

Is there a geographical difference in wolverine (*Gulo gulo*) home range size at different spatial and temporal scales in Scandinavia?

Elin Olsson



Photo: Lennart Halvarsson

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Elin Olsson

Supervisor: Malin Aronsson, Swedish University of Agricultural Sciences, Department of Ecology, Grimsö Wildlife Research Station
Assistant supervisor: Jens Persson, Swedish University of Agricultural Sciences, Department of Ecology, Grimsö Wildlife Research Station
Examiner: Gunnar Jansson, Swedish University of Agricultural Sciences, Department of Ecology, Grimsö Wildlife Research Station

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Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Ecology
Grimsö Wildlife Research Station

Abstract

A home range is the area that is covered by the animals normal day-to-day activity. The home range size may be influenced by factors such as abundance and distribution of food, sex, spatial organisation and population density. The spatial organisation is determined by different resources for each sex in polygamous mammals; females home range sizes are determined by food resources, whereas males home range sizes are determined by the number and distribution of females. The wolverine (*Gulo gulo*) is a solitary generalist predator and scavenger. Their home ranges are extremely large in relation to their body size.

The aim of this study was to assess geographical differences in wolverine home range size at two different spatial scales (i.e. total home range and core area) in Scandinavia, and to investigate if temporal scale (month and season), sex and reproductive status influence home range size.

I used wolverine location and reproductive data from 56 monitored wolverines, collected 2008-2018 from four study sites within the Scandinavian wolverine distribution; Sarek (mainly alpine area where reindeer is the main food resource), Jämtland, Värmland/Dalarna and Hedmark (boreal forest where moose is the main food resource). I used fixed-Kernel and MCP estimators to estimate 464 monthly home ranges and 157 seasonal total home ranges (MCP 95 and Kernel 90) and core areas (MCP 50 and Kernel 50).

Reproducing females had smaller total home ranges and core areas during spring-months (smallest in March) as well as smaller core area size during spring season than non-reproducing females. Juvenile survival did not influence reproducing females monthly or seasonal total home range or core area size. Neither season, month nor study site influenced non-reproducing females or males total home range or core area size. When using only wolverines in the forest landscape (i.e. Jämtland, Värmland/Dalarna and Hedmark study areas) the analysis showed that month had no effect on total home range size. However, reproducing forest females core area size followed the same pattern as when using the whole data set, with the exception that that core area size in October was the same as in April and May.

Reproductive status and temporal scale influenced female home range and core area size. That reproducing females' home ranges varied among months is probably because in the spring they restrict their movement to be close to the den. However, the pattern that reproducing females total home and core area size were smallest in the spring months, were different (pattern) when only using forest females. This indicates that there are some differences between the northern alpine study site and the southern boreal study sites. An important difference may be the main food resources; where reindeer is the main food resource in the alpine area and moose is the main food resources

in the southern boreal forest areas. When using the seasonal time scale, reproducing females core area size was influenced by season, but not their total home range size. This indicates that the season time-scale (3 months) might be too wide, because at the monthly time scale total home range size was smallest in March and then increased April and May. This could be due to that in March females restrict their movement pattern to be close to the den. However, in April/May as juveniles grow, the females movement pattern become less limited and she can move further away from the den, and consequently a reduction in total home range size is not visible at the seasonal time scale.

Keywords: home range, seasonal, monthly, Gulo gulo, wolverine, Scandinavia, spatial, temporal

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Introduction

What is a home range? Burt (1943) describes the basic concept of home range to be "That area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range." In other words, the area that is covered by the animal's normal day-to-day activities. An individual's movements and the spatial distribution of the population influences the location and home range size (Anderson et al. 2005). Factors that have been shown to influence the home range size are age, abundance and distribution of food, climate, body size, sex, social organization, population density and risk of predation (McNab 1963; Broughton & Dickman 1981; Damuth 1981; Sweeney and Sweeney 1984; Lindstedt et al. 1986; Akbar & Gorman 1993; Relyea et al 2000; Mysterud et al. 2001; Adams 2001). Species living in less productive habitat have larger home ranges sizes than species living in productive habitat, because they need larger areas to search for food (Harestad and Bunnell 1979). Unequal division of resources among competing individuals due to variation in home range sizes may result in differences in reproduction, growth rate and mortality (Adams 2001). Mammals' home range size differs among species, among individuals within a species, and even within individuals over time (Powell and Mitchell 2012). In solitary polygamous carnivores the spatial organisation is determined by different resources for each sex, where female home range sizes are determined by food resources, whereas male home range sizes are determined by the number and distribution of female (Sandell 1989).

The wolverine (*Gulo gulo*) is a medium-sized, solitary carnivore and scavenger. Its distribution is circumpolar and it inhabits taiga, tundra and forest in North America and Eurasia (Copeland et al. 2010). In Europe, the wolverine is divided into the "Scandinavian" and "Karelian" population and its distribution is limited to Fennoscandia and Russia (Chapron et al. 2014). Wolverines exhibit high intersexual territoriality and have a polygamous mating system, where one male overlap and mate with several females (Hedmark et al. 2007; Persson et al. 2010). Consequently, males have larger home ranges than females (Persson et al. 2010). In relation to

body size, wolverines have extremely large home range sizes throughout its distribution (Inman et al. 2012b; Copeland 1996). In Scandinavia home range sizes are approximately 200 km² for females and 700 km² for males, although the variation is large (Persson et al. 2010). Variation in abundance and distribution of food may explain the variation in home range sizes (Persson et al. 2010). Also, the timing of reproductive events in relation to food availability may also have an important influence on temporal variation in wolverine home range size (Inman et al. 2012b). Wolverine reproductive rate is low, where females rarely reproduce before they are 3 years old and the mean number of young/adult/year is 0.84 (Persson et al. 2006; Rauset et al. 2015). Mating occurs between May and August and they give birth to young in February-March, which is earlier than other non-hibernating northern carnivores (Inman et al. 2012b; Aronsson 2017). The young are kept in a snow-covered den, often in steep and rugged terrain (Magoun & Copeland 1998; May et al. 2012; Makkonen 2015).

According to harvest statistics, the wolverine was widely distributed in Scandinavia, where its main distribution was from the reindeer herding area in the north down to the counties of Värmland and Dalarna in the south (Aronsson & Persson 2012). Though in the middle of the 19th century the wolverine began to disappear from these regions and the population was reduced to a very low level due to human persecution, and was restricted to alpine areas in northern Scandinavia (Landa et al. 1998; Flagstad et al. 2004). In 1968, wolverines received legal protection in Sweden, 1973 in southern Norway and 1982 in northern Norway, after which the population slowly recovered (Landa et al. 1998; Persson & Brøseth 2011; Aronsson & Persson 2012). The wolverine population has increased in both size and distribution and is slowly expanding from the alpine region towards east and south, and has now recolonized large parts of central to northern Scandinavia (Aronsson & Persson 2017). In 2018, reproductions (the unit for the monitoring system) of wolverines were found in Norrbotten, Västerbotten, Västernorrland, Jämtland, Gävleborg, Dalarna and Värmland County (Tovmo et al. 2018).

When planning wolverine management it is of importance to have knowledge about wolverine home range sizes to determine population density, the carrying capacity in an area and where to find or search for reproducing females' den sites (Landa et al. 1998). Today, most information about wolverine space use, such as home range size, in Scandinavia comes from studies in northern regions, within the reindeer husbandry area. The wolverine is well adapted to harsh environments with low productivity and unpredictable food resources by being an opportunistic generalist predator and scavenger (Haglund 1965; Mattisson et al. 2011b; Mattisson et al. 2016). The wolverine also exhibits caching behaviour, which could be important to increase the predictability of food resources and reduces the energy spent on searching for food during challenging times (i.e. during lactation for females), and

decrease the time away from vulnerable new-borns (McNamera et al. 1990; Inman et al. 2012b). Therefore, it is important to investigate if reproductive ecology influences home range sizes on a temporal scale. Persson et al. (2010) showed that reproductive status did not have any effect on yearly home range size. Therefore, it is relevant to investigate whether another time-scale (i.e. months and seasons) would show that there could be any effects due to reproductive status. It is often stated that home range size variation can be due to prey population density (Carbone & Gittleman 2002). In northern Sweden wolverines primarily feed on migratory, semi-domestic reindeer (*Rangifer tarandus*; Persson et al. 2009; Mattisson et al. 2012a). However, in the forest landscape south of the reindeer husbandry area, moose (*Alces alces*) is the main food source, but beaver (*Castor fiber*), mountain hare (*Lepus timidus*), grouse (*Tetraoninae sp.*) and rodents is also an important food resource (Aronsson & Persson 2012). In Norway, wolverines also predate on free-ranging domestic sheep (*Ovis aries*) in the summer (Mattisson et al. 2016). The wolverine also scavenges on kills made by other, more efficient predators, as for example lynx (*Lynx lynx*; Mattisson et al. 2011b) and wolves (*Canis lupus*; van Dijk et al. 2008). During the yearly moose hunt, humans provide food for scavengers, and even though the remains from hunter harvests are generally available for only a few months during the hunting season in autumn, for caching species this food resource might last for longer periods (Wilmers et al. 2003; Wikenros et al. 2013). Because food resources may have a large influence on home range sizes it is important to investigate if there are any differences between the alpine and forest landscape, based on the differences in the main food resources, and if there are any temporal differences due to prey density during different months or seasons. Therefore, this study is important for management because the wolverine in central Sweden may not spatially behave as wolverines in the north. That is also why it is important to have the knowledge about the difference in main food resource for the different study sites. Also reproductive ecology should be considered (for example, if reproducing females home range size is smaller during spring because they are limited in their movements when the young is born [Aronsson et al. 2016]).

The aim of this study was to assess geographical differences in wolverine home range size at different spatial and temporal scales in Scandinavia, and investigate what factors may influence home range size (at different temporal and spatial scales). More specific aims were to: 1) Compare wolverine total home range and core area size in the northern alpine reindeer herding area, where reindeer is the main food source, and three areas in boreal forest at southern latitude, where moose is the main food source. 2) Compare total home range and core area size between months and seasons (seasons defined in relation to current knowledge about reproductive ecology, temporal food availability and climate, see methods) in all four

study areas. 3) Investigate if total home range and core area size differ in relation to reproductive status in four study areas.

Method

Data and study site

I used wolverine location and reproductive data collected from 2008-2018 from four study sites within the Scandinavian wolverine distribution; northern Sweden (Sarek 2008-2014), central Sweden (Jämtland 2015-2018, Värmland/Dalarna 2015-2018) and south eastern Norway (Hedmark 2016-2018). The Sarek study area represents the northern, alpine region while the Jämtland, Värmland/Dalarna and Hedmark study area represents the boreal forest region (figure 1). Wolverines were captured and handled using ethics-approved handling protocols (Arnemo & Evans 2017) and fitted with GPS collars (GPS plus mini, Vectronics Aerospace, Germany; Tellus Ultra Light GPS, Followit, Sweden). For determination of female reproductive status and juvenile survival, see Rauset et al. (2015).

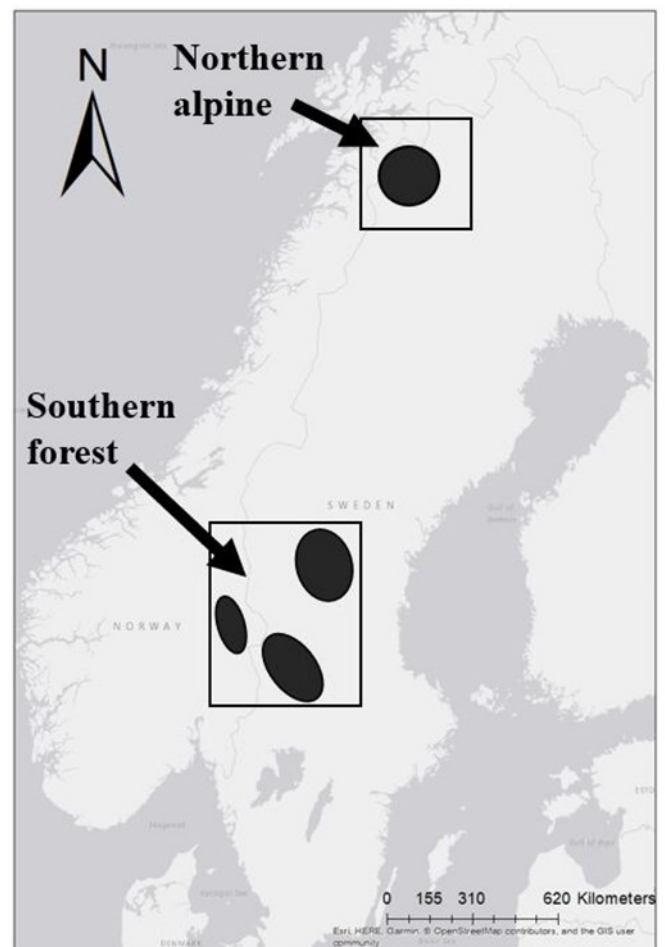


Figure 1. The four study sites in Sweden and Norway where wolverines were monitored.

The Sarek study area is located in and around Sarek national park (Kvikkjokk; 67°00'N, 17°40'E), above the Arctic Circle. The climate is continental, and the ground is usually snow-covered from November to late May. High plateaus with peaks up to 2,000 m above sea level, deep valleys and glaciers characterise this area. In the valleys' mountain birch (*Betula pubescens*), Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) dominate (Persson et al 2010). The tree line at 600-700 m above sea level is mainly constituted by mountain birch (Grundsten 1997). The Sarek area is within spring and summer grazing grounds of semi-domestic reindeer, exclusively and extensively managed by the indigenous Sámi people (Persson et al. 2006). Reindeer is the main prey for wolverines in this area, and other prey species are moose, mountain hare, grouse and rodents (Mattisson et al. 2016). Lynx, brown bear (*Ursus arctos*) and red fox (*Vulpes Vulpes*) also occur in the area.

The central study site (62°2'N, 17°17'E) is located in southeast Jämtland, southwest Västernorrland and northwest Gävleborg (referred to as Jämtland in this study). The habitat is dominated by mainly managed forest interspersed with mires and small settlements. Potential prey in the area are moose, beaver, mountain hare, and rodents. In the western part of the study site semi-domestic reindeer occur sporadically. Bears, lynx, red foxes and occasionally wolves occur in the area.

The most southern located study site is in southern Dalarna and northern Värmland (60°38'N, 13°20'E). As in Jämtland, the habitat is dominated by managed forest interspersed with mires, lakes and small settlements. Potential prey in the area are moose, beaver, mountain hare, and rodents. Lynx, red fox, wolf and a few bears also occur in the area (Aronsson & Persson 2017).

In Hedmark (61° 23'N, 11° 19'E) the habitat is characterized by mountain ridges and two main valleys, Glomma and Rena rivers. Boreal coniferous forest is dominating the area (Norway spruce and Scots pine), interspersed with deciduous trees of birch (*Betula pubescens*), aspen (*Populus tremula*) and willow (*Salix caprea*). The main food resource is moose (Nordli & Rogstad 2016). Free-ranging sheep graze in the forest and alpine-tundra areas during summer. Wolves, lynx and foxes occur in the area (Aronsson 2017).

Estimation of seasonal and monthly home range size

I estimated both seasonal and monthly home range sizes and core areas (km²) using two different estimators; fixed-Kernel method (Worton 1989) and minimum convex polygon (MCP; Mohr 1947) using the adehabitatHR Package (Calenge 2006) in R (R Core Team 2014). I used MCP 95% as total home range and MCP 50% as core area estimator to compare with other studies which used MCP as home range size estimator. The Kernel method estimates an utilization distribution (UD); where

kernel home range estimations are obtained as a function of an individuals' relative use of space (Marzluff et al. 2004). Fixed-kernel percentiles and bandwidth need to be adjusted to the data of the study (Kie et al. 2013). Therefore, I used six individuals (one female and male from Jämtland, Värmland/Dalarna and Norway, respectively) to determine which percentile and bandwidth that was optimal for this study. I tested bandwidth from 50-100% of the reference bandwidth (i.e. $0.5 \cdot h_{ref} - 1 \cdot h_{ref}$) and percentiles from 50-65 for core area and 80-95 for total home range. By plotting the home ranges estimated using the different bandwidths and percentiles, they could be compared to the underlying GPS locations to see if any "holes" in the home range appeared (i.e. selected the bandwidth and percentile for which the home ranges was a continuous area; Kie 2013). When comparing all home range size plots, I decided that 90% of the reference bandwidth (i.e. $0.9 \cdot h_{ref}$) and percentiles 90 (for total home range) and 50 (for core area) were the most optimal for this study.

Only resident adults were included in this study and by using ArcMap (10.6.1) I got an overview of all GPS-locations, and to determine if monitored individuals were resident or not (i.e. if locations were strictly confined to a distinct area [Powell 2000]). I randomly sampled 3 locations per day for individuals with multiple daily locations, to reduce biases from different sampling frequencies (Börger et al. 2006). I only estimated home ranges and core areas for months when the individual had ≥ 15 days with locations (i.e. the individual had to be monitored for 15 days or more during a month to be included in this study). For "seasons" I only estimated home ranges and core areas when the individual had been monitored for ≥ 2 months (which needed to have 15 days with locations, respectively) during spring (March-May) and summer (June-August), or 1 month during autumn (September-October). This resulted in 464 monthly and 157 seasonal home range sizes for 56 and 45 individual wolverines, respectively. I recognised three seasons based on the current knowledge about reproductive ecology, temporal food availability and climate; spring (March-May), summer (June-August) and autumn (September-October). Typical behaviours that define these seasons are; during spring the reproducing females are denning (Persson et al. 2010) and during summer the wolverines mate and their main prey give birth to their young (Inman 2012b). In autumn the food availability increases in the forest due to the start of the moose hunt season and the young starts to move outside their mother's home range (Aronsson & Persson 2012). In the monthly estimation the same months as in the seasonal estimation was used, March-October. There was not enough data from the study areas in the forest landscape to analyse November – February.

Statistical analysis

I used linear mixed models (*lmm*) with the “*lme4*” package (Bates et al. 2015) in R with log-transformed home range sizes as response variables in all analysis. To account for repeated measurements for the same individual and year, individual identity and year were fitted as random effect in all models. Model selection was done with the “*MuMIn*” package (Barton 2018) in R, using the Akaike information criterion for small sample (AICc) which estimates “best approximating model” by a simple, effective and objective selection for data analysis and inference (Brunham and Anderson, 2003).

Home range size analyses for each sex were done for the different spatial scales and home range estimators separately (i.e. total home range and core area sizes based on MCP and Kernel for males and females, respectively). As explanatory variables (x), I used study site (4-level factor) and temporal scale (season as 3-level factor or month as 8-level factor, respectively). For females I also included reproductive status as a 2-level explanatory factor (i.e. reproducing and non-reproducing). To assess if juvenile survival influenced home range size for reproducing females during months March-May or spring season, juvenile survival in April was included as a 2-level factor (i.e. if the juvenile lived after the 9th of April or not). At the seasonal scale, I included the interactions between season and reproductive status, and also the interaction between season and study site. However, at the monthly scale it was not possible to include any interactions due to sample size limitations. Consequently, when the model selection indicated that any of the fixed effects were important, I subsequently divided the dataset by female reproductive status to investigate whether months or study site had effect on reproducing or non-reproducing female home ranges, respectively. If months showed effect on home range size, I investigated how March-October was in relation to each other, by subsequently removing the earliest month and rerunning the model. The “*ez*” package (Lawrence 2016) in R was used to calculate model predictions and 95% confidence intervals (CI), using a bootstrap method suitable for mixed models.

All analyses were also made using only the three forest study areas, because the majority of my data were from Sarek and I wanted to make sure that the pattern I saw in the results was not just from the Sarek data. There was no non-reproducing female monitored in Värmland/Dalarna, and only one individual in Jämtland and one in Hedmark. Due to this I could not analyze if season, month or study site had effect on non-reproducing female home ranges using only the forest study areas. There was only one male monitored in Hedmark and he was a young male. Therefore, I decided to exclude him from all analysis because his space use might not represent an adult, resident individual.

Results

I present the result from the home range estimator Kernel, because when comparing the two different estimators I think that Kernel gives the most accurate home range size based on GPS-locations (see figures 5-7 in Appendix). There was a difference in both total home range and core area size between the two estimators, where home ranges based on Kernel were larger than MCP-based (table 3 and table 6). There were some small differences between Kernel and MCP, however no difference in the general spatial and temporal pattern. The MCP results are presented in Appendix 1 (table 10-13), and I will discuss the differences between the home range estimators in the discussion.

In total, 56 wolverines were monitored with GPS-collars from the four study sites (table 1).

Table 1. Information about the number of individuals from the four study sites separated on males and females

Individuals	Sarek	Jämtland	Hedmark	Värmland/Dalarna
<i>Total</i>	36	10	4	6
<i>Females</i>	26	4	4	1
<i>Males</i>	10	6	-	5

Monthly home range sizes

I estimated a total of 342 monthly home ranges for females and 122 monthly home ranges for males in the four study areas (table 2).

Table 2. Number of monthly home ranges from the four study sites separated on reproducing, non-reproducing females and males.

Number of monthly HR	Sarek	Jämtland	Hedmark	Värmland/Dalarna
<i>Reproducing females</i>	166	19	18	15
<i>Non-reproducing</i>	116	6	2	-
<i>Males</i>	74	28	-	20

Table 3. Mean \pm SE monthly home ranges size (km^2) estimates for all females and males from the four study areas, based on fixed kernel and minimum convex polygon (MCP) estimation models.

Monthly temporal scale		Sarek	Jämtland	Hedmark	Värmland/
Kernel					
<i>Females</i>	Home range	230 \pm 16	130 \pm 12	120 \pm 15	420 \pm 65
	Core area	60 \pm 5	35 \pm 5	35 \pm 5	125 \pm 25
<i>Males</i>	Home range	890 \pm 70	590 \pm 75	-	730 \pm 80
	Core area	275 \pm 20	170 \pm 25	-	215 \pm 25
MCP					
<i>Females</i>	Home range	140 \pm 10	80 \pm 8	80 \pm 10	245 \pm 38
	Core area	40 \pm 5	30 \pm 5	20 \pm 5	75 \pm 17
<i>Males</i>	Home range	490 \pm 34	370 \pm 50	-	420 \pm 50
	Core area	190 \pm 17	100 \pm 18	-	135 \pm 20

Total home range

Estimates of monthly total home range sizes (Kernel 90) showed that home range size for non-reproducing females were not influenced by month (predicted mean=225, CI: 391-125) and that reproducing females had smaller home range sizes than non-reproducing females during the spring months (figure 2, table 4a). For reproducing females monthly home range sizes could be divided into 3 groups, March home ranges were the smallest, and April-June were smaller than August-October (figure 2). If the young (i.e. the entire litter) survived or died had no effect on reproducing females home range size during spring months (table 4a).

For non-reproducing females, the AICc model selection showed that study site influenced monthly total home range size (table 4a). Total home range sizes in Sarek were larger than in both Hedmark and Jämtland (no data for non-reproducing females in the Värmland/Dalarna study area), although based on t-values, this difference was not significant (table 4b).

For the reproducing females from the forest areas (table 2), month and young survival had no effect on total home range size (predicted mean=135, CI: 225-80; table 5a). Consequently, the clear pattern that home range size was smaller during spring months (figure 2) was mainly caused by the data from the Sarek study area. The AICc model selection showed that study site influenced monthly total home range size for reproducing forest females (table 5a). Reproducing females in Hedmark had smaller total home range sizes than both Jämtland and Värmland/Dalarna, although based on t-values, this difference was not significant (table 5b).

For males neither month nor study site had effect on home range size, both when using all males (predicted mean=670, CI: 925-485; table 4a) and only forest males (predicted mean=551, CI: 885-340; table 5a).

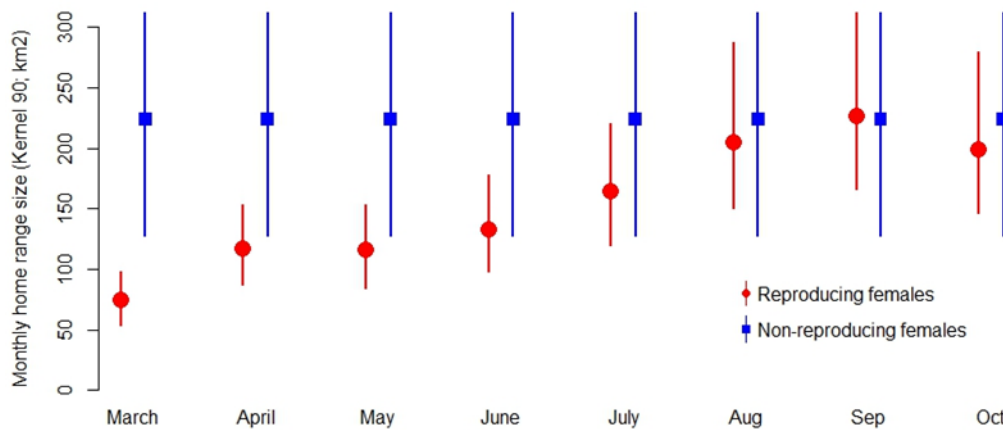


Figure 2. Predicted monthly total home range size (means with associated 95% confidence intervals) March-October for reproducing (red circles) and non-reproducing (blue squares) females from all study sites. Predictions are back-transformed to their normal scale for the figure. For model parameters see table 4b.

Core area

Estimates of monthly core area (Kernel 50) showed that reproducing females had smaller core area than non-reproducing females during the spring months, and that core area size for non-reproducing females was not influenced by month (mean=60, CI:110-35; figure 3). For reproducing females, core area could be divided into 3 groups, where area size in March was the smallest of all months, and April-May were smaller than July-October (figure 3). If the young survived or died during April

had no effect on reproducing females core area size during the spring months (table 4a).

For non-reproducing females, the AICc model selection showed that study site influenced monthly core area size (table 4a). Core area size in Sarek was larger than in both Hedmark and Jämtland (no data for non-reproducing females in the Värmland/Dalarna study area), although based on t-values, this difference was not significant (table 4b).

When only using females from the forest study areas (table 2), the reproducing females core area showed the same pattern as for all females, i.e. smaller during the spring months (figure 3). However, the core area size was smaller in October than during June-September for females in the forest study areas, which was not the case for females in Sarek (figure 3). If the young survived or died had no effect on home range size for forest females (4a).

Neither month nor study area influenced core area size for all males (predicted mean=197, CI: 275-140; table 4a) or forest males (predicted mean=160, CI: 255-100; table 5a).

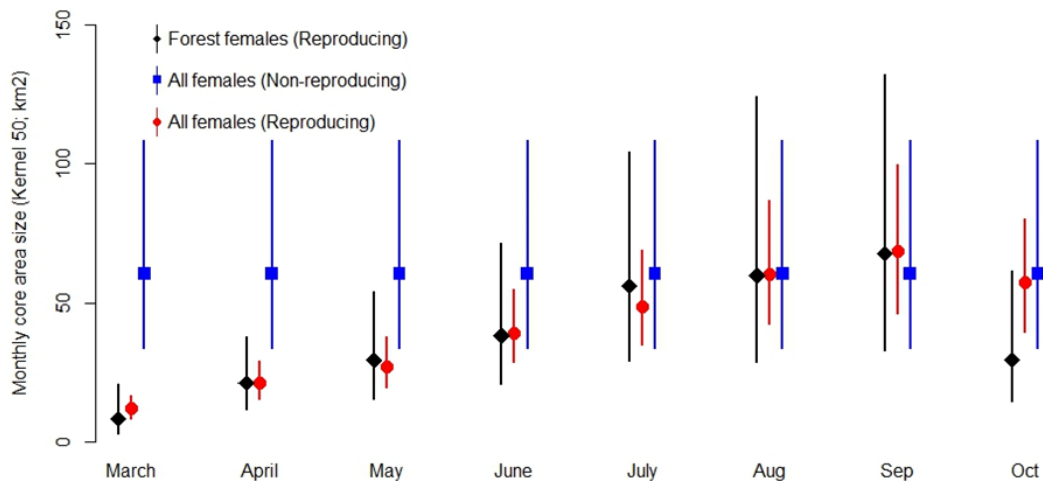


Figure 3. Predicted monthly core area sizes (mean \pm 95% Confidence interval) from March-October for all reproducing females (red circles), reproducing forest females (black diamonds) and all non-reproducing females (blue squares). Predictions are back-transformed to their normal scale for the figure. For model parameters see table 4b and 5b.

Table 4a. Model selection based on fixed kernel 90 and 50 estimates relating to monthly home range sizes (n=464) for all females, reproducing females, non-reproducing females, young survival and all males.

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
<i>All females</i>	Null	4	10.22	0.003	31.83	0.000
	Den	5	0.00	0.497	17.6	0.000
	Month	11	16.93	0.000	17.33	0.000
	Site	7	9.93	0.003	32.16	0.000
	Month + Den	12	6.95	0.015	0.00	0.999
	Site + Den	8	0.06	0.481	17.43	0.000
	Month + site	14	17.74	0.000	18.69	0.000
<i>Females, reproducing</i>	Null	4	28.59	0	70.78	0
	Month	11	0.00¹	1	0.00²	1
	Site	7	29.44	0	71.23	0
<i>Females, non-reproducing</i>	Null	4	2.36	0.235	2.49	0.224
	Month	11	25.15	0.000	26.80	0.000
	Site	6	0.00³	0.765	0.00⁴	0.776
<i>Females, reproducing, March-May</i>	Null	3	0.00	0.864	0.00	0.585
	Juvenile survival	10	3.69	0.136	0.69	0.415
<i>All males (excluding Norway)</i>	Null	4	0.00	0.72	0.00	0.688
	Month	11	28.18	0.00	22.42	0.000
	Site	6	1.89	0.28	1.58	0.312
	Month + Site	13	30.83	0.00	24.76	0.000

^{1, 2, 3, 4} For parameter estimates see table 4b.

Table 4b. Model parameters based on fixed kernel 90 and 50 for the top-models in table in 4a.

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept	4.2754	0.1677	25.490	Intercept	2.4734	0.1867	13.245
April	0.4768	0.1537	3.103	April	0.5792	0.1755	3.301
May	0.4570	0.1555	2.939	May	0.8116	0.1775	4.572
June	0.6287	0.1610	3.905	June	1.2140	0.1837	6.609
July	0.8502	0.1600	5.314	July	1.4343	0.1825	7.857
Aug	1.0731	0.1687	6.362	Aug	1.6565	0.1925	8.607
Sep	1.1945	0.1837	6.503	Sep	1.7955	0.2096	8.568
Oct	1.0706	0.1717	6.236	Oct	1.6376	0.1959	8.361
3.				4.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (Jämtland)	3.946	0.864	4.567	Intercept	2.5734	0.9327	2.759
Norway	0.570	1.089	0.524	Norway	0.7099	1.2184	0.583
Sarek	1.659	0.912	1.819	Sarek	1.7279	0.9823	1.795

Table 5a. Model selection based on fixed kernel 90 and 50 estimates relating to monthly home range sizes ($n=108$) for forest females, reproducing forest females, non-reproducing forest females, young survival and forest males.

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
Forest females	Null	4	0.62	0.241	2.96	0.087
	Month	11	10.97	0.001	0.00	0.382
	Site	6	0.00	0.329	2.96	0.087
	Month +	13	12.15	0.001	1.29	0.201
Forest females, reproducing	Null	6	1.34	0.333	6.91	0.029
	Month	11	7.62	0.014	0.00²	0.908
	Site	6	0.00¹	0.652	5.32	0.064
Forest females, reproducing, March-May	Null	4	0.00	0.859	0.00	0.782
	Juv.	5	3.61	0.141	2.56	0.218
Forest males (excluding Norway)	Null	4	0.00	0.612	0.00	0.592
	Month	11	17.84	0.000	13.43	0.001
	Site	5	0.91	0.388	0.75	0.407
	Month +	12	19.87	0.000	15.41	0.000

^{1,2} For parameter estimates see table 5b.

Table 5b. Model parameters based on fixed kernel 90 and 50 for the top-models in table 5a.

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (Jämtland)	5.0640	0.2955	17.139	Intercept	2.0985	0.4768	4.401
Norway	-0.6784	0.4315	-1.572	May	1.3404	0.4343	3.086
Värmland/Dalarna	0.7763	0.5660	1.372	June	1.6371	0.4449	3.680
				July	2.0002	0.4449	4.496
				Aug	2.1134	0.4663	4.533
				Sep	2.2013	0.4663	4.721
				Oct	1.4117	0.4663	3.028

Seasonal home range sizes

I estimated a total of 120 seasonal home ranges for females and 37 seasonal home ranges for males in the four study areas (table 6).

Table 6. Information about the number of seasonal home ranges from the four study sites separated by reproducing, non-reproducing females and males.

Number of seasonal HR	Sarek	Jämtland	Hedmark	Värmland/Dalarna
<i>Reproducing female</i>	55	8	7	6
<i>Non-reproducing female</i>	42	2	-	-
<i>Male</i>	22	10	-	5

Table 7. Mean \pm SE seasonal home range size (km²) estimates for all females and males from the four study sites, based on fixed kernel and minimum convex polygon (MCP) estimation models.

Seasonal temporal scale		Sarek	Jämtland	Hedmark	Värmland/Dalarna
Kernel					
<i>Females</i>	Home range	220 \pm 20	130 \pm 20	135 \pm 20	435 \pm 85
	Core area	60 \pm 5	35 \pm 5	40 \pm 10	120 \pm 30
<i>Males</i>	Home range	815 \pm 90	600 \pm 130	-	740 \pm 120
	Core area	250 \pm 30	160 \pm 40	-	195 \pm 40
MCP					
<i>Females</i>	Home range	190 \pm 15	105 \pm 15	115 \pm 20	340 \pm 70
	Core area	45 \pm 5	40 \pm 5	40 \pm 10	80 \pm 20
<i>Males</i>	Home range	585 \pm 60	420 \pm 90	-	555 \pm 85
	Core area	220 \pm 30	120 \pm 30	-	170 \pm 40

Total home range

Estimates of seasonal total home range size (Kernel 90) showed that neither season, reproductive status nor study site had an effect on female (predicted mean=165, CI: 210-130) or male (predicted mean=635, CI: 880-455) total home range size (table 8a).

The results were similar when only using forest study area females (predicted mean=130, CI: 230-75) and males (predicted mean=505, CI: 980-260) (table 4a) (table 9a).

Core area

Estimates of seasonal core area (Kernel 50) showed that reproducing females had smaller core area during spring season than non-reproducing females, while core

area size for non-reproducing females was not influenced by season (figure 4). Whether the offspring survived or not until April 9 did not influence reproducing females spring core area (table 8a).

When only using reproducing females in the forest study areas (table 6), they had smaller core area sizes during the spring season compared to during summer and autumn (figure 4). There was no effect of whether the young survived or not on reproducing forest females core area size in the spring (table 9a).

The estimate of male seasonal core area size showed that neither season nor study site influenced core area size (180, CI: 255-125; table 8a). The result was the same when only using forest males (130, CI: 260-65; table 9a).

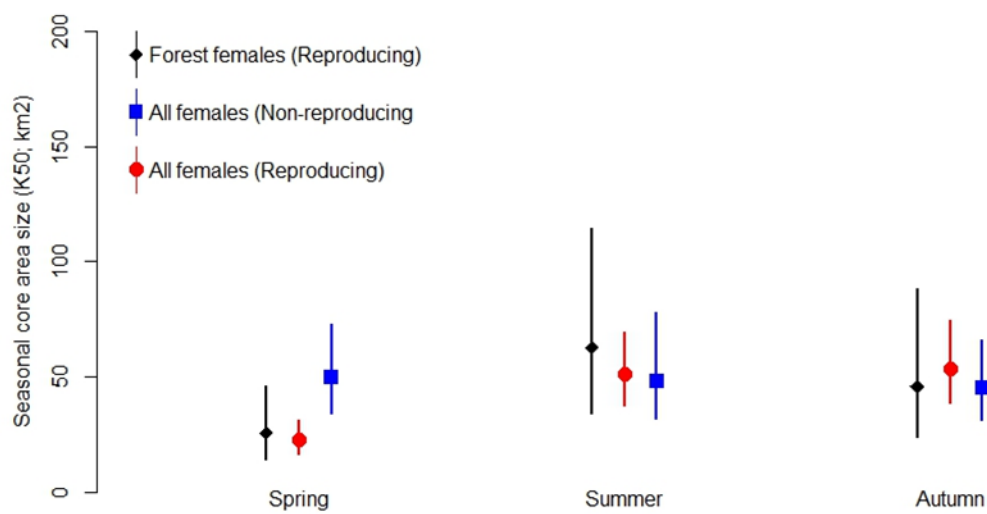


Figure 4. Predicted seasonal core area sizes (mean \pm 95% Confidence interval) from spring, summer and autumn for all reproducing females (red squares), all non-reproducing females (blue triangles) and only reproducing forest female (black diamonds). Predictions are based on the best model in table 8b for all females (reproducing and non-reproducing) and table 9b for reproducing forest females. Predictions are back-transformed to their normal scale for the figure.

Table 8a. Model selection based on fixed kernel 90 and 50 estimates relating to seasonal home range sizes ($n=157$) for all reproducing females, young survival and all males.

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
<i>All females</i>	Null	4	0.00	0.281	17.03	0.000
	Den	5	2.05	0.101	17.82	0.000
	Season	6	1.86	0.111	8.70	0.013
	Site	7	0.52	0.217	18.14	0.000
	Season + Den	7	4.32	0.032	9.57	0.008
	Site + Den	8	2.88	0.066	19.21	0.000
	Season + site	9	2.89	0.066	10.09	0.006
	Season x Den	9	1.63	0.124	0.00¹	0.972
	Season x Site	15	11.52	0.001	14.16	0.001
<i>Females, reproducing, Spring</i>	Null	4	0.00	0.785	0.00	0.857
	Juvenile survival	5	2.59	0.215	3.58	0.143
<i>All males (excluding Norway)</i>	Null	4	0.00	0.854	0.00	0.801
	Season	6	8.60	0.012	8.24	0.013
	Site	6	3.71	0.134	2.94	0.184
	Season + Site	8	12.98	0.001	11.96	0.002
	Season x Site	12	20.49	0.000	19.47	0.000

¹ For parameter estimates see table 8b.

Table 8b. Model parameters based on fixed kernel 90 and 50 for the top-models in table 8a.

1.

	Estimate	Std. Error	t value
Intercept (autumn)	3.82894	0.20105	19.045
Spring	0.07302	0.20135	0.363
Summer	0.03448	0.22230	0.155
Den	0.19609	0.22820	0.859
Spring; Den	-0.99222	0.26206	-3.786
Summer; Den	-0.11250	0.27292	-0.412

Table 9a. Model selection based on fixed kernel 90 and 50 estimates relating to seasonal home range sizes ($n=38$) for all forest females, reproducing forest females, young survival and forest males.

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
Forest females, all	Null	4	0.00	0.594	3.04	0.152
	Season	6	2.75	0.150	0.00¹	0.695
	Site	7	1.86	0.235	5.03	0.056
	Season + site	9	6.68	0.021	3.95	0.096
	Season x Site	15	31.11	0.000	24.96	0.000
Forest females, reproducing	Null	4	0.00	0.479	6.06	0.041
	Season	6	0.78	0.324	0.00²	0.858
	Site	7	2.16	0.163	8.48	0.012
	Season + site	9	5.26	0.034	4.54	0.089
	Season x Site	12	38.74	0.000	35.54	0.000
Forest females, reproducing, Spring	Null	4	0.00	1	0.00	1
	Juvenile survival	5	16.66	0	15.86	0
Forest males (excluding Norway)	Null	4	0.00	0.810	0.00	0.800
	Season	6	7.98	0.015	7.48	0.019
	Site	5	3.08	0.174	2.98	0.180
	Season + Site	7	14.11	0.001	13.62	0.001
	Season x Site	9	34.14	0.000	33.55	0.000

^{1,2} For parameter estimates see table 9b.

Table 9a. Model parameters based on fixed kernel 90 and 50 for the top-models in 9a.

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (autumn)	3.5565	0.3745	9.496	Intercept (autumn)	3.9659	0.3244	12.224
Spring	-0.5512	0.2485	-2.219	Spring	-0.7490	0.2049	-3.655
Summer	0.3381	0.2337	1.447	Summer	0.0794	0.2018	0.393

Discussion

Overall there were no differences between study areas in male or female monthly or seasonal home range size. In relation to other studies the home range sizes I observed (both based on Kernel and MCP) in Sarek, Jämtland, Hedmark and Värmland/Dalarna were within the range of home range sizes documented by Persson et al. (2010) and Bischof et al. (2015) and in the upper range of home ranges in Snøhetta, Norway (Landa et al. 1998). The only study area difference in space use was the tendency that non-reproducing females in Sarek had larger monthly home range and core area sizes than non-reproducing females in Jämtland and Hedmark (table 4b). However, in this comparison the Värmland/Dalarna study area was not included due to lack of data, and there is only data for one non-reproducing female in Jämtland and one in Hedmark. Furthermore, when only considering females in the three forest study areas, females in Hedmark had smaller home ranges than those in Jämtland and Värmland/Dalarna (table 5b), although this difference was not significant based on t-values (table 5b). I included study area as a 4-level factor in my analysis because I wanted to investigate if there was a difference between Sarek, in the reindeer herding areas (reindeer main food resource for wolverines), and each of the forest study sites (moose the main food resource) and among forest areas. The three forest study areas are far apart from each other and might be different, consequently I did not pool them in one group to compare with Sarek. However, when I redid all analyses using only forest wolverines the results were different from the total dataset, showing a different pattern for monthly home ranges in the spring months, which indicates that alpine and forest female wolverines' space use might be different (i.e. using the total data set both total home range and core area sizes were reduced during the spring months for reproducing females, using only the forest data set this size reduction was only visible for the core area). When using the whole dataset, the large sample size in Sarek was probably concealing this pattern.

Monthly home range and core area

When investigating if reproductive status influenced monthly total home range and core area size, it showed that reproducing females had smaller total home ranges and core areas during March-May than non-reproducing females (figure 2 and 3). This is probably explained by that reproducing females restrict their movements when the young are small and the female needs to be close to the den, which results in smaller home ranges (Magoun 1983; Banci 1994; Copeland 1996). However, by analysing only reproducing females in the forest study areas, I did not find this pattern of decreasing total home range size during the spring months (table 5a and 5b), indicating that the reduction in home range size for reproducing females were only the case in Sarek. That a temporal pattern (March-May smaller than the other months) could be seen in total home range size for all reproducing females (figure 2), was probably due to the Sarek data, because this was not seen using only females in forest areas (table 5b). This could be explained by the difference in food resources in the alpine study area compared to in the forests study areas. Reindeer is the main food resource in the Sarek study area and during winter reindeer body condition decreases and thereby natural mortality increases, creating a carrion supply (Tveraa et al. 2003; Mattisson et al. 2016). Lynx-killed reindeer are also an important food resource for wolverines in the alpine study area, where lynx often leaves a lot behind (Mattisson et al. 2011b). Persson (2005) and Rauset et al. (2015) showed that food availability at the time of pregnancy and early lactation is an important determinant of reproductive success, and females might be able to cache large pieces or much carrion during winter which they can use during denning. However, in the forest landscape outside of the reindeer husbandry area, moose is the main food resource for wolverines, where wolverines scavenge moose carrion left by wolves (Van Dijk et al. 2008), remains that are left behind after moose that are shot during the hunt, or at slaughter piles or bait sites (Wikenros et al. 2013; Persson et al. unpublished data). Consequently, in the forest landscape wolverines may not be able to find large pieces to cache, and reproducing females may need to search for food both further away from the den, and more often, compared to in the reindeer husbandry area. This may explain why the pattern of decreasing total home range size during the denning period did not show using only the three forest study areas. But because reproducing females are limited in their movements (i.e. they need to return to the den after they have searched for food), the pattern for reproducing females in the forest areas monthly core area was the same as when females in Sarek were included, i.e. that March-May were smaller than the other months (figure 3). Another difference compared to all females was that the core area in October was equally small as core area in March-May (figure 3). This highlights the importance of leftovers from the moose hunt (starting in September/October) as food for wolverines.

Wikenros et al. (2013) showed that the greatest amount of estimated available biomass for scavengers during the year was during October. Therefore, the decreased core area size in October is probably because the females concentrate their movements to scavenge on the moose remains after the moose hunt.

Seasonal home range and core area

When estimating if reproductive status had any effect on seasonal total home range or core area size there was only an effect for reproducing female core areas, where spring core area was smaller than both summer and autumn core area (figure 4, table 8a and 8b). The same results showed when estimating core area size for reproducing females in only the forest areas (figure 4, table 9a and 9b). As for the monthly home ranges and core areas, the spring season core area was smaller than summer and autumn core area because reproducing females restrict their movements when the young are small and the females need to be close to the den sites (Magoun 1983; Banci 1994; Copeland 1996). That the analysis showed that season had no effect on total home range size, even though the monthly analysis showed decreasing sizes during the spring months, could be because my seasonal time scale is too wide (i.e. 3 months in spring). The results from the monthly analysis showed that home ranges were smallest in March, and increased in April and May (even though the size in these months was smaller than in July-October). This gradual change during the denning season can explain why there was no effect of season on total home range size. Even though reproducing females need to spend a lot of time at the den during February/March when the young are born (Aronsson 2017), they are highly territorial within the sexes (Hedmark et al. 2007; Persson et al. 2010; Inman et al. 2012a) and they move around the edge of their territory to patrol their borders (Kersusan 2014). This movement pattern could also explain why there was no reduction of total home range size in the spring for reproducing females. When the young grows and becomes larger (April-May) the female movement pattern are not as limited as when the young is small, and she can move more often and further away (Aronsson 2017). Consequently, when the time scale widens from one month (March) to a season of three months (March-May), the increased movement during the last half of the denning season and GPS-locations near the territory border may have a larger influence on total home range size.

Some young survived and some reproducing females lost their young, but whether the young survived or not did not affect female monthly or seasonal total home range or core area size (table 4a and 8a). The females that lost their young did not have larger home ranges than other reproductive females. Persson et al. (2010)

showed the same pattern, that if the young died the female home range size was not larger than other reproducing females.

Male total home range or core area size was not influenced by neither month, season nor study site (table 4a and 8a). The same pattern was seen when only analysing forest males (table 5a and 9a). I suggest that this could be explained by the general prediction that home range size is determined by different resources for males and females; i.e. female home range size is determined by food resources and males by the number and distribution of female (Sandell 1989; Persson et al. 2010).

Differences between Kernel and MCP

There was no difference in the general spatial and temporal pattern using the two home range estimation methods. However, there were some small differences in the results from analyses using Kernel and MCP home range estimator, respectively. The influence of juvenile survival on reproducing females monthly core area size in the spring, where they had smaller core area size if the young lived in April compared to if they lost their young in April (Appendix). I decided to present the results based on the Kernel estimator because visual inspection showed that Kernel estimated the home range and core area size more accurate than MCP according to GPS-locations. For all males, Kernel estimated that there was no influence of study area on seasonal core area size. However, based on MCP estimate Sarek males had larger core area than males in Jämtland, and also that there was a tendency that males in Värmland/Dalarna had larger core area than males in Jämtland (Appendix). There were also some contrasting results when monthly total home range and core area size was estimated with MCP. Based on MCP estimates, forest males had smaller monthly core area size in July than during the other months (Appendix). This could be due to the mating system, where wolverines mate between May and August and could be that the males concentrate their movements to seek females (Wright & Rausch, 1955; Rausch & Pearson 1972; Magoun & Valkenburg, 1983). It is expected that male home range size is influenced by the density of females (Persson et al. 2010). All these differences could be due to that in this study MCP estimated home range sizes smaller than Kernel did, and therefore behavioural differences could be easier to detect in smaller home ranges.

Conclusions

In general, home range and core area size showed similar patterns among study areas. However, there were some differences when I separated the alpine and forest data sets. Reproductive status and temporal scale were the factors that influenced females home range and core area size, where reproducing females had smaller total home range and core area sizes during spring than other months (June-October) and seasons (summer and autumn). Reproducing females had also smaller home ranges than non-reproducing females during the spring months. These differences in home range size between reproducing and non-reproducing females is probably because reproducing females restrict their movements to be close to the den during spring, whereas non-reproducing females patrol their borders against other females. However, as the young grow the female are not as limited in her movements as when the young are small and during summer and autumn the food availability increases and the young can move around in their mothers home range. Therefore, it is important to use the right time scale when investigating differences due to reproductive status. In contrast to other studies my results showed that reproductive status influenced home range sizes. Because reproductive events occur during a short period of time, for example during the lactation period when reproducing females restrict her movement pattern to be close to the den and feed her young. This, I saw during March while in April and May the home range sizes began to increase.

The pattern that reproducing females total home range and core area size were smallest in the spring months, were not seen when only using forest females. This difference might be because of the difference in main food resource, where reindeer is the main food resource in the alpine area and moose is main food resources in the southern boreal forest areas. In the northern alpine areas reproducing females can cache food near the den during denning, because in the alpine area wolverines might find large pieces of reindeer carrions when the natural mortality increases during winter. However, in the southern boreal forest areas they cannot find as large pieces to cache as in the alpine area, because they scavenge on wolf-killed moose or moose remains from slaughter pits or bait sites. This indicates that when I analysed all

females and males, the pattern in monthly total home range size was dominated by the data from Sarek, and/or that the sample size from the forest study areas was too small to distinguish a potential monthly pattern. Therefore, I suggest that more data need to be collected in the forest landscape to continue to investigate whether there is a difference in home range size within the Scandinavian wolverine population in future studies.

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Appendix 1

Comparing Kernel and MCP estimators to GPS-location

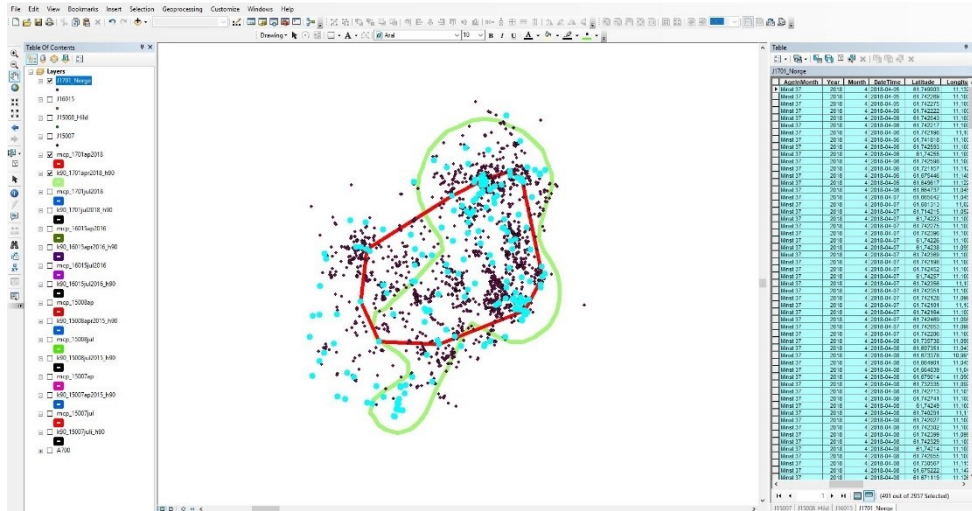


Figure 5. Comparing Kernel 90 (green circle) and MCP 95 (red circle) estimators to GPS-locations for individual 1701 in April 2018.

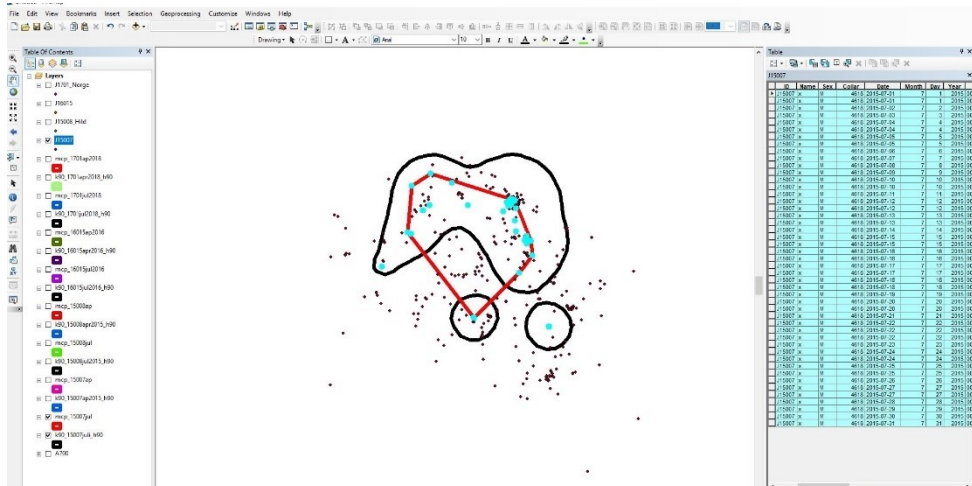


Figure 6. Comparing Kernel 90 (black circle) and MCP 95 (red circle) estimators to GPS-locations for individual 15007 in July.

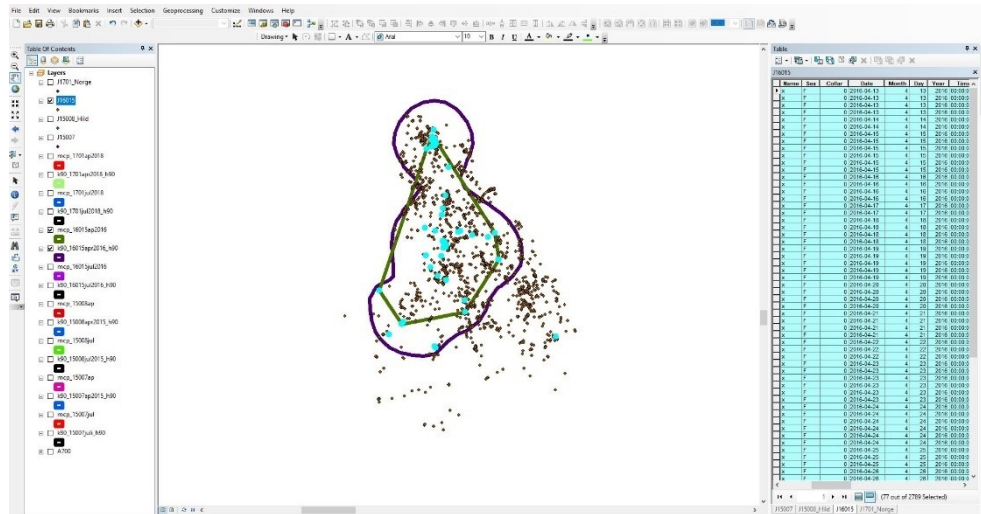


Figure 7. Comparing Kernel 90 (purple circle) and MCP 95 (dark green circle) estimators to GPS-locations for individual 16015 in April 2016.

Model selection for MCP 95% and 50% estimators

Monthly model selection for full data set

Table 10a. Model selection based on MCP 95 and 50 estimates relating to monthly home range sizes for all females (reproducing and non-reproducing females), young survival and all males.

	Model	df	Home range (MCP95)		Core area (MCP50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
All females	Null	4	10.71	0.003	50.29	0.000
	Den	5	0.00	0.590	43.00	0.000
	Month	11	26.38	0.000	10.27	0.006
	Site	7	11.19	0.002	51.96	0.000
	Month + Den	12	15.62	0.000	0.00	0.992
	Site + Den	8	0.76	0.404	42.47	0.000
	Month + site	14	27.10	0.000	12.63	0.002
Females, reproducing	Null	4	3.74	0.127	84.33	0
	Month	11	0.00¹	0.824	0.00²	1
	Site	7	5.64	0.049	84.88	0
Females, non-reproducing	Null	4	2.37	0.234	4.49	0.105
	Month	11	23.06	0.000	20.40	0.000
	Site	6	0.00³	0.766	0.00⁴	0.895
Females, reproducing, March-May	Null	4	0.00	0.851	2.97	0.184
	Juvenile	5	3.48	0.149	0.00	0.816
All males (excluding Norway)	Null	4	0.00	0.799	2.77	0.162
	Month	11	20.82	0.000	5.30	0.046
	Site	6	2.76	0.201	0.00	0.647
	Month + Site	13	24.24	0.000	3.00	0.145

^{1, 2, 3, 4} For parameter estimates see table 10b.

Table 10b. Model parameters based on MCP 95 and 50 for top-models in table in 10a.

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept	4.0114	0.1669	0.1669	Intercept	0.05385	0.34327	0.157
April	0.4097	0.1624	2.523	April	1.59405	0.38097	4.184
May	2.523	0.1643	0.1643	May	2.32403	0.38489	6.038
June	0.1643	0.1643	2.249	June	3.19071	0.39622	8.053
July	0.5888	0.5888	3.488	July	3.44850	0.39345	8.765
Aug	3.488	0.1780	0.1780	Aug	3.65536	0.41503	8.807
Sep	0.9016	0.1937	4.654	Sep	3.82870	0.45106	8.488
Oct	0.7798	0.1811	4.306	Oct	3.61065	0.42191	8.558
3.				4.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (Jämtland)	3.5063	0.8227	4.262	Intercept	1.8150	3.4738	0.522
Norway	0.4767	1.0327	0.462	Norway	0.9366	4.9139	0.191
Sarek	1.6168	0.8690	1.861	Sarek	1.0401	3.6310	0.286

Monthly model selection for forest data set

Table 11a. Model selection based on MCP 95 and 50 estimates relating to monthly home range sizes for forest females (reproducing and non-reproducing females), young survival and forest males

	Model	df	Home range (MCP95)		Core area (MCP50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
Forest females	Null	4	0.07	0.263	19.88	0.000
	Den	5	0.00	0.272	20.43	0.000
	Month	11	12.48	0.001	0.00	0.608
	Site	7	0.01	0.271	22.52	0.000
	Month + Den	12	13.46	0.000	1.62	0.271
	Site + Den	8	0.69	0.193	23.41	0.000
	Month + site	14	14.20	0.000	3.24	0.121
Forest females, reproducing	Null	4	0.43	0.446	21.48	0
	Month	11	11.78	0.002	0.00²	1
	Site	7	0.00¹	0.552	23.53	0
Forest females,	Null	4	0.00	0.842	0.00	0.842
	Juvenile survival	5	3.34	0.158	3.34	0.158
All males (excluding Norway)	Null	4	0.00	0.675	6.93	0.017
	Month	11	10.81	0.003	0.00	0.539
	Site	6	1.48	0.322	5.97	0.027
	Month + Site	13	13.87	0.001	0.51	0.417

^{1, 2, 3, 4} For parameter estimates see table 11b.

Table 11b. Model parameters based on MCP 95 and 50 for top-models in table in 11a

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (Jämtland)	4.5812	0.2853	16.060	Intercept	-0.6585	1.0023	-0.657
				April	2.2590	0.9759	2.315
Norway	-0.5526	0.4168	0.4168	May	3.7723	0.9775	3.859
Värmland/Dalarna	0.7360	0.5437	1.354	June	4.1287	1.0017	4.122
				July	4.6739	1.0017	4.666
				Aug	5.1288	1.0460	4.903
				Sep	4.4659	1.0460	4.270
				Oct	3.5935	1.0460	3.436

Seasonal model selection for full data set

Table 12a. Model selection based on MCP 95 and 50 estimates relating to seasonal home range sizes for all females (reproducing and non-reproducing females), young survival and all males

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
All females	Null	4	0.00	0.501	3.98	0.040
	Den	5	2.51	0.143	5.69	0.017
	Season	6	7.31	0.013	0.79	0.197
	Site	7	1.30	0.262	2.78	0.073
	Season + Den	7	9.96	0.003	2.39	0.089
	Site + Den	8	3.90	0.071	4.32	0.034
	Season + site	9	8.87	0.006	0.00¹	0.292
	Season x Den	9	12.53	0.001	1.89	0.113
	Season x Site	15	16.71	0.000	1.39	0.149
Females, reproducing, Spring	Null	4	0.00	0.794	0.00	0.797
	Juvenile survival	5	2.70	0.206	2.73	0.203
All males (excluding Norway)	Null	4	0.00	0.666	2.77	0.094
	Season	6	4.22	0.081	4.35	0.043
	Site	6	2.76	0.168	0.00	0.375
	Season + Site	8	7.06	0.019	1.72	0.159
	Season x Site	12	4.64	0.065	0.26	0.329

¹ For parameter estimates see table 12b.

Table 12b. Model parameters based on MCP 95 and 50 for top-models in table in 12a

1.			
	Estimate	Std. Error	t value
Intercept (autumn)	3.3686	0.9539	3.531
Spring	-0.3711	0.2098	-1.769
Summer	0.2969	0.2103	1.412
Norway	-0.3901	1.6142	-0.242
Sarek	-0.3049	1.0298	-0.296
Värmland/Dalarna	0.7918	2.0455	0.387

Seasonal model selection for forest data set

Table 13a. Model selection based on MCP 95 and 50 estimates relating to seasonal home range sizes for forest females (reproducing and non-reproducing females), young survival and all males

	Model	df	Home range (K90)		Core area (K50)	
			$\Delta AICc$	Weight	$\Delta AICc$	Weight
Forest females, all	Null	4	0.00	0.721	0.87	0.338
	Season	6	6.93	0.023	0.00¹	0.522
	Site	7	2.09	0.254	3.66	0.084
	Season + site	9	11.02	0.003	4.46	0.056
	Season x Site	15	33.00	0.000	17.67	0.000
Forest females, reproducing	Null	4	0.00	0.768	2.46	2.205
	Season	6	7.08	0.022	0.00²	0.701
	Site	7	2.61	0.208	5.63	0.042
	Season + site	9	12.09	0.002	5.20	0.052
	Season x Site	12	42.08	0.000	27.95	0.000
Forest females, reproducing, Spring	Null	4	0.00	1	0.00	1
	Juvenile survival	5	18.27	0	17.33	0
Forest males (excluding Norway)	Null	4	0.00	0.795	0.00	0.715
	Season	6	6.52	0.030	6.03	0.035
	Site	5	3.06	0.173	2.12	0.247
	Season + Site	7	12.57	0.001	11.45	0.002
	Season x Site	9	32.37	0.000	31.15	0.000

^{1,2} For parameter estimates see table 13b.

Table 13b. Model parameters based on MCP 95 and 50 for top-models in table in 13a

1.				2.			
	Estimate	Std. Error	t value		Estimate	Std. Error	t value
Intercept (autumn)	3.3386	0.4419	7.555	Intercept (autumn)	3.8531	0.3821	10.085
Spring	-0.4959	0.3489	-1.421	Spring	-0.7835	0.2940	-2.665
Summer	0.5080	0.3289	1.544	Summer	0.1451	0.2898	0.501