Territoriality and social organization in Scandinavian wolverines *Gulo gulo*

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Supervisor: Jens Persson   **20 Point, D-Level**

Department of Animal Ecology   **2006:1**
Swedish University of Agricultural Sciences
901 83 Umeå, Sweden

Abstract

Territorial behaviour can have strong effects on population structure and dynamics, and is therefore an important aspect in understanding an animal's ecology. Little information exists on territoriality in Scandinavian wolverines *Gulo gulo*. In this study I investigate territorial behaviour and spatial organization of a wolverine population in northern Sweden. I focus on spatial and temporal patterns in home range use, physical evidence of aggression and den positions within maternal home ranges. A total of 40 annual home ranges were estimated for 24 radio-marked individuals (17 females and seven males).

I found that wolverine males had considerably larger home ranges than females, and encompassed the ranges of several different females. Home ranges of males never overlapped. Females had either exclusive home ranges or ranges with relatively small overlaps with other females. Interacting females also showed little temporal association in overlap areas. Adults seemed to be tolerant towards subadults in home range overlaps, especially if they were related. Tolerance between kin was also observed for two adult females. Evidence of aggression was found for both male and female wolverines. Males had scars and wounds during the mating season whereas intraspecific killing was found in one subadult male and one adult female.

Wolverine females in this study showed a tendency towards a central placement of natal dens within their home ranges. Dens were also situated further away from neighbouring female's home ranges than expected, when these were close.

These results suggest that wolverines in Sweden have intrasexual territoriality and have a social organization resembling most solitary carnivores. I further hypothesize that wolverine females arrange and possibly extend their home ranges around suitable denning sites to reduce the risk of territorial defence and/or female infanticide.

Contents

1. Introduction

The wolverine *Gulo gulo* L. has been characterized as one of the northern hemispheres rarest and least known large carnivores (Banci 1994). It is the largest member of the Mustelidae family, a solitary generalist predator and a scavenger, occupying tundra, taiga and forest zones of North America and Eurasia (Haglund 1966, Banci 1994).

The Scandinavian wolverine population has increased in number and distribution, since the protection 1969 in Sweden, 1982 in Norway and 1979 in Finland (Landa et al. 2000, Naturvårdsverket 2003). Even so, population numbers are still low and the distribution is fragmented (Persson 2003). Wolverines in Scandinavia are also associated with several conservation problems, including depredation on livestock, illegal hunting and low genetic variability (Bjärvall et al. 1990, Willebrand et al. 1999, Walker et al. 2001). Consequently, wolverines are protected according to the Bern Convention in the Nordic countries (Landa et al. 2000, Naturvårdsverket 2003). All Nordic countries have agreed to maintain viable wolverine populations by the enactment of the Large Carnivore Initiative for Europe.

Because wolverine populations occur naturally in low densities and occupy remote and rugged habitats, relatively few studies of free-ranging wolverines have been conducted (Banci 1994, Persson 2003). Most information about wolverines originates from North American studies and from early studies based on snow tracking in Scandinavia (e.g. Krott 1959, Haglund 1966 and Bjärvall 1982). Limited up to date information exists from the Scandinavian population, and only in recent years has fundamental knowledge on wolverine demography and dispersal been gained (e.g. Persson 2003, Persson et al. 2003, Persson 2005 and Persson et al 2006). Social organization and behavioural aspects such as territoriality have been discussed for wolverines (e.g. Krott 1959, Haglund 1966, Pulliainen 1988), but there are no empirical studies concerning this in Scandinavia. This general lack of knowledge makes management less confident. Research from Scandinavian conditions is therefore needed to enable sound management of the wolverine (Landa et al. 2000).

The spacing pattern in a population is the result of the tactics chosen by the individual animals in their attempts to survive and maximize reproductive success (Sandell 1989). Animals compete for several resources including food, shelter and mates. One way to compete and possibly to maximize fitness, is to exclude potential competitors from the area containing the resources e.g. being territorial (Maher and Lott 1995). A "home range" is the area covered by the animals in their normal day-to-day activities e.g. food gathering, mating and caring for young (Burt 1943). A "territory" describes an area of exclusive use, irrespective of how the area came to be identified with the owner, but is often associated with a defended area (Maher and Lott 1995). Thus, by definition an exclusive home range is also a territory. Variation in home range size may lead to unequal division of resources among competitors, resulting in differential rates of growth, mortality and reproduction. Territorial behaviour can thus have strong effects on population structure and dynamics, and is an important aspect in understanding animal ecology (Adams 2001).

Like most mustelids, wolverines have been suggested to exhibit intrasexual territoriality, i.e. males are territorial against males, females against females, but there is an extensive overlap between sexes (Krott 1959, Powell 1979). Sandell (1989) argued that spatial organization in solitary carnivores, such as the wolverine, is determined by different resources for each sex. Female home range size and distribution is determined by food resources, whereas males underlie the number and distribution of females. This prediction is in agreement with the suggested multi-male mating system of wolverines (Ferguson and Larivière 2004). This mating system and intrasexual territoriality further predicts that male

home ranges should be larger than females, which coincide with studies of North American wolverines (App. 1). Sandell also hypothesized that when resources are evenly distributed, home ranges could be expected to be exclusive within each sex. Wolverines have been suggested to keep home ranges separated in space and time by marking the boundaries with scent, urine and excrements (Krott 1959, Haglund 1966, Koehler et al. 1980). However, Pulliainen (1988) suggested that scent marking only serves to keep temporal separation in wolverines and that home ranges overlap in space. There are few reports of territorial aggression in wolverines. However, Magoun (1985) reported that males exhibit scars and wounds during the mating season in May to August, indicating that fighting takes place and that male aggression increase during this period. During a study of wolverines in British Columbia, two adult and one subadult male were found killed by other wolverines during the mating season (Lofroth 2001).

Krott (1959) believed that both food availability and denning sites affected range size in wolverines. Wolverines tend to reuse denning areas, indicating that this may be a limited resource (Landa et al. 2000). This is evident in European badgers (*Meles meles*) where home range size and shape can be predicted from the positions of dens (Doncaster and Woodroffe 1993). Badger dens were often found placed towards the centre of home ranges. This strategy was suggested as an attempt to reduce investment in territorial defence. Wolverine mothers are known to be cautious when choosing denning sites and can go to great lengths to find secure dens for their young, suggesting that predation of young may be important (Banci 1994). Wolff and Peterson (1991) hypothesized that the primary function of territoriality in solitary female mammals could be to protect vulnerable young from infanticidal conspecific females. Infanticide is the most important cause of mortality in juvenile wolverines (Persson et al. 2003). There may be several explanations for infanticide (see Persson et al. 2003 for discussion), but one suggestion is that adult female wolverines kill non-related juveniles to reduce competition for resources.

My objective is to examine territorial behaviour and social organization of a wolverine population. I do this by investigating home range use, signs of aggression and natal den positions within maternal home ranges. I hypothesize that **a)** wolverines in Sweden are territorial and keep their home ranges exclusive from individuals of same sex in space and time **b** wolverines use aggression **c)** dens are placed in centres of home ranges and **d)** dens are placed with respect to potentially infanticidal neighbouring females.

2. Material and methods

2.1. Study area

This study was conducted in a 7 000 km^2 area in and around Sarek National Park in the county of Norrbotten (Kvikkjokk 67º00'N, 17º40'E) (Fig. 1). Wolverine density was approximately 1.4/100 km^2 during the study (Persson 2003). The population is not regulated by trapping or hunting, although some licensed and illegal hunting occurs (Persson 2003).

The climate is continental with cold winters (-10 to -13ºC in January) and medium warm summers (13-14 ºC in July). Annual precipitation is 500-1000 mm, and higher (2500 mm) in the western part of the study area (Påhlsson 1984, Ryvarden 1997). The ground is usually snow covered from October to May. The area is characterized by deep valleys, glaciers and high plateaus with peaks up to 2000 m. Valleys are dominated by mountain birch (*Betula pubescens)*, Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies).* Mountain birch forms the tree line at maximum 600-700 m a. s. l. (Grundsten 1997, Ryvarden 1997). There is little settlement or human activity in the area. Semi-domesticated reindeer (*Rangifer tarandus)* are managed extensively by indigenous Sámi people in the area. Moose (*Alces alces)* is the only wild ungulate found. There are also healthy populations of both Eurasian lynx (*Lynx lynx)* and brown bear (*Ursus arctos).* Wolf (*Canis lupus)* used to inhabit the area, but after many years of persecution, the species is now only an infrequent visitor.
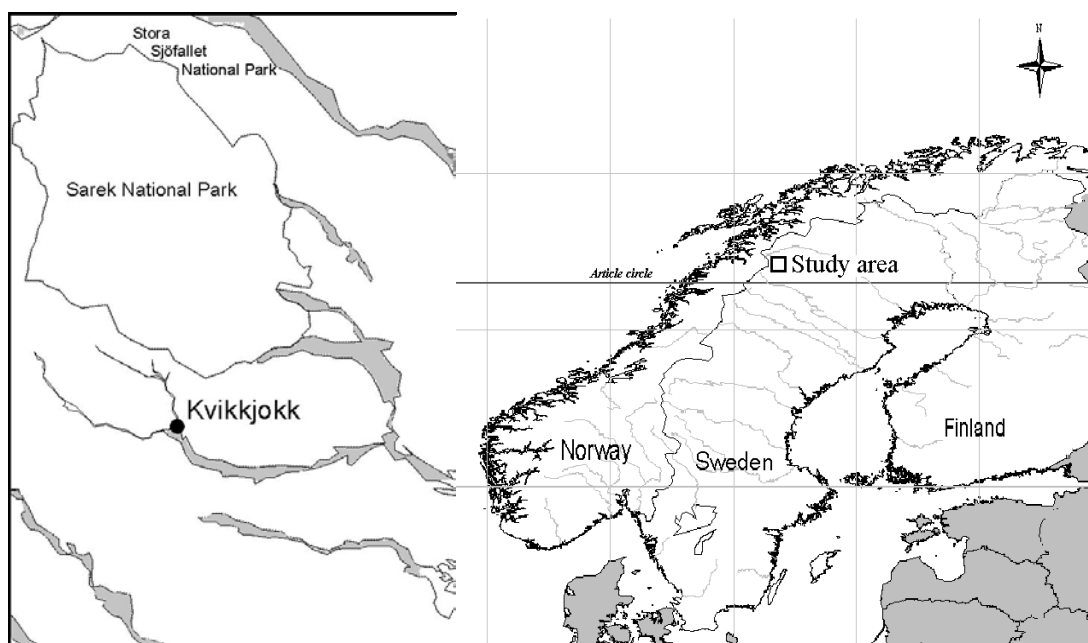
Figure 1. Scandinavian Peninsula with study area location. Field work was performed in and around Sarek National Park (Kvikkjokk 67º00'N, 17º40'E), northern Sweden.

2.2. Data collection

Wolverine location data used in this study were derived from the Swedish Wolverine Project (Persson 2003) during 1993-2004. Most adult females and juveniles were captured and marked at rendezvous sites from early May to early June. Most adult males were darted from helicopters. From 1993-1995 juveniles were equipped with transmitters glued

to the fur, and relocated during the summer and fitted with collar-mounted transmitters. From 1996 and onwards juveniles were fitted with implant transmitters. Adult wolverines captured 1993-1995 were fitted with collar-mounted transmitters and thereafter (1996-2004) with implant transmitters.

Radio-marked wolverines were relocated discontinuously weekly or biweekly, from fixed- wing aircraft and helicopter or from the ground. Locations were estimated with triangulation (Kenward 2001) and the precision was given in a subjectively estimated error-radius of 100 m-intervals around the location.

Location data on 54 natal dens were collected during 1993-2004. Den locations were usually determined by radio-tracking combined with visual observations and then by positioning (Global Positioning System). Denning behaviour, such as repeated use of excavated holes during extended periods, was used to confirm reproduction (Persson 2003). Twelve locations of natal dens used by unmarked females, but which were later marked, were also collected by County Administration personnel of Norrbotten during the annual monitoring of wolverine dens.

2.3. Home range analyses

Home range sample requirements
The number of locations required to estimate home ranges ought to be known before analyses begin (Harris et al 1990). This critical number can be found by examining at what number of locations home range size reaches an asymptote (Harris et al 1990, White and Garrot 1990, Kenward 2001). I used Minimum Convex Polygon (MCP) sample size bootstrap in Animal Movement extension (Hooge and Eichenlaub 1998) to find the required sample size for annual home ranges. I was unable to find an asymptote in number of telemetry locations, even when only adult resident individuals (n=15, 100 simulations) with $\geq$ 30 locations were used. Harris et al (1990) stated that some species never reach an asymptote even though a large number of locations have been collected. A possible explanation for this could be that occasional excursions by wolverines can have relatively larger influences on the range size than movement closer to the centre of the home range (Gautestad and Mysterud 1995).

As I was unable to find an asymptote, sample size requirements for home range analysis were based on scatter plots of annual home range size vs. number of locations collected. At 20 locations there was no positive correlation between fixed kernel range size and number of locations for neither adult reproducing females (Spearman's rank correlation; n=20, P=0.55, r_s = -0.1411), adult barren females (n =10, P=0.93, r_s = -0.035) nor adult males (n=6, P=0.23, r_s = -0.5798). The result was comparable for MCP. A minimum of 20 locations was therefore considered sufficient for estimating annual home range size of adult wolverines. Finally, only locations with a triangulation error less than 1 km were used.

Only resident animals that had locations distributed during most of the year were included. Animals were considered resident if locations were strictly confined to a distinct area (Powell 2000). Furthermore, only animals that were alive during the whole year under consideration were included. As annual home ranges were calculated in calendar years, second year wolverines (> 10 months) spanned two age classes, being both juveniles (0-12 months) and subadults (12-24 months) (Magoun 1985). These animals have been classified as subadults for simplicity here. Animals were classified as adults during their third year (>22 months), even though they may be regarded as subadults the first two months.

During the years 1993 to 2000, 24 out of 159 wolverine individuals (17 females and 7 males) fulfilled the stringent criteria for home range analyses and were used in the study. Several individuals (n=11) were monitored during multiple years. One male was used in calculations for both subadult home range and adult home range. Seven females were used in calculations of home ranges as both reproducing and barren. No subadult females had ≥20 locations, therefore one resident female with 16 locations was included. A total of 1198 telemetry locations were used and the mean triangulation error was estimated to be 583 m SE (± 52) (Fig. 4). Most locations were taken during March-August (Fig. 5). Mean numbers of annual locations were 30 for adult females and 27 for males (Tab. 1). Subadult males had fewer locations with a mean number of 23.
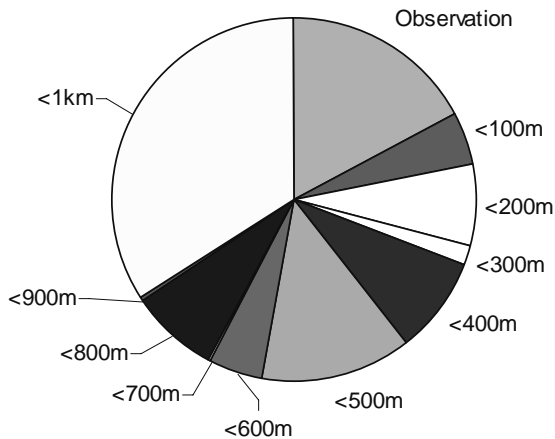
Figure 4. Proportions of wolverine telemetry locations (n=1198) separated in ten error-classes, for 24 individuals during 1993-2000 in Sarek, northern Sweden
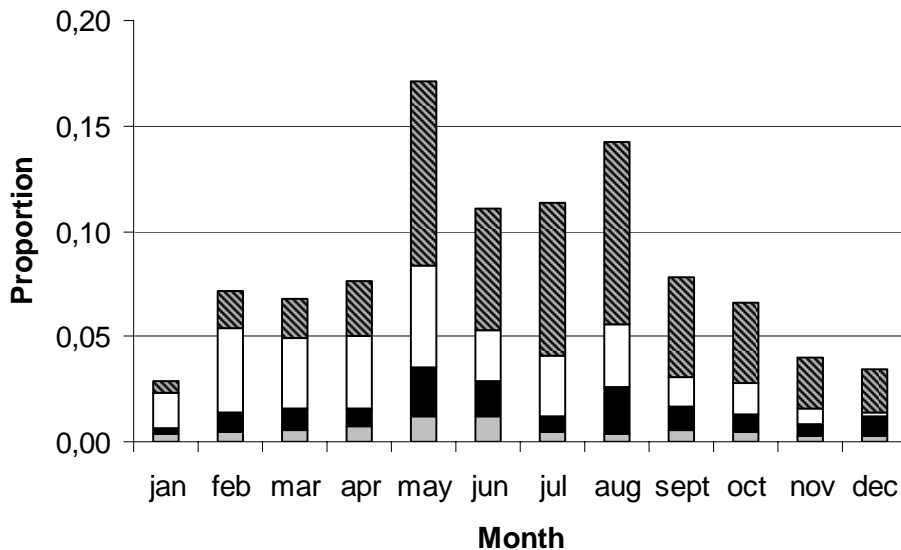
Figure 5. Proportions of wolverine telemetry locations (n=1198) separated per month and per age/sex class, for 24 individuals during 1993-2000 in Sarek, northern Sweden. ▨ Adult reproductive females, ▫ adult barren females, ■ adult males and ▫ subadults.

Autocorrelation analyses

Autocorrelation analyses examine how distances between locations change with sampling interval (White and Garrot 1990, Kenward 2001). If locations are recorded within short-time intervals, animals will not have travelled far and are not likely to reflect the use of the home range. As a result there will be a spatio-temporal correlation between successive locations and location data will not be statistically independent. Creswell and Smith (1992)

showed with simulated data that home range sizes can be underestimated if autocorrelated locations are used.

Even though it is advisable to consider statistical autocorrelation it is equally important to consider the biology of the study animal (Harris et al 1990, Kenward 2001). Lair (1987) concluded that it is possible to obtain unbiased estimates of home ranges even when successive locations are not independent statistically, provided they are biologically independent. For example, misleading autocorrelation can occur when animals are reusing and travelling along well-defined paths and when animal's activity and mobility change during the season e.g. during mating season and denning (Swihart and Slade 1985).

I used Schoeners' Index (Schoener 1981, Swihart and Slade 1985) to check for possible autocorrelation in the location data. I calculated Schoeners' index for all individuals with annual home ranges, and performed autocorrelation analyses with the Animal Movement extension (Hooge and Eichenlaub 1998) in ArcView 3.2. I considered location data statistically autocorrelated when index values were below 1 (Kenward 2001).

Home range size

To investigate the social organization and home range use of wolverines, I estimated annual home ranges for all individuals that met sample requirements. Various home range estimators have different statistical properties and a single method may not be appropriate to answer all research questions (Harris et al et al. 1990). Therefore I used two statistically different methods to estimate annual home ranges; the minimum convex polygon (MCP; Mohr 1947) and the fixed kernel method (FK; Worton 1989).

The fixed kernel method estimates home ranges on the basis of utilization distribution e.g. by drawing contours around the animals locations (Worton 1989, Kenward 2001). A minimum convex polygon connects the outer locations of an animal and calculates the enclosed area (Mohr 1947, Kenward 2001). Kernel estimators have been suggested to be a more accurate method in estimating home range size than earlier methods, such as MCP (Worton 1989, Seaman et al. 1999). Results of home range sizes, home range overlaps and the relative differences between individuals of different sex and age will therefore be referred to fixed kernel (FK95) estimates unless otherwise noted. I included minimum convex polygons (MCP100) because it is considered as the only valid method for direct comparison with previous studies on home range size of wolverines (Harris et al et al. 1990). I have used 95 % contours (e.g. FK95 and MCP95) to minimize influence of occasional excursions that could result in overestimates of range size (White and Garrot 1990). Fifty percent contours of kernel home ranges (FK50) were used as a measure of core area (Ackerman et al. 1990).

Fixed kernels were created with "least squares cross validation" (LSCV) for selection of the smoothing parameter "h", as recommended by Seaman et al. (1999). Grid coarseness was allowed to vary across individuals.

I performed all home range calculations in ArcView 3.2 a (ESRI, Redlands, California) with Animal Movement Extension 2.0 (Hooge and Eichenlaub 1998) and Home range Extension 0.9 (Rodgers and Carr 1998).

Home range overlaps

To test the hypothesis that wolverines are territorial and keep home ranges more or less exclusive within sexes, I calculated the proportion of exclusive home ranges of neighbouring individuals and estimated home range overlaps between individuals of different sex and age (e.g. dyads). Only animals that fulfilled sample requirements were used. Individuals were considered neighbours if they had contours (borders) within the distance of one home range radius (e.g. 8 km).

Overlaps of wolverine home ranges and core areas (FK95, MCP95 and FK50) were quantified using theme-overlay routines in ArcView. Sizes of overlaps were measured and percent overlap of interacting individuals' home ranges were calculated as "mean overlap" and were presented as an index (Minta 1992). Mean overlap in percent and size were later compared between dyads.

Mean overlap was calculated as $= \left(\dfrac{(\text{overlap area})}{HR \text{ of } a} * \dfrac{(\text{overlap area})}{HR \text{ of } b} \right)^{0.5}$

HR = home range
a = wolverine individual a
b = wolverine individual b

2.4. Temporal association in home range overlaps

To test the hypothesis that wolverines avoid each other both in space and time, I measured the proportion of locations that were temporally associated in the overlap areas. Wolverines were considered associating if they were present simultaneously within 24h in the overlap area. Temporal association was calculated and quantified with simple ratio association indices (Cairns and Schwager 1987, Ginsberg and Young 1992). An index value of 1 indicates that all locations of both animals have been recorded at the same time in the overlap. A value of 0 indicates that individuals have not appeared in the overlap area during the same time. Association indices of each dyad were compared to a reference index calculated on interactions between wolverine mothers and their young during one year. I assume that it is practically impossible to record an index value of 1 in the field. A natural reference representing high association-level may therefore be informative when evaluating the results.

Simple ratio index was calculated as: $\dfrac{x}{(x + y_{ab} + y_a + y_b)}$

a = wolverine individual a
b = wolverine individual b
x = number of locations of a and b together in the overlap area (within 24h).
y_{ab} = number of locations of a and b in respective home range outside overlap area.
y_a = number of locations of a alone in overlap area.
y_b = number of locations of b alone in overlap area.

2.5. Signs of aggression in wolverines

I evaluated records on mortalities and interviewed field staff for observations indicating wolverine aggression and territorial behaviour. Unfortunately, there were no available data to estimate the occurrence of scars and wounds on marked animals. As Persson et al. (2003) already discussed the role of infanticide in this wolverine population, I have not considered mortalities of juveniles.

2.6. Natal den positions

Den positions within maternal home ranges
I examined locations of 20 wolverine dens to see if there was a general pattern of den positions within maternal home ranges. Only reproducing females with annual home ranges based on ≥ 20 locations were used. MCP home ranges with 95%-contours were used, because they are more uniform in shape than kernel estimates. For each home range an arithmetic centre was estimated by the outermost locations in ArcView (e.g. "Spider Distance Analysis). This centre does not necessarily hold any biological significance, but rather represents a general estimate of the most internal point of the home range (Ciucci and Mech 1992). Direction and distance from the centre to the dens were recorded. Dens were further plotted in a circular home range with a mean radius of 5980m. Mean radius was calculated by measuring vectors (≥ 5 per home range) from the centre to the external locations of the home ranges (Fig. 2). The circular home range was then divided in 10 %-sectors of the mean radius length (Fig. 9).

Observed distribution of wolverine dens and their distance from home range centre (e.g. percent of mean radius) were compared to an expected uniform-probability assuming random placing (Tab. 4). This expected probability is proportional to the area encompassed by each percentage mean radius (Fig. 9).
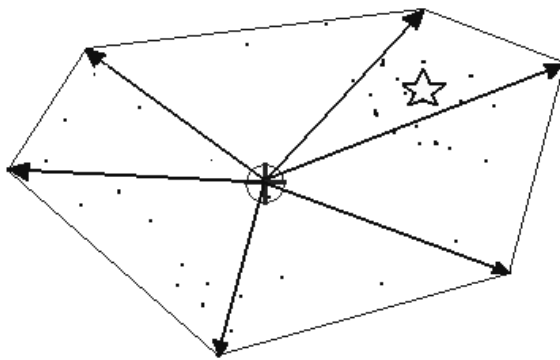

Figure 2. Centres (arithmetic) of wolverine home range were estimated by Spider Distance Analysis. Vectors from the centre to the most external locations (here six) were also used to calculate a mean radius (r=6.0 km) of 20 female wolverine home ranges in this study. The black dots are telemetry locations used to estimate the home range and the star is the maternal den.

Den positions in relation to neighbouring females
Because of difficulties in controlling for the effect of multiple neighbour home ranges and their relative placement around the denning home range, I only looked at females with one known neighbour (n=19). Adjacent female home ranges were considered neighbouring if they were either overlapping or had contours (borders) within the distance of one home range radius (e.g. 6 km). Criteria's for home ranges were the same as for den position within home ranges (see above). Two additional females with less than 20 locations were also included (19 and 10 locations).

I measured distance between natal dens and centres of neighbouring home ranges and compared these to an expected distance based on the distance between home range centres (Fig. 3). A relative distance was calculated to examine if dens were placed closer or further to the neighbour than expected. The relative distance was calculated as the expected

distance divided by the observed distance. Values > 1 thus indicates that dens are situated further away from the neighbour than expected and values < 1 indicate that dens are closer to the neighbour than expected (Fig. 10).
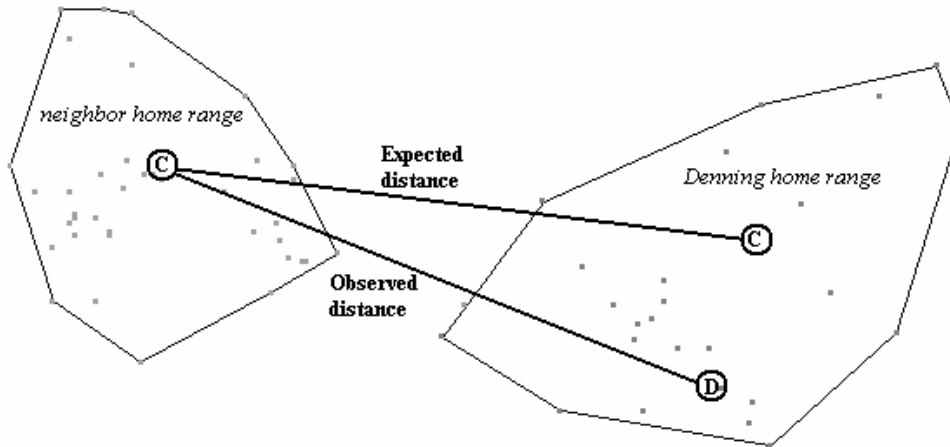

Figure 3. Annual home ranges of two wolverine females 1996 in Sarek, northern Sweden. Observed distances between natal dens (D) of wolverines and neighbour female home range centres (C), were compared to an expected distance of home range centres (C-C) to see if the nearness of neighbours influence den placing within home range.

2.7. Statistical analyses

Because most data failed to approximate normal distributions and sample sizes were small, I used non-parametric tests (Siegel and Castellan 1988). Wilcoxon-Mann-Whitney two-tailed tests for small samples were used to test for differences between two independent groups. The Kruskal-Wallis test was used when three or more groups were compared. A two-sample median test was used to test for differences of medians between two independent groups. Spearman's rank-order correlation coefficient were used when association of two variables were tested. A Chi-square test was used to test for differences between observed and expected distributions. Results of statistical tests were considered significant when $P < 0.05$. All statistical analyses were performed in JMP 5.1 (SAS Institute Inc., Cary, NC, USA. 2000).

3. Results

3.1. Autocorrelation analyses

I expected little or no autocorrelation because locations were taken discontinuously and rarely within 24 h. Generally, locations were not found to be autocorrelated (Tab. 1). However, locations for two individuals (one adult female and one adult male) were autocorrelated. Location data from both individuals continued to show autocorrelation even when locations within 48 h were removed. No further measures were done since resulting autocorrelation was most likely a result of some biological restrictions (see Methods; "Autocorrelation analyses"). Both individuals were used for home range analyses.

3.2. Home range size

Estimates of annual home range sizes differed significantly between methods (e.g. MCP100, MCP95 and FK95) (Kruskal-Wallis; n=40, P=0.043). The fixed kernel method generated larger home ranges on average than both polygon estimates (Wilcoxon; MCP100 and MCP95 pooled P=0.035) (Tab.1).

Mean annual home range size of adult males was 645 km^2 (SE ±37; n=6, 3 individuals, median 606 km^2), and ranged from 230 to 1246 km^2. Mean home range size of adult barren females was 162 km^2 (SE ±12; n =10, 8 individuals) and ranged from 25 to 347 km^2. Mean home range size for reproducing females was 145 km^2 (SE ±11; n=20, 15 individuals), and showed large variation in size (48-805 km^2). However, median home range size was 85 km^2 and 78 km^2 for reproducing and barren females, respectively. Annual home range sizes for resident subadults were approximately one third of adult ranges for one female (51 km^2) and for three male's (165 km^2, SE ±23).

Home ranges of adult females did not differ significantly between barren and reproducing females (Wilcoxon; means, P = 0.741, medians, P = 0.446). The two classes of females were therefore pooled together and compared to adult male home range size. Adult males had significantly larger home ranges than adult females (Tab.1, Fig. 6) (Wilcoxon; P = 0.001).

Core areas of adults (FK50) were approximately 15 percent of total home range size, for both males and females. There was no difference in core area size between the two classes of females (Wilcoxon; P = 0.947). Subadults had relatively larger core areas than adults (40% for males and 25% for the female).

Table 1. Home-range sizes of wolverines in Sarek, during 1993-2000, estimated with the minimum convex polygon method (MCP100), MCP-95 and the Fixed Kernel method using the 95% (FK-95). 50 % Kernel contours (FK-50) was used to estimate core areas of home ranges. All home range estimates are given as mean km^2 (± SE). Autocorrelation is measured with Schoeners index and given as mean (± SE). Numbers of telemetry locations are noted as mean (± SE).

Sex, status	Age	n	n telemetry locations	MCP 100	MCP 95	FK 95	FK 50	Auto-correlation
Females (reproducing)	ad	20	29.4 (1.8)	121 (27)	90 (18)	145 (11)	25 (8)	1.7 (0.1)
Females (barren)	ad	10	30.0 (7.6)	125 (53)	99 (41)	162 (12)	23 (9)	1.7 (0.2)
Females	subad	1	16	42	23	51	11	1.7
Males	ad	6	27.0 (1.9)	510 (165)	433 (140)	645 (37)	97 (28)	1.4 (0.2)
Males	subad	3	23.0 (5.1)	140 (35)	110 (26)	165 (23)	66 (47)	1.7 (0.3)

3

3.3. Home range overlaps

The number of home range overlaps differed depending on the method used (Tab. 2). Using the fixed kernel method resulted in a total of 40 overlaps, while the MCP method generated less than half of this, only 13 overlaps. Seven out of 30 (23%) female home ranges were found exclusive when using the fixed kernel method and 19 out of 30 (63%) when using MCP.

Home range overlaps (n=20) between adult females were generally small, with a mean overlap of 9% (SE ± 7) (Tab. 2, Fig. 6). Overlap sizes ranged from 0.01 km^2 to 46 km^2 and covered at most 24% of both female home ranges. Core areas were generally exclusive between adult females except from one case. However, this overlap was not generated by an actual visit, but a result of overlapping buffers (smoothing) around the locations, i.e. an artefact caused by the method.

Annual home ranges of adult males (n=6) were exclusive. However, there were only two neighbouring males in 1993 and three neighbouring males in 1994.

Home range overlaps between adult males and adult females (n=10) were significantly larger than those between adult females (Wilcoxon; P = 0.0176) (Tab.2, Fig. 6). Overlap sizes were up to 259 km^2 and covered at most 48 % of both home ranges. One male was partly covering home ranges of five adult females and another male overlapped three females within his home range. One female's home range was totally enclosed by a male home range. Mean percentage overlap between males and females (17% ± 15) were also larger than between females, but the difference was not significant (Wilcoxon; P = 0.084) (Tab.2, Fig. 6).

The largest overlaps were found between two pairs of subadult and adult males, covering an average of 29% (± 13) of integrated home ranges (Tab.2, Fig. 6). Overlap sizes were 61 km^2 and 164 km^2 respectively. Mean overlap of adult females and subadult males (n = 8; 20% ± 22), were similar to those of adult males and females (Wilcoxon; P = 0.1096), but overlap sizes were smaller, probably because of relatively smaller home ranges (Fig. 6). The subadult female had her home range exclusive of other marked individuals throughout the year.

Table 2. Home range overlaps of wolverine in Sarek, northern Sweden during 1993-2000 estimated with the fixed kernel method using the 95% and 50 %-contours (FK-95 and FK-50) and the minimum convex polygon method MCP95. Overlap sizes are given as mean km^2 (± SE). Dyad types consider adults if nothing else are given. Mean overlap is an index value (see Methods).

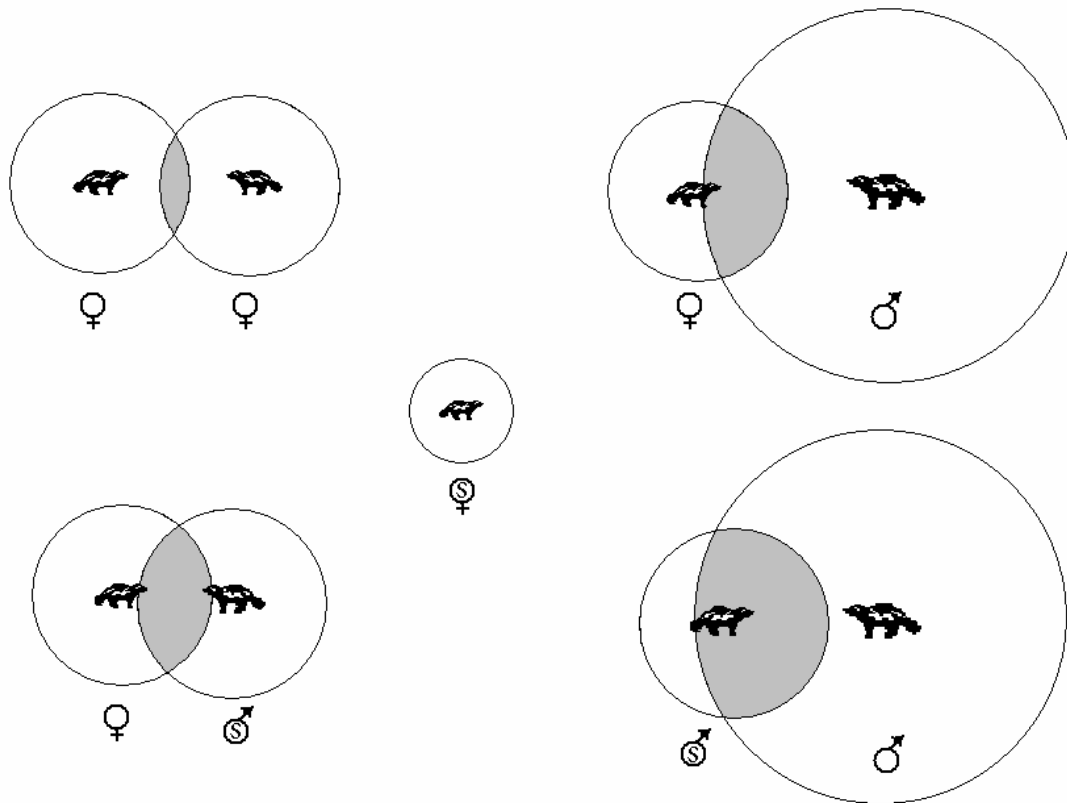| Dyad	FK-95			MCP-95			FK-50		
	n	Size	Mean overlap	n	Size	Mean overlap	n	Size	Mean overlap
♀♀	20	14 (3)	0.09 (0.07)	6	10 (5)	0.09	1	0.1	0.02
♂♀	10	66 (24)	0.17 (0.15)	3	109 (57)	0.29	0		
♂♂	0			0			0		
subad♀-ad♀	0			0			0		
subad♀-ad♂	0			0			0		
subad♂-ad♂	2	113 (51)	0.29 (0.13)	1	46.0	0.17	1	12	0.09
subad♂-ad♀	8	23 (7)	0.20 (0.22)	3	22 (8)	0.40	2	3 (2)	0.11

Figure 6. Visual presentation of relative home range sizes and home range overlaps of wolverines in Sarek, during 1993-2000, estimated with the Fixed Kernel method (FK95). Unmarked sex-symbols refer to adult home ranges. S stands for subadult.

3.4. Temporal association in home range overlaps

Wolverines were present simultaneously, within 24h, in only 30% of overlapping fixed kernel home ranges (n = 40),. With MCP95 home ranges, the corresponding numbers were four out of 13 overlaps (31%). Temporal association as measured by the simple ratio index generally resulted in low values as compared to the reference index (Tab. 3).

Adult males and females showed the highest temporal association (0.114). On seven different occasions (two and five days respectively) two pairs were recorded present simultaneously in the overlap area. Association took place during May and July (Fig. 7). When home ranges were analyzed with the MCP95 method, association between adult males and females was also recorded in August (Fig. 8).

Temporal association was found on five occasions in home range overlaps of four adult females. The association index was relatively low (0.056). Overlaps were often caused by short visits into the neighbouring home range, resulting in a low temporal association. Temporal association was recorded from July to December (Fig. 7 and Fig. 8).

Temporal association was found between three subadult males and five adults. One subadult male stayed for most of the year within an adult male's home range, resulting in an index value of 0.074. Both individuals were recorded twice simultaneously in the overlap, one time in April and one time in August. Another four cases of temporal associations were found between four adult females and two subadult males, resulting in a relatively low index value of 0.065. Temporal association took place during February-September.

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Table 3. Temporal association recorded in home range overlaps of wolverines in Sarek, northern Sweden during 1993-2000. Number of overlaps where temporal association was found is compared to the total number of overlaps (parenthesis). Temporal association among dyads is compared to a reference index calculated on juveniles-mothers, representing high association.

	FK-95		MCP-95		FK-50	
Dyad	*n* temp. ass. /total	Simple ratio index	*n* temp. ass. /total	Simple ratio index	*n* temp. ass. /total	Simple ratio index
♀♀	4/20 (0.20)	0.056	0/20	-	0/20	-
♂♀	2/9 (0.22)	0.114	2/9 (0.22)	0.139	0/9	-
♂♂	0/0	-	0/0	-	0/0	-
subad♀-ad♀	0/0	-	0/0	-	0/0	-
subad♀-ad♂	0/0	-	0/0	-	0/0	-
subad♂-ad♂	1/2 (0.50)	0.074	0/2	-	0/2	-
subad♂-ad♀	4/8 (0.50)	0.065	2/8 (0.25)	0.103	0/8	-
Ref. juvenile-ad♀	6/6 (1.0)	0.571				
Σ	12/40 (0.30)		4/13 (0.31)		0	

Figure 7. Number of days and monthly distribution of temporal association recorded in home range overlaps (FK-95) of wolverines in Sarek (1993-2000). Dyads; adF = adult female, adM = adult male and subadM = subadult male.
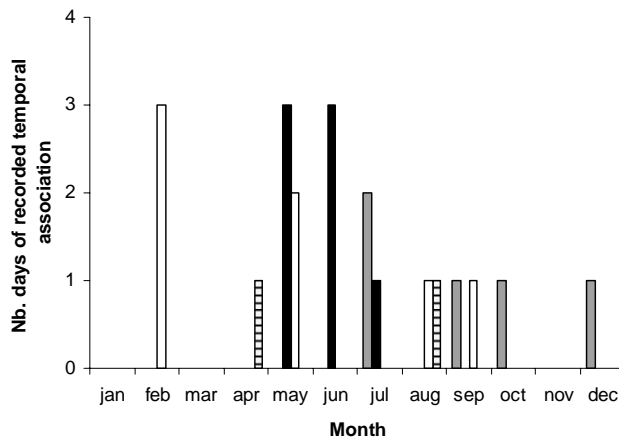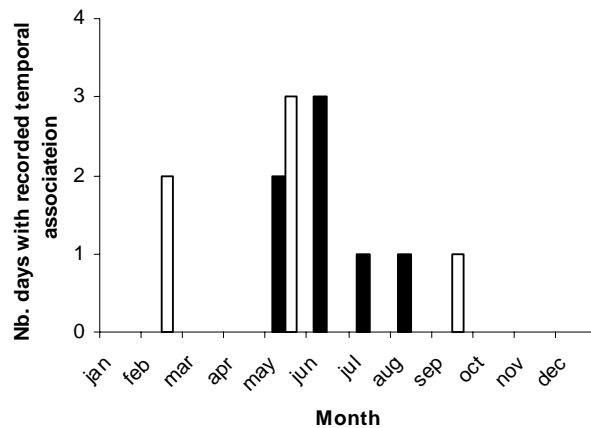

Figure 8. Number of days and monthly distribution of temporal association recorded in home range overlaps (MCP-95) of wolverines in Sarek (1993-2000). Dyads; adF=adult female, adM = adult male and subadM = subadult male.

3.5. Signs of aggression in wolverines

During marking of adult males in May-June, males frequently exhibited both old scars and sometimes fresh wounds (Peter Segerström pers.comm. 2004) (Fig. 11). In May 2003 a subadult male was found dead with injuries typical of wolverine attacks. The male died from severe wounds and crush damages inflicted to the upper part and back of the skull and the neck. Bite marks were corresponding to the dentition of wolverine. The male was left uneaten.

In January 2000 an adult female was found killed with injuries indicating intraspecific killing. This female died from injuries similar to the subadult male, but also had injuries on her front legs.

Figure 11. Wolverine males marked during the breeding season in Sarek, frequently showed scars and wounds indicating that fighting is used to defend home ranges. This male (marked in early June 2004) was exhibiting fresh wounds on the nose, old scars on the side of the head and had a cut in one of his paws. At the time of marking this male was overlapping home ranges of at least six different females and was considered a dominant male (Peter Segerström pers.com. 2004).

3.6. Natal den positions

Den position within home ranges

There was no obvious pattern in the positions of 20 natal wolverine dens within maternal home ranges. One den was situated approximately 5 km (centre-den distance = 10.3 km) outside the mean radius of home ranges and was not compared to the expected distribution. For that reason, the cumulative observed frequency, only reached 0.95. No dens were found within the 10%-radius, although dens were placed closer to the centre than expected. 50 % (n=10) of the dens were situated within the inner 50% of the mean radius, compared to an expected frequency of 25% (n=4) (X^2= 5.0, d.f. =1, P < 0.05). Only two dens were found in the outer 30% of the mean radius (plus the one outside 100% mean radius). Three females independently reused denning areas in consecutive years. Each female had her maternal dens located within a distance of <1 km. One female used the same mountain slope for four natal dens (1994, 1995, 1997 and 1998).

Table 4. Observed and expected (from a uniform probability distribution) frequencies of den locations (n = 20) within different classes of radius length. Mean radius is 6.0 km.

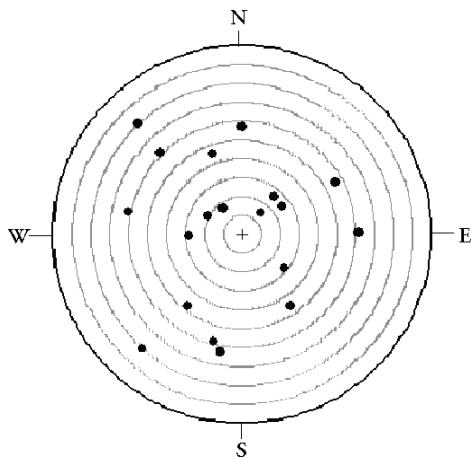| Radius class (%)	n	Observed	Expected	Cumulative observed	Cumulative expected	m from HR center
0-10	0	0.00	0.01	0.00	0.01	598
10-20	2	0.10	0.03	0.10	0.04	1196
20-30	5	0.25	0.05	0.35	0.09	1794
30-40	0	0.00	0.07	0.35	0.16	2392
40-50	3	0.15	0.09	0.50	0.25	2990
50-60	3	0.15	0.11	0.65	0.36	3588
60-70	4	0.20	0.13	0.85	0.49	4186
70-80	1	0.05	0.15	0.90	0.64	4784
80-90	1	0.05	0.17	0.95	0.81	5382
90-100	0	0.00	0.19	0.95	1.00	5980

Figure 9. Positions of 20 wolverine natal dens in relation to home range centres (estimated with MCP-95) in Sarek. Each circle represents 10 percent of mean radius (r= 6. 0 km).

Den positions in relation to neighbouring females

Mean distance between neighbouring home range centres was 10.2 km (SE ± 0.6). Distance between natal dens and neighbouring female home ranges (n=19) ranged from 6.1 km to 13.1 km, averaging 9.9 km (SE ± 0.4). The shortest distance between two natal dens in neighbouring home ranges was 5.7 km. Mean distances between all neighbouring natal dens were 13.1 km (n=37, SE ± 0.6 km).

As illustrated by the negative relationship between the relative distance from natal dens to neighbouring females home ranges (Fig. 10), dens were found to be located further away from adjacent neighbouring females' home ranges than expected (Spearman's rank correlation; rs = - 0. 7155, P = 0. 001). In this analysis three neighbouring home ranges had centres relatively far away from the dens (19 - 21 km), generating data points that differed considerably from the rest of the data set. These three home ranges were assumed to not influence the den placing within the maternal home range and were therefore excluded.
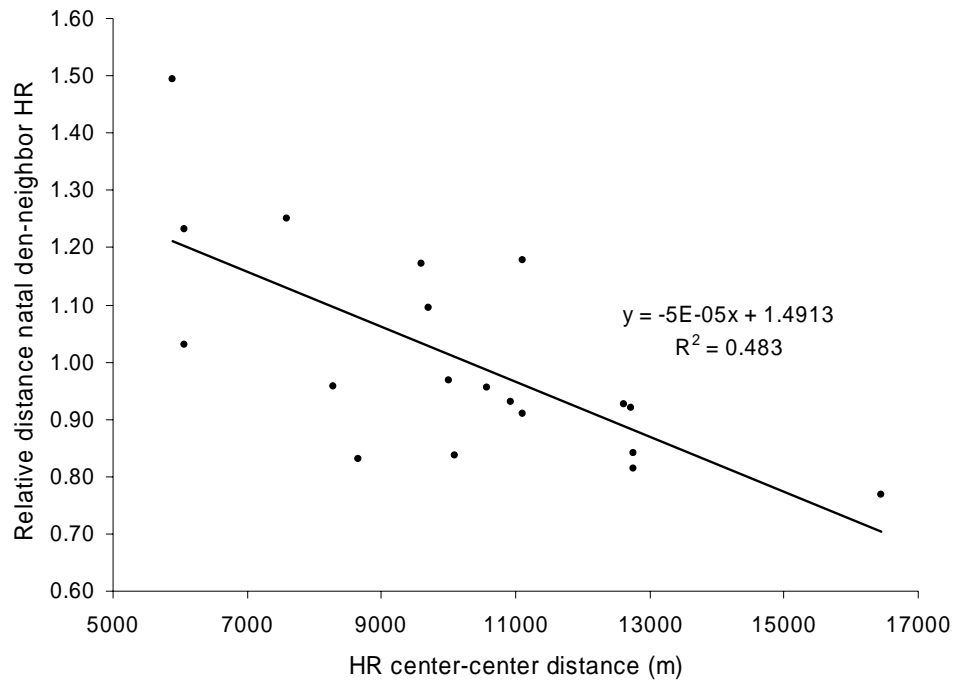
Figure 10. Relationship between natal dens within maternal home ranges (n=19) and the proximity of neighbouring female home ranges, of wolverines in Sarek. Observed distances between dens and neighbour home range (HR) centres were compared to an expected distance of mother-neighbour home range centres (x-axis). Values > 1 on the y-axis explains that dens are situated further away from the neighbour than expected and values < 1 explain that dens are closer to the neighbour than expected.

4. Discussion

Home range size

Wolverines in the study area showed considerable variation in home range size, within and between age and sex groups, ranging from 25 km^2 to 1246 km^2. Mean annual home range size of adults was 645 km^2 for males, 162 km^2 for barren females and 145 km^2 for reproducing females. Home range sizes in this study are within the range of home range sizes of wolverines in North America (App. 1, note that MCP100 is used for comparison). Variation of home range sizes in and among studies may partly be related to differences in area characteristics such as abundance and distribution of food, but also differences in data collection and analysis (Harestad and Bunell 1979, App. 1). Differences in home range sizes among studies could be a result of small sample sizes and variation within samples. Most studies have smaller sample sizes than this study.

Males had considerably larger home ranges than females in this study. This agrees with previous suggestions of intrasexual territoriality, mating tactics in wolverines and on the social organization of most solitary carnivores (Sandell 1989). Wolverines are polygamous with a multi-male mating system where males need large home ranges to include (monopolize) a number of females. Hence, male home range size is influenced by the density of females, and can thus be expected to be larger than females´. During the mating season, males increase their movements in order to monitor the breeding condition of females within their home range (Hornocker and Hash 1981, Magoun 1985, Copeland 1996). Therefore, male home ranges are normally larger than females on both seasonal and annual basis.

Krott (1959) suggested that female home range size is related to food availability and availability of denning sites. Magoun (1985) hypothesized that wolverine females in Alaska had small home ranges because of abundance in food resources. Reuse of denning areas in this study and in Norway (Landa et al 1998) also indicates that suitable den sites may be limited and possibly affect range size. Reproducing females in this study had larger home ranges than in most North American studies and were of similar size as barren females (App. 1). Core areas were of similar size for the two female categories in this study, even though the majority of telemetry locations were taken during the kit rearing period March-August. This was unexpected since previous studies suggest that females with kits restrict their movements resulting in smaller home ranges (Magoun 1985, Copeland 1996, Banci 1994). One reproducing female in this study had an unusually large home range (805 km^2), larger than previously reported. This female was shifting to a vacant home range during the year. However, excluding this female from home range calculations did not affect the results significantly. One reason for reproducing females having larger range sizes than in North America could be due to differences in area productivity. Hence, I would expect that barren females also have larger range sizes than female wolverines in North America. In contrast, barren females in this study have smaller home ranges than those in all North American studies (App. 1). Hornocker and Hash (1981) recognized the problem of determining home range size for wolverine individuals without known residency status. It is possible that previous studies have included occasional transient females in estimates of barren female home ranges, which could explain relatively larger home range sizes than reproducing females. In this study, only females of known status were included in the analyses. Another possible explanation for large home range sizes of reproducing females could be if females have lost their kits, early in the season. These females would then be restricted in their movements only during a short period. Two females lost their kits wolverines had been present simultaneously within 24h in April-May. These two females did however have smaller annual home range

sizes (148 km^2 and 155 km^2) than barren females. Differences in home range sizes between females in Scandinavia and North America could also represent natural differences in wolverine populations. Range sizes for barren females in this study and in South-central Norway were smaller than in North America (App. 1).

Subadults generally cover areas larger than those of adults, as these animals spend periods of time in different areas before they presumably set up their adult home range (Lofroth 2001). Subadults in this study had home range sizes approximately one third of adult ranges. Home ranges were also smaller than in previous studies. Subadults considered in this study were resident with no indications of exploratory movements outside their home ranges, which may explain smaller home range sizes. Home range sizes of subadults were also calculated on relatively few telemetry locations. Subadults in this study did however have relatively larger core areas than adults (40% for males and 25% for the female). This restless movement pattern might represent a pre-dispersal behaviour. The majority of subadult wolverines disperse at the age of 11-18 months (Vangen et al. 2001).

Home range overlaps
This study shows that home range overlaps are largely dependent on which method is used. Kernel home ranges were larger and generated more overlap than minimum convex polygons. This should be remembered when comparing results with other studies.

Adult males and females had relatively large home range overlaps. This is expected because males and females share a mutual interest in mating. One male partly covered home ranges of five adult females and another male had three females within his home range. Similarly, one adult male in Alaska covered at least four and possibly six females (Magoun 1985). Banci (1987) and Copeland (1996) report wolverine males covering three different female home ranges, in Yukon and Idaho. These findings indicate that male home ranges underlie the distribution of female home ranges. This "monopolization" of females by males supports previous suggestions of intrasexual territoriality and the suggested mating system of wolverines.

Home ranges of adult males were found to be exclusive. Females were distributed with home ranges basically lying border-to-border. As Sandell (1989) suggested, evenly distributed resources for males may explain exclusive home ranges.

Adult females had relatively small overlaps and core areas were always exclusive. This is consistent with previous studies, where females maintained home ranges essentially exclusive throughout the year (Magoun 1985, Banci 1987, Copeland 1996). A relatively large overlap was found between two reproducing females. This was unexpected, since the potential risk of female infanticide and an increased need for food resources ought to make females accompanied by kits intolerant to the presence of other females. Genetic analyses showed that these two females were closely related and most likely mother and daughter (Eva Hedmark, pers. comm. 2004). This supports Magoun's (1985) suggestion that females with overlapping home ranges might be mother-daughter combinations. I presume that their relatedness could explain their greater tolerance for home range overlap.

Subadult and adult home ranges showed relatively large overlaps, in accordance with previous studies (Magoun 1985, Banci 1987, Copeland 1996). Adults seem to be tolerant towards subadults, especially if they are related. At least four out of ten subadult-adult overlaps could be explained by relatedness. One subadult male stayed for most of the year within the home range of an adult male. Genetic analyses showed that the adult male was most likely father of the subadult. Similarly, three relatively large overlaps between subadult males and adult females were mother-son associations. As mentioned for the overlapping adult females, their relatedness is likely to explain the tolerance. It is also

possible that tolerance is given to subadults because they are of lower rank than adults and are not considered reproductive competitors. Genovesi et al. (1997) suggested that spatial behaviour in stone martens (*Martes foina*) is influenced by age-related social ranking. Erlinge (1977) showed that resident adult and dominant male stouts (*Mustela erminae*) were relatively unconcerned with subadult males within their home ranges. Banci (1987) oppositely suggested that altercations between young and adult male wolverines might be the proximate encouragement for subadults to disperse. This is likely to pertain to wolverine females too as Persson et al. (2003) report of four juvenile females being killed by other wolverines, presumably non-related territorial females, when they made excursions outside their mother's territory.

Temporal association
Temporal association was found in only 30 % of all home range overlaps in the population. Temporal association as measured by the simple ratio index generally showed low values. Temporal association could be low because of relatively small sample sizes in few telemetry locations. The results could also be interpreted as home range overlaps were caused by few and brief visits into neighbouring home ranges, when the owner were in some other part of its home range. It is unclear if the results of temporal association are different from interactions generated by random use of the animals. It would have been more informative if results were compared to random use of animals within their home ranges.

Temporal association between adult males and adult females took place during May to July. This period corresponds to the mating season (Rausch and Pearson 1972) and the association was likely a result of mating activity. Temporal associations between adult females were found from July to December. Landa et al. (1998) showed that resident females increase their activity in late autumn (September-November) when kits have become independent. It is also possible that the increased movement is a result of food resources becoming scarcer and that females need to travel more to meet energy requirements. Food availability during winter is critical for female wolverines since it affects their reproductive condition (Persson 2005).

Temporal association between adults and subadults were found from the beginning of the year until September. An association was found between a related adult male and a subadult male. Even though the subadult male stayed for most of the year within the adult's home range, both individuals were only recorded simultaneously twice in the overlap. Association took place during the breeding season (April to August). Four cases of temporal associations were found between two subadult males and four adult females. Two of the adult females were mothers of the subadult males and their home ranges were overlapping. The temporal association could have been a result of mother and sons seeking contact, but also a random result generated by independent use of their closely associated home ranges. Age of the subadults at time of temporal associations (e.g. 11-18 months) also coincide with the time when wolverines make pre-dispersal movements (Vangen et al. 2001). Increased movement by the subadults could be responsible for the association.

Territorial behavior and signs of aggression in wolverine
Adult males frequently exhibited fresh scars and wounds during the mating season, suggesting that territorial defence take place. This agrees with Magoun´s (1985) observations of scarred males and her suggestion that adult males become aggressive and intolerant of intruders during the mating season. The subadult male that was killed by

another wolverine in this study and Lofroth´s (2001) finding of intraspecific killing in two adult and one subadult males in British Columbia are also indications that aggression in wolverine males increases during the mating season.

The adult female that was killed by another wolverine in this study area, is interesting because there are no previous reports of aggression between either adult wolverine females or in other female mustelids. Persson et al (2003) suggestion that four juvenile females were killed by other resident females indicates that adult females use aggression to defend their home ranges. The adult female was killed in February and the juvenile females were killed when they left their maternal home ranges in August-September. Wolverine mothers may still be accompanied by kits during August-September and could be expected to be intolerant to intruders. In autumn and winter food resources becomes scarce and important. It is possible that aggression is more pronounced for females when they have kits and when food resources are limited. Even though predation of females imposed by other females seems most likely, it cannot be excluded that adult males killed the females.

Both male and female wolverines may use aggression to defend their territories, but it is not understood to what extent it is used or how important it is for territoriality in this species. Since males and females compete for different resources, it seems plausible that aggression is pronounced at different times of the year for each sex.

Den position within home ranges
Even though it was difficult to interpret the pattern of den positions within home ranges, there was a tendency for dens to be located closer to the centre of home ranges. As Doncaster and Woodroffe (1993) showed for badgers, arrangement of wolverine home ranges around suitable denning sites might be a strategy to reduce encounters and territorial conflicts. If neighbouring females pose a threat towards juveniles as Persson et al. (2003) hypothesized, keeping dens in the centre of the home range will reduce the risk of infanticide by a neighbouring female. Another possible explanation for central placing is that females will be able to cover their home ranges more uniformly when searching for food. Further analyses of this central-place foraging hypothesis would require detailed data on food abundance. However, Copeland (1996) found that wolverine females forage up to 19 km from den sites. Similarly, Bjärvall (1982) found that denning females can bring food from caches 22 km away from the den. These studies indicate that den site selection is based on factors other than food accessibility. Habitat characteristics, such as slope, snow depth, aspect etc, are likely to affect the selection of denning site and the position of dens within home ranges.

Den positions in relation to neighbouring females
Natal dens were located further away from female neighbours than expected, when these had home ranges near. If adult females kill non-related juveniles to reduce competition for resources, placing of dens further away from the neighbouring female might represent a strategy to reduce the risk of infanticide, consistent with Banci's (1994) suggestion that wolverine mothers are careful in selecting denning sites because of predation risk. At least three wolverine females in this population reused denning areas in consecutive years. Even though this is a small sample, it may indicate that suitable denning sites are limited. Reuse of denning areas contradicts the idea that wolverine mothers "place" dens within their home range, in relation to neighbouring females. As for badgers, it is more likely that female home ranges are arranged around known and suitable den areas. Wolverine mothers that have neighbours close may extend their home ranges towards neighbours to minimize

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risk of conflicts for denning sites and vulnerable young. It's also likely that they do have suitable denning sites close to the neighbour, but choose not use them. This could explain why dens are found relatively further away from close neighbours. Present but unknown neighbouring females could also have affected the position of dens, as well as the shape and size of home ranges in this study.

5. Conclusion

In this study, I have shown that wolverines in Sweden exhibit a spacing pattern in accordance with intrasexual territoriality. Males had significantly larger home ranges than females, encompassing or partly including up to five different females. Home ranges of males were totally exclusive and for females either exclusive or with relatively small home range overlaps. The previous suggestion that wolverine individuals keep home ranges temporally but not spatially exclusive (Pulliainen 1988) did not seem to pertain to my study population. Wolverine individuals of same sex generally showed both spatial and temporal separation. Home range sizes of Swedish wolverines were within the range of previous reports on home range sizes of wolverines in North America. Both male and female wolverines seemed to use aggression to defend home ranges. Males frequently exhibited scars during the mating season. One subadult male and one adult female were found killed by conspecifics.

Wolverine females in this study showed a tendency for central placing of natal dens within their home ranges. Dens were also situated further away from neighbouring female's home ranges than expected, when these were close. I hypothesize that wolverine females possibly extend their home ranges around denning sites or use suitable dens that are not close to the neighbouring females to reduce investment in territorial defence and avoid the risk of infanticide.

Knowledge of territoriality and social organization in wolverines can increase the understanding of why and how individuals are distributed in a population. It is clear that territoriality works as a spacing mechanism, but the ultimate causes are relatively unknown. More research is needed to find what specific resources or social attributes determine territorial behaviour and how this varies between populations. Identifying these attributes and critical resources for wolverines could simplify conservation. For example, understanding territoriality will help to predict consequences of management strategies such as removal of individuals and how this may affect the stability within populations. Advances in DNA-identification techniques and the development of GPS-transmitters will inevitably give opportunities to study territoriality in new ways. Finally, my data on home range sizes in Scandinavia will be valuable in planning the sizes of suggested recovery zones for wolverines (Landa et al 2000).

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Appendix 1. Annual home ranges (km^2) of wolverine in previous studies and in this study. All estimates are MCP100, unless nothing else is given (see bottom for notations on methodology).

Location	n	Mean		Range	Reference
Adult males					
NA Idaho	5	1506[a]		953-2400	Copeland 1996
NA Northwest Alaska	4	666		488-917	Magoun (1985)
Southcentral Norway	4	663		502-942	Landa et al 1998
NA Southcentral Alaska	4	535[b]		~340-620	Whitman et al 1986
Sarek, northern Sweden	**6**	**510**		**133-1131**	
NA Montana	9	422[c]			Hornocker and Hash 1981
NA Southwest Yukon	1	238			Banci 1987
Adult reproducing females					
NA Idaho	2	273[a]		107-438	Copeland 1996
Sarek, northern Sweden	3	170[d]		109-221	Bjärvall 1982
Sarek, northern Sweden	**10**	**120**		**31-560**	
NA Southcentral Alaska	3	105[b]		~60-120	Whitman et al 1986
NA Montana	2	100[c]			Hornocker and Hash 1981
NA Northwest Alaska	3	73		55-99	Magoun 1985
NA Southwest Yukon	1	47[e]			Banci 1987
Adult barren females					
NA Montana	1	388[c]		-963	Hornocker and Hash 1981
Southcentral Norway	4	335		273-397	Landa et al 1998
Idaho	4	320[a]		108-413	Copeland 1996
NA Southwest Yukon	2	155[e]		153-157	Banci 1987
NA Northwest Alaska	6	126		56-232	Magoun 1985
Sarek, northern Sweden	**20**	**125**		**45-575**	
Subadult males					
Southcentral Norway	1	3697			Landa et al 1998
NA Southwest Yukon	3	534[a]	534	438-619	Copeland 1996
NA Idaho	1	526			Banci 1987
Sarek, northern Sweden	**3**	**140**		**76-196**	
Subadult females					
NA Southwest Yukon	2	476[a]	476	370-582	Copeland 1996
Southcentral Norway	1	153			Landa et al 1998
NA Northwest Alaska	1	53			Magoun 1985
Sarek, northern Sweden	**1**	**42**			

a = Estimated with MCP95

b = Estimates derived from logarithmic curve analyses of home range size vs. time of monitoring

c = Estimated on locations from more than one year

d = Estimate based on tracking in snow

e = Estimates excluding long-excursions

SVERIGES LANTBRUKSUNIVERSITET Skoglig zooekologi

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1993:1 Olsson, Ulf. Bopredation i olika häckningsbiotoper och dess betydelse för kullstorleken hos skogshöns.

1993:2 Jarnemo, Anders. Spegeluppfällning hos rådjur; signal till predator eller artfränder?

1993:3 Ericsson, Göran. The impact from hunting on moose movements.

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