## Habitat selection and wolverine depredation-risk in freeranging sheep at an alpine pasture

Valg av habitat hos sau på beite i høgfjellet og risiko for å bli drept av jerv



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### Preface

This study has been a part of the Norwegian Wolverine Project. A research project at the Norwegian Institute of Nature Research (NINA), in Trondheim. It was done as a Master Thesis at the Agricultural University of Norway (NLH) at Ås.

First of all I would like to thank my supervisor Dr. Arild Landa at NINA for giving me the possibility to do this thesis, for all help and for giving me the chance to participate in the Norwegian Wolverine Project. Thanks also for showing me my first sight of playing wolverine cubs, at Breidslågåtangen.

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Now I want to announce some important words; As my study of Nature Management now ends here, I want to thank my study comrades for unforgettable memories through five fine years with friendship, through struggle and peace, and for now finally facing the end of this trail.

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### Summary

Habitat use and wolverine-caused mortality of domestic sheep was studied on an alpine range in south-central Norway during the grazing season of 2003. Radio telemetry was used to locate sheep and wolverines on the open range to document movements of both, and to recover sheep carcasses early to establish whether or not they were wolverine killed by wolverines. The question asked was whether sheep were killed in locations with different habitat characteristics than preferred habitat. The other central question was whether depredated sheep were found in habitats that were similar to the habitats utilised by living sheep during the time when wolverines are most active. Lamb mortality in relation to lamb sex and age of the mother were also documented.

Domestic sheep used different habitats throughout the season. Use of different habitats followed an altitudinal gradient, decreasing in altitude throughout the season. The utilisation changed from open grass habitat to more closed bush habitat in the end of the season. The flock size decreased throughout the season. The habitat utilization varied diurnally with consistent daily movements between day habitat to open bed site habitats at higher altitudes, containing fewer bushes and more rock. The flock size increased towards midnight and decreased until noon.

Sheep were killed by wolverines in different habitats than their preferred habitat. The probability mortality decreased with an increasing amount of rock and increased with and increasing amount of bush cover. The results also suggest that sheep were killed during the evening, as evening habitat of living ewes was most like the habitat around the sheep found to be killed by wolverines.

Carcasses which were deemed to have been moved after death were found closer to water than those who were not deemed to have been moved after death. I found no sex-specific differences in lambs killed by wolverines, nor total losses. Probability of lamb survival was positively related to age of the mother. Losses varied between different farmers. Home ranges were not related to age of ewe. The home ranges were relatively large compared to other studies in alpine ranges, but similar to other studies in coniferous habitats with predators present. The sheep appeared to be most vulnerable to wolverine depredation in bush habitat, outside their preferred habitat and during the evening. Domestic sheep in alpine habitats showed consistent movements to bed sites at higher altitudes, often containing rocky habitat which were less related to predation.

For management this implies that in alpine areas particular sheep and sheep breeds that consistently move to bed sites at night should be favoured. Individuals avoiding areas containing bushes at day should also be favoured. As both lamb loss and utilisation of bush habitat increases towards the end of the season, while grazing quality often is poor, collecting sheep earlier should seriously be considered, especially in Knutshø where lamb slaughterweights were high. That fewer lambs of young mothers survive the grazing season should be considered when planning age structure of the sheep flocks, and when choosing mothers for foster lamb.

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### **APPENDIX 1**

### **1** Introduction

The first sheep were domesticated approximately 8500 years ago (Squires 1975), traced to the areas south of the Caspian Sea (Hansen *et al.* 1998). The oldest traces from domesticated sheep (*Ovies aries*) in Norway come from the places Dønna, Fana and Leka approximately AD 1500. The origin of the domestic European breeds is *Ovis musimon* from Corsica and Sardinia in Italy (Berge 1942). The ancestor of *Ovis musimon* is the *Ovis vignei*; a steppe-living sheep, that live in the areas between Persia and Tibet. Today there are more than 200 breeds of domesticated sheep (Mason 1951).

During thousands of years of growers selection, the reproduction has gradually been human mediated to maximise wool, meat and offspring production. Humans have protected their livestock against depredation with tending, fences and by keeping them inside houses. Anti-predator behaviour has decreased during this period as a result of decreased selection pressure (Tømmerberg 1985).

The present Norwegian method of sheep husbandry is based on free-grazing mainly unguarded sheep released on open range areas in the middle of June, and collected in the middle of September. During the summer months June to September, domestic free ranging sheep are the most numerous large mammals in many areas of Norway (Berg 1990). Where large predators are temporarily or constantly present in the grazing areas containing thousands of free ranging sheep, depredation in some extent is unavoidable. Small populations of large predators since the turn of the 18<sup>th</sup> Century until recently, and a high demand for efficiency may be the reason why this vulnerable way of keeping sheep still dominates. Depredation on domestic sheep, however, is an increasing problem, as a result of the recovery of large carnivore populations (Landa *et al.* 1999).

The local variation in losses among adjacent grazing areas can be large, even when within the home range of a large predator. A normal loss of free-ranging sheep in areas without large predators is approximately 5% and 2% for lambs and ewes respectively (Mysterud & Mysterud 1995). In some areas lamb losses to wolverines (*Gulo gulo*) have exceeded 40% (Landa & Tømmerås 1997). In 2003, 31,700 domestic free-ranging sheep were lost because of depredation by wolverine, lynx (*Lynx lynx*), brown bears (*Ursus arctos*), wolves (*Canis* 

*lupus*), or golden eagles (*Aquila crysaetos*). The Norwegian government in total paid an amount of 45,637,170 Norwegian Kroner (553,4450 Euros) in compensation for domestic sheep killed by these predators in 2003. Same year the Norwegian government compensated owners for 14,500 wolverine-killed sheep based on 937 documented cases (Directorate for Nature Management, 2003).

Sheep have the ability to utilise the rough grazing resources in otherwise unproductive areas. Thus, they contribute to the possibilities for people to have a sustainable living in areas with few other sources of income. But the government also uses considerable amounts of money for the administration of compensation and on preventive measures (Landa and Tømmerås 1996). If studies of sheep and depredation could provide knowledge that could help to reduce the depredation, it would both favour the state and the economically stressed sheep owners.

Species experiencing predation develop strategies to avoid being predated, such the predation probability is minimised (Berge 1942). Prey display a variety of strategies to lower predation vulnerability, including fighting, flight, hiding and temporal and spatial distributions that minimize overlap with predators (Edmunds 1974). The wild sheep display strong antipredator behaviour; by staying in flocks, showing shy and attentive behaviour and escaping quickly. Also they are prepared to defend their offspring if necessary (Berge 1942). Antipredator strategies are also closely linked to selection and use of habitat. Species adapted to hiding, moving into cover or outrunning a predator all depend on appropriate habitat (Jarmann 1974). Animals also experience a trade-off between forage-acquisition and the cost of predator avoidance (Bell 1991).

The relationship between habitat and predation risk has been reviewed in detail in some species where predation is relatively easily measured, for instance in grey squirrels (*Sciurus carolinensis*) (Newman & Caraco 1987). In ungulates, however, very few studies have documented the actual risk associated with habitat use. It may be possible, given a relationship between habitat use and anti-predator strategy that ungulates use various terrain and vegetation features to decrease their vulnerability to predators, as was shown for domestic reindeer in Henaug (2000).

Despite the long period of human selection, domesticated sheep still display some of the daily behavioural traits as their ancestors (Tømmerberg 1985). This includes consistently daily

movements from low grazing sites at day to higher resting sites at night (Mysterud and Warren 1991), which could have been developed to avoid predators. But these consistently movements was by Welch (1981), suggested as shelter–seeking behaviour where sheep habitat preferences in Scotland ranged between rich open grassland to heather from day until evening and night.

Most bighorn sheep (*Ovis Canadensis*) migrate seasonally over an altitudinal gradient (Geist 1971), probably to have access to nutritious, growing forage for an extended time (Festa-Bianchet 1988). Several studies of domestic sheep have shown a daily pattern of habitat use where poor forest or habitat types were utilized in the evening and night, and richer types during the day (Warren and Mysterud 1991; Welch 1981). Bowns (1971) found that domestic sheep flock in the evening and in the middle of the day, while they are resting. (A study in Scotland in June also found that flocks of Blackface hill sheep were denser and larger during the night and evening, than during the day, even when there were no predators present (Hewson and Verkaik 1981). In a study of wild sheep by Festa-Bianchet (1988), bighorn-ewes with lambs chose poor grazing areas with good protection against predation over good grazing areas with less protection against predation.

It is well documented that domestic sheep in a variety of habitats prefer bedding sites on high ground (Bowns 1971; Welch 1981; Stensli 1988; Warren and Mysterud 1991) and display an altitude preference, going down slope in the morning from resting sites to grazing sites and upslope in the evening (Warren and Mysterud 1991; Bowns 1971). These diurnal behaviour patterns are more or less typical for both domestic sheep and wild sheep (Lynch 1971: merino sheep, Simmons 1980: desert big-horn sheep, Scott and Sutherland 1981: merino sheep, Welch 1981: Scottish blackface sheep, Seip and Bunnell 1985: stones sheep), and could have been developed to avoid predators. Diurnal behaviour patterns in Norway have also been documented for domestic sheep in forested habitat, in Trysil (Warren & Mysterud 1991), and Grue (Stensli 1988). In Norway few studies have examined anti-predator behaviour in domestic free-grazing sheep in alpine habitats.

The mortality patterns of free-ranging domestic sheep in Norway (Directorate for Nature Management 2003) are similar to patterns reported for other domesticated animals and wild ungulates (Linnell *et al.* 1995). The age of mother in wild ungulates has been shown to have a significant effect on lamb or calf mortality (Purser and Young 1959; Guinness et al. 1978: red

deer (*Cervus elaphus*), Festa-Bianchet 1988: Big-horn sheep). In a study by Warren & Mysterud (1995) in Hedmark, the factors ewe age, lamb sex, lamb body weight and lamb growth rate were found to influence sheep mortality. Factors that might explain why ewe age may influence lamb mortality are for instance: Young ewes give birth to lighter lambs (Purser and Young 1964), have higher lactation costs (Festa-Bianchet 1988), and generally have poorer rearing capacity (Hewson and Verkaik 1981; Petersson and Danell 1985). The younger dams may provide maternal care of lower quality, because lambs of young ewes are more vulnerable to predators than lambs of older ewes (Warren 1996). If this relation also exists in free-ranging sheep experiencing wolverine depredation in alpine areas is unknown.

Sheep grazing on open range usually adhere to a limited area or home range (Hunter 1964). The home range is an area with which the grazing animal is familiar. This familiarity enhances efficient use of resources, such as forage, salt and water (Provenca and Balph, 1987), and is also associated with lower rates of predation (Blakesley and Mcgrew, 1984; Nelson and Mech, 1991).

The sheep's choice of home range and the factors influencing home range size are many and complicated. Vertebrate home range size is generally related to body size and habitat productivity (Harestad and Bunnell 1979). Habitat quality is a function of both obtainable energy and predation risk (Brown 1992 and references therein). Increased predation risk decreases suitable habitat of animals, and this might force the animal to enlarge its home range (Brown 1988). Studies carried out in Troms County and on the Snøhetta showed an increase of sheep killed by wolverine towards the end of the summer season (Landa *et al.* 2003, in: Brainerd (red.) 2003). An increased use of areas containing sheep, by wolverine, was found in the end of the grazing season, which may explain the increase of depredation in this period (Landa et al. 2003, in: Brainerd (red.) 2003).

This study was designed to determine whether wolverine depredation on sheep during summer takes place in sites with specific terrain and vegetation attributes. The main question posed is whether sheep are killed in locations where the habitat characteristics differ from preferred habitat. The other central question is whether depredated sheep occur in habitats that are most like the habitats utilised by living sheep during the hour period when the wolverine is believed to be most active. Whether home range size was related to ewe age and whether mortality was related to lamb sex and age of the lambs' ewes were also tested. Hypotheses posed in this study are :

- HA1: Free-ranging domestic sheep change habitat preference during the season.
- **HA2**: Free-ranging domestic sheep show a diurnal habitat use changing from grazing sites during daytime to bedding sites during evening/night.
- **HA3**: Free-ranging domestic sheep show anti-predator behaviour by staying in larger flocks at evening/night.
- HA4: Flock size decreases as grazing quality decrease at the end of the grazing season.
- **HB1**: Depredated sheep that were apparently moved by wolverines after being killed, are found in different habitats than those that were apparently not moved.
- **HB2**: Free-ranging domestic sheep are not killed by wolverines in generally preferred habitat.
- **HB3**: At the end of the grazing season sheep are killed by wolverines in different habitat than that used by living sheep.
- **HB4**: Sheep are killed by wolverines in the habitats being preferred in the hour periods the wolverine is believed to be most active.
- H0C1: There is a higher mortality risk for lambs with younger mothers, and for male lambs.
- H0C2: Younger ewes use larger home ranges.

### 2 Material and Methods



Figure 1. The Study took place where the borders of Sør-Trøndelag, Oppland and Hedmark Counties meet.

#### 2.1 Study area

This study was concentrated in south central Norway, in the Knutshø Mountain Ranges at the borders of Sør-Trøndelag, Hedmark and Oppland counties (62°09' N, 9°41', Fig.1).

The habitat description around wolverine-killed sheep and the radio telemetry study were done in the mountain areas of Knutshøi, Heimtjørnshøi, and Elgsjøen. This was concentrated to the mountain range Knutshøi, generally east of E6, West of Råtåsjøhøi and Elgsjøtangen, south of the northern end of Elgsjøen, including Kvitdalen and the areas north of Kvitdalen in Oppdal-, Folldal- and Dovre Municipalities (Fig. 1).

The area is characterized by north-south directed mountain ranges with peaks up to 1690 m altitude with small valleys between, laying at 950 m.

The bedrock contains calcareous spar especially in the Knutshø area, and the areas east and northeast of Knutshø area consist of tuffite and green phyllite. The calcareous bedrock, which is easily weathered and the abundant ground water sources provide a good growth potential

for both grasses and herbs. This area is one of the Norwegian mountain areas with the richest flora, containing several rare and endemic species (Bretten *et al.* 1994).

The tree line is at about 1050 m, with birch (*Betula pubescens*) dominating at the highest altitudes, between 800 and 1050 m, and pine (*Pinus sylvestris*) dominating below the birch belt. The vegetation in the birch belt varies. In areas with an acidic soil, blueberry (*Vaccinium myrtillus*) forms the ground cover, and crowberry (*Empetrum nigrum*) dominates on dry places with low snowfall. Areas rich in nutrients and with stabile water sources have tall-fern woodland, with species like alpine blue-sow-thistle (*Cicerbita alpina*), wolf's-bane (*Acontium septentrionale*), Scandinavian small-reed (*Calamagrostis purpurea*) and ferns like lady-fern (*Athyrium filix-femina*) and northern buckler-fern (*Dryopteris expansa*) (Bretten *et al.* 1994).

In the ecotone from the birch belt to the open low alpine areas; locations rich in water and nutrients often contain different species of willow (*Salix spp.*) like (*Salix glauca*), downy willow (*S. lapponum*), tea-leaved willow (*S. phylicifolia*), woolly willow (*S. lanata*) and whortle-leaved willow (*S. myrsinites*). Especially at some places in the Knutshø mountain range, there are high willow belts in the low alpine zone (Bretten *et al.* 1994).

The low alpine zone on the south slopes of Søndre Knutshøi goes up to 1450 m, but decreases in altitude towards north and west. The highest part of this zone is the upper limit for dwarf birch (*Betula nana*), and is featured by species like blueberry, mountain avens (*Dryas octopetala*), and different species of willow (*Salix* spp.). The flora is characterized by species like bog bilberry (*Vaccinium uliginosum*), trailing azalea (*Loiseleuria procumbens*), bearberry (*Arctostaphylos uva-ursi*), mountain bearberry (*Arctostaphylos alpinus*) and crowberry (Bretten *et al.* 1994).

The middle alpine zone covers the highest parts of the Knutshø alpine range, 250-350 m above the low alpine zone. Wind and snow covering the ground during spring characterize the vegetation, which is dominated by grass and sedge species like three-leaved rush (*Juncus trifidus*), sheep's-fescue (*Festuca ovina*), stiff sedge (*Carex bigelowii*) and wood-rush species (*Luzula spp.*) (Bretten *et al.* 1994).

Areas with less nutrient-rich bedrock contain a fewer species and are characterized by vegetation like dwarf birch, greplyng<sup>1</sup> (*Loiseleuria procumbens*), crowberry (*Empetrum hermaphroditum*), blueberries , smyle<sup>1</sup> (*Deschampsia flexuosa*), gulaks<sup>1</sup> (Anthoxanthum odoratum), blålyng<sup>1</sup> (*Phyllodoce caerulea*), safranlav<sup>1</sup> (*Soloria croces*) and fjellmo<sup>1</sup>. The

<sup>&</sup>lt;sup>1</sup> Norwegian Name

areas surrounding Knutshø, with poor soil cover, are at many places featured by thick layers of lichens like Kvitkrull<sup>1</sup> (*Cladonia Stellaris*) (Gjærevoll *et al.* 1975).



Figure 2. Normal temperatures, normal precipitation, temperatures, and precipitation in 1961-1990 and in 2003, at Fokstua Weather station in Dovre Municipality.

The weather data was collected at Fokstua weather station (nr.16610) in Dovre Municipality, at 972 m. There is an inland climate, which is influenced by the more oceanic climate to the west (Gjærevoll *et al.* 1975). The mean temperature during June-Sept 2003 was 9.4°C, higher than the normal temperature from 1961-1990 which was 8°C. The total precipitation during the summer in 2003 was lower (194 mm) than the normal precipitation for the period 1961-1990 (222 mm) (Norwegian Meteorological Institute).

Generally the southern Norwegian wolverine population has increased in numbers and distribution during recent years. Based on the minimum of registered active natal dens during 2001-2003, the total Norwegian population was estimated to be 251 adult individuals, of which 79 are found in southern Norway (Brøseth & Andersen 2003). In 2003 17 dens of wolverines documented breeding or assumed breeding were found in the southern Norwegian population. In Folldal Municipality/ Knutshø wolverines were documented breeding/ assumed breeding in two dens in spring 2003, and also in the mountain plateaus surrounding Folldal (Snøhetta (3), Rondane(2), Alvdal(1)) dens were observed with wolverines documented-/ assumed breeding the same year (Brøseth & Andersen 2003). During winter and spring 2003,

at least one female gave birth to two cubs in the mountains of Knutshø. They were radio marked in April.

Two separate depredation-control permits were issued during August, and two wolverines were shot. One unmarked wolverine male was shot in Høggia on 3 August, and the radio-marked juvenile female was shot at Storhøi the 15 August. The depredation-control permits were issued because nine and ten sheep were killed respectively by wolverine in two small areas.

Many sheep graze unattended during summer in the Knutshøi area. Approximately 3700 sheep from Folldal municipality belong to the Kvitdalen Grazing Association (Odd Enget pers. com). Additionally approximately 1500 sheep belonging to Oppdal graze in Knutshø (Stein Lauritzen, pers.com.). The lamb slaughterweight for the area are high with mean weights above 19 kg during 2000-2002. Thus the grazing conditions are considered to be good (Informasjonssystem for beitebruk i utmark 2002).

The area has a population of wild reindeer (*Rangifer tarandus*) with a good balance between summer- and winter grazing areas (Forvaltningsplan for Knutshø villreinområde 2001-2005). Hare (*Lepidus timidus*), red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), rock ptarmigan (*Lagopus mutus*) and willow ptarmigan (*Lagopus lagopus*) are common. Scavengers like golden eagle (*Aquila crysaetos*), white tailed-eagle (*Haliaetus albicilla*) and ravens (*Corvus corax*) were often seen at cadavers. The presence of these scavengers caused corrion to disappear quickly, which made it necessary to discover the dead sheep and to perform the necropsies soon after death. A few sheep were depredated by lynx in Folldal 2003.

#### 2.2 Field Observations

A female wolverine and her two cubs (a male and a female) were caught in Knutshø in April 2003 by excavating their secondary den site. They were anaesthetized with medetomidine and ketamine, and a VHF radio-transmitter was implanted in their abdomens. The adult female was equipped with a Telonics® implant transmitter (IMP/400/L) with an expected operating life of 24 to 36 months. Both cubs were equipped with Telonics® implant transmitters (IMP/300/L) with an expected operating life of 9 to 13 months.

In mid-June eighteen adult ewes were marked with radio transmitters and 203 lambs were marked with transmitters with mortality sensors mounted on expanding collars. The ewes and lambs were marked on the home fields and inside the barns of four different sheep owners that participated in the radio-telemetry part of the study (Table 1). The ewes and lambs were chosen based on the owners' knowledge that they would graze in the study area. Lambs were born with primarily between 1 May and 1 June, and were four to eight weeks old when released to graze in the mountains. The ewe transmitters had individual frequencies (142MHz, SirTrack, New Zealand), which made it possible to localize, and follow specific individuals over time. The lamb transmitters were designed to start sending signals after they had been inactive for 2-3 hours.

We studied the radio marked sheep from 15 June until 14 September, and we divided the summer season into three grazing periods; 15 June -14 July, 15 July-14 August and 15 August- 14 September. Each day was divided into six four-hour periods. We excluded the hour-period from 00:00-04:00 in the third grazing period because of darkness.

Farmer	No. Marked	No.	No. Lambs	No.	No. Marked	No.
	lambs	Unmarked	totally	Unmarked	Ewes	Ewes
		lambs		ewes		totally
1	14	177	191	101	3	104
2	69	330	399	171	5	176
3	50	285	335	175	5	180
4	70	346	416	219	5	224
Total	203	1138	1341	666	18	684

**Table 1.** Number of lambs (collared and uncollared) and ewes from each cooperating sheep

 owner that participated in the study in Knutshø, 2003, Norway.

#### Radio tracking procedure for wolverines

Every day we attempted to radio track for the three radio-marked wolverines, but on average we managed to locate them once a week. Tracking was done using a three- element folding Yagi antenna (Sirtrack®) and a hand held receiver (ATM®, Advanced Telemerty Systems®). The positions of the animals were determined by triangulation in most cases and a position quality assessment was given by assigning a radius (meters) surrounding the position. We tried to get radio bearings from at least three different positions to calculate their position at the map (triangulation). The radio transmitters only sent signals during pre-programmed hours during a 48 hours cycle.

#### Radio tracking procedure of sheep

We tried to radio track the sheep such to obtain an evenly distributed number of observations on each ewe throughout the season and the 24-hour periods (Fig. 3., 4. and 5.). In each grazing period, we tried to obtain a minimum of one observation per radioed ewe for all the six four-hour periods. Tracking was done using a three element folding Yagi antenna (Sirtrack®) and a handheld receiver (ATM®, Advanced Telemerty Systems®). The ewes could move many km during a day. By walking up to higher terrain, we could receive signals from larger areas below, and determine which radioed ewes that could be reached in the next few hours. If there were many radioed ewes in a flock, it was possible to differentiate among them by reading the radio frequency on their radio collar, using binoculars.



Figure 3. Number of localizations of the collared ewes per four-hour period from 15 June until 14 July in Knutshøi, Norway, 2003.



Figure 4. Number of localizations of the collared ewes per four-hour period from 15 July until 14 August in Knutshøi, Norway, 2003.



Figure 5. Number of localizations of the collared ewes per four-hour period from 15 August until 14 September in Knutshøi, Norway, 2003.

In the first grazing period we obtained thirteen adequate observations of radioed ewes (with observations in more than three four-hour periods). In the second grazing period adequate observations were obtained from thirteen ewes and in the third grazing period we obtained eleven adequate observations.

When a radio-collared ewe was localized, we filled in a sheet (Habitatbruk sau) about date, observation number, time, weather, flock size, flock behaviour, and percentages of the surrounding habitats; Trees above 3m tall, Bushcover  $(3m>x>\pm0.5m)$ , Grass/Herbs, Heather/Berries, Marsh, Lichen, Rock/Cliff, Stream/river, Snow and "Other" (occupied by flock plus ±20m around flock).

When sheep carcasses were found, personnel from Norwegian Nature Inspectorate determined the cause of death by conducting a field necropsy following Landa (1999). If a wolverine had killed a sheep, a carcass sheet was filled out about specific marks that identified the predator, and a habitat sheet describing the habitat characteristics ( $\pm$ 5m) around the carcass as mentioned above, and whether it was deemed to have been moved after death.

#### Data analysis

For my statistical analyses I used the computer program Minitab version 14.11 and SPSS for Windows 11.0.1 (SPSS Inc. 2004). In all statistical tests the significance level were set at 0.05.

I used Arc View GIS 3.2 for Windows (ESRI inc. 3.2) to create maps, calculate kernel home range size, and calculate slope, aspect and altitude for the locations. The programme Ranges 6 was used to calculate areas for minimal convex polygon home ranges. I used digitalized maps from Folldal, Dovre, and Oppdal Municipalities that showed lakes, brooks, soil type and contour lines. In all maps I used the Geodetic datum: World Geodetic System 1984 (WGS 84) with grid zone designation UTM 33 V. All maps are contour maps with 20 m contour intervals.

#### Habitat and Predation Analyses

Quadratic regressions were made in Minitab. The tests are based on all of the 273 habitat observations of ewes. Quadratic regression was chosen because the quadratic model test fitted the data best (largest r-square).

The non parametric Mann-Whitney U test was used to compare the habitats around carcasses that had probably been moved and those not moved, based on the necropsies and where it was found. Only habitat characteristics ( $\pm 5m$ ) near carcasses that were "assumed killed" or "documented killed" by wolverine were used.

Minitab was used for a linear logistic test of the difference in habitat variables around documented carcasses only and the mean habitat variables throughout the season for each living ewe. The mean of all habitat observations through the grazing season were used from each individual ewe to avoid individual dependence. The statistical system for generalized linear interactive modeling (GLIM 4) (Francis *et al.* 1994) was used conducting a univariate analysis of variance (ANOVA), where the effects of one habitat characteristics on difference in habitat around carcasses and living, was estimated while controlling for the effect of the other habitat characteristics. Habitat variables that not were observed around living or dead sheep were noted as NC (Not calculated due to zero observations).

The Mann-Whitney U test was used to compare the habitats around depredated sheep and living sheep in the end at the grazing season.

Habitat observations  $\pm 20$  m around flock of living sheep were compared with the habitat observations around  $\pm 5$ m "documented" or "assumed" depredated sheep. The carcasses were found in the same period as the observations of the living ewes were made (27 august and the 14 September).

The Mann-Whitney U test also was used to compare the habitat around depredated sheep and living sheep in specific periods of the day.

Habitat observations occupied by flocks including  $\pm 20$  m around the flocks with living sheep were compared with the habitat observations around ( $\pm 5$ m) the "documented" or the "assumed" depredated sheep. Data from carcasses of sheep clamed to have been moved from place of death were not included. Habitats around carcasses found throughout the whole summer, but mainly the last part of the grazing season, were compared with habitat around living ewes in the last part of the grazing season (22 July until 14 September). Only data from living ewes in the last part of the grazing season were used, because most of the carcasses were found then. In all tests about missing lamb related to age of their mothers I excluded data from foster lamb, as these were not with their original mother. Lambs that died in home fields in autumn were also excluded. A chi-square test was used to determine whether there were more losses of lambs of a particular sex expected based on their sex ratio. The chi-square test was also used to determine whether the number of lambs missing was related to age of their mothers.

#### Home range analysis

A home range is defined as "the area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943). A one-way ANOVA was used to determine whether home range size was related to age of the ewe. Two different methods, minimal convex polygon and the kernel home range method, were used to calculate home range sizes. Home ranges for 50, 75 and 95 percent of their total home range were estimated for both methods.

The minimal convex polygon method calculates a home range by drawing a line around the outermost localizations, which makes the method sensitive for outliers (Harris *et al.* 1990). The home range size based on the minimal convex polygon may also depend on sample size, where increased sample size gives increased home range size (White & Garrott 1990). The kernel method is a nonparametric model that makes a continuous, smooth bivariate distribution (Worton 1987; 1989). The method assumes a symmetrical density function localized at every observation (Larsen 1997).

## **3 Results**

#### 3.1.1 Habitat utilisation during the season

The quadratic regression analysis display how free ranging domestic sheep's habitat preference varies during the season in an alpine biotope. The habitat preference varied significantly during the season for Bush, Grass, Marsh, Lichen, Rock and Altitude (Table 2).

#### Table 2.

Result from a quadratic regression analysis. Week numbers effect on habitat use throughout the grazing season.

Habitat use:	Bush cover	Grass	Heather	Marsh	Lichen	Rock	Water	Snow	Other	Altitude
P-value	0.000*	0.002*	0.081	0.010*	0.001*	0.006*	0.599	0.221	0.219	0.000*
Df:	2	2	2	2	2	2	2	2	2	2
F:	9,17	6,58	3,07	4,73	7,62	5,29	0,51	1,52	1,53	29,91
Square	0.064	0.047	0.013	0.034	0.047	0.038	0.040	0.011	0.011	0.183



**Figure 6.** Utilisation of habitats Bush, Grass, Marsh and Lichen by sheep in the Knutshøi area, Norway, in 2003, and how this preference varied by week number during the grazing season.



**Figure 7.** Utilisation of Rock habitat in the Knutshøi area, Norway, in 2003, and how this preference varied by week during the grazing season. Sheep utilisation of altitude through the grazing season is also displayed.

The quadratic regression lines in figure 6 and 7 show the dependence between the week number and the habitat variable. Sheep in Knutshøi show significant changes in preference for most habitat variables through the grazing season (Table 2) (Fig. 6 and 7).

The utilisation of habitats containing bush cover increased throughout the grazing season to high levels. The utilisation of marsh habitat was generally low but also increased throughout the season. Also rock habitat was generally little utilised but its use decreased throughout the season. The utilisation of lichen habitat was low in the beginning of the season, but increased significantly throughout the season. Grass habitat was generally highly utilised, but decreased throughout the season. The sheep were found at decreasing altitudes as the season progressed, but it increased some in the beginning of the season and decreased after the middle of July.

#### Flock Size throughout the grazing season

The flock size varied significantly throughout the season although the explanatory ability of the quadratic model was low (P=0.000, d.f=2, F=8.77  $r^2$ =0.062), Fig. 8).



**Figure 8.** Flock size of sheep by week throughout the grazing season in the Knutshøi area, Norway, 2003.

#### 3.1.2. Habitat utilisation throughout 24-hours period

The utilisation of marsh habitat and habitats containing bush cover decreased from noon until midnight, and increased from midnight until noon. The utilisation of habitat containing grass and rock increased from noon until midnight

Sheep used lowest altitudes at midday and highest at night. The sheep used increasingly steeper slopes from noon until midnight, and decreased in steepness from midnight until noon (Fig. 9), Table 3).

#### Table 3.

Utilisation of habitat variables by sheep grazing in the Knutshøi area, Norway, 2003, in relation to time of day. \* Denote significant values, where P<0.05, based on quadratic regression test.

Habitat use:	Bush cover	Grass	Heather	Marsh	Lichen	Rock	Water	Snow	Other	Altitude	Aspect	Slope
P- value Df:	0.000* 2	0.000* 2	0.839 2	0.030* 2	0.089 2	0.001* 2	0.402 2	0.606 2	0.402 2	0.000* 2	0.178 3	0.010* 3
F: R- Square	19,47 0.126	10,61 0.073	0,18 0.001	3,54 0.026	2,44 0.018	6,97 0.049	0,91 0.007	0,5 0.004	0,92 0.007	28,27 0.175	1,65 0.018	3,84 0.041



**Figure 9.** Utilisation of the habitats variables Bush, Grass, Marsh, Rock, Altitude and Slope by domestic sheep, grazing in the Knutshøi area, Norway, 2003, in relation to time of the day. All habitat variables displayed vary significantly with hour, based on quadratic regression.

#### Flock size through 24 hours

The flock size varied significantly through the day (P=0.000, d.f=2, F=32.87,  $r^2$ =0.198). It increased from noon until midnight, and decreased from midnight until noon (Fig. 10).



**Figure 10.** Flock size of domestic sheep grazing in the Knutshøi area, Norway, 2003, in relation to time of day. The flock size varied significantly at day, based on quadratic regression.

## **3.2.1** Habitat around carcasses moved after death compared with those not moved after death

The habitat characteristics were mainly the same  $\pm 5m$  around the carcasses that were "deemed moved" after kill, and those who were "deemed not moved" after kill (p>0.05). The exception was for the habitat characteristics water. There was significantly less water around carcasses that were not moved after death, than around carcasses that had probably been moved after death (Table 4).

#### Table 4.

Results from the Mann Whitney U-test, comparing the habitat characteristics between sheep carcasses "not deemed moved" after death and "deemed moved" after death, in the Knutshøi area, Norway, 2003.

NC=Not calculated due to zero observations. All p-values are adjusted for ties.

(+)&(-) Denotes significant values and direction, where +P<0.05,

++P<0.01,+++P<0.001,++++P<0.0001,(+) Denotes Mn<sup>1</sup>>Mn<sup>2</sup>

(- ) Denotes  $Mn^1 \le Mn^2$ 

Habit amor "dee move "dee move	tat use ng med not ed" vs. med ed"	Bush	Grass	Heather	Marsh	Lichen	Rock	Water	Snow	Other	Altitude	Slope	Aspect
<u>1/2</u>	<u>N1=13</u> <u>N2=5</u>	0,881	0,124	NC	0,871	NC	0,704	(-)	NC	NC	0,585	0,294	0,075
<u>Sum</u>	mary	1=2	1=2	NC	1=2	NC	1=2	1<2	NC	NC	1=2	1=2	1=2

### **3.2.2** Habitats used by living ewes and those around documented wolverinedepredated sheep

Several habitat characteristics around sheep documented depredated by wolverine were different from the habitat characteristics around living ewes. The habitat variables bush cover, lichen, rock and altitude were significantly related to the probability of being depredated by wolverine (p<0.05) throughout the whole grazing season (Table 5). However only bush cover and rock habitat had an independent effect on probability for sheep to be depredated by wolverine. Lichen and Altitude had no independent effect as they were dependent on each other and bush and rock (Table 6). There was a higher probability of finding dead sheep with an increasing amount of bush cover (p=0.006) and a lower probability of finding dead sheep with an increasing amount of rock in the habitat (Figure 11).

#### Table 5.

Comparison of habitat variables for living ewes and those around locations of documented wolverine killed sheep throughout the whole grazing season, in the Knutshøi area, Norway, 2003. NC= Not calculated due to zero observations.

Habitat use:	Bush cover	Grass	Heather	Marsh	Lichen	Rock	Water	Snow	Other	Alt.	Aspect	Slope
P-value Df: F: R- Square	0.006* 1 8.84 0.247	0.626 1 0.24 0.009	0.528 1 0.41 0.015	0.432 1 0.64 0.023	0.000* 1 24.18 0.472	0.005* 1 9.3 0.256	0.280 1 1.22 0.043	NC	NC	0.006* 1 9.05 0.251	0.427 1 0.65 0.024	0.908 1 0.01 0.001
	0.247	0.003	0.015	0.025	0.472	0.250	0.045			0.251	0.024	0.001

\*Denote significant values where p<0.05, based on logistic regression.

#### Table 6.

Univariate analysis of variance of the effects of the habitat characteristic bush cover, lichen, rock and altitude (left column) while controlling for the effect of one of other characteristics (upper row). (F/p-value, d.f.=1).(\*denotes significant values). Based on comparisons of habitat variables for living ewes and those around locations of documented wolverine killed sheep, throughout the grazing season, in the Knutshø area, Norway, 2003.

	Bush cover	Lichen	Rock	Altitude
Bush Cover		0.783/0.384	11,424/0.002*	1,121/0.3
Lichen	0,783/0.384		0.000/0.995	0.132/0.719
Rock	11,424/0.002*	0.000/0.995		4,240/0.050*?
Altitude	1,121/0.3	0.132/0.719	4,240/0.05*?	



**Figure 11.** The relationship between the occurrence of bush cover and rock at sites of dead (0) or living (1) domestic sheep throughout the whole grazing season, in the knutshøi area, Norway, 2003. The relationship is displayed with a smooth line.

# **3.2.3** Habitat around living sheep compared with that around depredated sheep at the end of the grazing season

Habitat around carcasses and living sheep were similar for the habitat characteristics slope, altitude, rock, marsh, heather, grass and bush (p>0.05). There was statistically significant more aspect (p<0.05) and more water (p<0.01), and less lichen (p<0.01) in the habitats in which the carcasses were found. The results for the habitat characteristics heather, lichen and water were not influenced by the fact that some carcasses had been moved after death (Table 7).

#### Table 7.

Comparison of habitat observed around living sheep (occupied  $\pm 20m$  around flock) and depredated sheep (habitat  $\pm 5m$  around) in the last period of the grazing season in Knutshøi, Norway, 2003. Result from the Mann-Whitney U-test, where all p-values are adjusted for ties. (+)&(-) Denotes significant values and direction, where +P<0.05, ++P<0.01. (+) Denotes M1>M2 (-) Denotes M1<M2. M1: Habitat around living sheep. M2: Habitat around depredated sheep. Plus, means that it was a significant more of the specific habitat around living sheep, than around dead sheep. Minus, means that it was more of the specific habitat type around cadavers than around living ewes. nM1 and nM2 means number of habitat observations of M1 and M2 the table is based on.

Habi obse arou Vs. P	tat rved nd Living redated	Test Of pop. median M:	Bush	Grass	Heather	Marsh	Lichen	Rock	Water	Altitude	Slope	Aspect
<u>1/2</u>	<u>nM1=44</u> <u>nM2=20</u>	M1≠M2	N.S	N.S	N.S	N.S	(++)	N.S	()	N.S	N.S	(-)

# **3.2.4 Habitat around depredated sheep compared with habitat around living sheep related to time of the day.**

The habitat observed around wolverine-killed sheep was most similar with habitats utilised by domestic sheep in the evening (hour period 5) during the main depredation period of the summer. In this time period the habitat characteristics around carcasses and living sheep only differed with more water (++) and less lichen (--) around the cadavers. The habitat characteristics around carcasses and living sheep were also quite similar in hour period 4 (day), whereas hour period 2 and 3 (night and midnight respectively differed more. The result for hour period 2 (night) was based on data from only 15 observations and may not represent the habitat use as well, as did the other periods with a larger number of observations. Assuming that the carcasses used in this test were not moved after death, I conclude that sheep were more often killed in evening habitat than morning and day habitat, whereas night habitat was more uncertain (Table 8).

#### Table 8.

Comparison of habitat around depredated sheep ( $\pm 5m$ ), and habitat utilized by living sheep (occupied  $\pm 20$  m around flock) in six-hour periods (M2-6), in the late part of the grazing season in the Knutshøi area, Norway, 2003. Results from the Mann Whitney U-test. All p-values are adjusted for ties. (+)&(-) Denotes significant values and direction, where +P<0.05, ++P<0.01, +++P<0.001, ++++P<0.0001 (+) Denotes M1>M2.

(-) Denotes M1<M2. NC=Not calculated due to zero observations. M1: Habitat around depredated sheep. M2-5: Habitat around living sheep in the late part of the grazing season in a particular hour period.

22 July-14 September. .

Carcasses M1:

Habitat observed in hour period M2: 22.00-04.00 (night) Habitat observed in hour period M3: 04.00-10.00 (morning) Habitat observed in hour period M4: 10.00-16.00 (day) Habitat observed in hour period M5: 16.00-22.00 (evening) 22 Observations.15 Observations.29 Observations.

52 Observations.

59 Observations.

Habitat observed Cadavers vs. living in hour period Mn	Bush	Grass	Heather	Marsh	Lichen	Rock	Water	Altitude	Aspect	Slope
<u>1/2</u>	(+++)	0.384	0.371	NC	()	()	0.085	()	0.698	0.913
<u>1/3</u>	0.231	0.059	0.130	(+)	()	0.365	NC	0.066	(+)	(+)
<u>1/4</u>	0.194	0.240	0.095	0.299	()	0.179	(++)	(+)	0.119	0.162
<u>1/5</u>	0.243	0.658	0.385	0.656	()	0.966	(++)	0.159	0.052	0.098
<u>Summary</u>	1=3&4&5	1=2&3&4&5	1=2&3&4&5	1=4&5		1=3&4&5	1=2	1=3&5	1=2&4&5	1=2&3 &4&5

#### 3.3.1 Missing lambs related to sex and age of their mothers

At the end of the grazing season farmers number 1, 2, 3 and 4 lost totally 9, 78, 53 and 43 lambs respectively, of which three, thirteen, four and six were depredated by wolverines. Two of the second farmers' ewes were also documented killed by wolverines. Of total number of lambs lost, 19.6 were found dead and 70.2 percent of lambs found were wolverine depredated. Farmer number 1 lost 5% of his released male lambs and 4.1% of his females (Fig. 12) (Appendix 1), even with the youngest livestock (Table 9). Corresponding loss rates were 23.6% and 21% for farmer 2, 17.9% and 15.1% for farmer 3 and 12.3% and 8.7% for farmer 4 (Fig. 12) (Appendix 1). Total losses for all four farmers were 15.7% of the released male lamb

and 13.2% of the released female lambs, or 14.5% for both sexes combined. There was no significant difference in loss rate between male and female lambs.

There was no significant difference in the sex ratio of wolverine-depredated lambs, compared with losses of lambs (Chi-square=2.25; DF=1; P-value=0.133).

However there was a significant difference between actual and expected losses of lambs related to age of the mother (Chi-square= 16.84; DF=6; P-value=0.009).

Young mothers lost more lambs than expected (Fig.13). This was particularly evident for yearling mothers, whereas mothers that were 5 and 6 years old lost noticeably fewer lambs than expected (Fig. 13).

There was not found a significant difference in sex of lambs missing, compared with expected losses of sheep from the four livestock (Chi-square=1.398; DF=1; P-value=0.315).



**Figure 12.** Rate of lamb lost in relation to sex of the lamb and the age of the mother (ewe). Data are from cooperating farmer 2, 3 and 4 from the Knutshøi area, Norway, in 2003. M is male and F is female.

**Table 9.** Age structure of released ewes of domestic sheep by different farmers, in the Knutshøi area, Norway, in 2003.

	Farmer	Farmer	Farmer	Farmer	
Ewe age	1	2	3	4	Total
1	24	21	20	66	131
2	30	22	23	42	117
3	15	31	29	44	119
4	38	24	25	31	118
5		37	37	14	88
6		14	14	12	40
7		10	10		20
8		7	4	2	13



**Figure 13.** Relationship between number of lambs actually missing and number of lambs expected to be missing related to age of their mother (ewe) in the Knutshøi area, Norway, 2003.

#### 3.3.2 Home range size related to age of ewe

There was no significant differences in home range size based on age of the ewes in the Knutshø area in 2003 for the home range methods Kernel 50%, 75% and 95%, and the home range methods Minimal Convex Polygon (MCP) 50%, 75% and 95% (Table 10). The Mcp 100% varied between the smallest home range to the largest from 4.1 km2 to 13 km2, with a mean size at 9.1 km2.



Figure 14. The relationship between home range size and ewe age. The results from one and two year old ewes reflect only one observation. The result from the two, four and six year old ewes reflects respectively two, five and four observations. The standard deviation as error bars.

Table 10. Results from one-way analysis of variance testing home range size in relation to age of ewes(1-6 years old) in the Knutshøi area, Norway, 2003.. Different estimated home range sizes from different home range methods are tested; Kernel 50%, Kernel 75%, Kernel 95%, Minimal convex polygon 50% (MCP), MCP 75% and MCP 95 %.

Home Range Method	Kernel 50%	Kernel 75%	Kernel 95%	MCP 50%	MCP 75%	MCP 95%
P-value	0.341	0.362	0.640	0.383	0.141	0.244
F	1,32	1,26	0,67	1,19	2,36	1,69
MS	1.44*10 <sup>12</sup>	4.55*10 <sup>12</sup>	2.42*10 <sup>13</sup>	3.33*10 <sup>11</sup>	3.53*10 <sup>12</sup>	3.10*10 <sup>13</sup>
SS	5.78*10 <sup>12</sup>	1.82*10 <sup>13</sup>	9.69*10 <sup>13</sup>	1.33'10 <sup>12</sup>	1.41*10 <sup>13</sup>	1.24*10 <sup>14</sup>
Factor	4	4	4	4	4	4
R-Square	0.397	0.385	0.251	0.374	0.540	0.458
Ewe Largest Km2				0.11		10.3
Ewe Smallest Km2				1.76		4,76
Mean size Km2				0.88		6.1



Figure 15. The Minimal convex polygon 100% home ranges of ewe number 02, 03, 33, 36, 37, 38, 39, 40, 43, 44, 46 and 49 in Knutshøi, Norway during the 2003 grazing season.

### **4** Discussion

#### 4.1 Source of error in collecting data

Four different persons participated in the habitat descriptions around the ewes and carcasses. There may have been differences from person to person, because the percentage of each habitat characteristic in the area around the ewes and the carcasses was estimated subjectively.

Anti-predator behaviour limits optimal grazing behaviour and is important for habitat choice, especially when caring for young offspring (Festa-Bianchet 1988; Kohlmann et al. 1996). Time spent looking for predators affects effective grazing time (Frid 1997), and Gluesing & Balph (1980) found that young ewes spent 25 percent more time grazing than more experienced ewes. Ewes being inexperienced with their home range also move more than more experienced ewes (Warren & Mysterud 1993). Light-weight breeds have better anti-predator strategies than heavier-weight breeds, which also may have influenced habitat preferences (Hansen *et al.* 1998). The experience, breed, age, number of offspring, and release date were not considered when we chose which ewe to carry radio transmitters. In this study I recorded the utilised habitat characteristics without considering the proportion of the different habitat characteristics available (Preference). I only studied habitat use and not habitat preferences. Thus my results are difficult to compare directly with other areas.

#### 4.2 Habitat utilization throughout the grazing season

I found that the sheep's habitat use of the habitat types, bush cover, grass, marsh, lichen, rock and altitude, changed throughout the grazing season. Altitude used increased slightly to a point in the middle of the season and then decreased towards the end of the grazing season, but in generally decreased throughout the season. The utilisation of habitats containing bush cover increased to almost a hundred percent towards the end of the season. The use of grass was high in the beginning of the season, but decreased throughout the whole season.

Past work has shown that plants that sheep use are utilized based on their phenological development, preferring young vegetation, which is rich in nutrients (e.g. Schoener 1971). In Norwegian mountains Albon & Langvatn (1992) found that crude protein content of graminoids and herb were positive correlated with altitude in early summer, but negative correlated with altitude in late summer. In Norway red deer (Cervus elaphus) also migrates seasonally over an altitudinal gradient, and in other regions e.g. Bighorn sheep (Ovis Canadensis) does (Geist 1971). The strategy of domestic sheep in Knutshø might have been to select plants in an early growth stage by choosing open habitats at higher altitudes in the first part of the summer, and more sun-protected sites in bush habitat in the end of the season. Studies done on domestic sheep in coniferous ranges have shown the same pattern as in this study for bush cover and grass, where the utilisation changed from open to closed habitat throughout the grazing season and where the utilisation of grass decreased throughout the season (Warren & Mysterud 1991). Sheep in Knutshøi increasingly used higher altitudes early in the grazing season probably because of larger access to nutrient-rich plants low in fiber, in the areas where fresh plants just had emerged after the melted snow. As a result of early snow melt, plants in sun-exposed sites mature earlier, reach a higher fiber content earlier, and reduce nutritional content earlier than in more sun-protected sites (Warren & Mysterud 1991).

The utilisation of rock habitat decreased throughout the summer probably due to the utilisation of lower altitudes throughout the grazing season, as the rockiest areas generally were at higher altitudes but this possible dependency was not checked. The use of habitats containing lichen was generally low throughout the whole summer, but increased from start of the summer to the middle of the summer and stayed at the same level towards the end of the season. Utilisation of habitats containing lichen was also found in Warren & Mysterud (1991). The reason for this is unsure. The use of habitats containing marsh was low throughout the whole grazing season, as found in coniferous habitats (Warren 1988; Stensli 1988; Berg 1990).

The habitat use changed throughout the season, as my hypothesis said.

#### 4.3 Diurnal habitat utilization

The habitat variables bush cover, grass, marsh, rock, slope and altitude varied significantly throughout the 24 hour-period. Altitude, slope and utilisation of grassy and rocky habitats decreased towards noon and increased towards midnight. On the other hand, the utilisation of bush habitat and marsh habitat increased towards noon and decreased towards midnight.

Several earlier studies have shown that sheep establish a daily pattern of habitat use where poor forest types are utilised in the evening and night, and richer types during the day (Warren & Mysterud 1991; Stensli 1988; Welch 1981). Berg (1990) and Movik (1992) found that the bed sites of domestic sheep in an area with predators present in coniferous habitat generally were more open than day habitat, and that resting sites during the day were denser. The consistent pattern of uphill and downhill movements to and from bed sites is a common behavioural pattern found in several earlier studies for both wild sheep and domestic sheep ranging in several different regions and types of habitats (Berg 1990: sheep, Movik 1992: sheep, Lynch 1971: merino sheep, Simmons 1980: desert bighorn sheep, Scott & Sutherland 1981: merino sheep, Welch 1981: Scottish blackface sheep, Seip & Bunnell 1985: Stones sheep). A preference for bedding sites on high ground with good visibility is also common for bighorn sheep (Ovis Canadensis) (Gionfriddo & Krausman 1986). In this study I can not conclude that poor habitat types were more utilized throughout evening and night as both grass and rock increased until night. The bed sites were probably more open with a better view than habitats utilised at day, as they were higher up with more grass, and as sheep often were observed sleeping in open habitats. A clear consistent pattern of uphill and downhill movements to bed site and grazing site was found, which supported my hypothesis.

The less dense vegetation and better view around bed sites found in Movik (1992), Berg (1990), Warren & Mysterud (1991) and Gionfriddo & Krausman (1986) is probably related to the fact that bed sites are found at higher altitudes. The main explanation given for the daily up- and downhill movements is anti-predator behaviour (Martin 1963; Hewson & Verkaik 1981). Hewson and Wilson (1979) in Scotland concluded that vegetation found on higher ground in bed sites consisted of birch trees and scrub giving better cover to foxes. Mountain ungulates are especially dependent on steep, rugged terrain for avoidance of predators (Berger

1978, 1991; Geist 1971; Nievergelt 1987; Shaller 1977). A study done on nursing Nubian ibexes (a wild goat) (Capra ibex nubiana) in Israel found that females being physically parted from their young while grazing at day time, more frequently selected densely vegetated habitats for foraging and foraged less on slopes and cliffs than females grazing with their young during daytime (Kohlmann et al. 1996). In a study in northern Norway wolverine kill sites of reindeer were characterised by lower visibility and less undulating terrain than where living reindeer were observed (Henaug 2000). Generally terrain that maximises visibility should decrease the risk of predation (Ouellet et al, 1996). Sites at high altitudes are often steep and open with good visibility, which make the view of the surrounding terrain better for predator detection. Sites at high altitudes also give many probable escape directions, probably giving escaping sheep a better and larger head start at an enclosing wolverine. An additional explanation may be that high and open terrain supports the sheep with more olfactory information from the surroundings, increasing the probability to detect predators (Warren 1988). More winds probably also keeps insects away. View and olfactory could be important since the wolverine is characterised as a predator that runs and catches its prey (Haglund 1966; Bjärval et al. 1990; Landa et al. 1997). In alpine grazing ranges containing wolverine, I believe that the bed sites by sheep on higher altitudes with a good view and favorable wind in alpine-terrain is anti-predator behaviour, since the probability to detect an enclosing wolverine increases.

## 4.4 Flock size throughout the grazing season and throughout 24-hours period

The flock size significantly decreased throughout the grazing season. The flock size throughout the 24-hour period decreased until approximately 15:00, and increased again towards midnight.

Important features reducing predation in group-living animals include the increased predatordetection probability and reduced individual vulnerability as group size increases (Pulliam & Caraco 1984). The flock size variation of domestic sheep throughout the grazing season has recieved little attention. However Stensli (1988) mentioned a generally more scattered grazing pattern at the end of the grazing season than earlier in the season. Dorrance & Lawrence (1976) found that domestic sheep flock sizes experiencing predation from mainly coyote (*Canis lactrans*) and dogs were largest in the open prairie and smallest in the more forested parkland. Kohlmann *et al.* (1996) found that females being parted from their young at daytime while grazing associated with smaller groups of ibexes, than did females followed by their young while grazing. As only young experienced predation risk, the mothers probably chose staying in larger flocks while with their young to decrease the predator risk. The study of Kohlmann *et al.* (1996) also indicated that staying closer to escape terrain, decreasing grazing time and a decreasing utilisation of densely vegetated habitat probably were knowingly anti-predator behaviour of nursery ibexes.

The grazing pattern found in Knutshø seems to be in accordance with the general grazing pattern observed by Dorrance & Lawrance (1976) and of Kohlmann *et al.* (1996). Flock sizes decreased throughout the season in Knutshø, which may be related to the quality of grass habitat, which supported my hypothesis. After flowering, plants decrease their grazing quality due to less nutrient content and increase in fibre content decreasing the digestibility (Nedkvikne & Garmo 1986; Syrjäla & Qvist 1986). Weight of increase in sheep is also strongly reduced in this period due to grazing quality. At the end of the season sheep utilised more bush habitat, and when the quality of grass habitat decreased, the flocks probably became smaller because of a more scattered grazing pattern.

Herbivores tend to experience a trade-off between vigilance and feeding (Illius & Fitzgibbon 1994; reviewed in: Lima & Dill 1990). Time spent grazing often increases throughout the grazing season (Southcott et al. 1962: Bowns 1971: Abel 1998) and Frid 1997) found that vigilance increased with decreasing group size. It seems that when sheep experience a tradeoff between poor grazing and predation at the end of the grazing season, they increase their depredation probability by spending more time in small flocks in bush habitat than earlier on in the season to maximise grazing. This could also increase individual vigilance resulting in decreasing grazing efficiency, and decrease the total vigilance as the flocks are smaller. This behaviour may be extra strong at the end of the grazing season, as a study by Landa et al. (2003, in: Brainerd (ed.) 2003) showed that wolverine family groups increased their use of habitat containing sheep towards the end of the season. Landa et al. (1999) found that loss of sheep was higher in wolverine cub areas than other areas. A more scattered grazing pattern with smaller flocks with more time spent grazing in bush habitats could also additionally increase the probability of encountering wolverines and being killed by them. Depredation as a result of the chance encounter rate was found to be the main explanatory factor regarding variation on sheep mortality caused by lynx and bear among grazing areas (Linnell et al. 1999; Herfindal 2000). This implies that the habitat use of lynx and bears

affects mortality of sheep more than an active selection for areas with high density of sheep. The conclusion in Landa *et al.* (1999) supports this theory, as sheep depredation by wolverines increased with increasing numbers of sheep, in an area with a stabile wolverine population, and as sheep losses were higher in wolverine cub rearing areas than other areas. A wolverine rearing cub areas is a more intensively utilised by wolverines, as the area utilised by the wolverine female is significantly smaller while she has dependant cubs (Magoun 1985), and as the oestrus season coincides with the cub-rearing period, attracting males and sub adults from previous litters (Landa *et al.* 1999). This results in a larger chance encounter rate between wolverine and sheep increasing predation within the area. Poor grazing conditions might cause the sheep to back into smaller groups that utilise bush habitat more often, reducing vigilance, increasing vulnerability and the chance that some sheep graze near wolverine cub rearing areas.

The flock size variations throughout the 24-hour period in this study generally showed the same pattern as observed in other studies, with flock size increasing in the evening and night, and decreasing again at the morning (Hewson & Verkaik 1981; Stensli 1988; Warren & Mysterud 1991). Warren & Mysterud (1991) found that flock size also increased at the middle of the day while animals were resting and ruminating, but this was not supported by this study. Increasing flock size towards midnight with large flock sizes at bed sites is probably in addition to moving up to higher altitude as discussed earlier, a part of the anti-predator behaviour of sheep (Martin 1963; Hewson & Verkaik 1981). My hypothesis of larger flocks at night was supported.

## 4.5 Wolverine-depredated carcasses that were deemed to have been moved, compared to those that had not been moved after death

I found that habitats with carcasses that were deemed to have been moved after death only differed from those deemed not moved after death, by containing more water.

Wolverines are believed to be surplus killers of sheep (Landa *et al.* 1997) and the wolverines hoard them for later use (Haglund 1966; Bjärvall *et al.* 1978). Therefore habitat characteristic between the two categories was expected to differ. Carcasses may have been hoarded in cold, and places wet or placed in marsh or shadow to slow decomposition.

It is difficult to say whether the depredated sheep deemed moved after death were found in specific habitats and places where the wolverine would prefer to hoard them. The low sample size (5 moved and 13 not moved) is a problem for inference. However these carcasses were assumed moved, and in most cases a wolverine probably moved them and not other predators, as the lambs are heavy in August and September. My results show at least a trend supporting my hypothesis.

## 4.6 Habitats around living sheep compared with wolverine-depredated sheep throughout the grazing season

Bush cover and rock had independent effects on the probability of sheep depredation by wolverines. I found that the probability of wolverine depredation increased with increasing bush cover in the grazing habitat and depredation risk decreased with an increasing amount of rock in the grazing habitat.

Several studies have detected a general relation between dense vegetation and a high depredation of losses for example for cattle (Dorrance 1982) and for goats and sheep (Nass *et al.* 1984). A study in Alberta found that predation on domestic sheep increased with a general increased forest cover in the ecosystem (Dorrance & Lawrence 1976). Dorrance & Lawrence (1976) reported that depredation rate on domestic sheep was large in forested habitats, but largest in mixed forest, whereas the depredation rate in habitats like southern parkland, prairie, and foothills was lower.

My results indirectly support the results of Henaug (2000), where less visibility was found around depredated than living semi-domestic reindeer, assuming that sites containing bush give less visibility than sites without bush.

That the depredation probability of domestic sheep was found to be low in rocky areas may be explained with that the sheep particularly in this period used anti-predator tactics. They used rocky habitats during evening and night when the sheep preferred staying in large flocks at higher ground with good visibility, and with better olfactory conditions. This might have decreased depredation probability. This strengthens my earlier conclusion that the consistent upward movement to bed sites at higher altitudes, thus increasing view and wind, can be seen as anti-predator behaviour (4.3). An important thing is that the differences in size of the area documented around living flocks and dead sheep, differed with minimum fifteen meters. The

difference in scale of the area recorded around the carcasses ( $\pm$ 5m around) and the living ewes ( $\pm$ 20m within and around flock), could have given different results for living than depredated sheep in both 3.6 and 3.7.

## 4.7 Habitats around living and wolverine-depredated sheep in the last part of the grazing season

Habitat around wolverine depredated sheep and living sheep were similar in last part of the grazing season for the habitat characteristics slope, altitude, rock, marsh, heather, grass and bush. I found significantly more of the habitat type lichen around living sheep, and more of the habitat type water and larger aspect around cadavers. Because the utilization of the habitats lichen and water was small related to the other habitat types, I can not conclude that the sheep were not depredated by wolverines in the habitat they mostly utilized. However, my hypothesis and conclusion is strengthened by the results that domestic sheep most probably were depredated in the evening (but depredation in night period could not be excluded because of lack of data in this period), and that depredation probability increased with bush cover (3.2.4 and 3.2.3). If the sheep depredation happened mainly in the evening or in the night in habitats containing bush cover, this means that sheep were killed outside their most utilised habitat, because the utilization of habitat containing bush cover decreased until midnight (3.1.2).

My conclusion may however be questioned, as the general utilization of bush habitat among sheep increased in the end of the grazing season and was high especially in the main depredation period. The different scales between living ewes and depredated sheep during the registrations is weakening the reliability of the results. Further studies are needed to clarify when wolverines are active and at what times domestic sheep are being depredated. This is important, especially as the habitat use among domestic sheep varies strongly throughout the 24-hour period.

## 4.8 Habitats around wolverine-depredated sheep compared with habitats utilized by living sheep at specific times

Habitat observed around wolverine-depredated sheep were most similar to habitats utilised by living sheep in the evening period from 16:00 to 22:00. As the data sample size from the night period was very small, the data from the night period could have been too small to be representative.

No earlier studies have studied wolverine diurnal activity pattern. The habitat types bush, grass, rock and heather, which were most utilised by sheep, were similar for morning, afternoon and evening, and were distinguished from less utilised habitat, like marsh and water. However the difference between day and evening habitat was small and the evening habitat was most like carcass habitat. From this I can conclude that there was a larger wolverine depredation probability for sheep in the evening period than in afternoon and morning period. As wolverines are believed to be most active evening and night, and my results indicates that sheep were killed in this period, my hypothesis was supported.

#### 4.9 Lambs mortality related to sex of the lamb and age of their mothers

Losses of male lambs were 5, 23.6, 17.9 and 12.3 % for the four farmers, and 4.1, 21, 15.1 and 8.7 % for female lambs, respectively. Totally losses were 15.7 % for male lambs, and 13.2 % for female lambs. There was no significant difference between males and females in loss probability related to sex ratio. The total loss of both sexes together was 14.5%. The farmers lost 3, 13, 4 and 6 lambs which were documented wolverine depredated. Of the total number of lambs lost, 19.6 % were found dead and 70.2 % of the dead lambs found were wolverine-depredated. There was no significant difference in lamb mortality based on sex, which does not support my hypothesis. However, lambs with young mothers were lost more often than lambs that had older mothers, supporting my hypothesis.

Most lamb mortality in the area occurs in late August and in September, when the female wolverine and her cub were in the area (Forland 2004). These losses happened in the same period as the wolverine female and her cub were in the same area. Normal loss in areas without large predators is approximately 5% and 2% for lambs and ewes respectively (Mysterud & Mysterud 1995), but this varies by area. The loss lambs in this study (14,5%) exceeds the normal loss rate, Suggesting that the wolverines killed more than were

documented. Wolverines are believed to be surplus killers on sheep (Landa *et al.* 1997), and earlier studies have concluded that some sheep disappear because the wolverine hoards them for later use (Haglund 1966; Bjärvall *et al.* 1978). The surplus killing and the increasing losses late in the season has been explained as a survival strategy related to the ineffectiveness of the wolverine as a hunter (Gudvangen 1995; Haglund 1966; Bjärvall *et al.* 1978). This may explain why the total losses are so high, and the part of lambs found so small.

In Snøhetta losses to wolverines also were high, and varied significantly from farmer to farmer (Gudvangen 1995). I also found losses to vary, as the loss of one farmer was a less than the other three farmers' losses. This could be explained by the fact that this livestock mainly grazed several kilometres north of the cub rearing area, and that the wolverines were seldom localized there. In 2002 the lamb losses in Knutshøi, north- and north-east of Knutshøi varied between 8-12, 6-8 and 4-6 percent respectively (Avansert beitebruk NIJOS, 2002), while a wolverine family group was localized in Knutshøi. A trend supporting that increasing losses in an area may be explained with documented wolverine breeding (Landa *et al.* 1999). Wolverine family group overlap of grazing areas of sheep was found increasing throughout the summer by Landa *et al.* (2003), which may be important in addition to what found in this study, where sheep were grazing more scattered in smaller flocks and are more often utilising high-risk habitat like bush in the end of the season.

Mortality studies on sheep have revealed many different factors to explain the causes of mortality with and without large predators (Skatter 2002). Higher mortality has been correlated with factors like low spring growth rate, low birth weight, litter size, lambs` age at release, breed, age of ewes and male lambs (Skatter 2002, and references therein). According to depredation theories, predators prefer prey animals that are weak such as; young, old, sick, parasite-infected or wounded animals or animals in a deviant group of the prey population (Curio 1976).

The survival probability for lamb throughout the grazing season increased with age of ewe, as has been found in other studies (Purser & Young 1959; Guinness *et al*.1978; Festa-Bianchet 1988; Warren & Mysterud 1995). Explanations include: Young mothers give birth to lighter lambs (Purser & Young 1964) have higher lactation costs (Festa-Bianchet 1988), and have generally poorer rearing capacity (Hewson & Verkaik 1981; Petersson & Danell 1985). All these factors negatively affect lambs` chances for survival (Warren & Mysterud 1995). Also if

ewes showing good rearing capacity have to escape, they are sure that their lambs are following before they start the escape, and the ewes escapes shorter than if they were alone (Alexander 1988; Pedersen 1993; Kohlmann *et al.* 1996). Other factors involved could be vigilance, as young ewes were found spending 25 percent time more grazing than experienced ewes (Gluesing & Balph 1980). Grazing efficiency also increases with experience which decreases grazing time and increases vigilance. This may be important in the end of the season while sheep were experiencing most losses because food resources are scarce, the sheep flocks are small, and time spent grazing is increased.

#### 4.10 Home range sizes related to age of ewes

There were found no significant difference in home range size among ewes at different ages in Knutshø, not supporting my hypothesis that home range size decreases with grazing experience in relation to age. Number of observations per home range was few (between 16-30 observations) in relation to other home range studies done, so increasing the number of observations would have improved the quality of the result, but however the result was as found in a forested range with home ranges based on more locations in eastern Norway (Warren *et al.* 1995).

The mean MCP 100% home ranges in Knutshø are smaller than found in coniferous habitats in Stensli (1988), and larger than in Movik (1992) and Berg (1990). The home ranges found in this study were twice as large as found in Jacobsen (2002) in an alpine habitat without predators for the MCP 100% method, and even more for the Kernel 50 and 95% methods. In Movik (1992) sheep were disturbed by wolves, but in Berg (1990) and Stensli (1988) predators were present but no predator attacks were observed. Whether the missing predator presence explains the small home ranges found by Jacobsen (2002) is unknown. However the relationship between resources and the attack risk of predators is a controlling factor of animal movements (Covich 1976). Ewes' choice of home range is dependent on access to water, food, predator pressure and climatic conditions (Bailey *et al.* 1996). Berg (1990) also found that home ranges within a livestock may vary from year to year, which makes it hard to comparison different areas. From my results I conclude that the home ranges found in Knutshø 2003 were larger than found in other alpine grazing areas in southern Norway, and about the same size as found in coniferous habitats in eastern Norway. If the home ranges were this large because of predator presence needs further studies.

#### 4.11 Conclusion

I found that habitat utilisation by sheep changed throughout the season along an altitudinal gradient and also between open and more closed habitats, probably due to change in plant phenology. Flock size also decreased throughout the season, probably related to plant phenology, as bush habitat, with a high depredation risk, was more utilised in the end of the season suggesting that food search was more important than predator detection when food resources were scarce.

Diurnal habitat utilisation which showed consistent movements to and from bed sites, were explained as anti-predator behaviour. Bed sites were found at higher altitudes, with few bushes giving a good view and probably good olfactory information. Bed sites contained less bushes and more grass which probably increased the view, but also more rock. Flock size was also largest in the bed site period. I concluded that the behavioural patterns of consistent movements to higher altitudes at evening and night, the flock behaviour and choice of bed habitat with a good view and few bushes to be anti-predator behaviour.

Throughout the grazing season bush cover and rock had independent effects on sheep depredation probability. Depredation risk increased with increasing bush cover. Explained with that bush habitat decreased view, bush was most utilised late in the season when the flocks were small, and more time were spent grazing late in the season and the wolverines killed most sheep in this period. That depredation risk decreased with an increased amount of rock was explained with that rock habitat was utilised at night while sheep showed most anti predator behaviour.

Wolverine depredated sheep that were deemed to have been moved after death, were found more closely to water than those who were not deemed moved. This suggests that wolverine might have a tendency to hoard food in sites with special habitat characteristics.

The habitat around depredated sheep was most like habitat around living sheep in the evening period, suggesting that sheep were mainly depredated in the evening period.

Domestic sheep were depredated outside their most utilised habitat, as more habitat containing lichen and less habitat containing water and less aspect were found around living sheep than wolverine depredated sheep. As depredation risk throughout the season increased with increasing bush cover, I concluded that domestic sheep mainly were depredated in the evening. The utilisation of bush habitat decreased towards midnight which strengthened this conclusion. However an alternative explanation is that depredation mainly happened in the end of the grazing season where the utilization of bush habitat was relatively high. Further studies are needed to clarify when wolverines depredate domestic sheep.

Male lambs were not found more prone to wolverine depredation or to loss. Lamb survival increased with age of the mother, probably due to increased rearing capacity with increasing age of the mother.

Home range size variations were not related to age of ewe. The home range sizes were similar to those in coniferous habitats with large predators present.

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### **APPENDIX 1**



Figure 16. Mothers age and portion of lambs lost, dependent on lambs' sex (Farmer 2). Males (M) and Females (F).



Figure 17. Mothers age and portion of lambs lost, dependent on lambs' sex (Farmer 3). Males (M) and Females (F).



Figure 18. Mothers age and portion of lambs lost, dependent on lambs' sex (Farmer 4). Males (M) and Females (F).