Examensarbete
i ämnet biologi

Spatial ecology and habitat selection of cub-rearing wolverine females

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Abstract

Suitable den sites is presumably important for reproduction of wolverines (*Gulo gulo*), but little information is available about selection of den and rendezvous sites for female wolverines. I examined patterns of den and rendezvous site selection in and around Sarek National Park, Sweden, from 1993 to 2004. I also assessed movements of females with cubs after den abandonment. The study included 81 den sites used by 36 radio-marked females and 177 rendezvous sites used by 33 females.

Female wolverines selected den sites in alpine heath/meadow at elevations between 700 - 800 and 900 - 1000 m a. s. l., and slopes between 10 – 40 degrees. Most dens were located in southwest aspects; where the greatest accumulation of snow was found, and northeast; where most snow drifts are built up and snow thaw is late. Nearly 50% of the dens were located within 100 meters from mountain birch tree line, and most dens were located in non-forested areas.

After den abandonment females moved their cubs further and further away from the den site. There was a declining pattern in the distance travelled between the den site and rendezvous sites by time. Early rendezvous sites were located at lower elevations compared to dens, often in or close to conifer forest. As spring thaw goes on cubs are moved to higher elevations above tree line and primarily in north-eastern aspects. There was a stronger preference for north-eastern aspects during the rendezvous period, indicating that snow is important also for rendezvous site selection. Females without tree cover within their home range located rendezvous sites at lower elevations than den sites, compared to females with forest within home range.

Keyword: wolverine, den, rendezvouz site, habitat, spatial, cub-rearing

1. Introduction

The wolverine is the largest terrestrial member of the weasel family (*Mustelidae*) and occupies remote areas of the northern hemisphere including alpine, tundra and taiga habitats (Magoun and Copeland 1998). Wolverines are solitary animals, with large area requirements, typically occurring at low densities in remote areas (Whitman et al 1986, Landa et al 2003). Consequently, ecological studies of the species are difficult and expensive and therefore the wolverine is one of the northern hemisphere's least known large carnivores (Persson 2003). The Scandinavian wolverine population has increased in size and distribution since it received protection 1969 in Sweden and 1982 in Norway, but is still considered endangered (criteria D) in the Swedish Red Data List and vulnerable in the global Red List of threatened species (Gärdenfors 2005). The annual number of registered wolverine dens in Sweden 1996 to 2007 varied between 41 and 78, with the highest number recorded for 2005 and 2007 (Viltskadecenter 2007). This is below the Swedish population goal with a interim minimum level of 90 annual reproductions and a more even distribution within the country (Regeringen 2000). Wolverines are also protected by the Bern Convention and the UNCED-Convention (Landa et al 2000, Swedish EPA 2003). The current distribution of wolverines in Sweden is mainly sympatric with that of semi-domestic reindeer, which is the main prey for wolverines. As a consequence, wolverines are in conflict with the indigenous Sámi people herding the reindeers.

To fully understand wolverine distribution we need detailed knowledge about their habitat requirements. A habitat is the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism (Hall 1997). Wolverine denning habitat is poorly described in literature (Pulliainen 1968, Myrberget 1968, Magoun and Copeland 1998) and knowledge about habitat needs for females during cub-rearing season are particularly limited (Magoun 2004). Wolverines tend to reuse den sites, indicating that this could be a limited resource (Pulliainen 1968, Magoun and Copeland 1998, Landa et al 2000). Knowledge of habitat requirements of females during cub rearing season can improve our understanding of what is affecting distribution and habitat suitability. Furthermore, knowledge about den site characteristics can also make monitoring of dens (cf. Landa et al. 1998) more effective by focusing search for dens to certain habitats.

Wolverine mating occurs from May to August (Wright and Rausch 1955, Rausch 1972, Magoun 1985) and the implantation is delayed until November to March (Banci and Harestad 1988). Gestation occurs for about 30–50 days (Rausch 1972, Mead et al. 1993, Pasitschniak-Arts and Larivière 1995). Most cubs are born in February and early March (Pulliainen 1968), and thus the peak of implantation probably occur in January.

Dens are typically dug out in snow-drifts or under snow-covered boulders, sometimes built up by a tunnel system up to 40 meters in length (Pulliainen 1968). There have also been reports of dens found in abandoned beaver lodges (Rausch and Pearson 1972), old bear dens (Seton 1929) and avalanche debris (Inman et al. 2007). Magoun and Copeland (1998) suggest several factors that might influence the selection of den sites. One potentially important factor is protection from predators, e.g. wolves, mountain lions, bears, golden eagles and conspecifics (Burkholder 1962, Boles 1977 Banci 1994, White et al. 2002, Magoun and Copeland 1998, Persson et al. 2003). Complex tunnels among boulders deep under the snow might represent too much effort for predators to find cubs, and could therefore provide suitable denning sites. Another factor which might influence den site selection is nearness to foraging areas. By locating the den close to foraging areas the female may reduce the energy cost. Finally, thermoregulatory effects and spring thaw might influence den selection. Cubs are born during one of the coldest periods of the year, therefore a thermoregulatory microhabitat, such as areas with deep snow or natural subnivean cavities, is favourable (Pullianen 1968, Bjärvall et al. 1978). The micro habitat should also be resistant against spring thaw. Magoun and Copeland (1998) found that den abandonment coincided with the period when maximum daily temperatures rose above freezing during several days.

After den abandonment wolverine females cache altricial cubs at rendezvous sites (Magoun and Copeland 1998). Rendezvous sites have only been described briefly in literature (Magoun and Copeland 1998), and no information is available on movements of females with altricial cubs and rendezvous site selection. Presumably, the selection of rendezvous sites is influenced by the same factors as the selection of den sites.

The aim of this study was to investigate den and rendezvous site selection for female wolverines in and around Sarek National park. I also investigated differences between den and rendezvous sites and movement patterns of females with cubs after den abandonment.

2. Material and methods

2.1 Study area

The study area (7,000 km²) is located in and around Sarek National Park in Norrbotten County, northern Sweden (Kvikkjokk: 67º00`N, 17º40`E) (Figure 1). The approximate density of wolverines is 1.4/100 km² (Persson 2003). Average temperature in Kvikkjokk is -16ºC in January and 13ºC in July (Alexandersson 2001). The annual precipitation is 500 – 1000 mm, but higher in the western parts (2500 mm) (Påhlsson 1984). The area is characterised by deep valleys, glaciers and high plateaus with peaks ranging up to 2,000 ma.s.l. The valleys are dominated by mountain birch (*Betula pubescens*) which forms the tree-line at a maximum elevation of 600-700 m a.s.l., Scots pine (*Pinus sylvestris*), and Norway spruce (*Picea abies*) and the ground is usually snow-covered from October to May, (Grundsten 1997, Ryvarden 1997). Semi-domestic reindeer are managed extensively by indigenous Sámi-people. Moose is the only wild ungulate occurring in significant numbers. Breeding populations of brown bear and lynx occur in the area (Persson 2003).

Figure 1. Location of the study area in and around Sarek National Park, Norrbotten County.

2.2 Data collection

The data used in this study was collected by the Swedish wolverine project in and around Sarek National park between 1993 and 2004. The study includes 81 den sites used by 36 radio-marked females and 177 rendezvous sites used by 33 females. Adult females were captured at rendezvous sites or darted from helicopter. All juveniles were captured at rendezvous sites by locating radio-marked females with cubs, or by snow tracking non-marked females with cubs. During 1993-1995 juveniles were initially equipped with transmitters glued to the fur during May-June, and relocated during summer and fitted with collar-mounted transmitters. From 1996 all juveniles were equipped with implanted transmitters. Adult wolverines captured 1993-1995 were fitted with collar-mounted transmitters and thereafter (1996 to 2004) with implant transmitters.

Dens and rendezvous sites were located by a combination of intensive radio-tracking, snow tracking and visual observations. Twelve locations of natal dens were collected by County Administration personnel of Norrbotten during the annual monitoring of wolverine dens. This was done before the females using the den were radio-marked. Movement patterns were derived from radio-tracking of females from fixed-wing aircraft or ground.

2.3 Habitat parameters

2.3.1. Den and rendezvous site habitat selection

Wolverine reproductive dens have been categorized as natal or maternal (Magoun and Copeland 1998). Natal dens are used during parturition and maternal dens subsequent to the natal den and before weaning. However, in this study I refer only to natal dens, as the differentiation of natal and maternal dens is dubious at northern latitudes (Magoun and Copeland 1998, J. Persson, pers. comm.). Selection of den and rendezvous sites was studied on macro scale.

Eight parameters were analysed; *Vegetation, elevation, slope, aspect, height and distance to conifer tree line and mountain birch forest tree line (hereafter defined as birch tree line).* All analyses described were conducted using Geographical Information System, GIS (ArcView 3.2, ESRI). Availability of these parameters was defined as that within all female home ranges (n = 66) pooled together, covering almost the entire study area. Each parameter was divided with the total home range area giving percentage as a result of availability.

Use of habitat was defined as contents of a buffer centred on a telemetry location (Rettie and McLoughlin 1999), also giving percentages of area as result of usage. The den site buffer zones were 100 m in radius, whereas rendezvous sites buffer zones ranged from 100 m to 2000 m in radius depending on telemetry error.

Considering use of area, rather than a point, has theoretical basis in reducing bias in habitat selection studies. Specifying a radius for each location point ensured that the true habitat used by wolverines, regardless of telemetry error, was included for analysis. However this method for measuring habitat use can result in conservative estimates of selection because buffers will include both used and unused habitats (Rettie and McLoughlin 1999).

The use of each parameter relative to availability within all home ranges pooled together was analysed using resampling without replacement. Den and rendezvous site selection is an example of Johnson´s (1980) third-order selection, which pertains to the usage made of various habitat components within the home range. To detect differences of habitat use during the rendezvous-period it was divided into three time periods; I = 27/4 – 17/5, II = 18/5 – 7/6 and III = 8/6 – 28/6.

In the vegetation analysis, 51 available vegetation types (appendix 2) were pooled into five discrete vegetation groups (table 1) (Buck 1994). These groups were classified based on structure and species composition. Digital vegetation coverage maps from SMD (Swedish ground data in 8-bit code) and Mountain-vegetation maps were used when analysing usage and availability of vegetation types.

Table 1. Vegetation types and description of five vegetation group's origin from 51 vegetation classes (Smd and mountain map) found within all home ranges pooled together.

Vegetation group	**Description**	**Availability (median)**
Water/ice	Lake, water course, bog, glacier and snow bed	12,5 %
Conifer forest	Conifer forest (pine and spruce)	17,5 %
Boulder	Block terrain and bare rock	20,0 %
Meadow/heath	Alpine heath, meadow grass and thicket	23,8%
Deciduous forest	Mountain birch forest	26,3%

Use and availability of elevations were analysed using a digitalised elevation map. Slope and aspect were derived directly from the elevation map using animal movement extension in ArcView 3.2. Dens and rendezvous sites were compared with snow accumulation in Tjakktjajaure area (67.05ºN, 18.50ºE) for different aspects using data from Andersson and Lundberg (2001).

For home ranges that included forested areas, height above and distance to tree line was calculated by comparing den and rendezvous sites elevation with that of conifer forest and birch forest tree line, respectively. No buffer zones were used in this analysis.

2.3.2. Spatial selection of rendezvous site within home range

Distance between den (n = 81) and rendezvous sites (n = 155) during the rendezvous period were calculated manually in ArcView 3.2 and grouped into nine weeks. Mean values for each of the nine weeks during the rendevous period were calculated to detect movement pattern. The number of independent locations during each week ranged from 10 to 22, except the first week which was based on three locations. Mean home range radius for reproducing females was derived from Wedholm (2006). To detect movements in elevation during the rendezvous-period, the difference in height between den and rendezvous sites was calculated in the same way as distance. All females were separated into three groups according to presence or abundance of tree cover within home range; a) *home ranges with coniferous forest, b) home ranges with conifer forest and mountain birch forest* and *c) home ranges without tree cover.*

2.4 Determination of home range

Home ranges were estimated by Minimum Convex Polygon (MCP100%) to accommodate the relatively small number of locations per animal. Only locations from the denning period and the period using rendezvous sites were included (February to June). For some females, I pooled positions from several years to obtain a sufficient number of locations for home range estimation. This was possible because of the homogenous distribution of home ranges over time.

2.5 Telemetry error
Telemetry error of locations used in the analysis varied from 100 to 2000 meters in radius. For all den sites and most rendezvous sites were telemetry error of <100 meter where used. Two rendezvous sites with telemetry error of <1000 meters were used for the habitat analyses and spatial selection within home range. When analysing distance and height between den and rendezvous sites telemetry error varied from 0 to 500 meters.

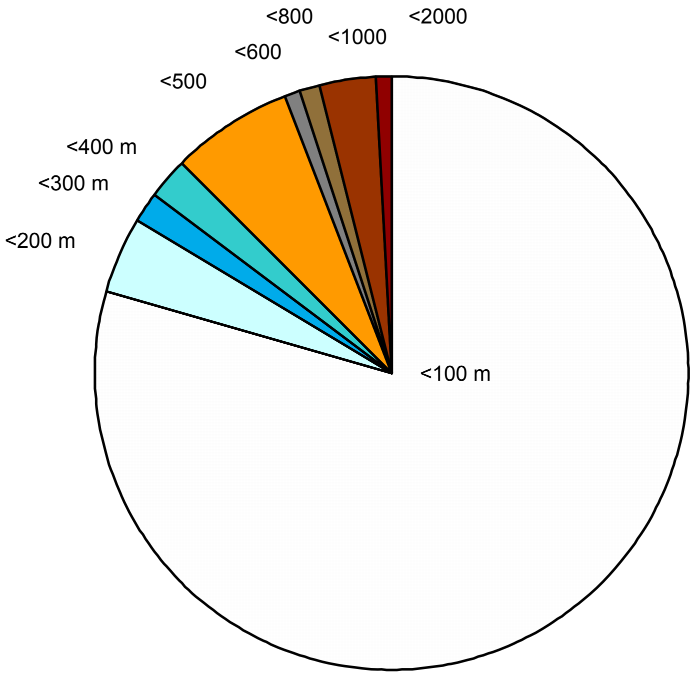

Figure 2. Proportion of telemetry locations of den and rendezvous sites divided into error-classes.

2.6 Statistical tests
The use of habitat parameters (elevation, vegetation, slope and aspect) compared with availability within home ranges for den and rendezvous sites was tested using resampling without replacement. Analyses were done with 1000 repetitions in Microsoft Excel's macro function. Differences in habitat selection between dens and RV-sites were compared using t-test. A linear regression analysis was used to test for increasing distance between den and rendezvous sites over time (Harrison 1999). Results of statistical tests were considered significant when $P < 0.05$. Statistical tests were performed in Minitab 14 and Windows Excel Analyse-It.

3. Results

3.1 Den site selection: *In which habitat do wolverine females prefer to locate their dens?*

3.1.1 Elevation
Dens were located at elevations between 486 and 1316 meters above sea level (mean = 799; 95% C.I. = ± 42, n = 81). Dens were located more often than expected at elevations between 700 – 800 m and 900 – 1000 m Forty-six percent of the dens (n = 37) were located

within 100 meter of birch tree line (716 ± 8 m). There was a strong tendency for avoidance of the lowest and highest areas (299 – 600 m and 1200 – 1600 m; Fig.3).

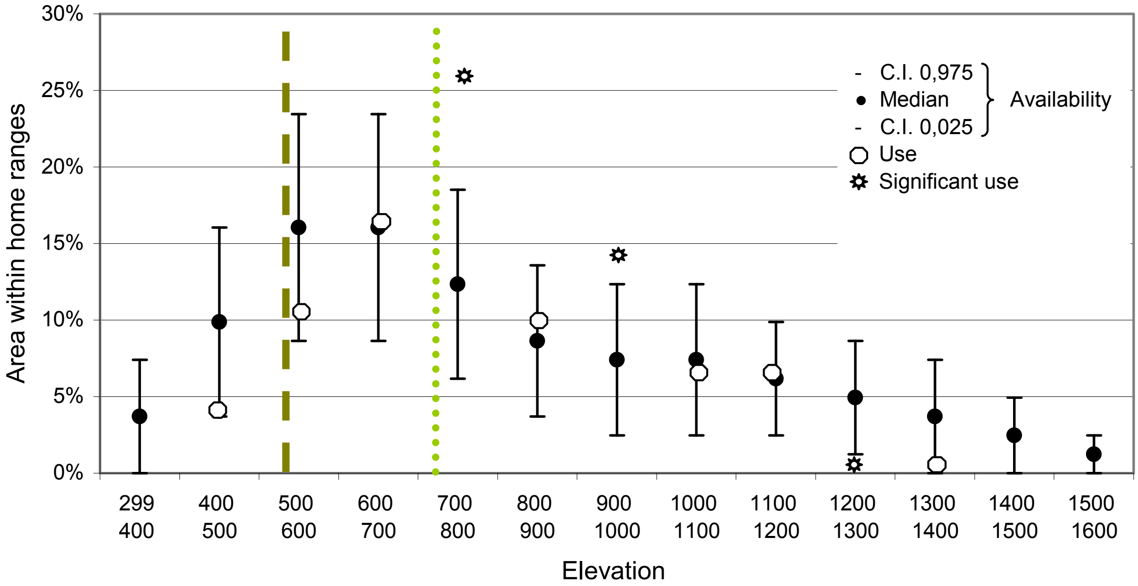

Figure 3. Distribution of den sites (n = 81) in relation to elevation. Availability of elevations is based on proportions of area within all home ranges. Habitat use that differs significantly from availability is marked with stars. The light green line represents birch tree line and the dark green line represents conifer tree line.

3.1.2 Vegetation

Dens were located in alpine heath/meadow (54.4%) more than expected (23.8%; Fig. 4). Eleven percent of dens were located in boulder terrain, which is similar to the lower confidence interval range of availability (11.3%). Water/ice and conifer forest were avoided (0.2% and 5.8 %, versus median availability of 12.5% and 17.5%, respectively). There was an unequal distribution of den sites among forested (coniferous and/or birch forest; 34%) and non-forested (66%) areas. Most home ranges (89%) included forest and the distribution within all home ranges was 44 % of the total area.

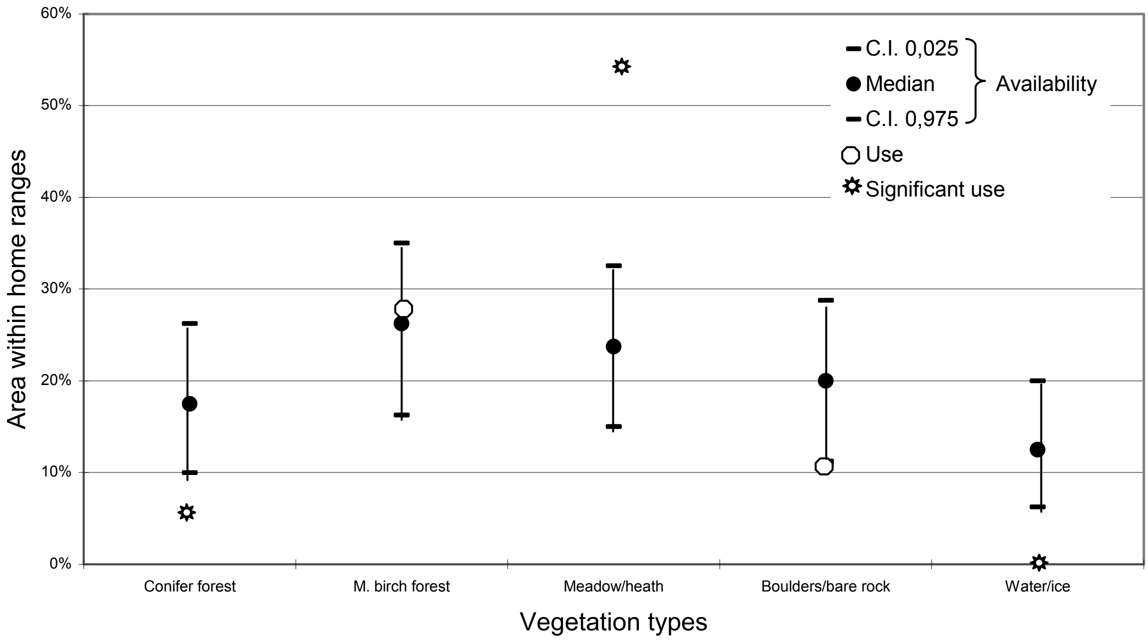

Figure 4. Distribution of den sites (n = 81) in relation to vegetation type. Availability of vegetation type is based on proportions of area within all home ranges. Habitat use that differs significantly from availability is marked with stars.

3.1.3 Slope

All dens were located at slopes below 42.6 degrees (mean = 20.1 degrees; 95% C.I. = ± 2, n = 81), and more often than expected at 10 to 40 degrees (Fig. 5). Most dens (65%) were found at slopes between 10 – 30 degrees. The most common slopes, 0 – 10 degrees, were selected against (Fig. 5).

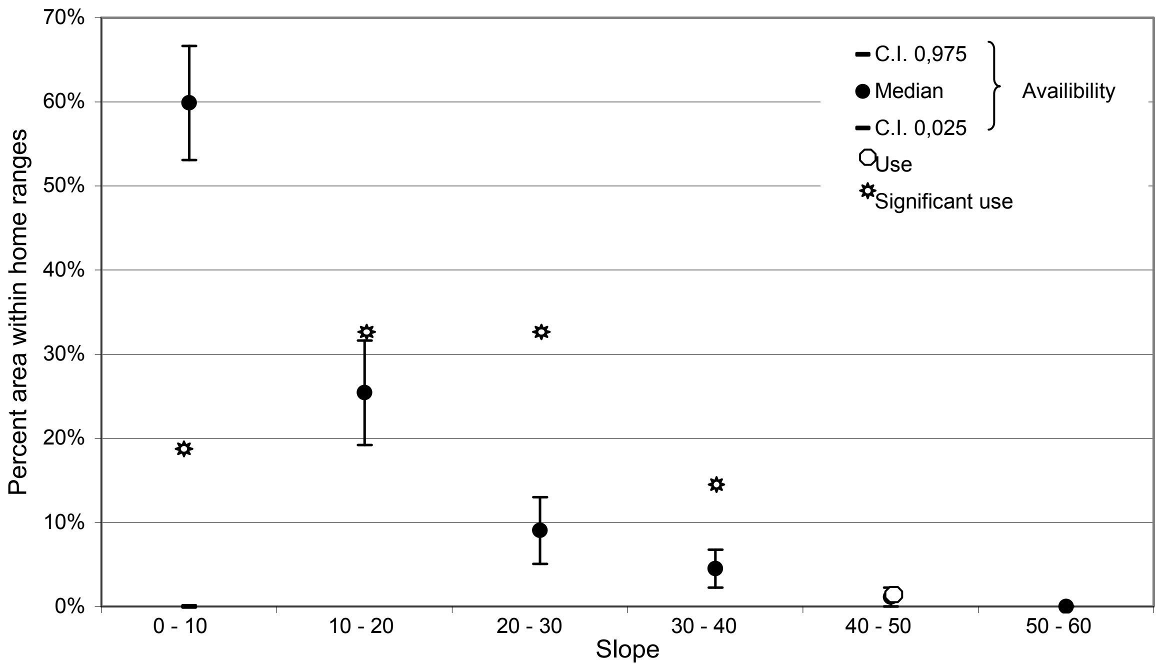

Figure 5. Distribution of den sites (n = 81) in relation to slope. Availability of slopes is based on the proportions of slopes within all home ranges. Use of slope that differs significantly from availability is marked with stars.

3.1.4 Aspect

Most of the dens (43%) were facing southwest or northeast, but neither of these aspects was used more than expected (Fig. 6). Northern aspects were selected against. According to Andersson (2005), the thickest snow layer is found at southern aspects, particularly south-west, and thinnest layers at northern aspects (Fig. 6). The greatest variation in snow depth was in north-eastern aspect (pers. comm. Andersson 2005).

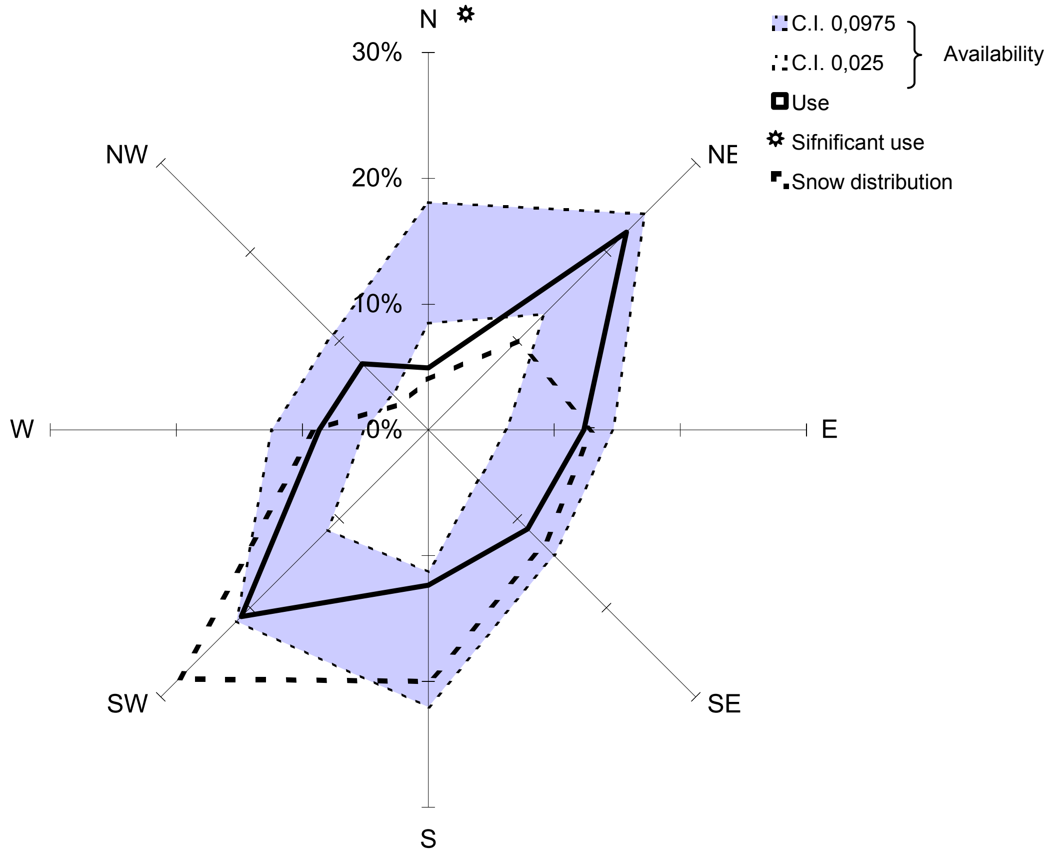

Figure 6. Distribution of den sites (n = 81) in relation to aspect. Use of aspect that differs significant from availability is marked with stars. Stroked line is representing snow depth during late April.

3.1.5 Distance to and height above tree line (conifer-/mountain birch forest)
Distance from dens to birch and conifer tree line showed a substantial variation. Nine home ranges did not include forest, therefore the distance from den to nearest tree line was great (1 478 m and 8 078 m to birch and conifer tree line, respectively) when all home ranges were included in the analysis. When home ranges without forest were excluded, the mean distance to mountain birch tree-line was 591 m (C.I. 95% = ± 249; range: 0 - 4700 meters), and to conifer forest tree line 2 540 m (C.I. 95% = ± 983; range: of 0–15 000 m).

When excluding home ranges without forest mean den site elevation was 731 m a.s.l. (C.I. 95% = ± 14, n = 72). Den sites were located closer to mountain birch tree line (C.I. 95% = 716 ± 8) than to conifer forest tree line (C.I. 95% = 530 ± 5 m).

3.2 Rendezvous site selection: *In which habitat do wolverine females choose to locate their cubs after den abandonment?*

3.2.1 Elevation
Rendezvous sites were located at elevations between 339 and 1457 meters above sea level (mean = 791; 95% C.I. = ± 40, n = 177; Fig. 7a). Female wolverines tended to locate rendezvous sites at higher elevation during summer (Fig. 7b-d). The lowest mean elevation was found for period I (mean: 671 ± 57 m C.I. 95%, n = 46). During period II rendezvous

sites were located in higher elevations (867 ± 57 m C.I. 95%, n = 85). The highest location of rendezvous sites was found for period III (918 ± 77 m C.I. 95%, n = 46).

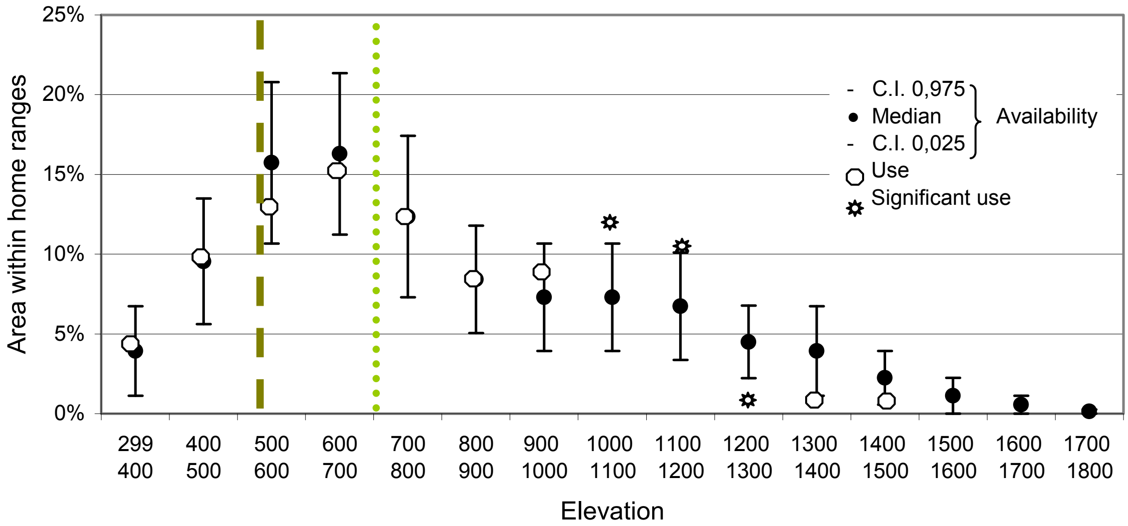

Figure 7a-d. Distribution of rendezvous sites (n = 177) in relation to elevation, during all rendezvous period (I, II and III): figure 7a, period I (27/4 – 17/5)(n = 46): figure 7b, period II (18/5 – 7/6)(n = 85): figure 7c and period III (7/6 - 28/6)(n = 46) figure 7d. Availability of elevations is based on proportions of area within all home ranges. Use of elevation that differs significantly from availability is marked with stars. The light green line represents birch forest tree line and the dark green line represents conifer forest tree line.

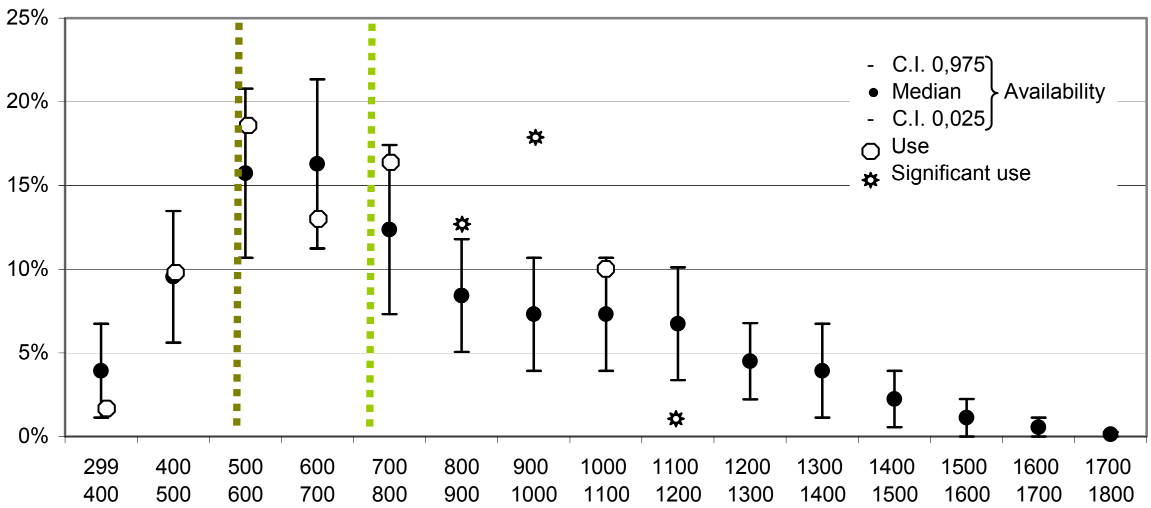

Figure 7b.

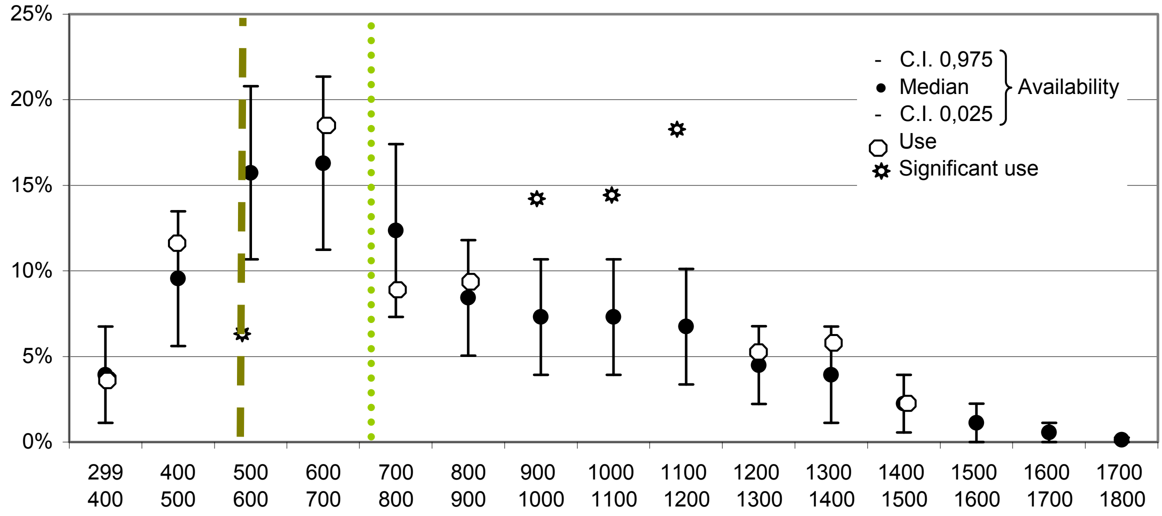

Figure 7c.

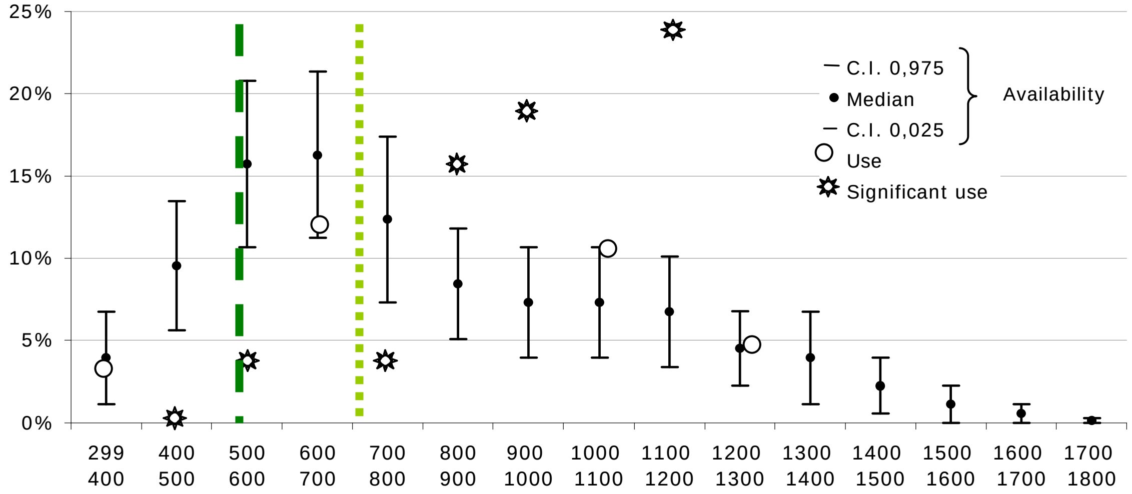

Figure 7d.

3.2.2. Vegetation

Rendezvous sites were found in all types of vegetations. Meadow/heath was selected for when all periods (I, II and III) were pooled together (Fig. 8a). However, conifer forest was selected for during period I and boulder terrain and water/ice were avoided during the same period (Fig. 8b). Meadow/heath was selected for during period II (Fig. 8c). During period III meadow/heath and boulder terrain were selected for, while birch forest was avoided (Fig. 8d). Rendezvous sites were located in forested (coniferous or/and birch forest; 64%) and non-forested (36%) areas. Most home ranges (89%) included forest and the distribution within all home ranges was 44 % of the total area.

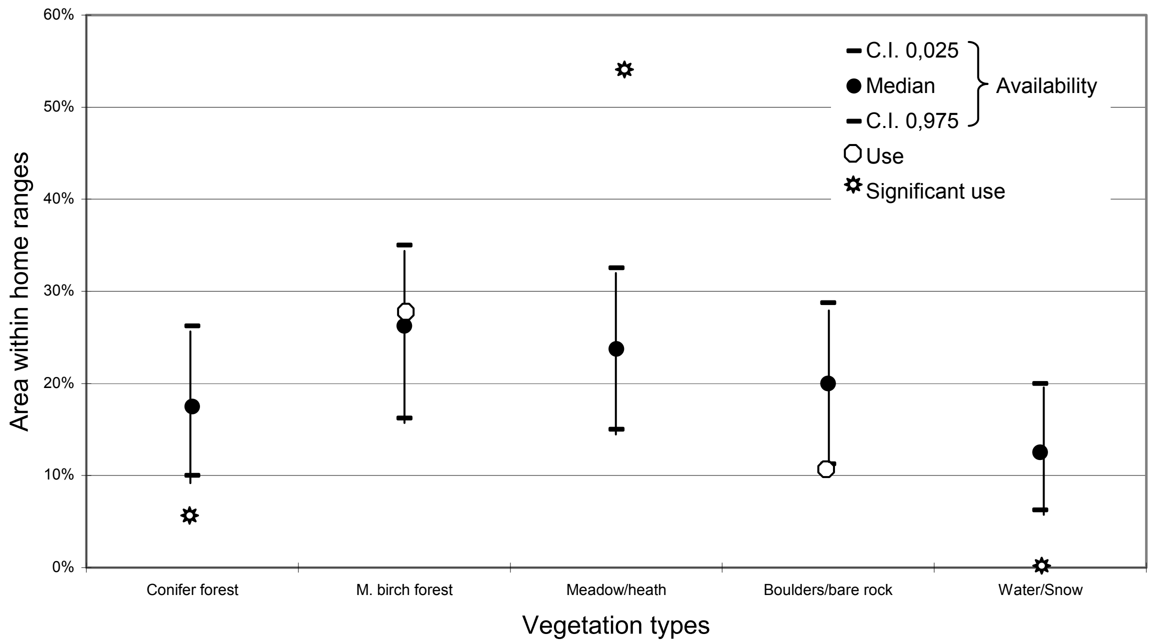

Figure 8a-d. Distribution of rendezvous sites (n = 177) in relation to availability of different habitat types during all rendezvous periods (I, II and III): figure 8a, period I (27/4 – 17/5)(n=46): figure 8b, period II (18/5 – 7/6)(n=85): figure 8c and period III (7/6 - 28/6)(n=46) figure 8d. Availability of vegetation is based on proportions of area within all home ranges. Habitat use that differs significantly from availability is marked with stars.

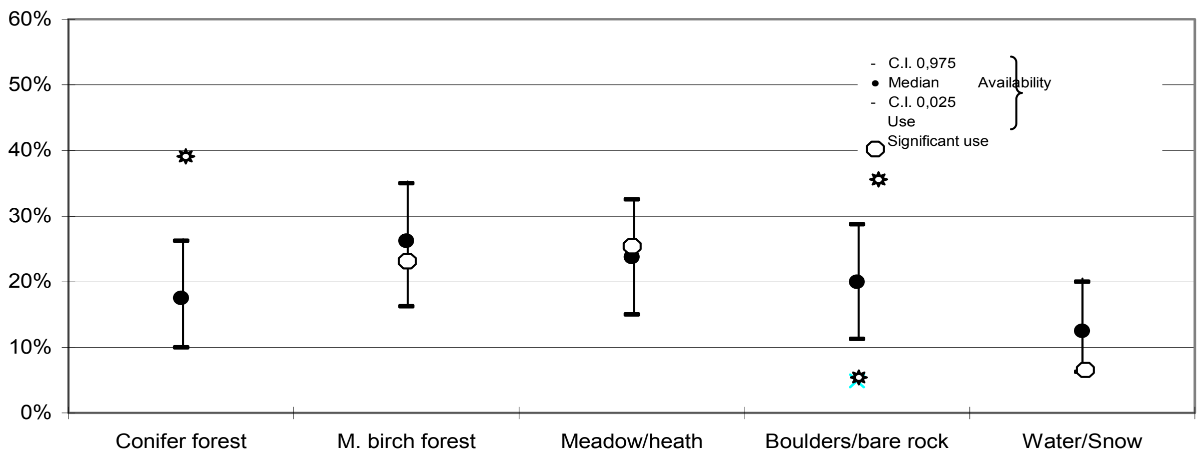

Figure 8b.

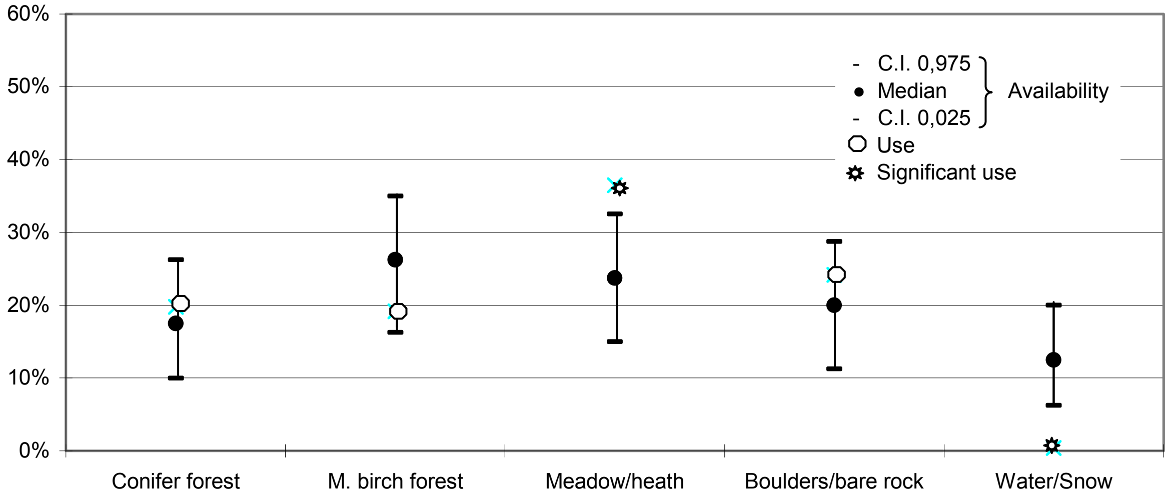

Figure 8c

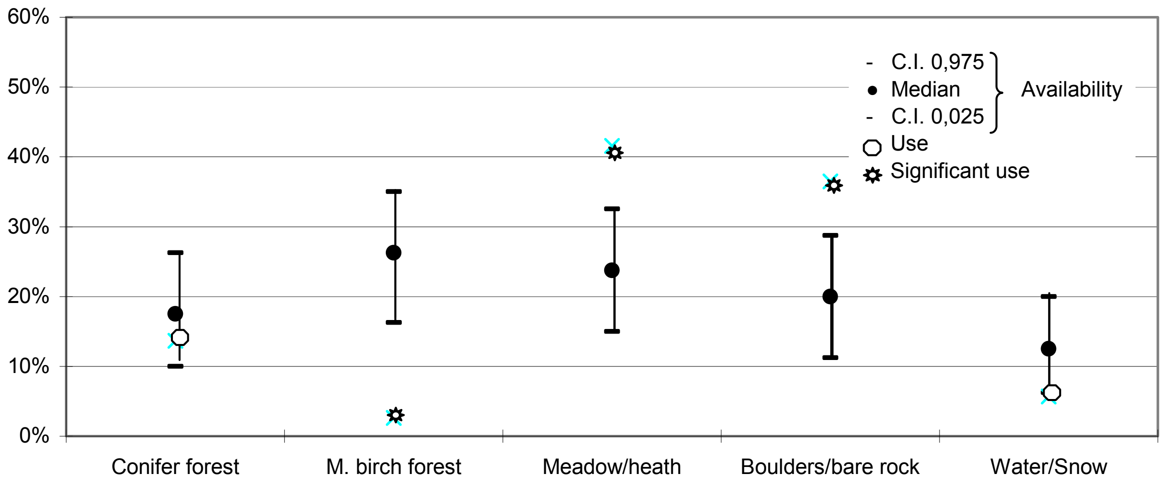

Figure 8d.

3.2.3. Slope

Rendezvous sites were located at slopes ranging from 2 to 36 degrees (mean = 14 degrees; 95% C.I. = ± 39, n = 177; Fig. 9). Slopes between 20–30 degrees were selected for, independently of period. Slopes between 10–20 degrees were selected during period I. No rendezvous sites were found at slopes steeper than 40 degrees (Fig. 9). Flat areas (0–10 degrees) were selected against during all periods.

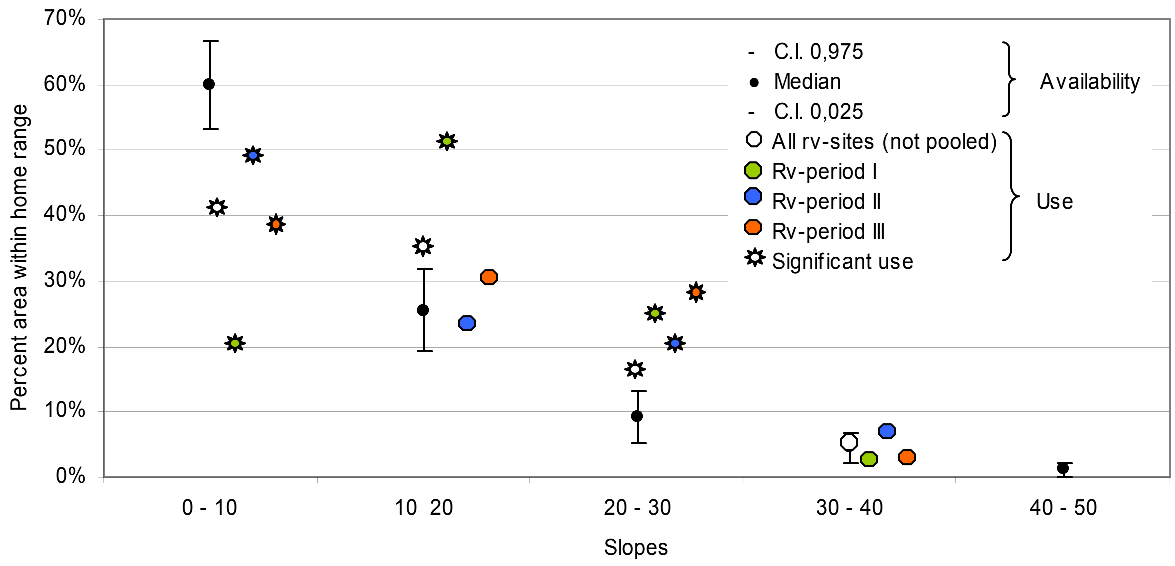

Figure 9. Distribution of rendezvous sites in relation to slope during all periods; period I (27/4 – 17/5) (n = 46), period II (18/5 – 7/6) (n = 85) and period III (7/6 - 28/6) (n = 46).. Availability of slopes is based on proportions of area within all home ranges. Use of slope that differs significantly from availability is marked with stars.

3.2.4 Aspect

North-eastern aspects were selected for when all periods (I, II and III) were pooled together (Fig. 10a) and for periods I and III (Fig. 10b-d). A high proportion (35 %) of the rendezvous sites was facing northeast during period III. Southern aspects were avoided during all periods (Fig. 10a).

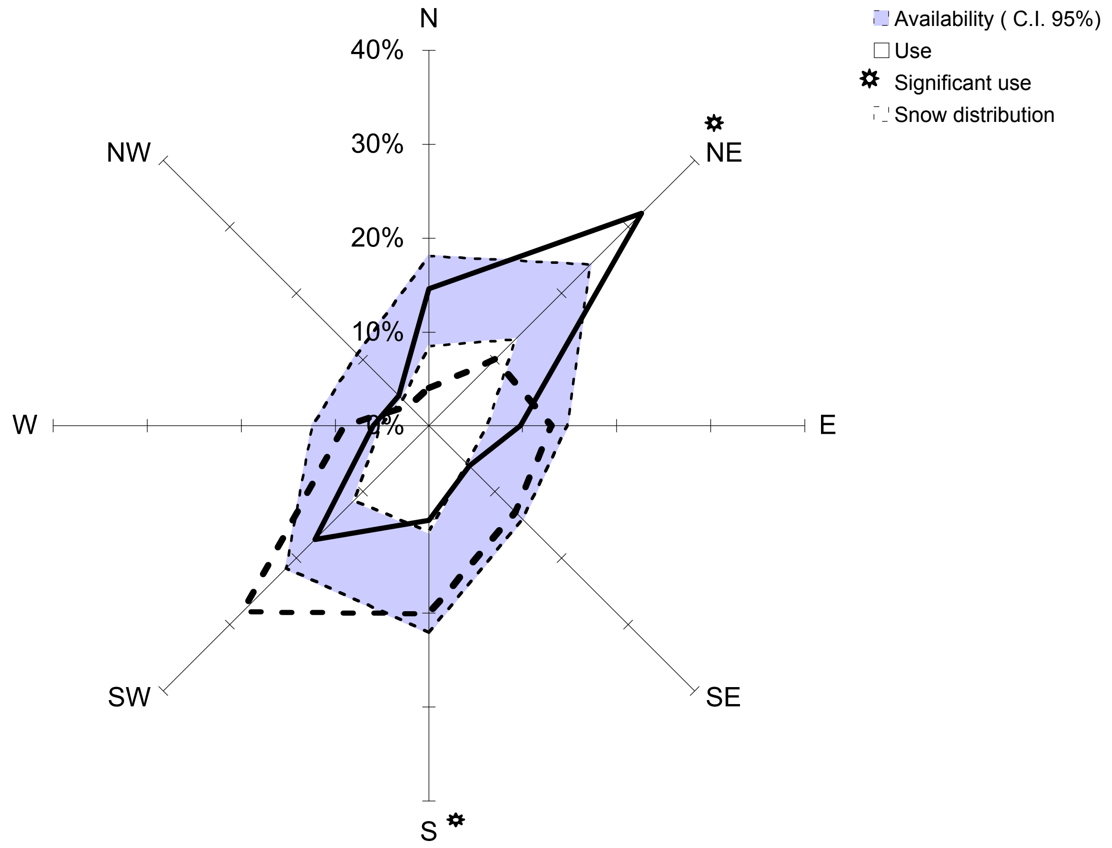

Figure 10a-d. Distribution of rendezvous sites (n = 177) in relation to aspect during all periods (I, II and III): figure 10a, period I (27/4 – 17/5)(n=46): figure 10b, period II (18/5 – 7/6)(n=85): figure 10c and period III (7/6 - 28/6)(n=46) figure 10d. Availability of aspects is based on proportions of area within all home ranges. Use of aspect that differs significantly from availability is marked with stars. Stroked line represents snow depth (snow distribution) in late April.

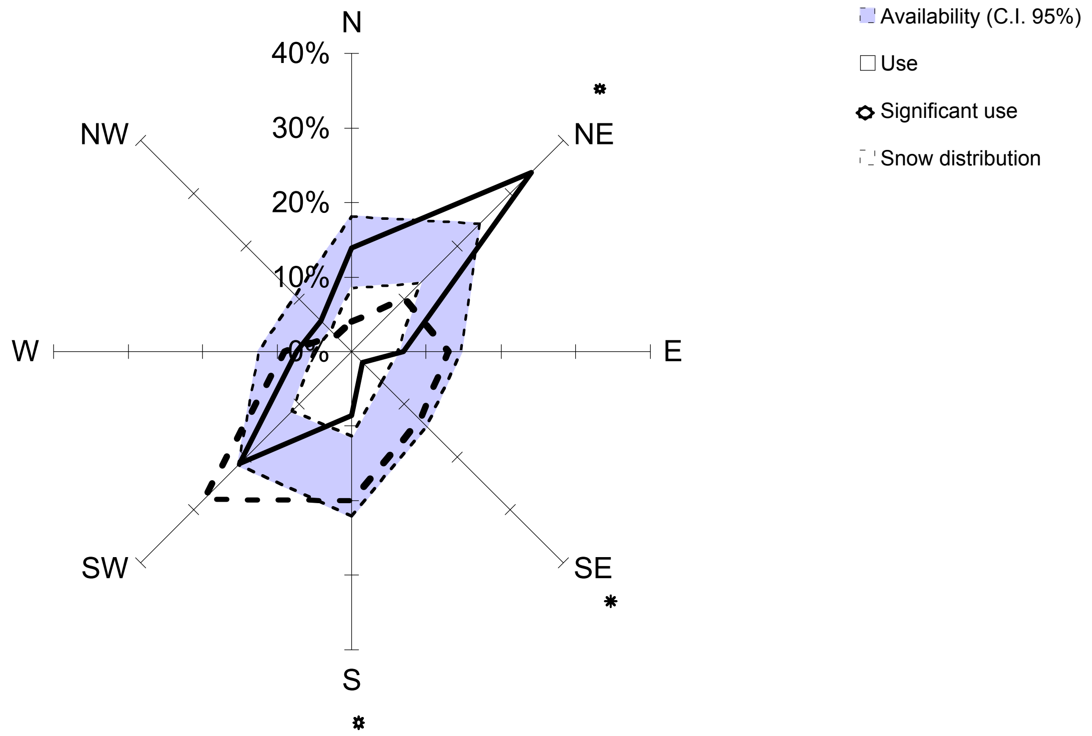

Figure 10b.

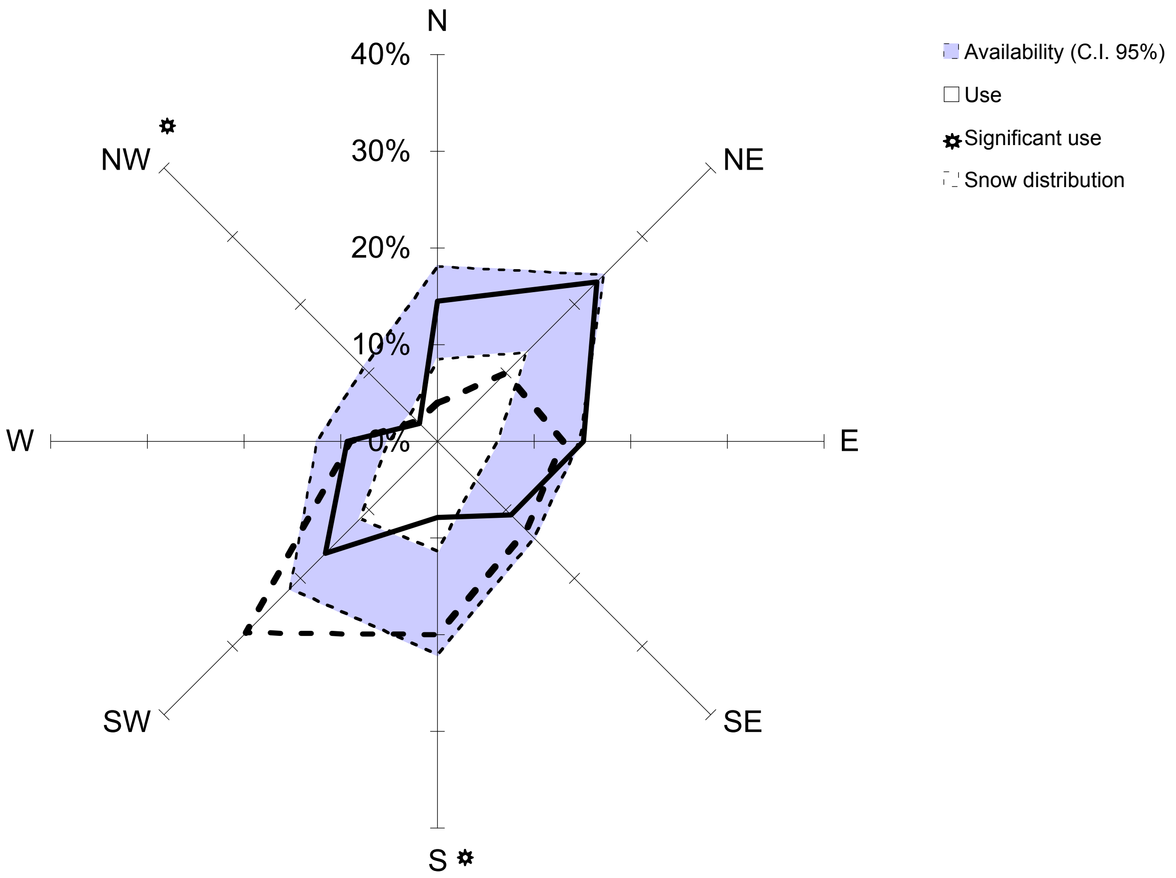

Figure 10c.

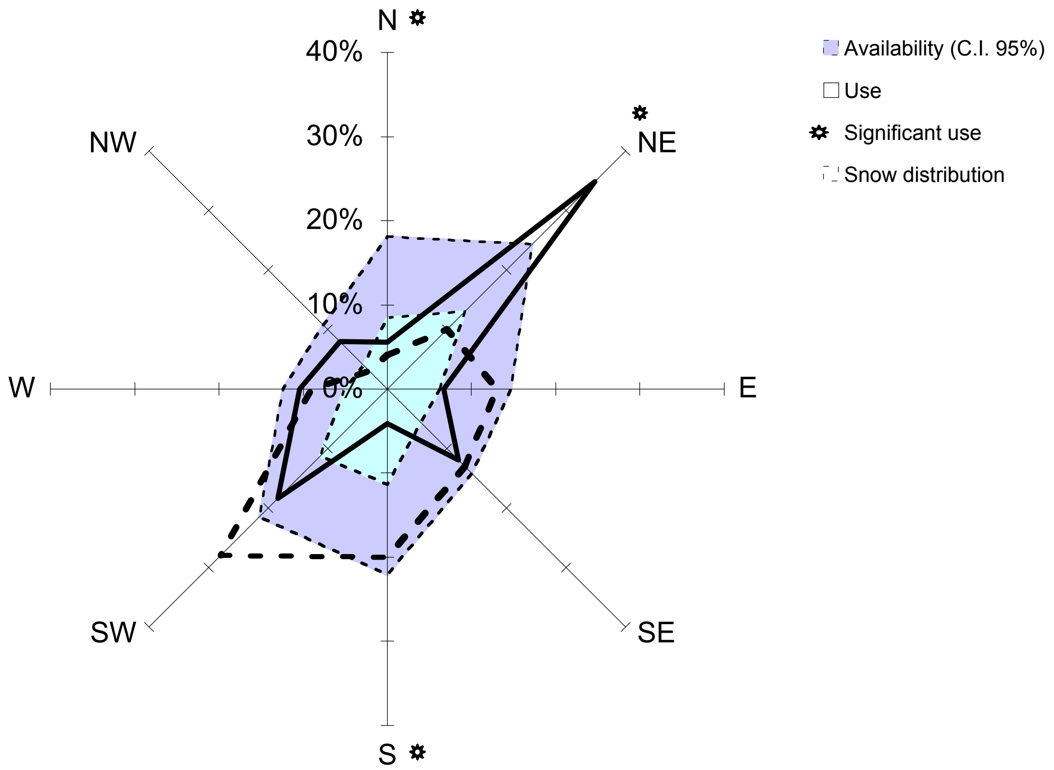

Figure 10d.

3.2.5. Distance to and height above tree line

When excluding home ranges without forest, mean distance to mountain birch tree line was (591 ± 249 m C.I. 95%) and (2 540 ± 983 m C.I. 95%) to conifer forest tree line. Ninety-eight (55%) of the rendezvous sites were located above birch tree line. Only 27 (15%) rendezvous sites were located in conifer forest and 27 (45%) in mountain birch forest. There was a correlation between periods and elevation of rendezvous sites (Fig. 11). During the first period ninety-five (54%) rendezvous sites were located below mountain birch tree line. During period II and III most rendezvous sites were located at higher elevations, above birch tree line.

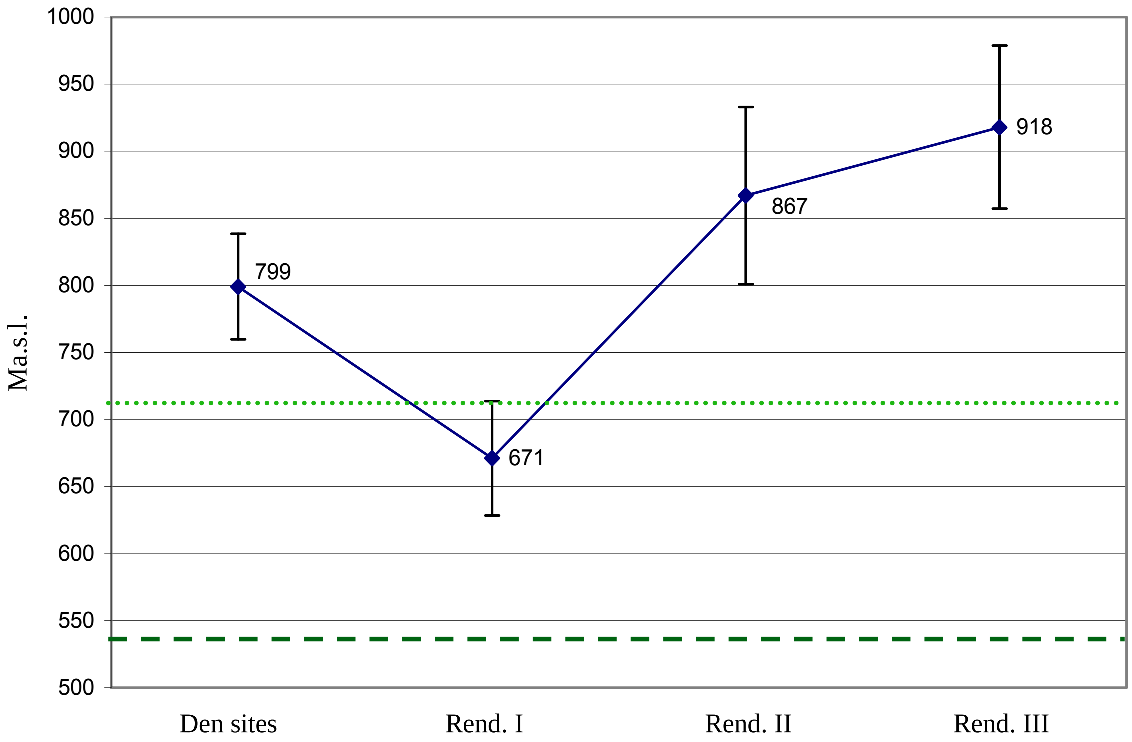

Figure 11. Mean elevation and 95% C.I. for den sites (n = 81) and rendezvous sites, separated into three periods; Rend. I (n = 46), Rend. II (n = 85) and Rend. III (n = 46). The light green line represents birch forest tree line and the dark green line represents conifer forest tree line.

3.3 Differences between den sites and rendezvous sites

Rendezvous sites from period III (918 m a.s.l.) were located at significantly higher elevations than den sites (799 m a.s.l.; t-test; P = 0.01). No difference were found between elevation of den sites and rendezvous sites during period I (t-test; P = 0.22), period II (t-test; P = 0,44) or when all rendezvous sites were pooled (t-test; P = 0.57).

There was an unequal distribution of rendezvous sites among forested (64%) and non-forested (36%) areas. Rendezvous sites were located significantly closer to conifer forest (1 182 ± 279 m C.I. 95 % t-test; P = 0.01) and birch forest (244 ± 89 m C.I. 95 % t-test; P = 0.01) than den sites (2 540 ± 532 m C.I. 95 %/685 ± 167 m C.I. 95 %) during period I. The opposite results were found for the last periods (II and III). During period II rendezvous sites were located further from birch forest (1 582 ± 435 m C.I. 95 %; t-test; P = 0.01) than den sites. I also found that rendezvous sites were located further from conifer forest (6045 ± 653 m C.I. 95 % t-test; P = 0.09) and birch forest (2 313 ± 342 m C.I. 95 % t-test; P = 0.64) than den sites during period III.

3.4 Spatial selection of rendezvous site within home range

After leaving the den site in late spring females move their cubs further and further away from the den site (P < 0.01). Weekly mean distance moved from den site was 508 m and ranged from 0 to 1050 m. The trend line (Fig. 12) illustrates how the increase in distance travelled between the den and rendezvous sites declines by time. During the nine weeks, 19 % (n = 29) of the rendezvous sites was located more than one mean home range radius (5

900 m) from the den site. The largest distance between den and rendezvous site was 10 910 meters. No significant difference in distance moved during the rendezvous period was found between females with one cub compared to females with two cubs.

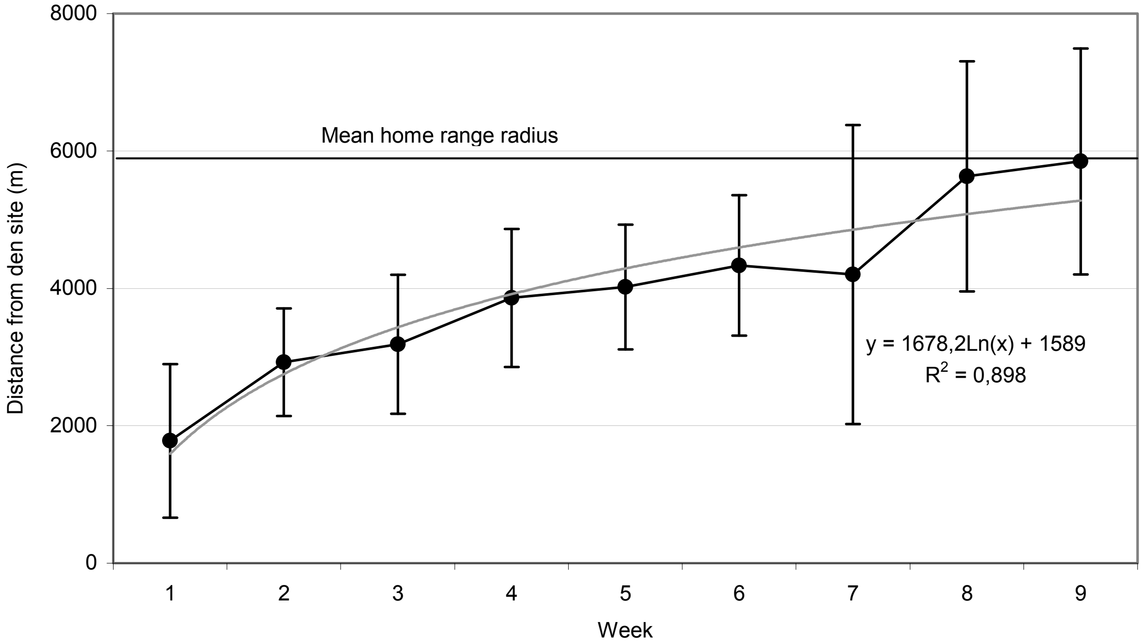

Figure 12. Mean distance moved (m) between den and rendezvous sites in May to July (n = 155). The horizontal line indicates mean home range radius for reproducing females based on 20 home ranges within the study area.

Females with presence of conifer forest and birch forest within their home ranges located den and rendezvous sites at approximately the same elevations. Females without tree cover within their home range showed a tendency to move cubs to lower elevation during the rendezvous period (t-test; P = 0.15; Fig. 13). I found that females that located dens below 800 meters showed a tendency to move their cubs to higher elevations during the rendezvous period compared with females locating their dens above 800 meters (Fig. 14).

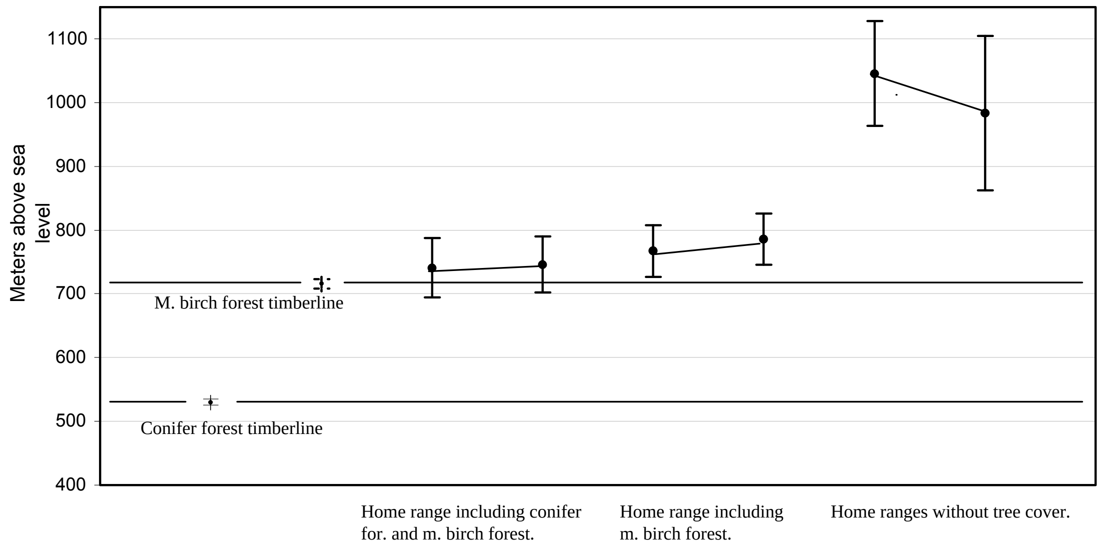

Figure 13. Den and rendezvous sites in relation to tree lines (conifer/birch). Den and rendezvous sites have been divided into three groups based on tree cover within home ranges.

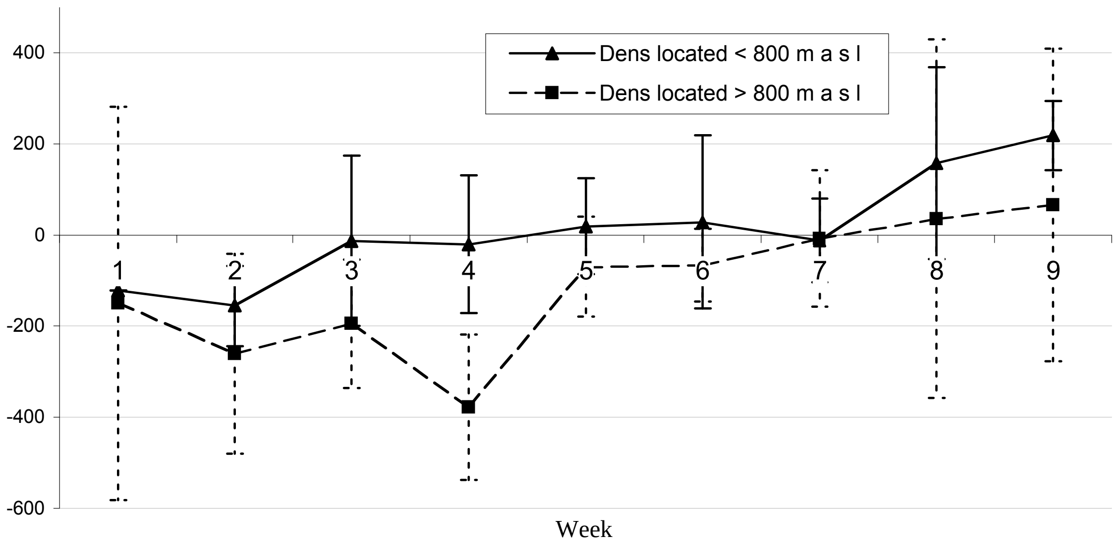

Figure 14. Change in elevation from den site to rendezvous sites by females with den <800m (n = 64) and >800 m (n = 60).

4. Discussion

4.1 Den habitat selection

The results in this study show that a typical wolverine den is located above or close to birch tree line, from 600-800 m a.s.l, at intermediate slopes (10-30), in alpine heaths and meadows facing south-west or north-east. I found that almost 50% of the dens were located within 100 meter from mountain birch tree line. This indicates that forested areas are important for wolverines, even though most dens are found above tree line. These results are in accordance with previous observations from Scandinavia (Pulliainen 1968, Myrberget 1968, Bjärvall 1982, Landa 1998). This study also shows that alpine heaths/meadows were selected for, and that boulder/bare rock-areas were selected against. However, many dens are located in connection to steep cliffs and boulder (Pulliainen 1968, Magoun & Copeland 1998 and Andersen 2002) and frequently in heath/meadow habitat (Persson & Segerström, pers.comm.). In connection to this, it is noteworthy that vegetation maps used in the analysis only show extensive boulder areas, while single boulders or small boulder areas which are suitable as denning sites might be excluded in macro scale vegetation analyses. Similarly, earlier studies show that denning areas are related to snow-covered ravines, rocky scree, and boulder taluses near or above tree line (Pulliainen, 1968, Andersen 2002).

Presumably, female wolverine den site selection is influenced by factors such as spatial structures, nearness to foraging areas and snow distribution. I suggest that the most important factor is availability of spatial structures, such as boulders, cliffs and fallen trees, which are the most common elements of a wolverine den site. Pulliainen (1968) hypothesized that one of the factors affecting the selection of a natal den site was the ease with which it could be adapted to a den. The reason why female wolverines prefer to locate their dens in connection to birch tree line is probably because of access to snow-covered structures above tree line and nearness to foraging areas in the forest. Snow drifts that are built up next to boulders above tree line are probably providing good den sites under the thick layer of snow. I suggest that deep snow is a critical feature for selection of den sites in accordance with previous suggestions from Pulliainen (1968) and Magoun and Copeland (1998). Female wolverines showed a tendency to locate dens in south-western and north-eastern aspects. Snow accumulation in this area is greatest at south-western aspects (Andersson 2001), where 21% of the dens were found. In the opposite aspect (north-east) 22% of the dens were found even though it receives less snow. In the Norrbotten mountains snow drifts often accumulate on north-eastern hill sides giving great variation in snow depth (Andersson 2001). This could explain why female wolverines choose north-eastern aspects in the same proportion as south-western. An additional explanation for use of north-eastern aspects with less snow is late snow thaw. A negative correlation was found between aspects with less snow accumulation and den positioning, as north and north-western aspects which receive the lowest amount of snow. Snow accumulation is influenced by a number of factors, such as; elevation, slope, aspect, vegetation and wind direction. At slopes exceeding 18° the accumulation subsides, probably due to snow slides (Andersson 2001). Earlier reports of den positioning in Scandinavia (Collet 1911–1912, Olstad 1945, Zetterberg 1945, Krott 1959 and Myrberget 1968) show that wolverine dens are mainly found in south or south-western aspects. Pulliainen (1968) reported that no particular aspect was favoured in Finland.

Bjärvall (1982) suggested that cub-rearing females rely more on cached food and less on hunting than the average wolverine. Haglund (1966) found that feeding on carrion was important during early winter and that hunting was less successful because of unfavourable snow conditions. Therefore it is likely that females locate their dens close to carrion, even though wolverines are capable of carrying food long distances (Bjärvall 1982). Female wolverines commonly cache food in the forest during early winter (Segerström, pers. comm.). These caches are important and more likely to be left alone during winter because bears are hibernating and insects are absent. Bjärvall (1982) found that four cub-rearing wolverines in my study area obtained almost all food in the coniferous forest, although their dens were located above birch tree line. However, if food availability is the only factor affecting den site selection, den sites would not be located above mountain birch tree line, where food is abundant during winter.

There was a clear tendency for avoidance of the highest elevations (>1 000 m) and steepest slopes. The highest elevations are dominated by low-productive, steep, rocky areas and glaciers and are probably avoided because of the energy loss associated with moving between such high elevation and the foraging areas in lower elevations. I also found that females showed preference for intermediate slopes between 10 – 40 degrees and avoided low elevation and flat areas. This might be explained by a high proportion of unsuitable denning habitat in low areas, e.g. mires and bogs. Most flat areas are found in low elevations with early spring thaw.

Females in this study preferred to locate dens in non-forested areas rather than forested areas. One third of the den sites were located in forested areas, of these, dens were more often located in birch forest than conifer forest which was selected against. In accordance with my results, Magoun and Copeland (1998) suggested that females prefer non-forested areas for denning even though forested areas are available, and contradict Banci's (1994) suggestion that preference for open habitat showed in previous studies was a result of research being biased to open areas.

4.2 Rendezvous habitat selection

I found that female wolverines locate the early rendezvous sites (rendezvous period I) in lower elevation than den sites. In spring cubs are moved to higher elevations and during period III most rendezvous sites are found above tree line.

During period I (27/4-17/5) most rendezvous sites (63%) were located at lower elevations in forested areas (conifer forest 40%; birch forest 23 %). The reason for locating rendezvous sites at lower elevations right after den abandonment might be related to food availability. During this period reindeer herds are moved to calving grounds and the first reindeer calves are born. Reindeer calves are probably an important food source for wolverines during spring (Bjärvall et al. 1990, Persson & Segerström pers. Comm). In addition, the snow conditions at lower elevations are still favourable for caching of food. Another factor could be human activities. Reindeer herders move reindeers to calving grounds at this time, which increases the snow mobile traffic in areas with sustainable snow conditions. Just a few rendezvous sites were found above 1100 m a.s.l. during the first period.

During period II, rendezvous sites were located at higher elevation, and during period III the highest mean elevation of rendezvous site locations were found. The low elevations (400 and 600 m a.s.l.) tended to be selected against during the same period. At this time there is little snow left at lower elevation and a lot of the cached food has been consumed by other scavengers. In contrast, high elevations might offer more favourable snow conditions for hunting newly born reindeer calves and caching of food and cubs. Furthermore, snowmobile traffic has disappeared from the area because of snow melting. This result supports earlier studies suggesting that wolverines choose higher elevation habitats during summer (Magoun and Copeland 1998, Banci and Harestad 1990, Whitman et al 1986, Gardner 1985, Hornocker and Hash 1981). The reason why wolverines use higher elevation during summer could be several and differ between areas. One important factor is probably related to the options for food storage (Magoun and Copeland 1998) and prey abundance (Whitman et al 1986) that high elevations provide during summer. In Scandinavia, reindeer is the most important prey, especially calves, which are easy prey during spring. Gardner (1985) hypothesized that the use of higher elevation during summer in Alaska was due to concentration of ground squirrels in alpine areas. Hornocker and Hash (1981) believed that wolverines in Montana used higher ranges during snow-free season to avoiding high temperatures and human recreational activity. Another reason might be related to intraspecific predation which is the most important cause of juvenile mortality in Scandinavia and occurs mostly during breeding season, April to August (Persson et al 2003). By occupying high elevations cub-rearing wolverines might be able to avoid confrontations with unrelated males and reduce the risk of infanticide.

Use of aspect might reflect the preference for snow discussed earlier. There was an even greater preference for north-eastern aspects during the rendezvous period than during denning, which indicates that snow is important also after denning. The reason for this pattern is probably late snow thawing and/or accumulation of snow drifts in north-eastern aspects. North-eastern aspects were selected for when all periods were pooled together and for period I and III. As much as 35 % of the rendezvous sites were facing this direction during period III. Southern aspect was selected against during all periods.

The differences found between the three period’s shows that rendezvous habitat analyses during a nine week period need to be divided to finer resolution. The total amount of rendezvous site locations for each female was pooled to avoid unequal influence of the different females. This is a weakness, because information is lost when data is pooled. By using equal numbers of locations from each individual pooling can be avoided.

4.3 Spatial selection of rendezvous site within home range

As expected, wolverine females locate their cubs further and further away from the den site (after den abandonment). The expansion rate of distance moved between den sites and rendezvous sites declined even though the cubs are able to travel greater distances when getting older (Fig. 10). This may correspond to the mean home range radius for wolverines (5 980 m) and indicate that females with cubs avoid the outermost parts of their home ranges, as a strategy to reduce territorial conflicts and the risk of infanticide by neighbouring wolverines. The mean home range radius is based on home ranges with homogenous shape and central placing of the den site, which not always is the truth. A female with a rectangular shaped home range could therefore move greater distances than 5 980 m before reaching the home range border.

4. 4 Den sites vs rendezvous sites

Den sites were found at elevations ranging from 486 to 1316 m and rendezvous sites from 338 to 1456 m. One reason that rendezvous sites were used in broader range is that the female spend a lot of time moving around her cubs within the home range. The higher number of rendezvous site locations (n = 177) compared with den sites (n = 81) might also contribute to the wider range. Period III differed most compared to den sites, e.g. den sites were located at lower elevations than rendezvous sites during period 3.

4.5 Den abandonment

Little information is available about den abandonment and the beginning of the period using rendezvous sites. In Scandinavia den abandonment takes place from late April to June, when cubs weigh 3-4 kg and are quite mobile (Landa et al 2000). In this study, the earliest rendezvous site was located in the end of April (28/4). Why females abandon the den is not fully understood. The difference I found in habitat selection, especially aspect, between den sites and rendezvous sites indicates that snow distribution is affecting den abandonment. Females avoid southern aspects when selecting rendezvous site but not when selecting den site. This is probably caused by greater sun exposure causing early snow melt in southern aspects compared to northern aspects, were most rendezvous sites were found. Magoun and Copeland (1998) found that den abandonment in Alaska and Idaho was associated with the first days of temperature above freezing. They found that wolverine females in arctic Alaska remained in the den until late April or early May, and that den abandonment differed with 1 month between their two study areas in Alaska and Idaho. I also found a preference for high elevation during the rendezvous-period which could be caused by several factors as later snow melting or food availability, or a combination of these factors. In that case, females with dens in sun exposed locations and lower elevations should abandon their den earlier than other females. There should also be a greater preference for north-eastern aspect when selecting den sites if these aspects are protected from early spring thaw. The reason why there is not could be that snow drifts in north-eastern aspects are build up after females choose their den sites.

5 Conclusion and implications for management

In this study, I have shown that denning wolverines show preference for elevations between 700 - 800 and 900 - 1000 meters, alpine heaths and meadows and slopes between 10 – 40 degrees. I also found that females tended to select den sites in aspects facing southwest; where the greatest accumulation of snow was found, and northeast; where most snow drifts are built up and snow thaw is late. Almost 50% of the dens were located within 100 meters from mountain birch tree line.

After den abandonment the cubs are cached in lower elevations, often in connection to conifer forest. During period II (18/5 – 7/6) and III (8/6 – 28/6) cubs are cached in rendezvous sites in higher elevations above tree line and primarily in north-eastern aspects. There was an even greater preference for north-eastern aspects during the rendezvous period then denning period, indicating that snow is important even after denning. A possible reason is that snow covered areas are used for food caching as late as possible.

I have shown that females move there cubs further and further away from the den site after den abandonment. And that the expansion rate of distance travelled between den sites and rendezvous sites declined during the rendezvous-period, even though the cubs are able to travel greater distances when getting older. My suggestion is that cub-rearing females avoid confrontation with neighbouring females and reduce the risk of infanticide by avoiding the outermost parts of the home range.

Knowledge about habitat requirements of cub rearing females can improve our understanding of what is affecting distribution and habitat suitability. Understanding denning habitat requirements can also improve monitoring by limiting search effort to certain habitats. These results do not tell which habitat parameter that is most important to denning wolverines. One important parameter not analysed in this paper is food availability, mainly reindeer distribution. By including this parameter one would probably get a picture of spatial distribution of denning wolverines, and wolverines as a species. More research is also needed to find what habitat is most favourable for cub-rearing females. By comparing habitat use with reproductive success one could get a better picture of how different habitats affect reproduction. This could help when predicting wolverine recovery zones where habitat quality is high.

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Appendix 1.

Den sites

Parameter	n	Mean	Range	Reference
Elevation				
North America, Alaska	?	66% above tree line		Rausch and Pearson 1972
North America, Idaho	2	>2500	1400 – 3279	Magoun and Copeland 1998
North America, Alaska	3	560 – 625		Magoun and Copeland 1998
Norway, (South)	10	1120 ± 125[a]	960 – 1300	Landa 1997
Finland	31	Near or above tree line		Pulliainen 1968
Norway	25	Most above tree line	200 – 1500	Myrberget 1968
Sweden, Sarek[d]	17	772 ± 164[b]	510 – 1120	Löfstrand 2000
Sweden, Sarek	4	700 – 800		Bjärvall 1982
Sweden, Sarek[d]	**81**	**799 ± 42[a]**	**486 – 1316**	*****
Slope				
Sweden, Sarek[d]	17	17 ± 10	6 – 38	Löfstrand 2000
Sweden, **Sarek[d]**	**81**	**20 ± 2**	**4 – 39**	*****
Distance to conifer treeline.				
Sweden, Sarek[d]	17	2650 7	0 – 15120	Löfstrand 2000
Sweden, **Sarek[d]**	**81**	**2540 ± 983[c]**	**0** – 10170	*****
Mountain spruce				
Sweden, Sarek[d]	17	842,5	70 – 2200	Löfstrand 2000
Sweden, **Sarek[d]**	**81**	**1290 ± 356[c]**	**0** – 4760	*****

a = Confidence interval, C.I
b = Standard deviation, S.D
c = Only female with forest within home range
d = Studies partly based on same individuals.

Appendix 2.

Vegetation groups

Veg. code (SMD)	Type of vegetation	Vegegation group
40	Broad-leaved forest not on mires / Lövskog ej på myr eller berg i dagen	Mountain birch forest
41	Broad-leaved forest on mires / Lövskog på myr	Mountain birch forest
42	Broad-leaved forest on open bedrock / Lövskog på berg-i-dagen	Mountain birch forest
43	Coniferous forest on lichen-dominated areas / Barrskog på lavmark	Conifer forest
56	Coniferous forest not on lichen-dominated areas / Barrskog, ej på lavmark	Conifer forest
44	Coniferous forest 5-15 meters / Barrskog ej på lavmark 5-15 meter	Conifer forest
45	Coniferous forest > 15 meters / Barrskog ej på lavmark > 15 meter	Conifer forest
46	Coniferous forest on mires / Barrskog på myr	Conifer forest
47	Coniferous forest on open bedrock / Barrskog på berg-i-dagen	Conifer forest
48	Mixed forest not on mires / Blandskog ej på myr eller berg i dagen	Mountain birch forest
49	Mixed forest on mires / Blandskog på myr	Mountain birch forest
51	Natural grassland / Naturligt gräsmark	Meadow/heath
52	Moores and heathlands / Hedmark (utom gräshed)	Meadow/heath
53	Thickets / Busksnår	Meadow/heath
54	Clear-felled areas / Hygge	Meadow/heath
55	Younger forest / Ungskog	Mountain birch forest
59	Bare rock / Berg i dagen	Block
60	Sparsely vegeated areas / Områden med sparsam vegetation	Block
63	Grass tundra / Gräshed	Meadow/heath
64	Meadow grasses / Örtäng	Meadow/heath
70	Inland marshes / Limnogena våtmarker	Water/ice
71	Wet mires / Blöt myr	Water/ice
72	Other mires / Övrig myr	Water/ice
80	Water courses / Vattendrag	Water/ice
81	Lakes and ponds, open surface / Sjöar och dammar, öppen yta	Water/ice

Veg. code (Mountain map)	Type of vegetation	Veg. group
101	Boulder and flat rock / Block- och hällmark	Block
108	Glacier / Glaciär	Water/ice
109	Water / Vatten	Water/ice
111	Alpine grass heath / Alpin gräshed	Meadow/heath
112	Twig heath / Skarp rished	Meadow/heath
113	Dry heath / Torr rished	Meadow/heath
114	Fresh heath / Frisk rished	Meadow/heath
115	Wet twig heath / Fuktig-våt rished	Meadow/heath

121	Alpine low-herb meadow / Alpin lågörtäng	Meadow/heath
122	Alpine high-herb meadow / Alpin högörtäng	Meadow/heath
123	Meadow / Ängsmark	Meadow/heath
131	Cultivated land / Kulturmark	Meadow/heath
132	Snowbed / Snölega	Water/ice
141	Bog with twigs / Rismyr	Water/ice
143	Dry marsh / Torrt kärr	Water/ice
144	Marsh in slope / Backkärr	Water/ice
145	Wet marsh / Vått kärr	Water/ice
146	Mixed bog / Blandad myr	Water/ice
150	Osier / Vide (Salix)	Meadow/heath
161	Heath birch forest / Lavrik hedbjörkskog	Mountain birch forest
162	Heath birch forest / Mossrik hedbjörkskog	Mountain birch forest
163	Meadow birch forest / Ängslövskog	Mountain birch forest
171	Coniferous forest rich in lichens / Lavrik barrskog	Conifer forest
172	Coniferous forest rich in mosses / Mossrik barrskog	Conifer forest
173	Meadow spruce forest / Ängsgranskog	Conifer forest