examine the influence of spatial and temporal factors on the probability that the female would shift den site during the denning season. The results show a difference in daily hazard rate (the probability to shift den site) between the two habitats; alpine and forest. In the alpine habitat, the den shift probability increased with increasing cub age and was higher for den sites located on reindeer calving grounds. In the forest habitat on the other hand, the probability of shifting a den site decreased by increasing female experience and increased with increasing day-time temperature. Snow cover did not influence the probability of females to shift den sites, as snow is a crucial factor for wolverine ecology, this result was unexpected. However, the influence of temperature in the forest habitat could be related to snowmelt and poorer snow conditions. Calving grounds are especially important from the beginning of May, when the reindeer arrive to the area and give birth. Additionally, higher human activity levels will occur during this time of the year as reindeer herders patrolling the area to guard the reindeer herds. Consequently, the increase of den site shifts occurring on calving grounds in comparison to outside these areas, may be explained by the potential increase of food availability and/or the increase of human activity (i.e. disturbance). Previous studies on other species have shown that the experience of female individuals can be influential on the reproduction. Due to the more unstable denning conditions in the forest, female wolverines might need to learn to adapt their denning behaviour while denning in the forest region. Further research is encouraged to focus on the impact of climate change, especially on snow conditions, and the denning behaviour of females on lower latitudes in the boreal forest.

Keywords: Wolverine, Gulo gulo, den, denning, denning behaviour, den shifts, habitat, environmental conditions, female experience, resource availability, survival analysis, reproduction, snow, climate

Introduction

Reproduction plays a crucial role in the persistence and growth of all animal populations (McEvoy & Robinson, 2003; Manlik, 2019). Therefore, species have developed and refined multiple ways of raising their offspring during the early stages of their life (Klopfer, 1981; Gittleman & Thompson, 1988; Royle *et al.*, 2012). Parental care strategies vary within and between species (Hofer, 1981; May & Rubenstein, 1985; Keverne, 1985; Clutton-Brock, 1991a; Webb *et al.*, 1999). In some species the parent(s) stay in close proximity to their offspring at all times to increase survival, while others invest higher amounts of energy to give birth to juveniles that are highly mobile soon after birth (Royle *et al.*, 2012). Another common strategy is building a nest, or use holes dug into the ground or located in existing conditions, such as snow. These sites are used as a strategy to survive unfavourable resource and weather conditions and offer security from hazards and for resting. Many mammal and bird species use this strategy especially to safely raise their offspring, for mammals often referred to as “den sites” (Clutton-Brock, 1991b; Webb *et al.*, 1999; Royle *et al.*, 2012).

Denning strategies in mammals

Mammals exhibit different strategies when it comes to den site use, some use few and the same den sites several consecutive years, while others adapt to yearly changing conditions and utilize occurring opportunities in their home range (Royle *et al.*, 2012). For example, species such as Brown bears (*Ursus arctos*) make use of a den site to safely hibernate during the winter, and to give birth and wean offspring for a period of time before emerging (Ciarniello *et al.*, 2005; Manchi & Swenson, 2005; Mannaart, 2016). There are also species which have several den sites during a denning season. Wolves (*Canis lupus*) make use of one natal den site and some maternal den sites (up to 3), before they switch to using rendezvous sites (Theuerkauf *et al.*, 2003; Alfred  n, 2006; Sidorovich *et al.*, 2017). Arctic foxes (*Alopex lagopus*) can use several den sites simultaneously within one denning season, and they may also reuse these den sites over many years (Eberhardt *et al.*, 1983). Red foxes (*Vulpes vulpes*) are known as a highly adaptable species, which also corresponds with their den site selection and use, as they utilize so-called den groups consisting of several den sites in close proximity (Nakazono & Ono, 1987; Carter *et al.*, 2012; Reshamwala *et al.*, 2018).

The Mustelid family (*Mustelidae*) is a highly diverse group of mammals, that occur all around the globe. Mustelids have developed rather distinctive denning strategies. The European badger (*Meles meles*), one of the bigger mustelids, use year round communal den sites and have high residency with only occasionally long distance replacements (Weber *et al.*, 2013). The fisher (*Pekania pennanti*) use den sites exclusively found in hollow trees (Powell, 1993; Powell *et al.*, 1997). On average, fishers use 1-3 tree den sites during a reproductive season (Powell, 1993; Powell *et al.*, 1997). Both American martens (*Martes americana*) and European pine marten (*Martes martes*) can have den sites both in structures on the ground (rocks/fallen trees) and tree cavities (Kleef & Tydeman, 2009; Nichols, 2016). Similar to fisher, European martens use a low number of den sites during one denning season (Kleef & Tydeman, 2009). American martens may use many more den sites, ranging from 3-24 (Ruggiero *et al.*, 1994; Ruggiero *et al.*, 1998).

One may ask, why do animals shift den sites? Shifting den sites may cause energy loss for the parents (Bronson, 1989) and vulnerable offspring could be exposed to hazards during the movements between sites. On the other hand, movements to other den sites may prevent offspring from being harmed. Human disturbance is known as a main factor for den abandonment in various species (Ciarniello *et al.*, 2005; Reshamwala *et al.*, 2018). Still, polecats (*Mustela putorius*), stoats (*Mustela erminea*) and stone martens (*Martes foina*) appear to use human infrastructure to their advantage (Weber, 1989; Murphy & Fechny, 2003; Herr *et al.*, 2010).

Wolverine denning and factors influencing wolverine denning behaviour

Wolverine (*Gulo gulo*) females give birth between late January and early March, with February 15 as average date (Aronsson, 2017). The female enters the natal den site just before parturition, and the

denning season (i.e. when the young are kept in one or several den sites) may continue until the end of May or early June (Magoun & Copeland, 1998; May, 2007; Inman *et al.*, 2012; Aronsson, 2017). Den site selection is presumably influenced by several factors, which include resource availability, security from conspecifics and other predators, thermoregulatory capabilities of the site and also the level of human disturbance (Magoun & Copeland, 1998; May *et al.*, 2012). Previous studies have focused on den site habitat selection (Mattsing, 2008; Dawson *et al.*, 2010; May *et al.*, 2012), den site characteristics (Magoun & Copeland, 1998; Makkonen, 2015) and impact of reproduction on the condition of female wolverines (Rauset *et al.*, 2015). To date, denning behaviour aspects, such as how many den sites are used, for how long the den sites are used and why they shift den sites, has not received much attention.

Snow has been suggested as a crucial factor for wolverine ecology (Copeland *et al.*, 2010). Wolverines benefit from snow for their hunting success on larger ungulates, for favourable conditions for caching and for favourable denning conditions (Inman *et al.*, 2012). It has been suggested that reproducing females rely on scavenging and winter-food caching as a predictable food resource during the first months of the denning period, which coincides with cold temperatures and stable snow conditions (Inman *et al.*, 2012). Also, during this stable snow period, snow influences the temperature inside the den site, which is referred to as thermoregulation (Knudsen & Kilgore, 1990; Patil *et al.*, 2013). In the open and rugged alpine habitat, snow may accumulate by the wind in drifts, which creates favoured conditions for wolverines to den as the den site often consist of tunnels in deep snow drifts (Magoun & Copeland, 1998). In forested regions or other areas where the snow is less deep, wolverines may have to use additional features such as boulders and fallen trees under the snow as those structures may enhance snow accumulation (Magoun & Copeland, 1998; Makkonen, 2015). As time progresses during the denning season, temperatures rise and snow starts to melt. This change may expose or flood the den site and the thermoregulation advantages of the snow decrease, causing the den site to become less favourable or even uninhabitable.

The rise in temperature and snowmelt, also sets other natural processes in motion which can influence food availability for the wolverine. For example, later in the spring and early summer rodent species become available and ungulates and other prey species gave birth. This influx of food resources may influence wolverine denning behaviour as cache sites and other winter food sources may be depleted (Inman *et al.*, 2012; Mattisson *et al.*, 2016; Aronsson, 2017). Also, as the cubs grow older, they become more mobile and start to eat solid food (are weaned for 10 weeks (Iversen, 1972)). This may result in more den shifts as females bring the cubs to den sites closer to food resources (Aronsson, 2017).

Experience is assumed to increase survival capacity and reproductive output of animals (Royle *et al.*, 2012). Parental age or breeding experience has been used in earlier studies, assuming young reproductive individuals have lower offspring survival, prime-aged individuals have high offspring survival and older individuals showing a decrease in offspring survival again (Lunn *et al.*, 1994; Côté & Festa-Bianchet, 2001; Weladji *et al.*, 2006). Although the effect of breeding experience on reproductive output has been debated (Pärt, 1995), it has been shown that primiparous female brown bears have significantly smaller litters and higher cub losses in comparison to multiparous females (Zedrosser *et al.*, 2009). Suggested reasons for this higher loss of cubs were the lack of behavioural skills, such as foraging and parental care (e.g. defending or avoiding potential infanticidal individuals) (Zedrosser *et al.*, 2009). Wolverines reproduce for the first time at 2-5 years of age, and as their reproductive output is influenced by winter food availability and previous reproductive costs, they might only reproduce successfully every other year (Persson, 2005; Rauset *et al.*, 2015). As wolverines generally occur in an unpredictable environment, experience could have an impact on foraging capabilities and parental care skills. Finding suitable den sites could be an essential skill for cub survival, which may need to be acquired by experience. Therefore, unexperienced individuals with fewer breeding attempts may have to shift den sites more often in comparison to more experienced individuals.

All the above factors can change over short periods of time and differ between years, which may force female wolverines to adapt quickly to both positive and negative transitions. Stable cold weather conditions may result in favourable denning conditions, but unpredictable food resources. Whereas, warmer weather conditions later in the season may result in predictable food resources, but may decrease the suitability of den sites.

Research aim and hypotheses

The research question I will explore and answer in this thesis, is: “*What factors influence den shifting behaviour of female wolverines?*” To answer this question, I used data on den site locations and use during multiple denning seasons (2004-2014) from 18 GPS-collared adult wolverine females in Northern Sweden. The aim of this study is to gain insight into the den use behaviour of reproductive wolverine females, focussing on exploring the spatial and temporal influences causing den shifts. This may lead to a better understanding of wolverine denning strategies. Furthermore, my results can be used to compare denning behaviour of wolverines in other parts of their range, and especially to wolverines further south which may contribute to our understanding of potential effects of climate change on wolverine denning behaviour.

In the northern half of Scandinavia, semi-domesticated and migratory reindeer, owned by the native reindeer herding Sámi people, are the main food source for wolverines and other carnivores (Mattisson *et al.*, 2016). Wolverines both kill reindeer and scavenge lynx (*Lynx lynx*) killed or natural death reindeer carcasses (Mattisson *et al.*, 2011; López-Bao *et al.*, 2016). My study area is located within the summer grazing area of the reindeer husbandry area, consequently reindeer availability show high seasonal variation; with large herds during the summer and only a few and scattered individuals remaining during the winter (Andrén *et al.*, 2018). Furthermore, the return of the reindeer in late April to early May coincide with the calving season, and my study area constitutes important calving grounds for the reindeer herding practice (Aronsson, 2017). Aronsson (2017) determined that the number of den sites used during a reproductive season is highly variable between individuals in my study area, with an average of 10 den sites (range = 3-24) during one season. The natal den sites were used on average 47 days (range = 10-84), while the maternal den sites were used for 1-54 days. Shifts occurred more often towards the end of the denning season (April – May).

I have formulated several hypotheses for this study:

- 1) My study area consists of both alpine and forest habitat. Alpine habitat promotes more possibilities to create extensive and secure den sites in deep snow drifts, whereas the forest habitat has a less deep and less reliable snow cover as well as earlier snowmelt, which makes using additional structures such as boulders and uprooted trees necessary. Consequently, I expect the den sites in the forest habitat to be less suitable and therefore I predict that there is a higher rate of den site shifting in forest habitat compared to alpine habitat.
- 2) When temperatures are increasing later in the season snow conditions will change due to spring thaw, which may cause den sites to be flooded and/or exposed. This could lead towards unfavourable denning conditions for both the female and the cubs. I therefore predict that temperatures above freezing will increase the rate of den site shifts in comparison to temperatures below freezing. However, later in the denning season when the snow disappears, temperature will most likely be less important compared to earlier.
- 3) Food resources are important for reproducing females and their offspring. Females denning on calving grounds might have more access to resources during the calving season. Although, during the calving season human activities may be higher on these calving grounds due to reindeer herding practices. I therefore predict den sites within the calving grounds have a higher shifting rate in comparison to the ones outside, both due to the pursuing of easy resources and higher human activity.
- 4) The cub age (i.e. vulnerability and mobility) may influence den site shifting. As older cubs will be more mobile, I predict that the rate of den site shifts will increase with increasing cub age.
- 5) Experience is assumed to increase survival in animals (Royle *et al.*, 2012). Indices for experience can be age or number of prior reproductions. I predict experienced females to have a better understanding of the suitability of den sites, timing and changing circumstances, therefore older females or females with a higher number of reproductions should have a lower rate of den shifts.

Methods

Study area

The study area (ca. 2200 km²) is located in and around Sarek National Park in northern Sweden, with Kvikkjokk as the nearest human settlement (67°00'N, 17°40'E) (Figure 1). The area is characterized by rugged terrain, shifting between high mountain peaks (range: 1700-2100 m a.s.l.) and plateaus, glaciers, deep valleys, tundra and forests. The area consists of alpine habitat at higher altitudes, with the tree line (ca. 600-700 m a.s.l.) made up by mountain birch (*Betula pubescens pumila*), and coniferous forest habitat in the valleys dominated by Scots Pine (*Pinus sylvestris*) and Norway Spruce (*Picea abies*) (Rauset *et al.*, 2013). The climate is continental with daily mean temperatures ranging from 3 to 10°C in May and from -10 to -13°C in January, but mid-winter temperatures can reach as low as -38°C. The ground is usually snow-covered from October to May (Persson, 2003). Snow cover and depth are highly variable during winter with factors such as habitat, elevation, slope, ruggedness and aspect determine snow depth at the local scale. Wolverines in the area have shown preference for den sites on higher elevations (700-1000 m.a.s.l.), on steep slopes (10-40 degrees) and slopes facing towards southwest or northeast (Mattsing, 2008).

Semi-domestic reindeer are the most important prey species for the three large carnivores (wolverine, brown bear and lynx) present in the area. Wolverines use lynx-killed reindeer carcasses to a great extent, but are capable of killing reindeer themselves (Mattisson *et al.*, 2011; Mattisson *et al.*, 2016). From spring to autumn, the reindeer roam around freely within the study area. However, as reindeer presence is seasonal, wolverines also use other prey like mountain hare and grouse (Mattisson *et al.*, 2016). Moose also occur in the area, which are another possible resource (Persson, 2003). Wolverines also cache food, which helps them to survive low-resource periods, such as the winter (Inman *et al.*, 2012).

Within the study area only a low amount of human activities occurs and therefore risk for human disturbances is minimal (Persson *et al.*, 2009; Rauset *et al.*, 2016). In late winter and spring, the main source of possible human disturbance is recreational skiing, the use of snow scooters (only allowed for use by County Administrative Board rangers and reindeer herders within the National Park). Later in snow free part of the denning period, there are recreational use of hiking paths both inside and outside of the National Park. Importantly, the den sites included in this study were not approached by County Administrative Board rangers nor by researchers during the denning season.

Determining den sites

The data was collected during a 11-year period (2004-2014) from 18 adult female wolverines equipped with GPS collars. The wolverines were captured by darting from a helicopter or from the ground, immobilised with a mixture of ketamine and medetomidine and equipped with GPS-collars (2004-2006: Televilt Posrec C300; TVP positioning, Lindesberg, Sweden, and 2008-2014: GPS plus mini, Vectronic Aerospace GmbH, Berlin, Germany) and intraperitoneally implanted VHF-transmitters (iMP/400/L, Telonics inc., Mesa, Arizona, USA). All captures and handling were done using ethically approved handling protocols (see Persson *et al.*, 2010).

By closely monitoring the GPS-collared females (8-48 locations per day), distinct clusters of GPS-locations could be detected by using GIS software (ArcMap 10.7.1, ESRI). The clusters were visited in the field after the denning season to confirm use as a den site and to separate den sites from other activities, such as feeding sites or daybeds (cf. Mattisson *et al.* 2011; Mattisson *et al.* 2016). The identification of den sites was further supported by visual observations of the females. The combination of detailed investigation of high-resolution GPS data and field observations provides reliable identification of den sites. However, it became increasingly difficult to identify den sites during the later stages of the denning season. Females move frequently with the cubs after mid-May (Aronsson, 2017), therefore sites used after 1st of June were not included in this study. The day of parturition was determined by using integrated temperature sensors, which showed a significant and characteristic increase in body temperature related to the birth of the cubs (Jens Persson, personal communication,

May, 2019). Furthermore, wolverines enter the den site when giving birth, therefore the parturition date could also be investigated by using the GPS-locations. All gathered information was used to determine the correct location, date of entry and date of abandonment for every den site, which resulted in a complete overview of the denning season per female.

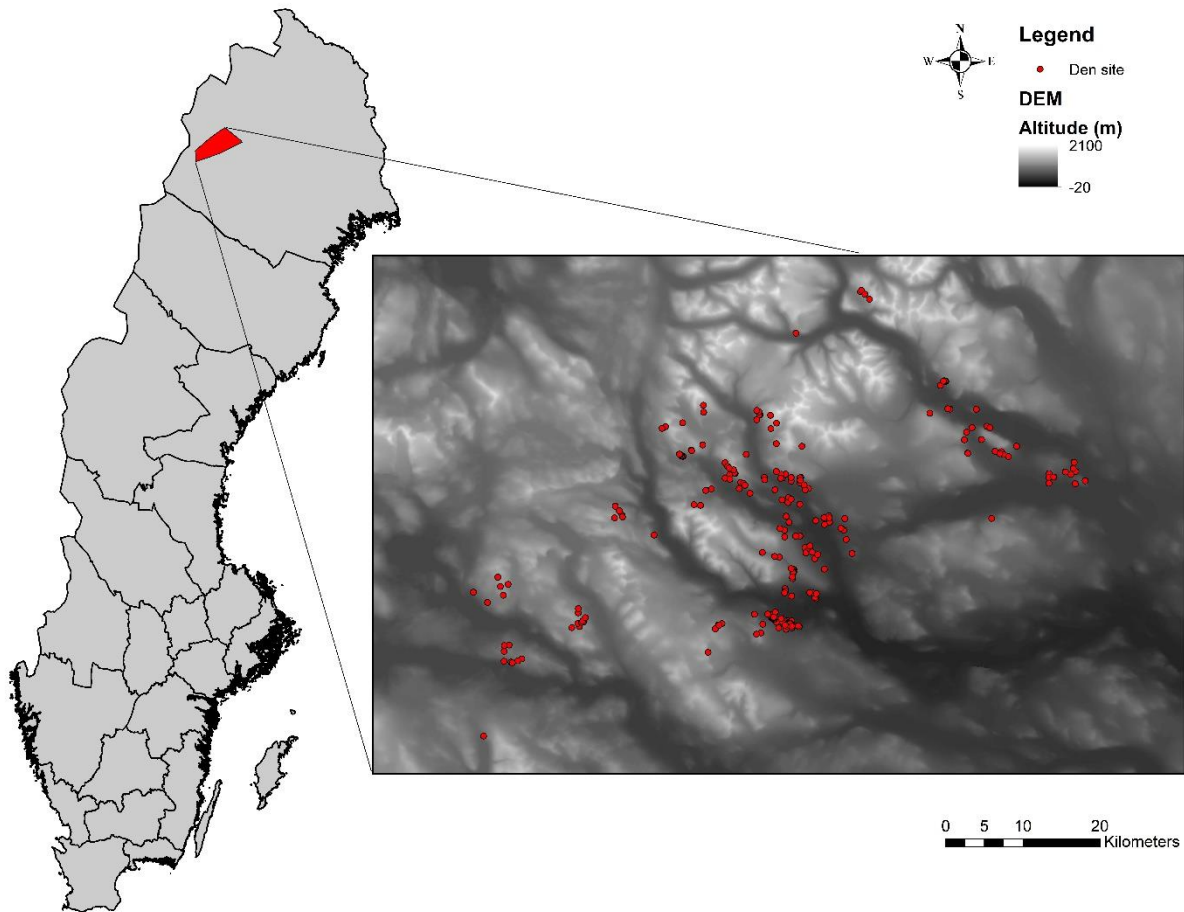


Figure 1: Map of research area, Sarek National Park. Showing elevation (metres) and the den site locations.

Extracting variables and build dataset

The Swedish Land Cover (SMD; National Land Survey of Sweden), including habitat classifications for the whole of Sweden, was used as habitat data. The SMD was reclassified to 3 classes; alpine, mountain birch and other forest. I extracted habitat data for each den site using the ‘*raster*’ package (Hijmans & van Etten, 2012) in R (R Development Core Team, 2020) and checked it using GIS (ESRI, 2020). The habitat classification was compared with photos from the den site being visited in the field and/or satellite images. Before the main analyses, the habitat data was investigated to check for significant differences in the survival time of den sites between the three habitats, using the Kruskal-Wallis test. There was no significant difference found between mountain birch and alpine habitat ($\chi^2 = 2.97$, $df = 1$, $p = 0.87$), a possible reason could be because during the winter the conditions in mountain birch forests are the same as in alpine habitats. Therefore, for the main analyses, mountain birch and alpine were grouped together which resulted in two habitat variables (alpine & forest; ($\chi^2 = 5.52$, $df = 1$, $p = 0.02$)). Additionally, for every den site I determined if it was within or outside known reindeer calving areas, using a polygon layer regarding all the calving areas in the study area. Reindeer calving areas are both found in the forest and alpine habitat.

Snow and temperature data was obtained by using the ‘*MODISsp*’ application in R, which is part of the ‘*MODISsp*’ package (Busetto & Ranghetti, 2016). By using this application, satellite images were extracted for the study area, containing information about temperature and snow conditions. I used

the MOD10A1 Daily NDSI Snow Cover (Hall & Riggs, 2016) and MOD11A1 V6 daily Land Surface Temperature and Emissivity datasets (Wan *et al.*, 2015). The daily snow cover estimate was extracted from the daily images on a 500 x 500 m grid scale. The range of snow cover was from 0 (no snow) to 100 (grid fully covered by snow). The daily day-time and night-time ground temperature estimates were extracted by using the daily satellite images on a 1 x 1 km grid scale. The night-time estimations were used as a lagged variable, which means the estimate of the night before the exit date was used and not the estimate from the exit date itself. Missing data for snow and temperature due to for example, cloud cover were handled by using the ‘*imputeTS*’ package (Moritz & Bartz-Beielstein, 2017) and given a value based on a weighted moving average (i.e. four known extracted values were used to calculate the most probably value).

Other variables such as cub age, female age and number of prior reproductions were added to check for individual differences and to add a time dependent variable (cub age). The date of parturition was defined as the first day at the natal den sites (Aronsson, 2017). By using this date, the cub age could be determined for every day of the denning season. The female age was either known (i.e. she has been monitored from birth) or age was determined by tooth sectioning. Besides female age, the experience of the female was determined by summing up the number of previous reproductive attempts for each denning female, where both successful (i.e. ≥ 1 cub surviving after the denning season) and unsuccessful (lasting for ≥ 1 month before interrupted) attempts were included. The number of attempts was used to quantify the reproductive experience. It might be difficult to confirm reproductions when cubs died early, however, in this study the females were monitored intensively since birth or first capture, and therefore their reproductive history was known.

I built up the dataset in a way that is suitable for a daily survival analysis approach (Murray & Bastille-Rousseau, 2020) in order to include all the temporal and daily changing variables, such as snow and temperature (Appendix I). Some general variables were added to complete the dataset:

- **Den ID** – Each den site was given a unique ID. This was the same for all the days the den site was used. Den ID was used as the cluster variable in the survival analysis models.
- **Wolverine ID** – Referring to the female id, included to explore individual differences. Wolverine ID was used as the ID variable in the survival analysis models.
- **Day of den entry (Julian date)** – The Julian date referring to the date of entry. For example, the 15th of February is Julian date 46.
- **Day of den exit (Julian date)** – The Julian date referring to the date of exit. This is always one day after the day of entry, due to the daily structure of the dataset.
- **Fate** – This variable defines den use per day as 0 = used and 1 = left (shift). For example, if a wolverine entered a den site on the 80th day and left on the 85th, the fate for day 80-84 would be 0 and for 85 it would be a 1.

Before the analysis, a set time period was determined. As start date (in dataset as day 1), the average parturition date was used (15th of February, Julian date 46). The end date of the model period was set at the 1st of June (Julian date 151; for leap years Julian date 152; in dataset as day 105-106). Due to uncertain dates of entry and exit in late May and beginning of June, some den sites were excluded from the analysis (n = 11).

Survival analysis approach

To analyse potential factors influencing den site shifts, I used a survival analysis approach (Cox, 1972; Cox & Oakes, 1984; Andersen & Gill, 1982). This approach is mainly used in medical or clinical research, but it is increasing in popularity for ecological research (Murray, 2006; Murray & Patterson, 2006). The reason for this is the late extensions for survival analysis models such as Cox Proportional Hazard (CPH) models (Kelly & Lim, 2000). Survival data can be described as two different probabilities, namely the survival and hazard (Clark *et al.*, 2003). The survival probability is the chance of survival (remaining in the den site) from a certain point in time (entering the den site) until a specified future event (shift to another den site) and the hazard is the probability that the individuals (den site) at a specific time experiences a shift (Clark *et al.*, 2003). The CPH is a multiple linear regression model,

which describes the relation between an event expressed by the hazard function and the covariates tested in the model (Bradburn *et al.*, 2003a; Muenchow, 1986). The hazard ratio (exponentiated coefficients) produced in the test, give the effect size of the covariates (Bradburn *et al.*, 2003a). I mainly focused on the hazard function, which gives the probability a specified event (shift) is occurring and not on how long a certain den site “survives”.

I used the extended CPH model approach for the analysis of potential factors influencing the probability of den shifts (Kleinbaum & Klein, 2012; Murray & Bastille-Rousseau, 2020). This semi-parametric survival model approach makes it possible to use both left truncated and right censored data (which makes it possible to include interrupted seasons by death of female/cubs or transmitter failure), include continuous variables and analyse daily hazard rates (Murray & Bastille-Rousseau, 2020).

For all analyses the software R was used (R Development Core Team, 2020). I used the ‘*survival*’ package (Therneau, 2020) to execute all the pre-analysis, model assumptions and CPH models (Hosmer *et al.*, 2008; Fox & Sanford, 2019; Murray & Bastille-Rousseau, 2020). The CPH model assumes proportional hazards, meaning the baseline hazard should be a multiple constant between groups (Bradburn *et al.* 2003a). Assumption of proportional hazards was tested on all variables using an integrated function in the survival package. A p-value below 0.05 would indicate that the hazard would be non-proportional, meaning it significantly changes with time. This variable (i.e. showing non proportional hazards) may then be used to fit a stratified model or fit separate CPH models based on the different groups (Bradburn *et al.*, 2003b). I used the ‘*survminer*’ package to visualize hazard rates (Kassambara *et al.*, 2019), and visualized the baseline hazards by using the ‘*bshazard*’ package (Rebora *et al.*, 2018) which show how the hazard rate changes over the whole denning period.

First, I used a univariate analysis to investigate single explanatory variable influence and significance. After that, the significant variables were put into a multivariate extended CPH model and checked for correlation. The den ID was used as cluster variable and wolverine ID was added to correct for repeated measurements (i.e. the same female monitored during multiple denning periods). The model selection was done by using the sample-size corrected Akaike Information Criterion (AICc) (Akaike, 1973; Burnham & Anderson, 2002). The model with the lowest AICc was selected as the most parsimonious. After acquiring the top model, the ‘*simPH*’ package (Gandrud, 2015) and “Greg” package (Gordon & Seifert, 2020), were used to simulate graphical predictions based on the model estimations.

Results

Denning Behaviour

During the study period (2004-2014), 271 den sites (172 in alpine and 87 in forest habitat) were found and confirmed in the research area. The den sites were used by the 18 different females during 33 denning seasons, resulting in 2203 denning days. In total, 7 seasons were interrupted by transmitter failures, 2 due to death of the female and 2 due to death of the cubs.

On average a female used 12 den sites during one denning season (range = 4 – 28, median = 10, n = 22). The natal den site was on average used for 43 days (range = 10 – 83, median = 44). The days spend in the first four den sites make up approximately $\pm 80\%$ of the total denning season (range = 30-100%, median = 85%). This corresponds to the wolverine spending about 74 days in the first four den sites (range = 22-111, median 80, n = 22). In total, the females used den sites for approximately 93 days before the end of May (range = 57-124).

Den site shifting

The different baseline hazards were significantly higher in the forest habitat compared to alpine habitat ($\chi^2 = 16.5$, df = 1, $p < 0.001$), violating the assumptions of the CPH model. Therefore, I did all further analyses separately for the two habitats. The hazard rate increased over time for both the alpine and forest habitat (no covariates included; Figure 2 & 3). The probability for a den shift was higher in forest habitat, and similarly increasing patterns were visible at the end of denning seasons in both habitats.

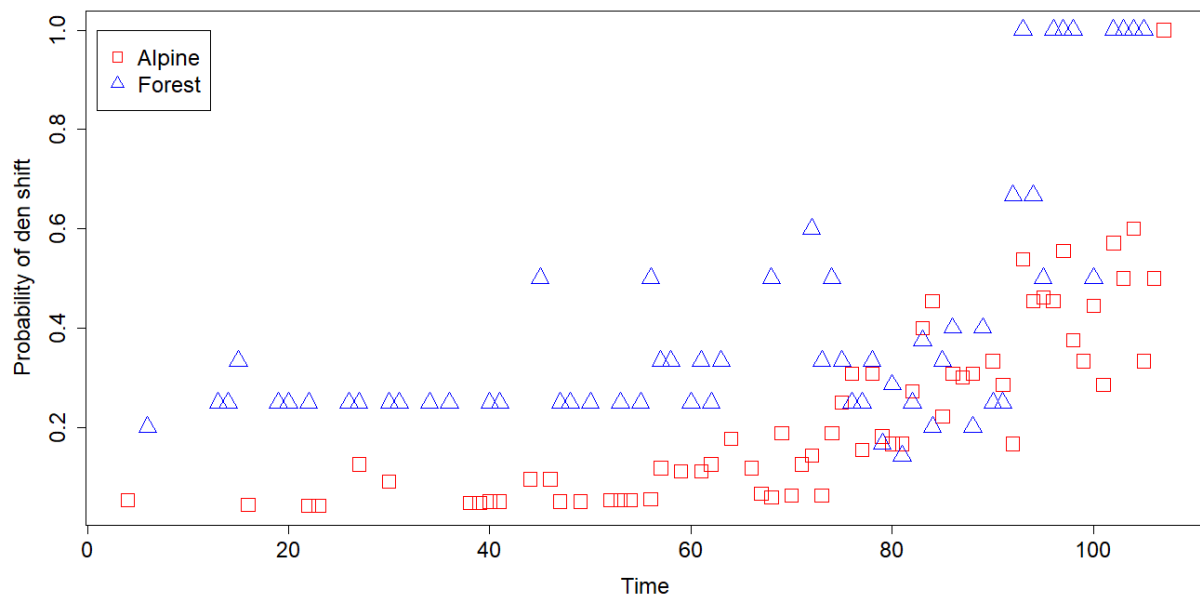


Figure 2: The probability to leave a den site and shift to another den site over the whole denning period (alpine: red squares; forest: blue triangles). The probability was calculated by dividing the number of dens shifted on that particular day by the total number of dens in use.

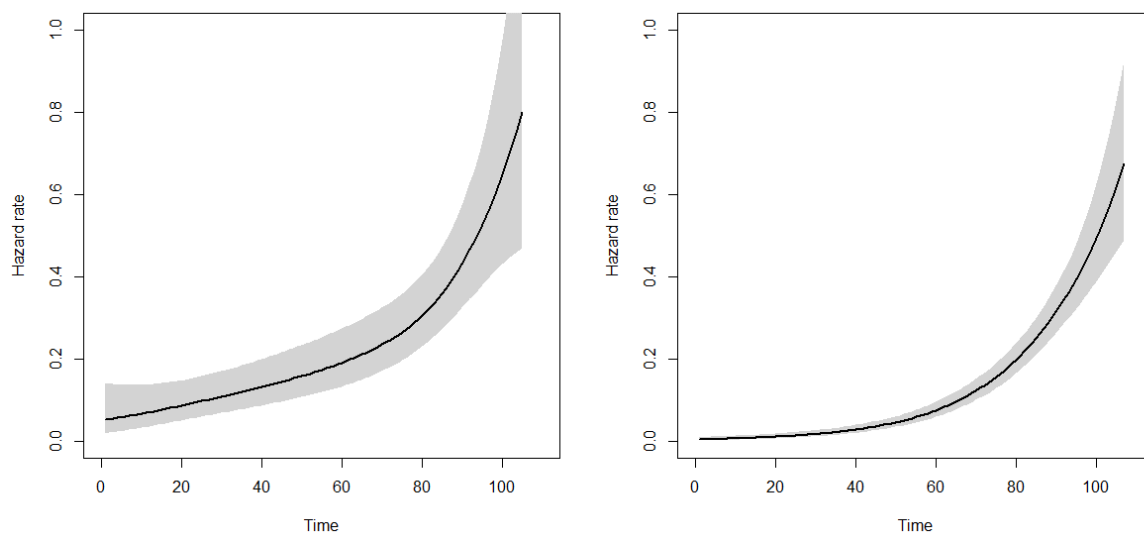


Figure 3: The baseline hazard rate (probability to leave den site) shown for both the forest (left) and alpine (right) habitat.

Cox Proportional Hazard models

To apply extended CPH models per habitat, subsets were made from the main dataset. The univariate analysis results are shown in table 1. Den shifts occurring in alpine habitat were mostly influenced by the age of the cubs and if the den site was located within calving grounds or not. Shifts in forest habitat were influenced by temperature (day and night), age of the female, experience of the female and age of the cubs. All significant variables were used in the multivariate models.

Table 1: Univariate analysis of the explanatory variables separated between the two habitats (alpine – forest). Stating the exponential coefficient (estimate), standard error of the estimate, lower/upper 95% confidence interval (lower/upper 95%) of the estimate and p value (Pr (>|z|)).

Subset: Alpine					
<i>Variable</i>	Estimate	SE	Lower 95%	Upper 95%	P value
Snow	1.001	0.007	0.988	1.015	0.826
Temp. day	1.009	0.026	0.960	1.063	0.703
Temp. night	1.037	0.021	0.994	1.081	<u>0.093</u>
Female age	0.951	0.032	0.893	1.012	0.115
Experience	0.933	0.077	0.801	1.086	0.368
Cub age	1.041	0.011	1.020	1.063	< 0.001
Calving	2.601	0.267	1.542	4.387	< 0.001

Subset: Forest					
<i>Variable</i>	Estimate	SE	Lower 95%	Upper 95%	P value
Snow	0.997	0.005	0.988	1.006	0.526
Temp. day	1.037	0.018	1.001	1.074	0.043
Temp. night	1.045	0.020	1.004	1.087	0.029
Female age	0.852	0.052	0.770	0.942	0.002
Experience	0.764	0.069	0.667	0.875	< 0.001
Cub age	1.083	0.023	1.036	1.132	< 0.001
Calving	0.611	0.318	0.328	1.139	0.121

Before the multivariate analysis all variables were checked for correlation. This showed a correlation between female age and experience, as well as between day-time and night-time temperature. Consequently, female age and experience nor day-time and night-time temperature could not be included into the same model. Tables 2 and 3 show the AICc tables for the alpine and forest habitat subsets respectively. The top model for alpine habitat included the variables age of the cubs and calving ground and for the forest habitat the variables experience and temperature during the day.

Table 2: AICc table for the alpine habitat candidate models.

<i>Model</i>	AICc	ΔAICc	AICc weight
Cub age + calving	734.79	0.00	0.69
Calving	736.56	1.77	0.28
Cub age	741.30	6.51	0.03
Female age	752.80	18.01	0.00
Temp. night	753.86	19.07	0.00
Null	755.48	20.69	0.00
Experience	755.49	20.70	0.00
Temp. day	757.24	22.45	0.00
Snow	757.36	22.57	0.00

Table 3: AICc table for the forest habitat candidate.

<i>Model</i>	AICc	ΔAICc	AICc weight
Experience + temp. day	188.58	0.00	0.32
Experience	190.00	1.42	0.16
Experience + temp. day + cub age	190.50	1.92	0.12
Experience + temp. night	190.53	1.95	0.12
Experience + cub age	191.72	3.14	0.07
Experience + temp. night + cub age	192.48	3.90	0.05
Female age + temp. day	192.52	3.95	0.04
Female age	194.12	5.54	0.02
Female age + temp. day + cub age	194.29	5.71	0.02
Female age + temp. night	194.32	5.75	0.02
Female age + cub age	194.47	5.89	0.02
Cub age	194.82	6.24	0.01
Female age + temp. night + cub age	195.33	6.75	0.01
Temp. night + cub age	195.86	7.28	0.01
Temp. day + cub age	196.12	7.54	0.01
Calving	203.63	15.05	0.00
Temp. night	204.88	16.30	0.00
Null	205.53	16.95	0.00
Temp. day	205.54	16.96	0.00
Snow	207.36	18.78	0.00

Table 4: Top model output for both two habitats (alpine – forest). Stating the exponential coefficient (estimate), standard error of the estimate (SE), lower/upper 95% confidence interval (lower/upper 95%) of the estimate and p value (Pr (>|z|)).

Subset: Alpine					
<i>Variable</i>	Estimate	SE	Lower 95%	Upper 95%	P value
Cub age	1.022	0.012	0.998	1.046	<u>0.071</u>
Calving	2.027	0.312	1.100	3.733	0.023
Subset: Forest					
<i>Variable</i>	Estimate	SE	Lower 95%	Upper 95%	P value
Experience	0.759	0.072	0.659	0.873	< 0.001
Temp. day	1.051	0.018	1.015	1.090	0.006

In the alpine habitat, calving grounds increase the probability of den shifts occurring (hazard rate) by 200% on average (estimate = 2.03), when the den site is located on reindeer calving grounds (Table 4). The general trend is that the probability of den site shifts increases after the reindeer arrive during the end of April (Figure 4). Also the cub age increases the probability of a den site shift occurring in alpine habitat (Table 4). The hazard rate increases with 2% per day (estimate = 1.02) and overall there was a positive relation between cub age and the hazard ratio (Figure 5).

In forest habitat, female experience had a negative influence on the probability of a den shift occurring (Table 4). The probability declines with about 24% (estimate = 0.76) per year of experience, meaning that more experienced females shift den sites less often in comparison to in-experienced females (Figure 6). Also the day-time temperature increases the probability of den shifts in the forest habitat (Table 4). The relationship with the hazard ratio is positive (Figure 7), where an increase of temperature by 1°C increases the hazard rate with 5% (estimate = 1.05).

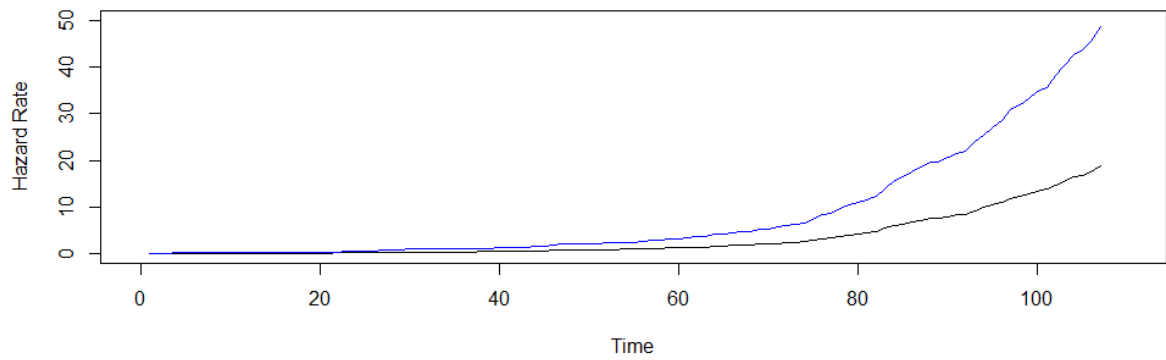


Figure 4: Hazard rate estimations for the den sites on and outside calving grounds (on = blue and upper line; outside = black and bottom line) in alpine habitat (time 0 = Julian date 46 referring to 15th of February).

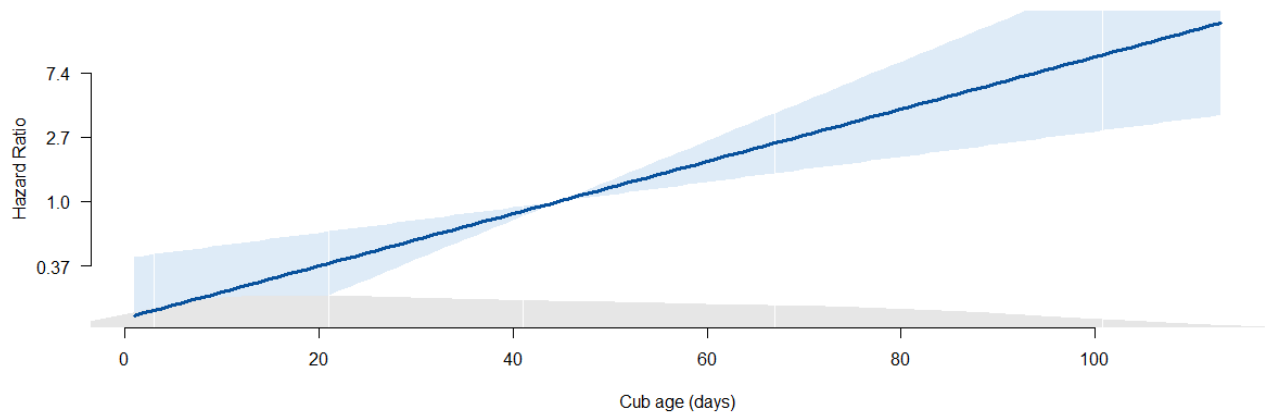


Figure 5: The hazard ratio estimations for when the age of the cub is increasing in the alpine habitat (light blue = 95% confidence intervals; grey = amount of data).

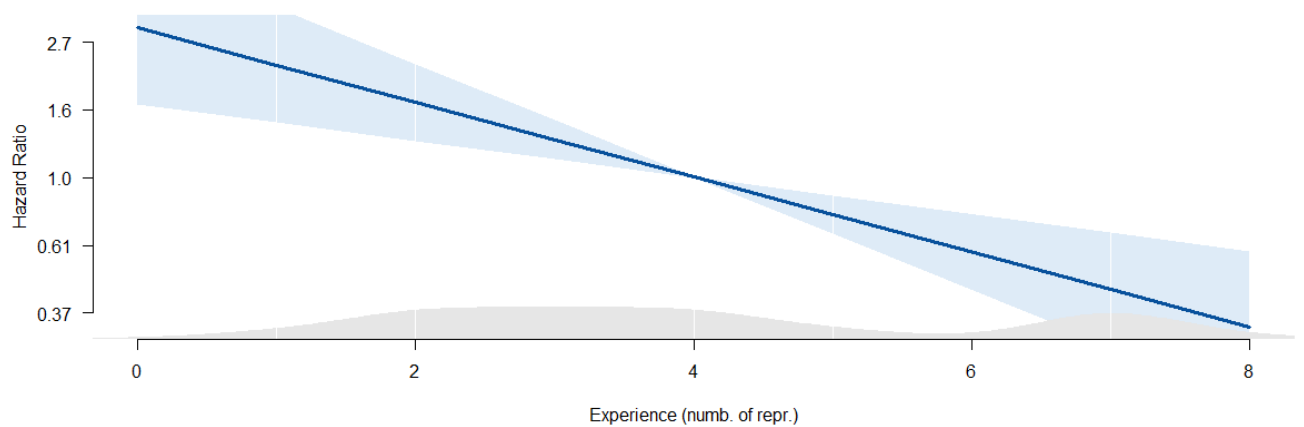


Figure 6: The hazard ratio estimations for the number of reproductions the female had before the denning season when denning in the forest habitat (light blue = 95% confidence intervals; grey = amount of data).

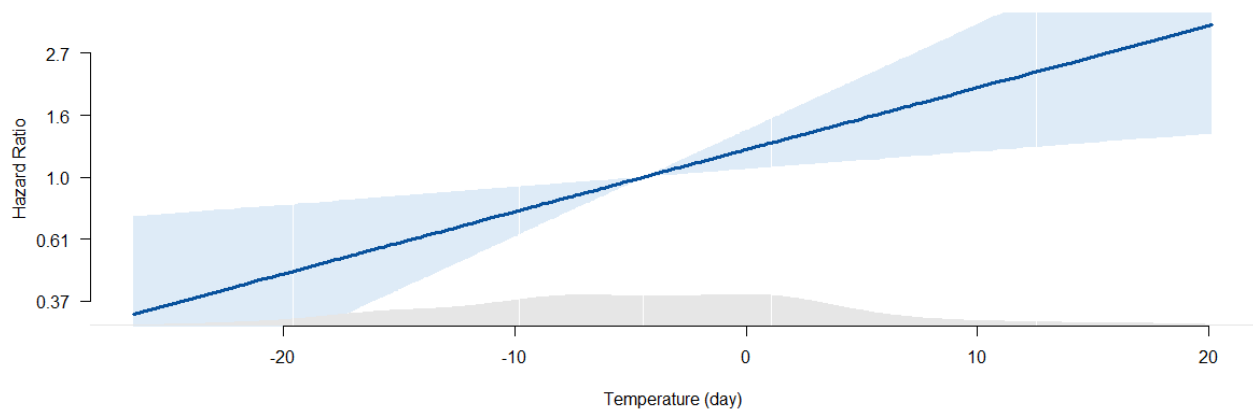


Figure 7: The hazard ratio estimations for the temperature during the day when denning in forest habitat (light blue = 95% confidence intervals; grey = amount of data).

Discussion

Female wolverines showed high variation in den use and den shifting patterns, although the general pattern was an increased probability of den site shifts over time during the denning period. This variation was explained by the habitat the den site was in, reproductive experience of the female, temperature, resource availability (i.e. in this case represented by reindeer calving grounds) and the increasing age of cubs during the denning season. Especially if the female was denning in alpine or forest habitats had an great influence on the shifting of den sites (Figure 2 & 3).

Habitat

As hypothesized, habitat appears to be a decisive factor for den shifting behaviour of female wolverines in my study area as there was a lower probability for den site shifts in alpine habitat compared to in forest habitat (Figure 2). This is probably explained by the different denning conditions. Den sites in alpine habitat often consist of a tunnel system in snow and are almost unreachable for other predators. Thermoregulatory conditions under the snow are assumed to be stable in the alpine habitat for a great duration of the denning season. Besides that, Mattsing (2008) reported a preference for altitude, slopes and aspects which favoured stable snow conditions in the alpine habitat. In the forest habitat, snow conditions are less stable (Musselman *et al.*, 2008). Due to the lower altitude and habitat characteristics in the forest habitat, snow might be a less decisive factor for den site selection and cover should instead be provided by structures, such as boulders and (fallen) trees (Makkonen, 2015). The snowpack in the forest habitat may be impacted earlier by snowmelt than in alpine habitat (Molotch *et al.*, 2009), causing den sites to become uninhabitable earlier in the forest habitat. Therefore, finding suitable and stable den sites could be more challenging in forest habitat and making “wrong” denning decisions may cause the higher probability of den shifts in forest habitat. Though, females may need to shift more often in forest habitats, distances between consecutive den sites may be short and therefore reduce the risk for the cubs. Short and a higher number of shifts may be the way female wolverines adapt to the unstable environmental conditions in forest habitat.

Calving ground

Resources are of great importance for current and future reproductions in most mammals (Fuller & Sievert, 2001), as also showed for the wolverine (Persson, 2005; Persson *et al.*, 2006; Rauset *et al.*, 2015). Not only for the offspring during the maternal care, but also for the female to successfully reproduce in the future (Harrison *et al.*, 2011; Shaw & Levin, 2013). In most areas where wolverines occur, food resource availability is highly variable between seasons and areas (Mattisson *et al.*, 2016). In my study area, reindeer are the main food resource for wolverines. Wolverines are also known for their food caching capabilities (van der Veen *et al.*, 2020). Therefore, they can buffer for low resource

availability periods, such as when females with cubs are denning and have a limited movement range. During spring, reindeer arrive to the study area and start to give birth on the traditional calving grounds in early May. My results, partly in line with my hypothesis, show that females denning in alpine habitat shift den sites on the calving grounds more often in comparison to den sites outside of calving grounds (Table 4). Until day 70 (the end of April), the probability of shifting den sites is low, after this day the probability increases rapidly (Figure 2, 3 & 4). This corresponds to the influx of resources into these areas. Besides that, most wolverine cubs have reached an age at which they are mobile enough to follow their mother (Inman *et al.*, 2012) and therefore they could move closer to where the reindeers are located. On the other hand, one may think these resources should keep females more stationary and spend less energy on moving the cubs. However, it could be more beneficial to move the cubs to the resources instead of bringing the food to the cubs. The observed pattern could also be explained by a higher amount of human activity in the calving areas. Reindeer herds are patrolled more intensively by reindeer herders during the calving season, which could lead to increased disturbance. Human disturbance has been suggested as a main factor for den abandonment (Magoun & Copeland, 1998). Due to lack of data, this factor could not be included in this analysis, and needs to be further investigated.

Cub age

Wolverine cub development has mainly been studied in zoos (Shilo & Tamarovskaya, 1981). Cubs are born blind, deaf and immobile, making them vulnerable and relying completely on the female. The relocation of these young cubs is not without risk as intraspecific predation is a major cause of juvenile mortality (Persson *et al.*, 2003) and the female needs to spend energy carrying them separately when moving them. Therefore, the natal den site should be chosen well, to avoid most potential threats. After about 10 weeks of nursing, the cubs start to eat solid food and can start to travel short distances with the female (Inman *et al.*, 2012). In line with my hypothesis, the probability of den shifting increases with increasing cub age (Figure 5). The increasing mobility of the cubs could make it possible for the female to relocate the cubs closer to food resources and to move away from den sites when they become uninhabitable.

Female reproductive experience

The effect of learning to survive and adapt to changing conditions, such as resource availability, can be expressed as experience. My results, partly in line with my hypothesis, for the forest habitat show that wolverine females with more experience (i.e. number of previous reproductions) have a lower den shift probability in comparison to less experienced females (Figure 5), while this effect of experience was not visible in the alpine region (Table 1 & 2; Figure 8 in Appendix II). Royle *et al.* (2012) stated that experience is assumed to increase survival, both of the parents and their offspring. The lack of behavioural skills, such as foraging and parental care (e.g. defending or avoiding potential infanticidal individuals) could lead to higher loss of cubs (Zedrosser *et al.*, 2009). More experienced females might have a better understanding of the suitability of den sites, timing and changing conditions. One conclusion could be that females need to learn how to find suitable den sites in forest habitats more than in alpine habitats. This may be traced back to the unstable climate conditions in the forest habitats compared to in the alpine habitat, that females need to cope with. Additionally, suitable denning possibilities might be more limited in forest habitats and wrong decisions may be more frequent. If den sites are a limited resource in forest habitats, females may need to choose less suitable sites (Royle *et al.*, 2012). In contrast, suitable den site possibilities might not be limited in alpine regions due to favourable snow conditions and the formation of snow drifts.

Climatic variables

Spring snow conditions has been suggested to be a crucial factor for wolverine denning (Magoun & Copeland, 1998; Copeland *et al.*, 2010; Dawson *et al.*, 2010; McKelvey *et al.*, 2011; Inman *et al.*, 2012; May *et al.*, 2012; Magoun *et al.*, 2017). Snow conditions are influenced by temperature and habitat characteristics, which may vary on a small scale. Therefore, the influence of temperature may be different for both habitats. Magoun & Copeland (1998) found that natal den abandonment coincided

with the time when temperatures rose above freezing for several days. My results show that increasing day-time temperatures positively influenced the probability of shifting den site in the forest habitat (Table 4, Figure 7). However, I found no influence of temperature in the alpine habitat, nor that wolverines shift den sites after a couple of days with temperatures above freezing. This result was partly in line with my hypothesis, as temperature was only influential in the forest habitat and not in alpine habitat. Snowmelt is probably an important cause of den shifts when temperature increases, especially in the forest habitat. However, it is hard to measure snowmelt and accurate local data was lacking for this study. In the future, local scale measurements are needed to investigate snowmelt at den sites.

Snow cover was non-significant for both habitats (Table 1). This may be caused by snow cover being a limited index for snow conditions around the den site. Snow cover estimates are difficult to relate to the actual snow conditions at a den site, due to the coarse scale of the data used. Other methods should be investigated regarding snow conditions at den sites.

In the next decades, snow will be increasingly influenced by the warming climate (Jones *et al.*, 2000; Armstrong & Brown, 2008). Especially further north, the climate is warming up faster (Larsen *et al.*, 2014). Higher temperatures will result in less suitable snow conditions for wolverines and may lead to a shortened season of snow cover (Hörnfeldt, 2004; Hörnfeldt *et al.*, 2005; McKelvey *et al.*, 2011; Myrsterud, 2016). Besides that, snow conditions might only be suitable for denning for a short time period especially in the southern range of the wolverine distribution (Peacock, 2011). This may make it more difficult for wolverines to find suitable den sites in the future, which may affect cub survival and thus recruitment. Less suitable den sites may be disturbed more easily or exposed earlier by the environmental elements. Studying wolverines occurring more south, in boreal forest, will be of great importance to be able to explore the reproductive success of wolverines in areas with less snow (or altered snow conditions) during the denning period. As the wolverines have been expanding more southwards in Sweden (Aronsson & Persson, 2017), they apparently are able to reproduce under conditions which have not been studied yet.

Conclusion

The denning behaviour of wolverines in northern Sweden varies greatly. During and between reproductive seasons, many factors change and influence each other. All the above mentioned important variables (calving grounds and cub age in alpine habitat; female experience and temperature in the forest habitat) cannot fully explain the reason for den shifts by themselves. For example, both the reindeer moving towards the calving grounds and the increased mobility of the cubs occur during the same period of time in the denning season and might therefore enhance each other, and this needs to be investigated further.

Wolverines seem to time reproduction perfectly, though might be surprised by small scale but rapid changes which cause den shifts. The reasons for den shifts at the beginning of the denning season are most likely taking place at a too small scale to be detected in my analysis.

Especially the denning habitat is a critical factor regarding den shifts. Climatic factors, such as snow and temperature, only appear to have influence in forest habitat. This may support the suggestion that forest habitats are more challenging to have a den site in. The alpine habitat may sustain preferable conditions during the denning period, nevertheless wolverines do make use of den sites in forest habitat throughout the whole denning period. This might also be influenced by wolverine density, as with increasing density less suitable areas will be used for denning as well. Besides habitat, both resource and individual factors influence den shifts as well. The reindeer calving grounds increased the probability of den site shifts in alpine habitat, which may be because wolverines move towards and follow the herds or because of increased human disturbance. Whereas, the reproductive experience decreased the den shift probability in forest habitat.

The expansion southwards has created new challenges for wolverines. Studying wolverines occurring in these most southern ranges can lead to answers regarding their adaptability. The ongoing global climate change may affect crucial factors of the wolverine life-history and these individuals could give a critical insight into, for example, how they cope with less snow or no snow at all. For upcoming denning behaviour studies on wolverines, several factors should be considered; exploring most suitable snow and temperature estimation method at the den site scale. Most reliable would be to use camera

traps near den sites, which make photos of a reference pole for snow depth and that uses time-lapse settings to investigate daily and small scale snow changes at the specific sites in combination with temperature loggers inside and outside the den sites. Besides that, include data on cache sites (resource availability), include female specific variables and use these to explore denning behaviour of wolverines in their southern ranges.

Hopefully, this thesis has led to a better understanding of wolverine denning behaviour and opened up ideas for future research. In the coming years, this study also offers reference data to compare to the denning behaviour of wolverines further south and to evaluate the effects climate change might have on the species and mainly their denning behaviour.

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Appendices

- I. Dataset Survival Analysis example.
- II. Additional plots.

Appendix I: Dataset Survival Analysis example

Table 5: The dataset for the survival analysis dataset was build up on a daily pattern, this made it possible to include daily changing variables such as temperature and snow. The example dataset is showing the den ID, wolverine ID, year, entry (julian date), exit (julian date), start_t (0 = julian date 45), exit_t, den number, fate (0 = stayed in den site, 1 = den shift occurred), age of the cub(s), habitat, day-time temperature and age of the female. The other variables were excluded, to make sure the daily set-up was clearly visible.

den_id	w_id	year	entry	exit	start_t	end_t	den_number	fate	c_age_exit	habitat	temp_day	age
2	J-11270	2012	45	46	0	1	1	0	2	Alpine	-16.61	3
2	J-11270	2012	46	47	1	2	1	0	3	Alpine	-15.57	3
2	J-11270	2012	47	48	2	3	1	0	4	Alpine	-16.6	3
2	J-11270	2012	48	49	3	4	1	0	5	Alpine	-15.75	3
2	J-11270	2012	49	50	4	5	1	0	6	Alpine	-13.79	3
2	J-11270	2012	50	51	5	6	1	0	7	Alpine	-14.89	3
2	J-11270	2012	51	52	6	7	1	0	8	Alpine	-11.63	3
2	J-11270	2012	52	53	7	8	1	0	9	Alpine	-11.63	3
2	J-11270	2012	53	54	8	9	1	0	10	Alpine	-9.87	3
2	J-11270	2012	54	55	9	10	1	0	11	Alpine	-11.99	3
2	J-11270	2012	55	56	10	11	1	0	12	Alpine	-10.13	3
2	J-11270	2012	56	57	11	12	1	1	13	Alpine	-10.69	3

Appendix II: Additional plots

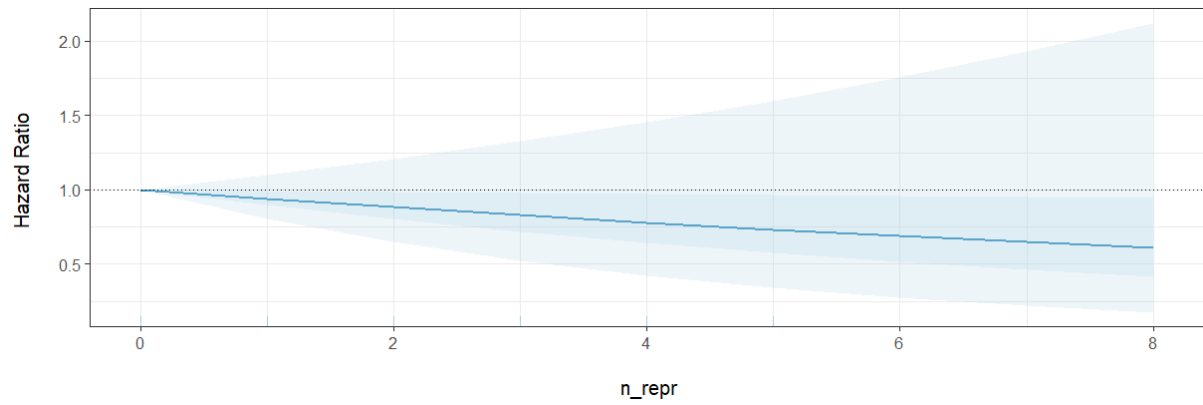


Figure 8: The hazard ratio estimations for the number of reproductions the female had before the denning season when denning in the alpine habitat (light blue = 95% confidence intervals; grey = amount of data).