

Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia

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Abstract Space use and territoriality influence population structure and dynamics and is therefore an important aspect in understanding the ecology of animals. We investigated spatial and temporal space use of wolverines (*Gulo gulo*) in northern Scandinavia. We estimated home ranges of 24 radio-marked individuals (17 females and seven males). Male home ranges (mean 669 km²; SE=211) were significantly larger than female home ranges (mean 170 km²; Wilcoxon–Mann–Whitney; $P=0.001$) and encompassed or included parts of up to five different females. Home range sizes of reproducing (170 km²; SE=51) and barren (171 km²; SE=63) adult females did not differ. Wolverines in Scandinavia exhibit intrasexual territoriality, with male home ranges totally exclusive and female home ranges either exclusive or with little home range overlap. Overlap between wolverine territories is most likely explained by intrasexual tolerance and kinship.

Keywords Carnivore · Home range · Mustelid · Overlap · Social organisation

Introduction

The spacing pattern of animals is the result of the tactics used by individual animals in their attempts to survive and

maximise reproductive success (Sandell 1989). Animals compete for different resources, such as food, shelter, and mates (Maher and Lott 1995). One way to compete is to exclude potential competitors from the area containing the resources (i.e., being territorial; Noble 1939; Schoener 1968; Brown and Orians 1970). A home range is defined as the area covered by the animals in their normal day-to-day activities and territory as that area which is defended against conspecifics (Burt 1943). Variation in home range size may lead to unequal division of resources among competitors, resulting in differential rates of growth, mortality, and reproduction (Adams 2001). Territorial behaviour can, thus, have strong effects on population structure and dynamics and is an important aspect in understanding animal ecology (Adams 2001).

The wolverine (*Gulo gulo*) is a solitary generalist predator and scavenger, occupying tundra, taiga, and forest zones of North America and Eurasia (Banci 1994). Because wolverine populations generally occur at low densities and occupy remote and rugged habitats, few studies of free-ranging wolverines have been conducted. Only in recent years has fundamental knowledge on wolverine demography been gained (Persson et al. 2003, 2006, 2009; Krebs et al. 2004; Persson 2005). Published information about wolverine spatial dynamics originates from a few telemetry studies (Hornocker and Hash 1981; Whitman et al. 1986; Landa et al. 1998; Vangen et al. 2001).

Like most mustelids (Powell 1979), wolverines exhibit intrasexual territoriality and varying degrees of intrasexual overlap (Banci 1994). Spatial organisation in solitary carnivores is determined by different resources for each sex; female home ranges would be determined by food resources while male home ranges would be determined by the number and distribution of females (Sandell 1989). This corresponds with the polygamous mating system of wolverines, which predicts that male home ranges should be larger than females (Hedmark et al. 2007).

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Globally, the wolverine is classified as vulnerable (Mustelid Specialist Group 1996). Conservation concerns include primarily habitat fragmentation, overexploitation, and depredation conflicts with sheep and reindeer husbandry (Landa et al. 2000; Slough 2007; Zhang et al. 2007). The Scandinavian wolverine population's distribution and size declined markedly during the 1900s (Flagstad et al. 2004). Currently, $\geq 1/2$ of the Scandinavian wolverine population, estimated at about 780 individuals, reside in Sweden (Persson 2007) where it is classified as endangered (Gärdenfors 2000). The distribution of wolverines in Sweden largely overlaps with that of semi-domestic reindeer (*Rangifer tarandus*), which is the predominant prey of wolverines (Persson 2005). Locally, reindeer husbandry suffers from heavy predation by wolverines and other predators (Swenson and Andrén 2005). As a result, poaching and lethal control forms a substantial part of wolverine population dynamics in northern Scandinavia (Persson et al. 2009).

In light of current conflicts and lack of knowledge, more information is needed to understand spatial ecology of wolverines and to enable sound management of the species. Therefore, in this study, we examine space use and social organisation in wolverines. In particular, we assess age and sex specific home range size and territoriality.

Materials and methods

Study area

This study was conducted in and around Sarek National Park in northern Sweden above the Arctic Circle (Kvikkjokk: 67°00'N, 17°40'E). The climate is continental, and the ground is usually snow-covered from November to late May. The area is characterised by deep valleys, glaciers, and high alpine plateaus with peaks $\leq 2,000$ m above sea level. The valleys are dominated by mountain birch (*Betula pubescens*), Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*), while mountain birch forms the tree line at 600–700 m above sea level (Grundsten 1997). Semi-domestic reindeer are managed exclusively and extensively by the indigenous Sámi people in the study area. The approximate density of wolverines were 1.4/100 km² in the study area (Persson et al. 2006).

Animal capture and monitoring

We monitored wolverines from 1993 to 2000. We captured and equipped juveniles (2–3 months old) with transmitters at rendezvous sites in early May to early June. All animals categorised as subadults were captured as juveniles and were hence of known age. Adults were captured on ground or were darted from helicopters (Arnemo and Fahlman 2007).

We radiotracked wolverines on average every second week by plane, complemented with additional ground-based telemetry. We estimated locations with triangulation (Kenward 2001), and the precision was given as estimated error-radius of 100-m intervals around the location. Reproduction of adult females was determined from documentation of denning behaviour or observations of offspring or their tracks by means of radiotracking and observations on the ground (Persson et al. 2006).

Home range sample requirements

We used minimum convex polygon (MCP) sample size bootstrap in Animal Movement Extension (Hooge and Eichenlaub 1997) to find the required sample size for annual home ranges (Harris et al. 1990; White and Garrott 1990; Kenward 2001). We were unable to find an asymptote in a number of telemetry locations, even when only adult resident individuals with ≥ 30 locations were used ($n=15$; 100 simulations). Therefore, we based sample size requirements for home range on a regression analysis to find a cut-off point where there was no positive correlation between home range size and number of locations (Dahl and Willebrand 2005).

Animals were considered resident if locations were strictly confined to a distinct area (Powell 2000). Furthermore, only resident animals that were alive and whose locations were distributed during the entire year under consideration were used. Annual home ranges were calculated in calendar years.

During 1993 to 2000, 24 individuals (17 females and seven males) fulfilled the stringent criteria for annual home range analyses and were used in analyses. Eleven individuals were monitored multiple years and provided sufficient data for multiple (two to four) estimates of home ranges. Their annual home ranges were used separately for comparison of different home range estimators (40 separate home ranges). Adult female home ranges from the same individual from different years were treated as individual units if they represented years with different reproductive status (reproductive or barren). However, when sufficient data were collected for a single individual for multiple years (with the same reproductive status), a mean annual home range was calculated (one barren and four reproducing adult females, two adult males) to avoid pseudoreplication.

Autocorrelation analyses

We used Schoener's index (Schoener 1981; Swihart and Slade 1985) to control for autocorrelation in the location data (White and Garrott 1990; Kenward 2001). We calculated Schoener's index for all individuals with annual home ranges and performed autocorrelation analyses with the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcView

3.2. We considered location data statistically autocorrelated when index values were below 1 (Kenward 2001).

Home range size

We estimated annual home ranges for all individuals that met the sample requirements. Home range estimators have different statistical properties, and a single method may not be appropriate to answer all research questions (Harris et al. 1990). Therefore, we used two statistically different methods: the MCP (Mohr 1947) and the fixed kernel method (FK; Worton 1989). We used 95% contours (FK95 and MCP95) to minimise influence of occasional excursions that could result in overestimates of range size (White and Garrott 1990). Fifty percent contours of kernel home ranges (FK50) were used as a measure of core area (Ackerman et al. 1990). Kernel estimators are suggested to be more accurate for estimation of home range size (Worton 1989; Seaman et al. 1999; Kernohan et al. 2001). Thus, home range sizes, overlaps, and relative differences between individuals of different sex and age are referred to FK95 estimates unless otherwise noted. We included MCP (100%) for comparison with previous studies (Harris et al. 1990).

Fixed kernels were created with least squares cross validation for selection of the smoothing parameter h (Seaman et al. 1999). Grid coarseness was allowed to vary across individuals. We performed all home range calculations in ArcView 3.2a (ESRI, Redlands, CA, USA) with Animal Movement Extension 2.0 (Hooge and Eichenlaub 1997) and Home Range Extension 0.9 (Rodgers and Carr 1998).

Home range overlaps

To examine territoriality, we calculated the proportion of exclusive home ranges and overlap between neighbouring individuals. Individuals were considered neighbours if they had contours (borders) within the distance of one home range radius (8 km). We quantified overlap of wolverine home ranges (FK95, MCP95), and core areas (FK50) were using theme-overlay routines in ArcView. We measured overlap size and calculated percent overlap of interacting individuals' home ranges as mean overlap and present it as an index (Minta 1992). We compared mean overlap in percent and size between age and sex categories. We calculated mean overlap as $= ([\text{overlap area}/\text{HRA}] \times [\text{overlap area}/\text{HRb}])^{0.5}$, where HR=home range, a=wolverine individual a, and b=wolverine individual b.

Temporal association in home range overlaps

We measured the proportion of locations that were temporally associated in overlap areas simultaneously within 24 h. 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. We assume that it is practically impossible to record an index value of 1 in the field. Therefore, we used a natural reference representing high association-level to evaluate the results. Association indices of each dyad were compared to a reference index calculated on interactions between wolverine mothers and their offspring during 1 year.

Simple ratio index was calculated as $= x/(x + y_{ab} + y_a + y_b)$, where a=wolverine individual a, b=wolverine individual b, x =number of locations of a and b together in the overlap area (within 24 h), 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, and y_b =number of locations of b alone in overlap area.

Statistical analyses

Because most data failed to approximate normal distributions and sample sizes were small, we 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. Kruskal–Wallis test was used when three or more groups were compared. Spearman's rank correlation was used to analyse correlation between home range size and number of locations. Statistical significance was inferred at an alpha level ≤ 0.05 . All statistical analyses were performed in JMP 5.1 (SAS Institute 2000).

Results

We estimated 40 annual home ranges, which were used for comparison of home range estimators. After pooling multiple home ranges from the same individual, we used 28 home ranges from 20 adult wolverines for further analyses. We used 1,198 telemetry locations, and the mean triangulation error was estimated to be 583 m (SE \pm 52). We used only locations with a triangulation error <1,000 m. Most (68%) locations were taken during March to August. Locations were reported to be autocorrelated for only two individuals (one adult female and one adult male). Location data from both individuals continued to show autocorrelation even when locations within 48 h were removed, most likely a result of some biological restrictions, and they were included in the analyses.

Home range size

At 20 locations, there was no positive correlation between fixed kernel range size and number of locations for adult reproducing

females (Spearman's rank correlation; $n=15$, $P=0.55$, $r_s=-0.1411$), adult barren females ($n=9$, $P=0.93$, $r_s=-0.035$), or adult males ($n=4$, $P=0.23$, $r_s=-0.5798$). The result was similar for MCP. Thus, we considered a minimum of 20 locations sufficient for estimating annual home range size. However, one subadult resident female with 16 locations was included because no subadult females had ≥ 20 locations.

Estimates of annual home range ($n=40$) sizes differed significantly between methods (MCP100, MCP95, and FK95; Kruskal–Wallis test; $P=0.043$). The fixed kernel (95) method generated larger home ranges on average than both polygon estimates (MCP100 and MCP95 pooled; Wilcoxon–Mann–Whitney; $P=0.035$).

Mean annual home range size (FK95; Table 1) of adult males ($n=4$) was 669 km² (median 599 km²) and ranged from 230–1,246 km². Mean home range size (FK95) of adult barren females ($n=9$) was 171 km² and ranged from 25–603 km². Mean home range size (FK95) for reproducing females ($n=15$) was 170 km² and ranged from 48–805 km². Median home range size (FK95) was 105 and 80 km² for reproducing and barren females, respectively. Because neither mean (the same) nor median (Wilcoxon–Mann–Whitney; $P=0.57$) home range size differed between barren and reproducing females, all females were pooled and compared to adult male home range size. Adult males had significantly larger home ranges than adult females (Wilcoxon–Mann–Whitney; $P=0.001$).

Core areas (FK50) of adults were 15–20% of total home range size, for both males and females (Table 1). There was no difference in core area size between the two classes of females (Wilcoxon–Mann–Whitney; $P=0.52$).

Annual home range sizes for resident subadult males (165 km²) were approximately one third of adult ranges. One female resident subadult had a home range of 51 km². Core areas of subadults were 40% for males and 25% for the female.

Home range overlaps

Home range overlap differed depending on the home range estimation method used (Table 2). Fixed kernel 95 resulted

in a total of 40 overlaps, while MCP95 generated only 13 overlaps. Sixteen adult females provided 30 pairs of neighbouring home ranges (same year). Ten (33%) home range pairs were exclusive, and 20 overlapped. Home range overlaps between adult females were generally small, with a mean overlap of 9% (Fig. 1; Table 2). Overlap sizes ranged from 0.01 to 46 km² and covered at most 24% of both female home ranges. Core areas were generally exclusive between adult females except for one case. However, this overlap (0.1 km²) was an artefact generated by overlapping buffers (smoothing) around the locations. Annual home ranges of adult males ($n=6$) were totally exclusive. However, there were only two neighbouring males in 1993 and three neighbouring males in 1994.

Home range overlaps (Table 2) between adult males and adult females ($n=10$) were significantly larger than those between adult females (Wilcoxon–Mann–Whitney; $P=0.018$). Overlap sizes were up to 259 km² 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 home range was totally enclosed by a male home range.

The largest overlaps were found between two pairs of subadult and adult males, covering an average of 29% of integrated home ranges (Table 2). Overlap sizes were 61 and 164 km², respectively. Mean overlap of adult females and subadult males (20%) were similar to those of adult males and females (0.17), but overlap sizes were smaller, probably because of relatively smaller home ranges. The subadult female had her home exclusive of other marked individuals throughout the year, but this was expected because there were no other marked individuals close to her home range.

Temporal association in home range overlaps

Wolverines were present simultaneously, within 24 h, in only 30% of overlapping FK home ranges ($n=40$). With MCP95 home ranges, the corresponding numbers were four

Table 1 Home range sizes of radiotracked wolverines (1993–2000) estimated with the minimum convex polygon method (MCP100 and MCP95) and the fixed kernel method (FK95)

Sex (status)	Age	Number	Number of telemetry locations	MCP100	MCP95	FK95	FK50	Autocorrelation
Females (reproducing)	Adult	15	29 (2)	131 (34)	99 (23)	170 (51)	30 (10)	1.7 (0.1)
Females (barren)	Adult	9	30 (2)	132 (58)	104 (45)	171 (63)	24 (10)	1.7 (0.2)
Females	Subadult	1	16	42	23	51	11	1.7
Males	Adult	4	26 (1)	403 (53)	434 (143)	669 (211)	105 (38)	1.4 (0.2)
Males	Subadult	3	23 (5.1)	140 (35)	110 (26)	165 (23)	66 (47)	1.7 (0.3)

Fifty percent fixed kernel contours (FK50) were used to estimate core areas of home ranges. All home range estimates are given as mean square kilometre (\pm SE). Autocorrelation (Schoener's index) and number of telemetry positions are given as mean (\pm SE)

Table 2 Home range overlaps of radiotracked wolverines (1993–2000) estimated with the fixed kernel method using the 95% (FK95) and 50% contours (FK50) and minimum convex polygon method (MCP95)

Dyad	FK95			MCP95			FK50		
	Number	Area	Proportion	Number	Size	Proportion	Number	Size	Proportion
♀♀	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		
Subadult ♀–Adult ♀	0			0			0		
Subadult ♀–Adult ♂	0			0			0		
Subadult ♂–Adult ♂	2	113 (51)	0.29 (0.13)	1	46	0.17	1	12	0.09
Subadult ♂–Adult ♀	8	23 (7)	0.20 (0.22)	3	22 (8)	0.40	2	3 (2)	0.11

Overlap sizes are given as mean area (square kilometre; ±SE) and mean proportion (±SE). Dyad types consider adults if nothing else are given

out of 13 overlaps (31%). Temporal association generally resulted in low simple ratio index values compared to the reference index (Table 3).

Adult males and females showed the highest temporal association (0.11). On seven different occasions (2 and 5 days, respectively), two pairs were recorded simultaneously in the overlap area. Association took place during May and July (Fig. 2). When home ranges were analysed with the MCP95 method, association between adult males and females was also recorded in August.

Temporal association was found on five occasions in home range overlaps of four adult females. The association

index was relatively low (0.06). 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. 2).

Temporal association was found between three subadult males and five adults. One subadult male stayed for most of the year within an adult male 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 to September.

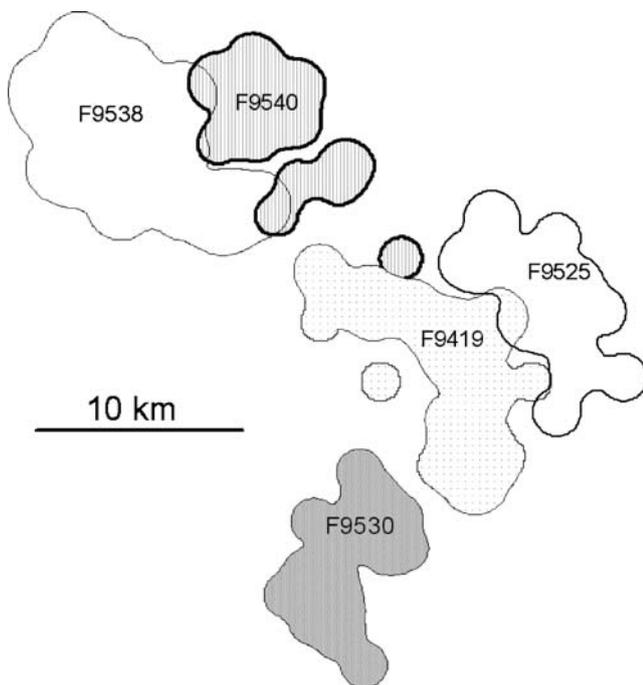


Fig. 1 Spatial distribution of five adult female wolverine home ranges (fixed kernel 95%) and their overlap during 1995 in Sarek, northern Sweden

Discussion

Home range size

Wolverines in our study showed considerable variation in home range size, within and among age and sex groups, ranging from 25–1,246 km². Mean annual home range size of adult males (669 km²) was significantly larger than those of females (170 km²). Home range sizes in this study are within the range of those of North American wolverines, although variation is large within and among studies (Appendix). Variation in home range sizes among studies may partly be related to differences in area characteristics such as abundance and distribution of food, but also differences in data collection, analyses, and sample sizes (Banci 1994; Harestad and Bunnell 1979).

Male wolverines had 3.9 times larger home ranges than females. This agrees with the polygamous mating system (Hedmark et al. 2007) and the social organisation of most solitary carnivores (Sandell 1989). Hence, male home range size is expected to be influenced by the density of females. It has been suggested that males increase their movements during

Table 3 Temporal association recorded in home range overlaps of radiotracked wolverines (1993–2000)

Dyad	FK95		MCP95		FK50	
	Number of temporal association/total	Simple ratio index	Number of temporal association/total	Simple ratio index	Number of temporal association/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	–
Subadult ♀–Adult ♀	0/0	–	0/0	–	0/0	–
Subadult ♀–Adult ♂	0/0	–	0/0	–	0/0	–
Subadult ♂–Adult ♂	1/2 (0.50)	0.074	0/2	–	0/2	–
Subadult ♂–Adult ♀	4/8 (0.50)	0.065	2/8 (0.25)	0.103	0/8	–
Reference index	6/6 (1.0)	0.571				

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 (juveniles–mothers) representing high association. Temporal associations were recorded in home range overlaps calculated with the fixed kernel method with 95% (FK95) and 50% (FK50) contours and the minimum convex polygon method (MCP95)

the mating season (Hornocker and Hash 1981; Copeland 1996) possibly influencing annual range size. Female home range size is assumed to be related to distribution and availability of food (Magoun 1985; Banci 1994).

Both home range size and core areas of reproducing females were similar to that of barren females, even though the majority of telemetry locations were taken during the cub-rearing period (March to August). In contrast, previous studies suggest that females with offspring restrict their movements resulting in smaller home ranges (Magoun 1985; Banci 1994; Copeland 1996). It can be problematic to determine home range size for wolverine individuals without known residency status, and it is possible that previous studies include transient females in estimates of

barren female home ranges (e.g., Hornocker and Hash 1981), which could explain larger home range sizes in barren females than reproducing females in previous studies. In this study, we included only females of known residency status in the analyses. Two reproductive females lost their cubs in April to May and would therefore only be restricted in their movements during a short period. They did not, however, have larger home ranges than other reproductive females. Furthermore, our study population is largely saturated with female territories giving little room for females to expand home ranges years without offspring if we assume territoriality. In lower density populations, home ranges might be more flexible between years. Two females in this study had unusually large home ranges (603 and 805 km²). This was presumably the result of extraterritorial excursions preceding territory shifting the following year. However, excluding these females from the home range analysis did not affect the results significantly.

Home range overlaps

As expected, adult males and females had relatively large home range overlaps. 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 four to six females (Magoun 1985), and male home ranges encompassed those of three different females in Yukon and Idaho, respectively (Banci 1987; Copeland 1996). This suggests that female home ranges underlie the distribution of male home ranges in accordance with the wolverine mating system (Hedmark et al. 2007).

Home ranges of adult males were found to be exclusive. Sandell (1989) suggested that evenly distributed resources for males (i.e., females) may explain exclusive home

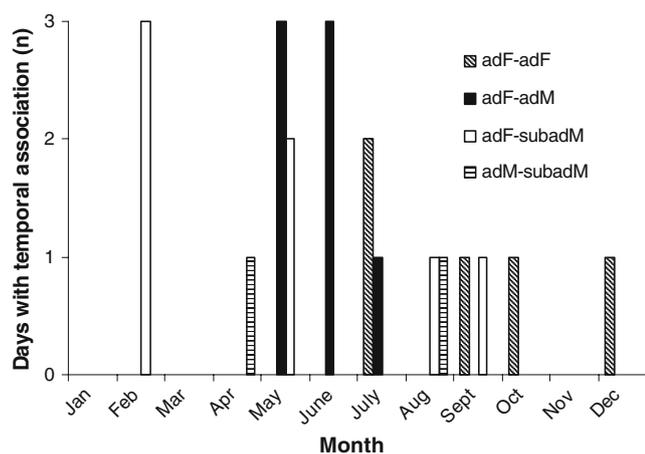


Fig. 2 Number of days and monthly distribution of temporal association recorded in home range overlaps (FK95) of wolverines in Sarek, northern Sweden (1993–2000). Dyads: *adF* adult female, *adM* adult male, and *subadM* subadult male

ranges. Adult female home ranges were basically distributed border-to-border. Adult females had 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). However, a relatively large overlap (26 km²) was found between two reproducing females. Genetic analyses showed that these two females were most likely mother and daughter (Hedmark et al. 2007), presumably explaining greater tolerance.

Subadult and adult home ranges showed relatively large overlaps, similar to previous studies (Magoun 1985; Banci 1987; Copeland 1996). Adults seem to be tolerant towards subadults of the opposite sex. Furthermore, at least four out of ten subadult-adult overlaps were between closely related individuals. Of two opposite sex overlaps, one was between father and son, and three relatively large overlaps between subadult males and adult females were mother-son associations. In addition to opposite sex tolerance and kinship, it is possible that tolerance is given to subadults because they are of lower rank than adults and not considered 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 erminea*) were relatively unconcerned with subadult males within their home ranges. However, juvenile and subadult wolverines are occasionally killed by conspecifics (Persson et al. 2003; Lofroth 2001), suggesting that non-related wolverines of all ages can be seen as competitors.

Temporal association

Temporal association indicates whether wolverines avoid each other in space and time. We found temporal association in only 30% of all home range overlaps in the population. Temporal association generally showed low values (Table 3) indicating strong territoriality and that home range overlaps were caused by few and brief visits into neighbouring home ranges, when the owners were in another part of its home range. However, low values of temporal association could be a result of relatively few telemetry locations.

Temporal association between adult males and females were documented from May to July. This coincides with the mating season (Rausch and Pearson 1972). Temporal associations between adult females were found from July to December. Landa et al. (1998) showed that resident females increase their activity in late fall (September to November) when their offspring were independent. It is also possible that increased movement at this time is related to foraging and food hoarding, before the winter, as food availability during winter is critical for female wolverine reproductive success (Persson 2005).

Maintenance of territoriality

Wolverines are assumed to keep home ranges separated in space and time by marking the boundaries with scent, urine, and excrements (Koehler et al. 1980). In addition, direct aggression presumably an important role in maintaining exclusive territories. Juvenile (Persson et al. 2003) and adult females (Persson et al. 2009) are killed by conspecifics. Persson et al. (2003) suggested that unrelated territorial females killed four juvenile females when they left their maternal home ranges in August to September. Furthermore, adult males frequently exhibit fresh scars and wounds during the mating season (Magoun 1985; Wedholm 2006), and intraspecific mortality among subadult and adult males have been documented during the mating season (Lofroth 2001; Persson et al. 2009), which suggests that males become aggressive and intolerant of intruders during the mating season. Hence, assuming that intraspecific strife primarily involves individuals of the same sex, we suggest that both male and female wolverines use aggression to defend their territories. Because males and females compete for different resources, it seems plausible that aggression is pronounced at different times of the year for each sex.

Conclusion

Knowledge of wolverine space use and social organisation derived from this study increases our understanding of why and how individuals are distributed in a wolverine population. Knowledge of home range size and use is necessary for deciding appropriate management scale for the species. Understanding home range size and territoriality can help us to predict effects of management actions, such as harvest. It can also contribute to improvements of monitoring methods. More research is needed to find what specific resources or social attributes (e.g., kinship) determine territorial behaviour and dynamics. Identifying these attributes could simplify conservation of wolverines, e.g., understanding the consequences of removal of individuals and how this affects the stability within populations. Advances in DNA-identification techniques and the development of global positioning system transmitters will give opportunities to study territoriality in more detail.

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Appendix

Table 4 Annual home ranges (square kilometre) of wolverine in different study areas

Location	Number	Mean	Range	Reference
Adult males				
Idaho, USA	5	1,506 ^a	953–2,400	Copeland 1996
NW Alaska, USA	4	666	488–917	Magoun 1985
SC Norway	4	663	502–942	Landa et al. 1998
SC Alaska, USA	4	535 ^b	340–620	Whitman et al. 1986
N Sweden	6	510	133–1,131	This study
Montana, USA	3	422 ^c	–	Hornocker and Hash 1981
SW Yukon, Canada	1	238 ^e	–	Banci 1987
Adult reproducing females				
Idaho, USA	2	273 ^a	107–438	Copeland 1996
N Sweden	3	170 ^d	109–221	Björvall 1982
N Sweden	15	131	31–560	This study
SC Alaska, USA	3	105 ^b	60–120	Whitman et al. 1986
NW Alaska, USA	3	73	55–99	Magoun 1985
SW Yukon, Canada	1	47 ^c	–	Banci 1987
Adult barren females				
SC Norway	4	335	273–397	Landa et al. 1998
Idaho, USA	4	320 ^a	108–413	Copeland 1996
SW Yukon, Canada	2	155 ^c	153–157	Banci 1987
NW Alaska, USA	6	126	56–232	Magoun 1985
N Sweden	9	132	45–576	This study
Subadult males				
SW Yukon	3	534	438–619	Banci 1987
Idaho	1	526		Copeland 1996
N Sweden	3	140	76–196	This study
Subadult females				
SW Yukon	2	476	370–582	Banci 1987
SC Norway	1	153		Landa et al. 1998
NW Alaska, USA	1	53		Magoun 1985
N Sweden	1	42		

All estimates are MCP100, unless nothing else is given

^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 1 year

^d Estimates based on snow-tracking

^e Estimates excluding long excursions

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