Høgskolen i Innlandet

Faculty for applied ecology, agricultural sciences, and biotechnology

May Britt Trydal

Master thesis

Spatial and temporal movement patterns of wolverine *(Gulo gulo)* females during the denning period in the boreal coniferous forest

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Contents

Abstract

Knowledge about how individuals move in time and space in different seasons is important because it affects both the population structure and how individuals are distributed in the landscape. When reproduction occurs the spatial temporal movement patter often change. The wolverine *(Gulo gulo)* inhabits a highly seasonal environment and the female give birth to altricial offspring in a den in mid- February, earlier in the year than other non-hibernated, solitary northern predator species. My main objective was to describe the spatial and temporal movement pattern of reproducing female wolverines during the denning period. In this study, I present GPS data from 12 breeding seasons of n=7 reproductive dwelling female wolverines from parturition or day of capture until 1th June. To investigate the distance the female was from the den site, I used a non-linear regressive time series analysis (GAMM) with the additive effect of time of the year and time of day. The result showed that the female reduced her activity early in the denning period. The distance from the den site gradually increases until the distance stabilises around Julian day 100 (10th April). The female was more active during the nocturnal hours with an increase in activity pattern from 15:00 and beyond until 05:00. Wolverine equipped with GPS collar have a larger proportion of 0-positions (No-Fix) because they are associated with rough terrain and the den is under deep snow often in connection with boulders or rocks. To investigate the probability of No-fix position in relation to day of year and time of day I used a binomial GAMM. The proportion of missing positions decreased with time of year, while the proportion of missing positions was highest in the middle of the day. This may indicate that the female reduces the time she spends on the den gradually over the denning period and she spent most of her time on the den during the day. The female used a home range size of 25-30 km^2 early in the denning period, but the size gradually increased to week 15, when the home range size stabilized at 85-90 km^2. I conclude that a reproductive female reduces her spatial and temporal movement pattern during the denning period. After parturition, the female has short excursions from the den. In relation to the cub’s growth and gradually getting used to solid food, she takes longer excursions to gradually move the cubs closer to food storage. Home area use is significantly reduced early in the denning period, but after 2 months it appears that the entire home area has been taken into use.

Keywords: *Gulo gulo*, Reproduction, Temporal, Caches, Spatial, No-Fix, Coniferous Forest, Wolverine.

Norsk sammendrag

Kunnskap om hvordan individer beveger seg i tid og rom i ulike årstider er viktig fordi det påvirker både bestandsstrukturen og hvordan individene er fordelt i landskapet. Reproduksjon kan påvirke individers romlige og temporale bevegelsesmønster. Jerven (Gulo gulo) er tilknyttet leveområder med stor variasjon mellom årstidene. Tispa får valper i hi i midten av februar, som er tidligere på året enn andre arter som ikke har vintersøvn eller går i dvale. I dette studiet presenterer jeg GPS-data fra 12 ynglesesonger av n=7 reproduktive jervetisper fra fødselstidspunkt for valper eller fra merkedato til 1. juni. Hovedmålet mitt var å beskrive det romlige og tidsmessige bevegelsesmønsteret for reproduserende jervetisper i under hiperioden. For å undersøke avstanden tispa var fra hiplassen benyttet jeg en ikke- lineær regressiv tidsserieanalyse (GAMM) med additive effekter for tid på år og tid på døgn. Resultatet viste at tispene reduserte aktiviteten tidlig i hiperoden, men avstanden fra hiet øker gradvis inntil avstanden stabiliserer seg 10. april. Tispa var mer aktiv i de nattlige timene med økt aktivitetsmønster fra kl. 15.00 og utover til kl. 05.00. GPS merket jerv har en større andel 0 – posisjoner (No-fix) fordi det er tilknyttet ulent terreng samt at hiet er under djupt snø ofte i forbindelse med store steiner eller berg. Jeg brukte en binomial GAMM for å undersøke sannsynligheten for manglende posisjoner i forhold til dag på året og tid på døgnet. Sannsynligheten for 0 - posisjoner ble redusert med tid på året, mens sannsynligheten for 0 - posisjoner var høyest midt på dagen. Det kan tyde på at tispa reduserer tiden hun bruker på hiet gradvis utover hiperioden og tispa brukte mest tid på hiet på dagtid. I forhold til størrelsen på hjemmeområde reduserte tispa områdebruken og tidlig i hiperioden brukte hun et 25-30 km^2 stort område. Hjemmeområde økte gradvis, men fra uke 15 stabiliserte hjemmeområdestørrelsen seg på 85-90 km^2 stort område. Resultatet mitt stemmer overens med tidligere studier om at ynglende jervetisper har redusert aktivitetsmønster tidlig i hiperoden og aktiviteten foregår hovedsakelig om natta.

Nøkkelord*: Gulo gulo*, reproduksjon, barskog, hi, matlager, døgn, aktivitet, 0- posisjoner, jerv.

1. Introduction

Life history strategies are related to reproductive and survival traits (Stearns, 2000; Zedrosser, 2006), and through evolution various strategies have been developed to achieve as high a level of reproduction and survival of offspring as possible (Bronson, 1989). A species limitation of nutrients has to be used for growth, maintenances and reproduction (Varpe et al., 2009), and nutrient supply is often a limiting factor on reproductive success (Banci, 1994; T. Clutton-Brock & Iason, 1986; Persson, 2005). To compensate for the increased need for resources, there are two general tactics which are at each end of a continuous scale, "income breeder" finance reproduction with concurrent available resources, and “capital breeder” which uses stored resources to pay for reproduction attempts (Jönsson, 1997; Stephens et al., 2009). The stored resources can be both extrinsically and intrinsically stored resources. In species that breed several times and lives in unstable environment, it is predicted that capital breeding will be the most prevalent (Ejsmond et al., 2015). In general, females have a greater investment in reproduction because it requires more energy to reproduce and lactation is the most demanding phase of the female reproductive cycle (Inman et al., 2012; Smith & Smith, 2015).

Knowledge about how individuals move in time and space in different seasons is important because it affects both the population structure and how individuals are distributed in the landscape. Most adult reproductive individuals have a home range. Home range is defined as the area an individual uses to perform its normal activities of food gathering, mating and caring for young (Burt, 1943). Home range size and utilization and how these change throughout the year, are basic descriptors in movement ecology (McNab, 1963; Peery, 2000). Resources such as food as well as mating system and social organization can often explain individual and species-specific differences in home range size and utilization. In mammals, home range size is related to the body size of the species. In general, large mammals use large areas because they need more energy and therefore lager areas containing enough resources. Carnivores require usually larger home ranges than herbivore and omnivores of comparable body size, and males and adults have larger home ranges than females and juveniles, respectively (Burt, 1943; McNab, 1963; Smith & Smith, 2015). The spatial and temporal movement patterns are also affected by intra- and interspecific competition, environmental condition and in most cases a combination of all these factors as well as human disturbance (Aronsson, 2017; COSEWIC, 2017; Eriksen et al., 2011; Manchi & Swenson, 2005; Merrill & Mech, 2003; van

Beest et al., 2013). The circadian rhythm can, for example, be affected by predators that will avoid other dominant predators or predator- prey interactions (Bischof et al., 2014; Ji et al., 2022). Reproduction is essential for a species' survival (Comizzoli et al., 2009; McEvoy & Robinson, 2003), and when reproduction occurs, the spatial and temporal movement patterns often changes to avoid intra- and interspecific competition and to increase the reproductive success (Aronsson & Persson, 2018; Ballard et al., 1991; Magoun, 1985; Moen et al., 2008; Nordli, 2018). Intraspecific competition such as infanticide – the killing of conspecific young is relatively common behaviour in mammals (Palombit, 2015). In some mammals both females and males are contributing for bringing up the offspring (Kleiman, 1977). In these monogamous species, such as the wolf, the spatial and temporal movement patterns of the female will be more concentrated near the den in the time after parturition (Ballard et al., 1991; Mech, 1974). However, the most common in mammals is polygyny where the female is essentially alone raising the offspring (Clutton-Brock, 1991; Smith & Smith, 2015). The female must constantly make decisions to ensure the survival of the offspring, as well as take care for her own survival and condition (May et al., 2009). The brown bear *(Ursus arctos)* is a capital breeder and gives births in December -January during hibernation. When the female and her cubs leave the den in April - May, the cubs are exposed to infanticide (Swenson et al., 1997). A strategy for the female to avoid infanticide is to have a different spatial and temporal movement patterns than males, such as restricting area use, selecting areas close to human settlements, and being more active during the day (Dahle & Swenson, 2003; Zedrosser, 2006). A study done in Netherlands on natal den activity patterns in female pine martens *(Martes martes)* shows that the activity pattern of the female during nursing is strongly related to kitten`s development and time of day (Kleef & Tydeman, 2009).

The wolverine is a solitary, territorial, facultative predator as well as a scavenger in *Mustelidae* family. The wolverine has a polygamous mating system and an intrasexual territoriality, (Banci, 1994; Bjärvall, 1982; Dawson et al., 2010; Hedmark et al., 2007; Persson et al., 2010). The wolverine has a large home range in relation to its body size (females 10 kg, males 15 kg) and the average home range for females is 70-400 km^2 and for males 400 km^{2}-1500 km^2 (Persson et al., 2010). The spatial organisation depends on different resources for males and females. While the male home ranges depend on the density of females and can cover home ranges of several neighbouring resident females, female home ranges are assumed to be related to food availability(Sandell, 1989). It is suggested that reproducing female have the smallest home range size, compared to males and non-reproducing females (Banci & Harestad, 1990; Magoun, 1985). The wolverine can cover long distances in one day (Haglund, 1966; Pulliainen, 1968), and except breeding and females with cubs, the movement is mainly motivated by foraging (Banci, 1994). Although the wolverine is not a particularly good hunter compared to other apex carnivores, and largely uses carcasses as a food source, the wolverine is enduring and can pursue prey for several kilometres (Bjärvall et al., 1978).

The wolverine inhabits an highly seasonal environment in boreal forest and alpine tundra (Banci, 1994) and a strategy for the wolverine to survive and reproduce in an highly seasonal environment, is to store food in various caches (Haglund, 1966; van der Veen et al., 2020). The parturition occurs earlier in the year than other non-hibernating, solitary northern predator species (Inman et al., 2012). The average parturition date is in mid-February (Aronsson, 2017), but can vary from late January to early April (Aronsson, 2017; Bjärvall, 1982; Haglund, 1966; Johnsen, 1947; Myrberget & Sørumgard, 1979; Persson et al., 2010; Pulliainen, 1968). The female gives birth to usually 2-3 altricial cubs (Myrberget & Sørumgard, 1979; Pulliainen, 1968) in a den that often is located under boulders or felled trees buried under the snow, or structures in the snow layer itself (Bjärvall et al., 1978; Johnsen, 1947; Magoun & Copeland, 1998; Myrberget, 1968). Persistent and deep snow cover is suggested as an important factor for denning habitat because the snow cover provides both thermal advantages for the cubs as well as protection against predation (Pulliainen, 1968). The cubs suckle for about 10 weeks, with a gradual transition to solid food (Iversen, 1972). How long the cubs are in the natal den can vary (Magoun & Copeland, 1998), but the wolverine can use several maternal dens until she starts using rendezvous sites in May or June (Magoun, 1985). Like most of the other members of the Mustelid family, the wolverine has a short period of growth and by September or October the cubs are nearly full-grown (Iversen, 1972; May et al., 2009). During the denning period the female must produce enough milk, forage, take part in territorial defence activities, parental care, and take care of her own survival and condition. She must constantly consider whether to stay in the den and take care of the dependent young that may be vulnerable to predation and infanticide, or to go out to search for food (Magoun & Copeland, 1998; May et al., 2009; Persson et al., 2003a). Intraspecific predation is a major cause of death in altricial cubs and young individuals (Persson et al., 2003a).

Following the protection, the wolverine population in Scandinavia has mainly been associated with the northern mountain areas in the border areas between Norway and Sweden. In recent years, the wolverine has temporarily recolonized former habitats such as the coniferous forest in Scandinavia (Aronsson & Persson, 2017; Johnsen, 1929; Persson & Brøseth, 2011). Therefore, most of the research on wolverines are from alpine areas (Aronsson & Persson, 2012; Linnell et al., 2015) and basic knowledge about wolverines ecology from forest habitat is scarce. Moreover, the spatial and temporal movement patterns in the wolverine's denning period are rarely studied, especially in forested areas.

In this study, I present unique GPS data from 12 breeding seasons of n=7 reproductive forest dwelling female wolverines. My main objective was to describe the spatial and temporal movement pattern of reproducing female wolverines during the denning period. I made the following predictions: I predict that **1)** throughout the denning period the female will gradually increase her daily movement away from the den, this due to pups' growth and increased food consumption and according to their changing nurturing needs. Moreover, since wolverines are primarily nocturnal, I predict **2**) that the female will be more active during the night. Wolverines are associated with rugged terrain and place their dens in inaccessible places, and therefore No-fix positions (missing positions) is more common in wolverines equipped with GPS collars and therefore, I predict **3)** that the probability of No-fix position decreases with day of year because the female use less time at the den site and **4)** is higher during daytime than during night. Lastly, since I expect that the female will gradually increase her daily movement away from the den and use less time at the den, I predict **5)** that the female uses a smaller part of her home range early in the denning period, and this will gradually increase as time progresses and the cubs grow.

2. Method

2.1 Study area

The study area comprises 12,215 km^2 and is geographical located in the southeast part of Norway more accurate formerly Hedmark county (61˚25´N, 11˚25´E; Figure 1), now Inlandet county, east for the river Glomma (Grensevilt, n.d.). Due to the county's extent and the topographical conditions with different altitudes, there is great variation in the length of the different seasons, snow cover and temperature conditions. The climate is typically continental climate, with cold winters and warm summers, with an average temperature between -6 to -13^o and between 13 to 16 in January and July respectively. Winter length can vary from about 180 - 115 days and snow covered 3-6 mouth of the year (Lystad, 1978; Milleret et al., 2017; Zimmermann et al., 2015). The landscape is dominated by boreal conifers forest of Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies*) and has a high incidence of bogs. Among these wide forests, it is typical with a hilly landscape and mountain peaks. Elevation in the study area range from 250 to 1050 m above sea level (m.a.s.l), and the tree line is at approximately 750 m a.s.l. Inlandet county is Norway's largest forest county with 40% of all Norwegian timber harvesting. Because of this intensive forest management it has also created an extensive network of forest roads (Sand et al., 2008). The study area is without free-ranging domestic sheep, and south of the southern border for Sami domestic reindeer in Norway. Together with Trøndelag county, Inlandet has the largest population of moose *(Alces alces)*, and in 2021, 8 716 moose were shot during moose hunting in Inland county (Statistisk sentralbyrå, 2021b). Other cervid species are reed deer (*Cervus elaphus*) and roe deer *(Capreolus capreolus).* Parts of the study area are within the wolf breeding range, and in addition there are red fox *(Vulpes vulpes)*, brown bears and Eurasian lynx (*Lynx lynx)*(Grensevilt, n.d.). Smaller species include beavers, capercaillie *(Tetrao urogallus)*, black grouse *(Lyrurus tetrix)*, willow ptarmigan *(Lagopus lagopus)* and mountain hares *(Lepus timidus)*(Lystad, 1978). Human population density in the study area is 8 inhabitants per km^2 land area (Statistisk sentralbyrå, 2021a).

2.2 Study animal

To answer the study question, I have used data consisting of position data from reproductive wolverine females equipped with GPS collars from 2017 to 2021. All the data are provided from the Norwegian Forest Wolverine Project (SKOGSJERV), Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University. To study wolverine females' spatial and temporal movement pattern in the study area, I used n=7 confirmed reproducing female wolverines with GPS transmitters for a total of 12 reproduction seasons (1-4 seasons per individual) (Table 1). All wolverines, except one who was darted at a den-site (J1702), were trapped in life - traps made of solid wood. All captures were approved by the Norwegian Animal Research Authority of the Norwegian Food Safety Authority (FSA,

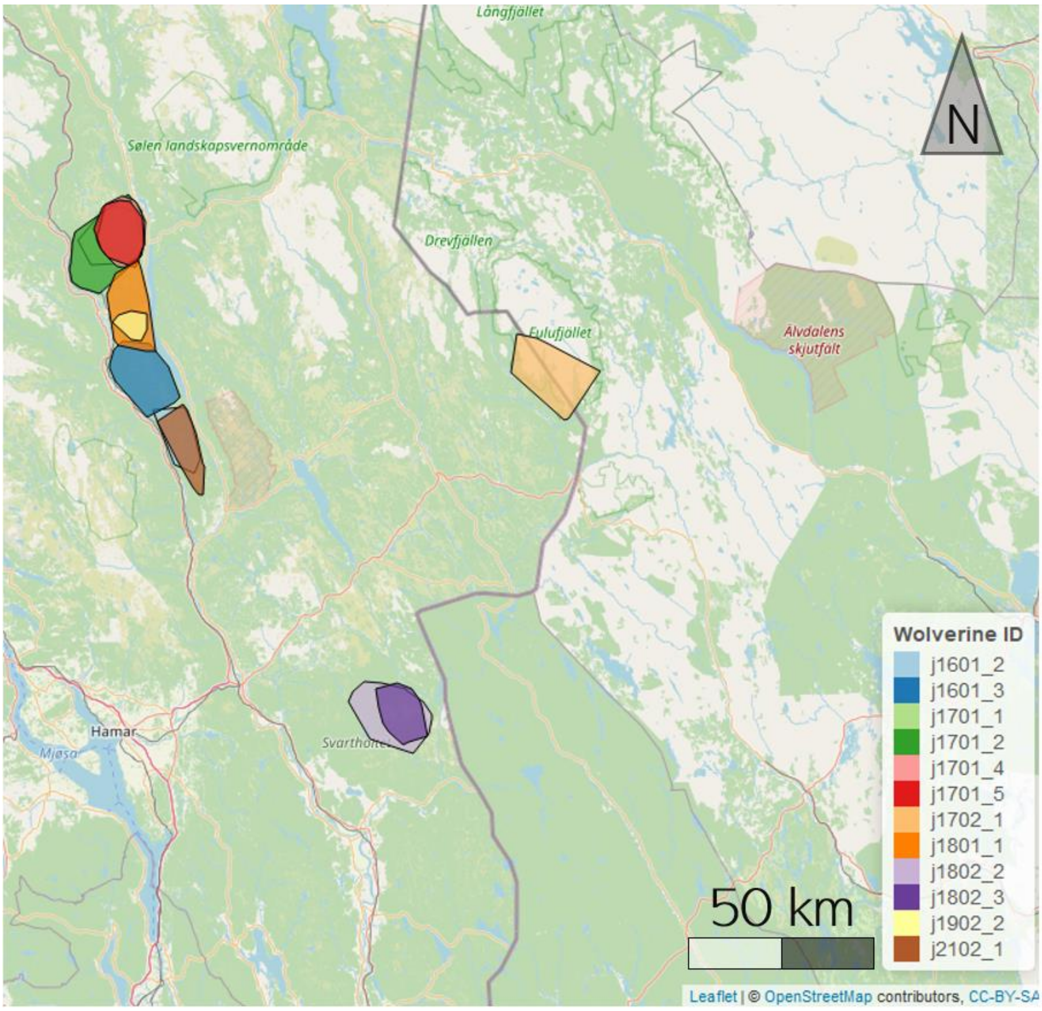


Figure 1. *100% Minimum Convex Polygon (MCP) for 12 breeding year of 7 wolverine females from 2017 -2021.*

FOTSID-16-22/: 29148), and the Norwegian Environmental Agency and all the captures were following detailed, standardized biomedical procedure for animal anaesthesia and handling techniques (Arnemo & Evans, 2017). The wolverine was darted with a CO_2 powered dart-gun and immobilized with a combination of ketamine and medetomidine. The wolverines were equipped either with a GPS-GSM Vertex Lite Collar or Tellus UltraLight neck collar (Vectronic, Berlin, Germany or Followit, Lindesberg, Sweden). When the capture was finalized, the wolverine was put back in the trap that was open but disarmed and reversed with anti-sedan.

Table 1. *Data overview used in the statistical analysis. From parturition date or from the time of capture and summarized censored days with GPS - positions for each individual and year.*

WOLVERINE_ID	2017	2018	2019	2020	2021	N=days
1601		06.04-01.06			10.03-01.06	139
1701	28.04-01.06	05.04-01.06		06.03-01.06	18.04-01.06	222
1702	10.05-28.05					18
1801		05.04-27.04				22
1802			04.04-01.06		07.03-01.06	144
1902					*12.02-21.03	37
2102					08.03-01.06	85
N=days	52	135	58	87	335	667

**Infanticide. The cubs were killed by a male 19th March.*

To capture the wolverines, there has been an extensive fieldwork. Several people have done this, including me from the winter 2017. The live - traps were placed at relevant locations with wolverine activity and the placement was approved by municipalities and landowners. Various preparatory field work has been carried out, such as baiting and maintenance of the traps. Bait used was moose, roe deer, red deer, and beaver. Two notification systems, one satellite-based and one GSM system were mounted on the traps. In addition, one to two game cameras with motion sensor were located at the traps that sent images on command. During the capture periods, there was always a team consisting of a veterinarian team and field crew who were ready to move out to the trap if a wolverine was caught. Most of the capture were performed in March and April, except one female which was GPS collared in January 2021 (Supplementary Table 1). Since I was interested in the denning period, I used data from parturition- or capture date, to 1st June (Table 1). The collars were mainly programmed to acquire a GPS fix every fourth hour, but in periods the collars were programmed to acquire

GPS fix every hour. In this study I only used 4 hourly positions. This gave six regular positions per day at 03:00, 07:00, 11:00, 15:00, 19:00, 23:00 (GMT). Captures may have a disruptive influence on animal's spatial and temporal movement patterns (Cattet et al., 2008; Nordli, 2018; Teräväinen, 2016). In this study I have chosen to not exclude positions, because reproducing females have the den sites as a holding point compared with males and subadults.

2.3 Documentation of reproduction and cubs alive during study

Several different methods were used to determine whether female with GPS collars reproduced. Females captured during the reproduction period were examined to document lactation. The GPS position from females during the reproduction was analysed to see if they showed movement patterns that are typical of females that have cubs in a den and to identify the den site (Aronsson, 2017). By analysing the GPS positions, it was possible to see a sudden change in the movement pattern of the female. For example, when female J1902 lost her cubs she took a long excursion away from the denning site, in a straight line the distance was 25 km and into the territory of another female. Other methods for documenting or confirming cubs was to sneak or scout with a telescope (Figure 2, Table 3 Supplementary) on marked females to see if she still had young and sometimes the cubs could be confirm being alive in later summer by game cameras.

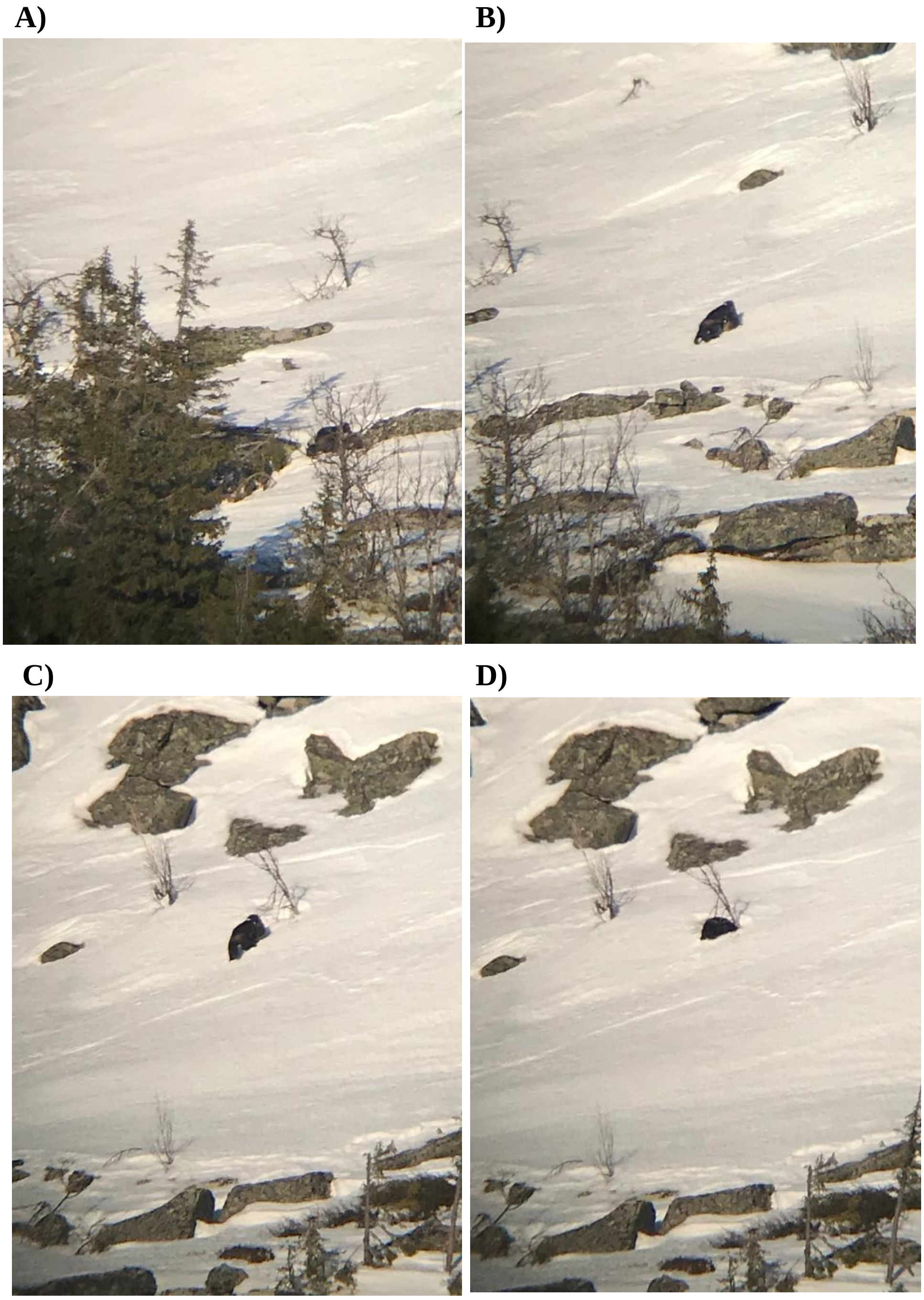


Figure 2. *Observation of female J1701 moving her cubs from one denning site to another at 19:00. She carried 2 cubs, one at the time, 15-20 meters from a den site next to some boulders **A)** to a den site beside a small birch **D)**. I could not see any sign of that these den-sites were connected under the snow when I checked these den sites in the field 30. May 2021. Den sites **A)** and **D)** are **A)** and **B)** in Figure 3. Photo: May Britt Trydal 27. April 2021.*

2.4 Identification of den sites

The GPS positions also give information about where a den site is located, as well as the movement pattern. If a cluster of positions has been created for several days and with few or no positions outside this cluster in the first days, it is an indication for that the female has given birth to the young. Most often, the females have the young in the natal den the first two months (Aronsson, 2017). For various reasons such as the environment, disturbances and age of puppies, the female moves the puppies to the maternal dens eventually. The GPS positions can identify the distance the female travels in the denning period as well as how far the female move the cubs. In early summer the female can move the puppies so often that position clusters no longer identify obvious den sites. Therefore, I have used data until June 1st.

An assumption for the analysis is that the puppies have been on den sites. For as good documentation as possible, a cluster check has been performed every year (2017-2021) and to collect samples of DNA from pups and/or to document denning and maternal dens (Table 3). To not disturb the female while caring for her young field documentation of den sites was carried out after the snow had melted, and the females had left the denning area. In May and June of 2021, I conducted these cluster checks (Figure 2). For quantitative and comparative reasons, we used a similar protocol as the Norwegian Environmental Agency (Miljødirektoratet) to document denning-sites on bare ground (Table 2).

Table 2. *Indications used to register den -and rendezvous sites for female wolverines suspected to be accompanied by cubs (Rovdata, 2021)*

1) Remains from several prey animals found.
2) There must be plenty of faeces in the form of at least two toilets.
3) Several den-bed sites have been found.
4) There are plenty of wolverine grey – white wool hair.
5) Bitemarks on vegetation are found in at least two different places.
6) Walking/tunnel system with branches is documented in snow residues, on bare ground or in the vegetation.

In the period from May to June 2021, I checked 29 clusters of 4 reproducing females that we assumed were denning locations based on GPS positions (Table 3). I was able to document denning locations based on the guildlines from Rovdata (Table 2), among other things by finding bed sites after cubs (Figure 3) (Rovdata, 2021), and I collected DNA samples for documenting cubs.

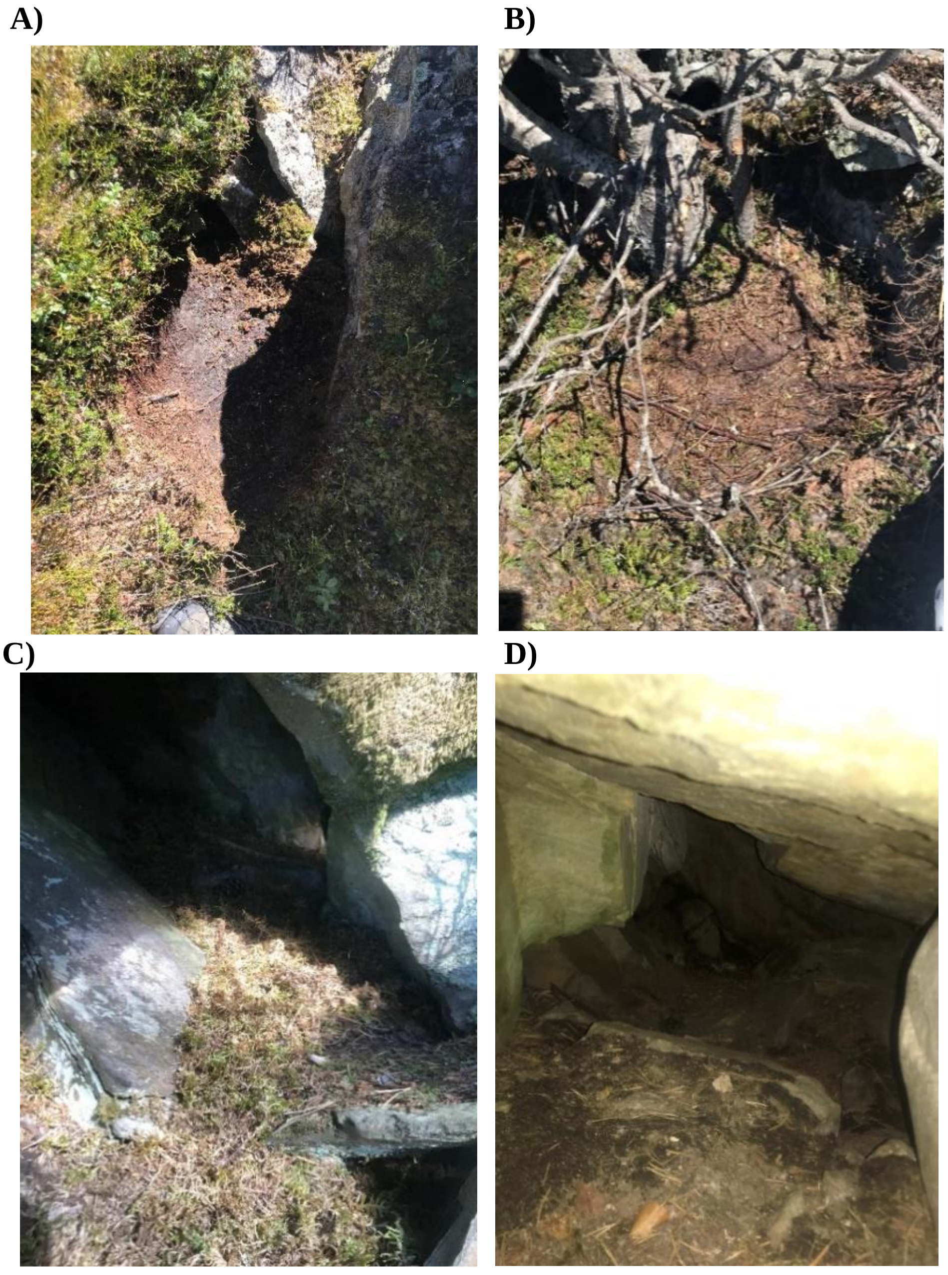


Figure 3. *Identified denning sites during checks of clustered GPS-positions.* ***A)*** *Denning site beside boulders (Figure 1****A****).* ***B)*** *Denning site by a birch tree. (Figure 2****D****)* ***C)*** *Denning site under / inside stone cave. Could look like the female had collected moss as a base.* ***D)*** *Under / inside stone cave with soil as a base. Photo: May Britt Trydal 2021*

The DNA samples was sent for individual identification, and for kinship analysis to determine if the sample was from a puppy. But only three new individuals from 2 different denning sites were confirmed (Supplementary Table 2). The analyses were performed with Single Nucleotide Polymorphism (SNP) DNA analysis. SNPs are variations in individual bases in DNA (Aitken et al., 2004).

Table 3. *Cluster check that is examined in the different years for each female (n=7) of a total of 12 breeding seasons. This is used as a standardized method to prove / make probable that pups were at the den and alive with the mother at the time the data were analysed. I followed up the cluster check in 2021.*

WOLVERINE_ID	1601	1701	1702	1801	1802	1902	2102
2017		1	1	2			
2018	2	2					
2019					4		
2020		3					
2021	12	9			1	3	4

2.5 Statistical analyses

All analyses were run using R version 4.1.1 (R Development Core Team, 2021) with the integrated environment RStudio (RStudio Team, 2021). Except for the home range analysis, a Generalized additive mixed model (GAMM) was used to investigate the spatial and temporal movement pattern of reproductive wolverine females. The data is a time series, and it also became clear in the data exploration that the response could fit the non-linear function. GAMMs are particularly suitable handling non-linear relationships and handling autocorrelation if present. Animal behaviour, terrain, and vegetation can have an effect on fix rate success on GPS collars (Mattisson et al., 2010). The wolverine often prefers habitat with large boulders, often in rugged terrain and at the same time is relatively short-legged animal, which means that the GPS collar will be close to the ground. These can negatively affect the GPS collar's ability to acquire satellites for positions fix (Mattisson et al., 2010).

When preforming data cleaning and management, I used the R packages "lubridate" (Grolemund & Hadley, 2011), "tidyverse"(Wickham & RStudio, 2021), "dplyr" (Wickham et al., 2022) and “datatable”(Xie et al., 2022). To calculate Euclidian Distances and extract weekly 100% MCP home range estimates (Mohr, 1947) I used the package “adhabitatLT” and “adhabitatHR” (Calenge, 2006). For making the map over all the years of reproducing females in this study I used the package “Leaflet”(V. Agafonkin, 2010). I standardized GPS positions at 4-hourly positioning intervals, this gave six regular positions per day. To investigate the spatial and temporal movement pattern I calculated the Euclidean distance for series of consecutive 4- hourly GPS positions for each female wolverine. For the data analysis and for model validation I used the packages "mgcv" and "itsadug" (van Rij et al., 2015) with the functions check_resid and gam.check. I used the package "ggeffects" (Lüdecke, 2018) to extract predictions with the function ggpredict, and finally I used the "ggplot2" (Wickham, Hadly, 2016) for plot visualization.

For my first model I tested the response variable Euclidean distance to the den site in relation to Julian day (s(DOY)) and time of day (s(HOUR)) according to predictions P1 and P2. My response variable was not normally distributed, so I used a gamma distribution supplied with a log link to improve fit. I did not detect any autocorrelation, potentially due to the excess of missing positions and scarce positioning interval. For my second model, where I wanted to investigate the probability of a missing position, I fitted a binomial GAMM with a link logit function to investigate the relationship of missing positions in relation to *X* Julian day (s(DOY)), and *X* time of the day (s(HOUR)) according to my predictions P3 an P4. To visualize cumulative home range size from the 15th February to 1st June I first summarized all positions within a calendar week. Second, I added all positions from a previous week to the following week and created a 100% Minimum Convex Polygon (MCP) for each cumulative week, which resulted in cumulative home range estimations over time.

3. Results

The distance (meters) (y) travelled from day 46 (15th February) to day 152 (1st June) (x), increased daily before the distance stabilized from day 100 (10th April) (Figure 4A). The female had highest activity during the crepuscular and nocturnal hours to 05:00 (Figure 4B). Thereafter the distance travelled decreased drastically, and in the middle of the day there was very little movement. From 15:00 onwards, the average distance to the den site increased again.

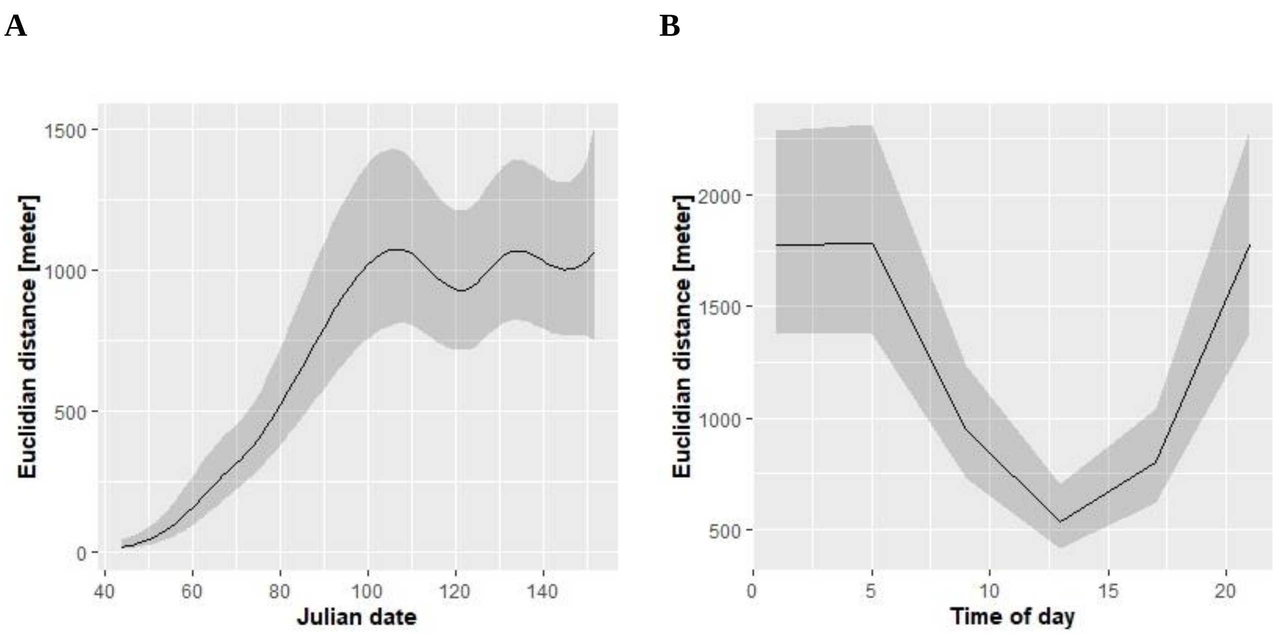


Figure 4. *The predicted Euclidean distance the female travelled from the den site in relation to Julian date* ***A****) and time of day* ***B****).*

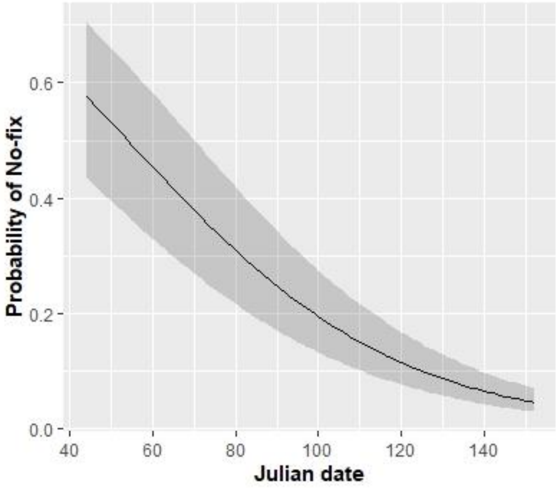
Table 4. *Model summary from the response variable Euclidean distance to the den site in relation to Julian day (s(DOY)) and time of day (s(HOUR))*

A: Parametric coefficients	Estimate	Std.error	t-value	p-value
Intercept	7.2820	0.1363	53.43	<0.001
B: Approximate smooth terms	Edf	Ref.df	F	p-value
s(DOY)	8.328	10.38	13.76	<0.001
s(HOUR)	1.980	2.00	106.73	<0.001
s(ID_EVENT)	8.159	9.00	11.63	<0.001

R-sq(adj) = 0.11, deviance explained = 9.17%, REML 5329.8.

The possibility of No-Fix decreased with Julian date (DOY) (Figure 5A), while the possibility of No-Fix increased in the middle of the day (Figure 5B), but from 15:00 the possibility of No-Fix decreased.

A **B**



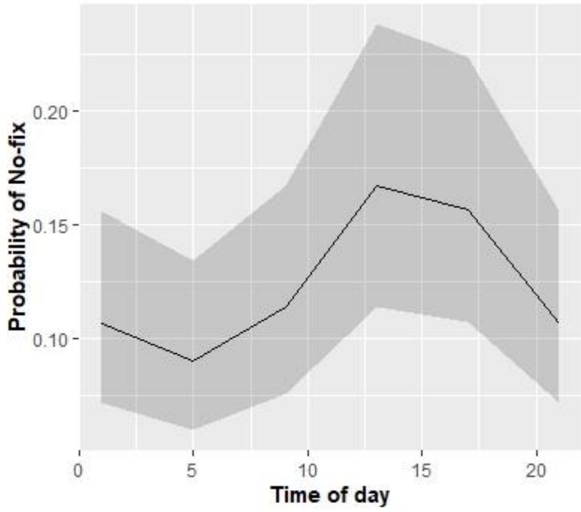


Figure 5. *The predicted probability of No-Fix in relation to the Julian date (s(DOY)* ***A)*** *and time - of - day* ***B****).*

Table 5. *Model summary from the probability of no-fix modell (GAMM) on Julian day s(DOY) and hour of the day s(HOUR).*

A: Parametric coefficients	Estimate	Std.error	t-value	p-value
Intercept	-1.673	0.231	-7.242	<0.001
B: Approximate smooth terms	Edf	Ref.df	F	p-value
s(DOY)	1.001	1.001	198.07	<0.001
s(HOUR)	1.902	2.001	39.17	<0.001
s(ID_EVENT)	8.477	9.000	204.85	<0.001

R-sq(adj) = 0.14, deviance explained = 12.8%, ML 5270.

The weekly cumulative home range size in square kilometres increased from February 15 (date of birth) to week 15 (Figure 6). At week 15 the home range size stabilized at 85- 90 km^2. Minimum home range size the female used was 30 km^2 and maximum home range size was 155 km^2.

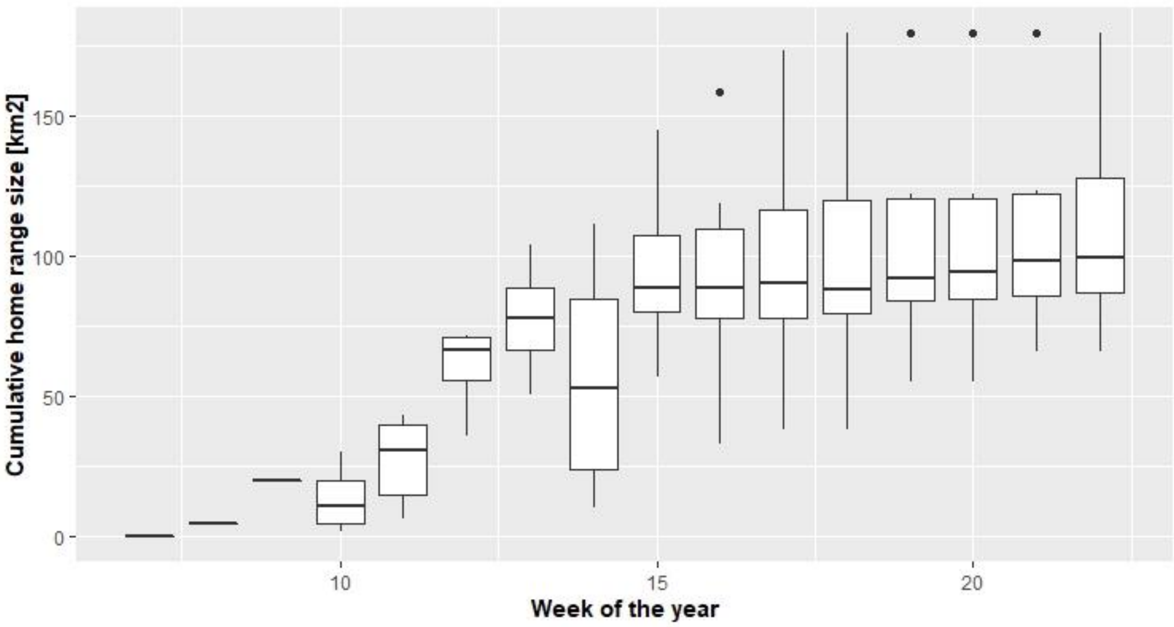


Figure 6. *Cumulative frequency distribution of 100% MCP weekly home range sizes of seven reproductive female wolverines with cubs during the time from February 15 (date of birth) to June 1. Black horizontal line in the boxplot shows the median home range size.*

4. Discussion

In this study I show how the spatial and temporal movement pattern of reproductive female wolverines change over time during the denning and rendezvous period. Consistent with my first prediction the female gradually increases the distance from the den until the distance stabilises around Julian day 100 (10th April) (Figure 4A). According to my prediction **2)** the female was more active during crepuscular and nocturnal hours. There was an increase in activity pattern from 15:00 and beyond until 05:00. (Figure 4B). My predictions **3)** and **4)** about No-fix positions was also supported, with decrease in No-fix position related to Julian date (DOY) (Figure 5A) and increase of No-fix positions related to time of day (HOUR) (Figure 5B). And finally, my prediction **5)** was also supported, reproductive females use a smaller part of the home range early in the denning period, and the proportion increases with week of year (Figure 6). From week number 15 the home range size use stabilized at 80-90 km^2. In the following I will discuss the result from this study of spatial and temporal movement pattern in female wolverine in denning period in coniferous forest habitat.

Like previous studies, this study indicate that the female spends more time in the den early in the denning period and don't travel so far from the denning site (Aronsson, 2017; Bjärvall, 1982; Johnsen, 1957; Magoun, 1985). This is probably since the neonatal cubs may need to suckle more often and the female don't have to bring solid food back to the cubs. The cubs might also need extra warm in the beginning, although snow cover is suggested as a thermal regulator (Pulliainen, 1968). An adult female might also have a surplus of caches close to the den early in the denning period. The distance increased with day of year until day 100. The cubs grow rapidly (Iversen, 1972; May et al., 2009), and the female must increase her milk production. This can lead to an increase in distance the female has to pass to find enough food. It may also be a possibility that the food caches that may have been near the den are empty (Aronsson & Persson, 2012), and the female must travel longer distances to find food. The cubs suckle for 10 weeks (assuming the parturition is 15th February, weaning takes place 26th April), but cubs are gradually accustomed to solid food (Iversen, 1972). The natal den might be the most secure and often the den the female is using for the longest period (Aronsson, 2017). May results showed that the distance was stabilizing at day 100 (10th April). This can be when the female starts using maternal dens. When the female starts using maternal dens the cubs are moved more regularly to new ones that might be nearer the food sources and may be a cause for the stabilizing of the distance the female travels daily. Aronsson (2017) found that the females start move the cubs more often after 15th April. Wolverine can use several maternal dens until she starts using rendezvous sites in May or June (Aronsson, 2017; Magoun, 1985). The behaviour of wolverines indicate that it selects for habitats that contain large boulders and inaccessible areas, which it uses for food caches and resting places. Thus, zero positions can also be when the female has been on a food cache or has rested, not only in the den. The decrease of zero position late in the denning season which I have conclude that the female spending less time on the den can also be due to the decline in snow cover late in the denning period as well as the maternal den are in more open areas so there are fewer zero positions and not because the female spends less time on the den.

The number of pups is also a possibility that can affect the distance the female travels. First, a higher number of cubs needs more food, and the second the number of young can cause the female to move the cubs more often due to space, parasites, and faeces in the den. The age and experience of the reproducing female can also be a factor that can affect the movement pattern (Côté & Festa-Bianchet, 2001; Heeres, 2020; Weladji et al., 2006). An inexperience female may not have a surplus of caches or may be a poorer hunter which can lead to an increasing distance travelled and more away from the den. Early in the denning period it might be important for the female to stay close to den not only for maternal care, but also defend the cubs against predation and infanticide (Agrell et al., 1998). One of the females (1902), most likely a young primiparous female, lost her cubs due to infanticide around March 19th , 2021. These cubs were born around 14th February.

With regards to the circadian rhythm of the wolverine, my result was in according to previous study's (Bjärvall, 1982; Haglund, 1966; May et al., 2009; Thiel et al., 2019). It was a higher activity in the crepuscular and nocturnal hours until 05:00 when de activity decreased. In the middle of the day there was very little activity before the activity increased again at 15:00. Personal observation of a reproducing female in the spring of 2021 (Figure 2), was that the female left the den at 15:00. She returned to the denning site at 18:10. and stayed in the den until 19:00. Then she came out of the den and carried 2 cubs, one at the time, about 20 meters to a new denning site (Figure 2A and D). I did not see her or her cubs again until I left the vantage point at 20:15. Haglund (1966) mentions that the wolverine, like the other large predators, is most active during the evening, night-time and in the morning. Likewise, it is the wolverine that is mostly seen during the day in comparison to the other large predators (Haglund, 1966). However, Bjärvall (1982) mentions that there can be a difference in the circadian rhythm of the wolverine depending on age, sex, and status. While juvenile individuals may have a higher activity rate during the day, breeding females who have a surplus of cached food are mainly nocturnal. At the same time, it has also been shown that the wolverine increases its activity with day length and increasing temperature (Thiel et al., 2019). Forage is an important factor that affects the movement pattern. The wolverine in this study inhabits forest habitats where moose are hunted. Slaughter remains and carcasses of traffic-killed moos can be a great food resource for scavengers such as wolverines. In the forest landscape in central Sweden, it is proposed that there is approximately 24,000 kg of meat available in an area equivalent to 900 km^2 (Wikenros, 2011). These are factors that can affect the distance the female travels, and that can contribute to increased food supply for the wolverines in the study area. Caches are important for wolverines, and for successful reproduction it is probably decisive (Persson, 2005; van der Veen et al., 2020). This may indicate that the female in this study has good access to food, and that they can limit their activity to crepuscular and nocturnal hours, in accordance with what has been proposed in previous studies (Bjärvall, 1982). Reproductive wolverines with poorer access to food, or food resources available at different times of the day can have a different circadian rhythm (Magoun, 1985). In northwestern Alaska in a treeless study area Magoun (1985) found that the reproductive females hunting ground squirrel in the mid-day. Bjärvall (1982) mention that the nocturnal behaviour might have a relation to the previous persecution. Large carnivores adjust their spatial and temporal activity to avoid humans and also in the hunting season (Ordiz et al., 2011).

Home range size increased with day of year. Early in the denning period the home range size was under 30 km^2 and increased to 85-90 km^2 from week 15. A reduction in home range use for reproducing females early in the denning period has been shown in previous studies (Aronsson, 2017; Magoun, 1985). Also in other carnivore the female reduced the home range size early in the denning period (Kleef & Tydeman, 2009; Moen et al., 2008) In contrast, Persson et.al. 2010 didn’t find differences in home range size in reproducing females and barren females. This was in alpine areas which may explain why the female must use the whole area to find food. In this study I have only looked at reproducing females, but since the home range size increased with age of cubs it is likely that the female will have a larger home range if she does not have cubs. Food availability is the proposed factor that determines home range size for females, thus food availability is a limiting factor for reproductive success for females (Persson, 2005). Population density can affect the home range size and can increase the chance for infanticide, because an increasing competition for resources. Infanticide preformed of males are related to sexual selection and occur when the cubs are altricial (Palombit, 2015; Swenson et al., 1997). Reduction in home range size early in the denning period, when the cubs are vulnerary can reduce the chance for infanticide because the female are nearby and can defend the cubs (Agrell et al., 1998; Balme & Hunter, 2013). It is somewhat uncertain why wolverine male kill altricial young because there are no immediate benefits. Perhaps by killing the cubs early, it might improve the female's condition in the following season thus the infant male gets an advantage and increases his reproductive success (Persson et al., 2003b). The mating season for wolverines is distributed from April to August. It may be that a female who loses her cubs will come into heat earlier than a female who has the cubs with her. Infanticide performed by female occurs more often when the cubs have become independent and female juveniles are more vulnerable (Persson et al., 2003a). Resources such as food are suggested as the most important factor for females' reproduction success (Persson, 2005) and infanticide performed by females can be seen in the context of it.

One of the assumptions in this study was that the cubs were born around 15th February, which is suggested as an average time of birth for wolverines (Aronsson, 2017). However, it is proposed that the time of parturition in wolverines can vary from late January till early April, (Collett, 1911; Pulliainen, 1968). This may be a factor that may influence the study design. Most of the capture took place in March and April after the females had given birth to cubs and the time of birth could not be documented. At the same time, by analysing the positions, it turned out that in J1902 she gave birth to pups on 14-15 February. In spring 2021 I checked cluster we assumed was denning site. Although we were able to document several denning sites, it is also possible that we have missed some denning sites. There may be disturbances that cause the female to move the cubs several times in a short time and it might be difficult to register the den site and it may be a failure in personal observations and time and opportunity to check all positions. Either way, it can affect the results. Due to the behaviour of wolverine such as have denning site in deep snow and under boulder etc as well as the GPS collar are closer to the ground, it is more common with zero positions in wolverine than in other species (Mattisson et al., 2010). However, it has been shown in previous studies of underground denning species that zero positions can be related to the den site (Walton & Mattisson, 2021). The GPS positions used in the analysis are registered every 4 hours at fixed times. A wolverine can move relatively long within this time. It must be considered that the size of the home area and the distance the female have covered in this study is the minimum size and distance.

In contrast to most other studies done on wolverines, this study has been carried out in the coniferous forest areas south of the domestic reindeer area and without sheep on open pasture. It can be assumed that even if the wolverine does not have access to the above proposed important prey (Landa et al., 1997) in this study area, humans influence the wolverine's food supply considerably. Anthropogenic subsidies that likely make the wolverine have good access to food range from human hunting behaviour as well as a traffic killed ungulates, and sites. More research is needed to understand the wolverine's ecology in these "new" re-established habitats. It could be interesting to investigate further how the slaughter remains impact the reproductive rate, how common infanticide as well as the spatial movement pattern of independent cub are in wolverine population with home ranges in coniferous forest without sheep and south for the Sami domesticated reindeer area. Establishment of wolverines in the forest landscape can reduce the conflict with sheep farmers as well as reindeer husbandry and at the same time it is possible to increase the population of wolverines in Norway, so the wolverine no longer is endangered.

Takk

Et lærerikt masterforløp er avsluttet her på Høgskolen i Innlandet, avdeling Evenstad. Økologi er et stort tema, og rovdyrene er bare en liten del av dette. Uansett så er det noe spesielt med disse store rovdyrene, de er og blir fascinerende. Jeg har vært så heldig å få muligheten til å få et lite glimt inn i denne verden, og selv om læringskurven har vært bratt, så har jeg skjønt at her blir man ikke utlært med det første, verken innen økologi eller rovdyr. Det er mange som skal takkes for at jeg har fått denne muligheten. Først og fremst skogsjervprosjektet og veilederne mine Kristoffer Nordli, Petter Wabakken, Barbara Zimmermann. Petter- man blir målløs når man er i samme rom som deg, ikke bare fordi du snakker mye, men mest av alt fordi det er fascinerende og inspirerende å høre på all kunnskapen du sitter med og ikke minst det pågangsmotet og alle mulighetene du ser. Barbara- kan ikke unngå å kommentere det gode humøret ditt og din positivitet. Man får alltid svar når man lurer på noe. Takk for tilbakemelding og ikke minst kommentarer på språk. Kristoffer- du har lært meg alt som har med jervefangst. Det har vært utrolig moro og spennende å få være en del av Skogsjerv prosjektet. Takk for gode og konstruktive tilbakemeldinger på innhold, språk og ikke minst statistikken. En stor takk for muligheten dere har gitt meg og ikke minst for at jeg har fått muligheten til å oppleve jerv, ulv og bjørn på nært hold i norsk natur! Erling Maartmann skal ha en stor TAKK for hjelp med DNA prøvene til denne oppgaven, og ikke minst behjelpelig da jeg hadde en av mine største naturopplevelser, fikk se ei jervetispe med valper i norsk natur. Jeg vil takke Oddmund Kleven i NINA/Rovdata for analyse av DNA prøvene. Wencke Lind på biblioteket for god hjelp med å finne litteratur og Melanie Spedner for hyggelige turer og samtaler her på Evenstad. I forbindelse med feltarbeid så vil jeg spesielt nevne Ingvild Svarstad, Rune Elnan og Erlend Furuhovde; takk for godt samarbeid og hyggelig samvær i felt. Det er også mange andre som skal nevnes av ulike grunne; Paul og Ragnhild Granberg mange hyggelige samtaler over en kaffekopp, Marius Rogstad både for opplæring i jervefangst, men ikke minst for husrom, samt mange gode venner og familiemedlemmer som har bidratt på ulike måter. Til slutt, jeg hadde ikke fått til dette uten den nærmeste familien min; Håvard, Netta og Tom Olav og mamma og pappa, ja dere er alltid der, uansett hva slags sprell jeg finner på. Tusen takk!

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5. Supplementary

Table 1. *Overview of periods reproducing wolverine females have sent GPS positions. Summarized days with GPS - positions for each individual and year.*

WOLVERINE_ID	2017	2018	2019	2020	2021	N=days
1601		06.04-27.07			10.03-03.10	292
1701	28.04-22.10		05.04 - 31.12	01.01-22.01 ,06.03-23.09	18.04-31.12	931
1702	10.05-28.05					19
1801		05.04-27.04				23
1802			04.04-20.10		07.03-31.12	500
1902					02.01-31.12	364
2102					08.03-31.12	299
N=days	197	135	471	224	1401	2428

Table 2. *Results of 64 DNA samples collected in May and June 2021 from 29 clusters.*

DNA-ID	Sex	WOLVERINE_ID	Number of samples	Comments
JI403930 Ind3573	F	J1701	5	
JI406054 Ind3709	F	J1601	36	
JI408839 Ind3751	F	J1802	7	
JI412928 Ind3808	F	J2102	6	
JI412958 Ind3827	F	J1902	3	
JI416926 Ind6694+	F		3	Cluster J1601, also detected in Alvdal 10.4.2021, shot 24.10.2021.
JI417248 Ind6717	M	A new individual	1	Denning location J2102
JI417249 Ind6718	F	A new individual	2	Denning location J2102
JI417250 Ind6719	F	A new individual	1	Denning location J1601
			64	

Table 3. *Number of cubs documented for the females from 2017-2021, and minimum for how long the cubs have been alive.*

Year	Wolverine_ID	Age	Comments	How long did the cubs live the least?	**Lifespan of young** (last time young from the respective breeding year have been observed, checked via DNA-rovbase, intern picture-database, Facebook/skandobs/ local tips/SNO (The Norwegian nature inspectors).
2017	J1701	Adult		?	No information
2018	J1701	Adult	Frightened + tracks of 2 kids + female on snow. 2 pups also confirmed by DNA	?	06.11.2021 offspring shot during license hunt, Ind3812 (unmarked)
2019	J1701	Adult	Cub radio tagged with mother late August.	August	09.12.2020 offspring shot during license hunt, Ind3862 ()
2020	J1701	Adult		?	No information
2021	J1701	Adult	Visual observation of 2 cubs with the female, seen by field personnel on snow in 27.05.	In April	Visual observation of 2 cubs and the female 27.04.2021. Field personnel
2018	J1801	Adult	Mother of J1902		Still alive, J1902, 22.01.2022
2021	J1902	Adult	First litter. Number of pups currently unknown (DNA collected). 1 young killed by aa wolverine v / Infanticide	No cubs left after a dead kid was found? (Looks like cubs was gone after about March 18 in positions)	1-2 cub(s) killed (cub nr. 1 dead, blood DNA cub nr. 2), found dead the night of 19.03.2021.
2020	J1601	Adult	3 cubs together with the female photographed on game camera in May and June	In June	Photo (Norwegian Forest Wolverine Project) of female and 3 cubs, 03.06.2020
2021	J1601	Adult	Number of pups currently unknown (DNA collected)	?	DNA from1 cub probably in April 2021.
2018	J1601	Adult	First litter. 2 cubs v / DNA. Field data indicate 3 pups. More DNA is available.	?	DNA from a cub collected 14.03.2021.
2021	J2102	Adult	Number of pups currently unknown (DNA collected)	?	A video from hunters 03.06.2021 shows 3 cubs. DNA from 2 cubs.
2017	J1702	Adult	Excavated. DNA taken from cubs	?	No registration after capture 10.05.2017

2019	J1802	Adult	First litter	?	No information
2021	J1802	Adult			