

## Factors associated with wolverine *Gulo gulo* predation on domestic sheep

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### Summary

1. Following a long history of eradication campaigns against predators, wolverine *Gulo gulo* distribution and numbers became critically low in Norway in the 1960s. Consequently, wolverines were protected by law during the 1970s and 1980s. This led to an increase in wolverine numbers and re-establishment in some formerly occupied habitats, resulting in increased depredation on domestic reindeer *Rangifer tarandus* and sheep *Ovis aries*. Wolverine control and licensed hunting have been used increasingly as tools to reduce the depredation since protection was introduced. However, the factors influencing the level of this depredation have not been studied. We therefore examined losses of domestic sheep grazing unattended on upland summer ranges in the Snøhetta plateau of south central Norway during 1979–94, in relation to wolverine population numbers, reproduction and control measures. This area was recently re-occupied by wolverines and reproduction has been recorded regularly from the beginning of the study period.

2. The number of ewes and lambs recorded in organized grazing areas increased more than fivefold during the period, and losses increased proportionally with sheep numbers. The differences in losses among municipalities and grazing co-operatives were probably related to sheep breeds and local variation in wolverine density.

3. The heavy Dala sheep breed was most at risk, whereas losses from the lighter Norwegian short-tailed and Norwegian fur-bearing breeds were lower than expected.

4. Killing of wolverines led to fewer lambs being lost in the same year that the wolverine killing took place, but the effect quickly declined, implying a rapid re-establishment of wolverines in the local area.

5. Lambs were more vulnerable to wolverine predation than ewes, and losses were higher in wolverine cub-rearing areas than in the area as a whole.

6. We conclude that: (i) control programmes for wolverines, as practised today, will have little long-term effect in reducing sheep losses, unless wolverines are eradicated or severely reduced in numbers; (ii) the introduction of more agile sheep breeds will probably reduce losses; (iii) in areas where wolverine control to protect sheep is a threat towards wolverine conservation, the present sheep husbandry system of grazing unguarded sheep in the mountains should be replaced by alternative forms that provide the sheep with more protection. This is particularly important in wolverine denning areas.

**Key-words:** carnivore management, livestock depredation, predator control, Norway.

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## Introduction

Wolverines *Gulo gulo* L. have attacked domestic animals in the Nordic countries for centuries (Brehm 1873; Bjärvall, Franzén & Nilsson 1978). In recent years, the number of reported wolverine kills in Norway has increased following the introduction of a compensation scheme (Miljøverndepartementet 1992, 1997). Domestic sheep *Ovis aries* L. and semi-domestic reindeer *Rangifer tarandus* L. are particularly at risk of attack by wolverines (Aanes, Swenson & Linnell 1996; Landa *et al.* 1997).

Until the beginning of this century, the wolverine had a wide distribution over most of Norway (Landa, Lindén & Kojola 1999). It received protection in southern Norway in 1973 and in northern Norway in 1982. By that time the wolverine was functionally exterminated from southern Norway, but survived in central and northern Scandinavia in the most remote upland areas along the Norwegian–Swedish border (Landa, Lindén & Kojola 1999). However, some recovery in numbers and re-occupation of former range has occurred since protection was granted. Today, wolverines are found mainly in mountainous areas in south central Norway and along the Norwegian–Swedish border from Hedmark County (south-eastern Norway) and northwards. The wolverine has not re-occupied all of its former range and densities are still low compared with former distribution. In Norway the minimum populations in 1995–97 were estimated to be 120 individuals in northern Norway and  $27 \pm 7$  in southern Norway (study area plus surrounding plateaux), with the southern Norwegian population being isolated from the larger continuous population by approximately 100–200 km (Landa *et al.* 1998c).

Special permits to kill wolverines in local areas with high depredation on domesticated reindeer and sheep have been issued since the enactment of protection. Additionally, licensed hunting was introduced to reduce wolverine numbers and conflicts with the livestock industry in 1993 in northern Norway (Nordland and Troms counties) and in 1997 in Finnmark County (north-eastern Norway) and southern Norway. The use of these control measures and their effects on depredation levels must be evaluated in order to judge whether viable populations of wolverines are being conserved (Miljøverndepartementet 1997).

Wolverine attacks on sheep vary greatly in time and space, but certain areas have always been noted for high losses. That wolverines kill domestic sheep, mainly lambs on summer pasture, has been well documented from the Snøhetta plateau and north Norway for the past 20 years (Landa *et al.* 1998a, c). However, different sheep breeds vary in awareness and anti-predator strategies in controlled trials (Hansen, Hansen & Christiansen 1998). This implies

that wolverine predation on sheep could be expected to vary among the different sheep breeds.

The abundance of prey can influence the depredation behaviour of predators. For example, in Australia Lugton (1993) showed that red foxes *Vulpes vulpes* began to kill and eat sheep when their natural food items were in short supply, or when the population density of foxes was high and old foxes dominated in the population. In Spain, brown bears *Ursus arctos* appeared to be opportunists and did not take particular species or age classes of domestic animals, but instead preyed upon those that were most common (Clevenger, Campos & Hartasánchez 1994). Kvam *et al.* (1994), however, found that brown bears preferred ewes rather than lambs in Norway. Boggess, Andrews & Bishop (1978) found no relationship between the number of sheep killed by coyotes *Canis latrans* and the number killed by dogs in Iowa, USA. However, they did find a positive relationship between the number of sheep killed by dogs and the sheep numbers in the area, and also showed that a positive relationship existed between the number of lambs born annually and the number killed by predators. They suggested that the losses were more closely related to the availability of sheep than to the number of predators.

The wolverine's ability to exploit many different sources of food, and to hoard food (Haglund 1966; Landa *et al.* 1997), makes it probable that wolverine depredation on sheep will vary with the number of grazing sheep. If so, and if the wolverine population is stable, it can be expected that an increased number of grazing sheep will lead to increased predation. A reduction in the wolverine population will, on the other hand, be expected to result in a reduction in the number of sheep killed by wolverines.

No one has described whether certain age or sex categories of wolverines are responsible for sheep depredation, but it has often been claimed that large sheep losses occur in areas where wolverines raise offspring. The home range of females with cubs is limited while the cubs are growing up (Hornocker & Hash 1981; Banci & Harestad 1990). Because the cub-rearing period coincides with the mating period (Rausch & Pearson 1972), adult males visit cub-rearing areas. Young wolverines from previous litters, and particularly female offspring, will sometimes live within the home range of a female with dependent young (Magoun 1985). In addition to the greater energy requirements of the females when they are bringing up young, the cub-rearing areas therefore function as 'traffic centres' for many categories of wolverines, and such areas will probably contain the highest density of wolverines (Landa *et al.* 1998a). Hence, we expect that the losses of sheep in such areas will be higher in years when wolverines have litters.

We tested the following hypotheses: (i) increased numbers of sheep grazing in an area with a stable wolverine population leads to greater losses; (ii) different sheep breeds vary in their susceptibility to wolverine predation; (iii) killing of wolverines reduces losses among grazing sheep; and (iv) sheep losses are highest in wolverine cub-rearing areas.

## Materials and methods

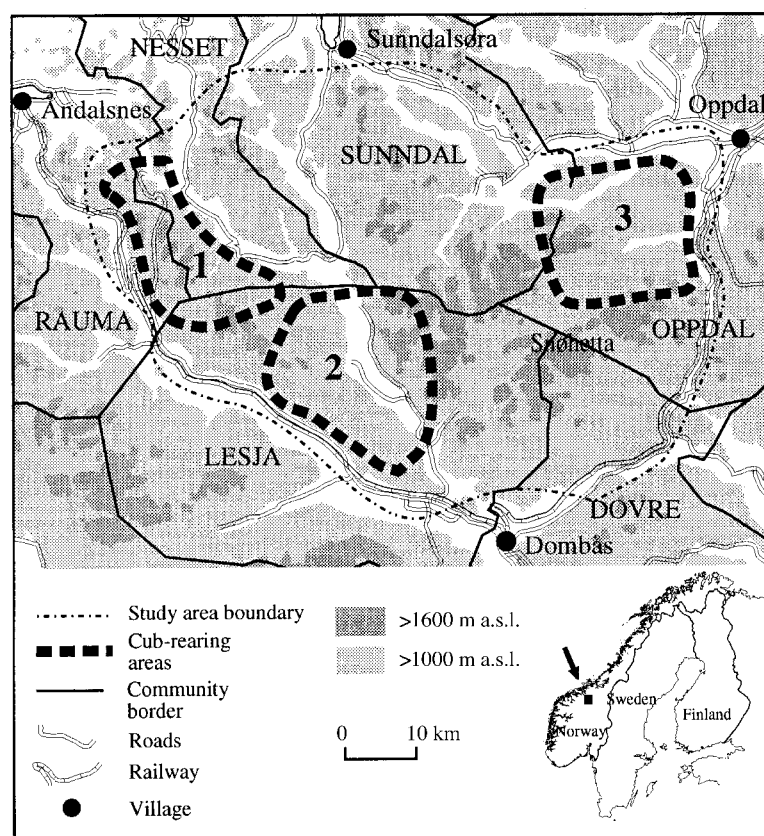
### STUDY AREA

Data were collected within parts of the municipalities of Rauma, Nesset and Sunndal in the County of Møre and Romsdal, Lesja and Dovre in Oppland County, and Oppdal in Sør-Trøndelag County, which occur on the Snøhetta plateau (Fig. 1). This is a high plateau (4400 km<sup>2</sup>) with peaks above 2000 m a.s.l. Valleys, which typically cut into the area, are dominated by mountain birch *Betula pubescens* Ehrh. woodland, with Scots pine *Pinus sylvestris* L. and Norwegian spruce *Picea abies* Karst. at the lowest altitudes. Some of the valleys also contain roads, summer dairy farms and clusters of recreational cabins. Other upland plateaux adjoin the Snøhetta

plateau on all four sides and are similarly separated by valleys containing permanent settlements and transport corridors. The climate has a greater oceanic influence in the west, where the timberline is at about 800 m a.s.l., and a more continental climate in the east, where the timberline is at about 1000 m a.s.l.

### WOLVERINE POPULATION ON THE SNØHETTA PLATEAU

Censuses of wolverines have been undertaken on the Snøhetta plateau nine times since 1979, with the results varying between seven individuals in 1979 and 17 in 1995 (mean = 12.2, SE = 1.05). Until 1990, censuses were based on winter tracking surveys. Since 1990 they have been supplemented by tracking of radio-tagged wolverines (Landa *et al.* 1997). In years when no tracking of any kind was undertaken, we estimated the population figures by simple extrapolation, using the mean of estimates from the year before and after. The tracking was carried out under the auspices of the Game Research Department at the Directorate for Nature



**Fig. 1.** Location of the Snøhetta study area showing areas where wolverine reproduction was recorded within areas of organized grazing (1–3) during the study period.

Management, later the Norwegian Institute for Nature Research, and from 1990 under the auspices of the Environmental Divisions of the respective county authorities. The Directorate for Nature Management authorizes the issuance of permits to kill wolverines, and 10 wolverines were killed during the period 1980–87. Additionally five wolverines were documented as having been killed illegally, and three were found dead due to natural causes during 1980–94 (Landa *et al.* 1997).

#### NUMBERS OF GRAZING SHEEP AND LOSSES ON THE SNØHETTA PLATEAU

The Norwegian Government provides subsidies to promote sheep farming. The applications for this financial support contain information on the number of ewes and lambs that each co-operative released on to the grazing area and the number that disappeared. Copies of the applications were obtained from the county environmental offices and local authority agricultural offices. In our study area we recorded 20 herding co-operatives, with an average of 1100 sheep, during the study period. The participation of sheep owners in co-operatives varied between 70% and 95% by municipality on the Snøhetta plateau. This meant that the total number of sheep grazing in the area was, in reality, somewhat higher than the number we have used in this study. In this study, sheep refers to ewes and lambs, as rams are not released on to the same ranges as ewes and lambs in Norway. We obtained data about the sheep breeds on the Snøhetta plateau in the period 1989–93 from the Livestock Control Office at Norwegian Dairies in Ås.

#### NUMBER OF SHEEP KILLED BY WOLVERINES

With the enactment of protection in southern Norway in 1973, a compensation scheme for livestock killed by protected predators was introduced. We used the number of ewes and lambs for which compensation was paid as the basis for determining relationships between the population of wolverines and sheep losses. An investigation from the Snøhetta plateau showed that 50–85% of the dead sheep that were found could be documented as having been taken by wolverines (Børset 1995; Mortensen 1995). Based on this, the total number of lambs that were reported to have disappeared while grazing was used to analyse the variation in losses among the various sheep breeds. We used only the documented cases of sheep killed by wolverines in the period 1991–93 to analyse the predicted and observed losses of ewes and lambs.

#### SHEEP LOSSES AND WOLVERINE REPRODUCTION

All located natal dens and reported observations of females with young, or of young alone, from May to September, have been recorded annually since 1979 (Landa *et al.* 1997). The cub-rearing areas, encompassing seven grazing co-operatives, were delimited on the basis of field data from radio-tagged animals, tracks and observations of breeding in the period 1979–93 (Fig. 1). Thirteen grazing areas did not contain a documented cub-rearing area during this period.

#### STATISTICAL ANALYSES

We employed correlation, regression and variance analyses in SPSS for Windows 6.0. The Kolmogorov–Smirnov one-choice test was used to test whether the variables were normally distributed. As normal distribution was not attained, we used non-parametric tests, except where otherwise stated. Spearman rank correlation was used to investigate the relationship between continuous variables. Despite the lack of normal distribution, regression analysis of non-ranked data was employed to determine the best-fit equation for the graph. Stepwise multiple regression of non-ranked data was used to indicate the importance of the wolverine population on the percentage losses relative to the importance of the number of grazing sheep. These parametric tests were used for lack of better alternatives and because the central limit theorem states that non-normally distributed selections approach normal distribution when the sample size increases (Zar 1984).

### Results

#### WOLVERINE POPULATION, NUMBERS OF SHEEP AND LOSSES

We lacked data about the numbers of grazing livestock in the years when no subsidy was given for organized grazing. Because this varied from one local authority and year to another, data are lacking for some local authorities in certain years. As the study was based on a large volume of data, few data were lacking overall, and these were randomly distributed across the material, we chose to allow these values to remain as zero. Tabachnick & Fidell (1989) believed this to be a good method for handling this kind of missing data.

The wolverine population on the Snøhetta plateau has apparently remained quite stable since 1979, with possibly a slight increase during the last few years (Landa *et al.* 1997). However, the number of sheep in organized grazing has increased more than

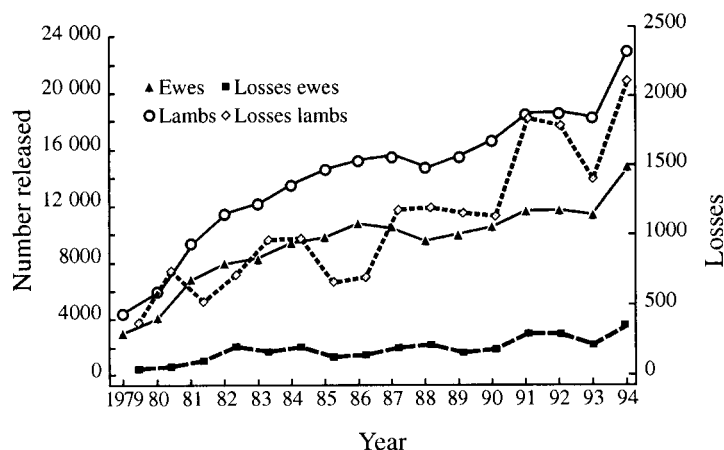


Fig. 2. Numbers of ewes and lambs released on summer pasture and numbers lost on the Snøhetta plateau during 1979–94 (data from Landa & Tømmerås 1996).

fivefold, with an average of 375 sheep in each herding co-operative in 1979 and 1890 sheep in 1994. Losses on summer pasture rose throughout the study period (Fig. 2). However, it was often the same owners who suffered large losses.

Analyses from the Snøhetta plateau as a whole showed a statistically significant positive relationship between numbers of sheep lost and numbers on summer pasture. Losses increased for both ewes and lambs, but lamb losses were relatively higher (Fig. 3a,b). There were no statistical relationships between compensated ewes and lambs and the number of wolverines on the Snøhetta plateau viewed as a whole (Fig. 4a,b). The loss was explained by the number of grazing sheep alone; adding the population of wolverines did not increase the explained power of the model significantly (Fig. 4c,d and Table 1). The proportion of sheep lost did not vary by year for the area as a whole ( $P > 0.54$ ), nor by municipality (Kruskal–Wallis test, 10, 12, 14 d.f.,  $\chi^2 < 20.49$ ,  $P > 0.11$ ).

#### DIFFERENCES IN LOSSES BETWEEN DIFFERENT SHEEP BREEDS AND LAMBS VERSUS EWES

Thirteen breeds of sheep were on summer pasture on the Snøhetta plateau in the period 1989–93. The  $\chi^2$  test was used to examine the relationship between sheep breed and losses, and the wolverines' choice of lambs vs. ewes. When the global test gave a significant result, the Bonferroni Z-test (Neu, Byers & Peek 1974) was used to determine which sheep breeds suffered significantly different losses than expected. There was significant heterogeneity in lamb losses among the various breeds ( $\chi^2 = 34.54$ , 3 d.f.,  $P < 0.001$ ). The Dala breed had a significantly higher loss than expected, whereas the Norwegian short-tailed and Norwegian fur-bearing breeds had significantly lower losses than expected (Table 2). Wolverines chose lambs rather than ewes (23 ewes and 209 lambs were documented as having been killed by wolverines during 1991–93,  $\chi^2 = 80.09$ , 1

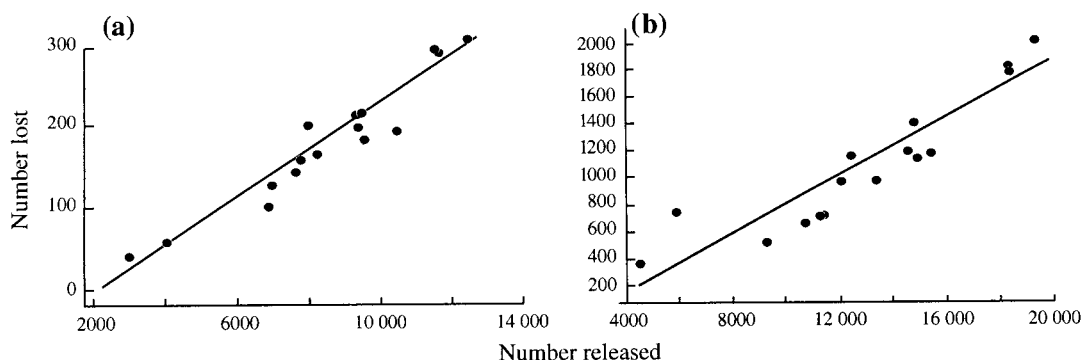
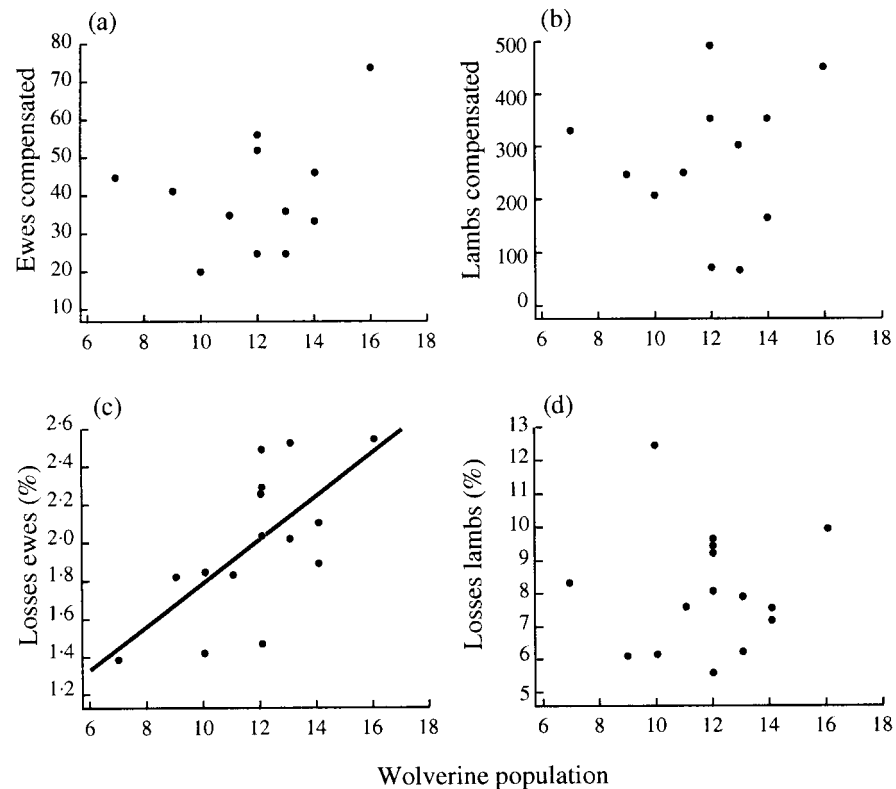


Fig. 3. Relationship between the number of sheep on summer pasture and the number of sheep lost during 1979–94. (a) Ewes,  $r_s = 0.89$ ,  $P < 0.001$ ,  $n = 16$ ; (b) lambs,  $r_s = 0.93$ ,  $P < 0.001$ ,  $n = 16$ .



**Fig. 4.** Relationship between the wolverine population on the Snøhetta plateau and the number of sheep compensated as killed by wolverines (a, b), and between the wolverine population and the percentage of sheep lost (c, d). (a) Ewes,  $r_s = 0.22$ ,  $P = 0.482$ ,  $n = 12$ ; (b) lambs,  $r_s = 0.12$ ,  $P = 0.710$ ,  $n = 12$ ; (c) ewes,  $r_s = 0.71$ ,  $P = 0.003$ ,  $n = 15$ ; (d) lambs,  $r_s = 0.06$ ,  $P = 0.831$ ,  $n = 15$ .

d.f.,  $P < 0.001$ ). Lambs were six times more at risk of being killed by wolverines than adult ewes.

#### SHEEP LOSSES FOLLOWING THE KILLING OF WOLVERINES

The Spearman rank correlation and the Mann-Whitney  $U$ -test were used to investigate the effect of killing wolverines on sheep losses. We first investigated sheep loss in the group of years when wolverines had been killed against the rest of the years. To test the effect of the killing over a period of time,

the years following the killing were grouped and compared with the remaining years as a group. There was a negative relation between the number of wolverines killed and the combined loss of ewes and lambs on the whole Snøhetta plateau in the same year as wolverines were killed, but the effect declined rapidly and was not measurable the following years. There was no observed effect of killing wolverines on loss of ewes (Table 3). Testing the effect by municipalities where wolverines had been killed showed no effect, but the combined losses of lambs and sheep were lower in years when wolver-

**Table 1.** The loss of sheep on the Snøhetta plateau in relation to the number of sheep released on summer range and the number of wolverines present (stepwise multiple regression)

|       | <i>n</i> | Variable          | Coefficient | $r^2$ | d.f. | <i>F</i> | <i>P</i> |
|-------|----------|-------------------|-------------|-------|------|----------|----------|
| Ewes  | 15       | Constant          |             |       |      |          |          |
|       |          | No. of ewes       | 0.95        | 0.89  | 13   | 119.4    | < 0.001  |
|       |          | No. of wolverines |             |       |      |          | > 0.05   |
| Lambs | 15       | Constant          |             |       |      |          |          |
|       |          | No. of lambs      | 0.90        | 0.79  | 13   | 54.7     | < 0.001  |
|       |          | No. of wolverines |             |       |      |          | > 0.05   |

**Table 2.** Losses of lambs of the most frequent breeds of sheep (Dala, Rygja, Norwegian short-tailed and Norwegian fur-bearing sheep) on summer range on the Snøhetta plateau during 1989–93. Percentage losses in parentheses, Bonferroni Z-test. H = significantly higher losses than expected, L = significantly lower losses than expected ( $P < 0.05$ ), NS = not significantly different from expected ( $P > 0.05$ )

| Breed                  | No. of lambs on pasture | Proportion of total number on pasture | Observed losses | Difference from expected |
|------------------------|-------------------------|---------------------------------------|-----------------|--------------------------|
| Dala                   | 3877                    | 0.486                                 | 403 (10.4)      | H                        |
| Rygja                  | 428                     | 0.054                                 | 28 (6.5)        | NS                       |
| Norwegian short-tailed | 2986                    | 0.375                                 | 225 (7.5)       | L                        |
| Norwegian fur-bearing  | 681                     | 0.085                                 | 33 (4.9)        | L                        |
| Total                  | 7972                    |                                       | 689 (8.6)       |                          |

ines were killed. The effect did not carry over to subsequent years (Table 4).

#### RELATIONSHIP BETWEEN WOLVERINE REPRODUCTION AND SHEEP LOSSES

We used Spearman rank correlation to examine the relationship between wolverine reproduction and the percentage of sheep losses. The Mann–Whitney  $U$ -test was employed to test the relative loss in years with and without reproduction. The data were grouped in the same way as when the effect of killing was investigated. There was a statistically positive relationship between recorded number of wolverine cubs and the losses of lambs and of all sheep when the cub-rearing areas were combined, but not for the individual cub-rearing areas (Table 5). We found no relationship between loss of ewes and wolverine reproduction.

When the data were split by cub-rearing areas, a difference was found in the percentage loss of ewes among areas ( $\chi^2 = 16.14$ ,  $P < 0.001$ ) but not of lambs ( $\chi^2 = 2.49$ ,  $P = 0.29$ ). However, there were no significant differences in losses among years when reproduction took place and when it did not (Mann–Whitney  $U$ -test, 1 d.f.,  $P > 0.11$ ). Cub-rearing area 1 had a significantly higher loss of ewes

than areas 2 and 3 (Mann–Whitney  $U$ -test, 2 d.f.,  $P < 0.05$ ). Because the data could not be divided further than in to herding co-operatives, some flocks that did not graze within the approximate boundaries of the cub-rearing areas were also included in the analyses. Moreover, as observation sites of wolverine females with cubs also varied from year to year, the definitions of the denning areas may be inaccurate. Landa *et al.* (1998a) found a strong relationship between recorded cub-rearing and sheep losses in four trial areas, where one of the options for selection of trial area was that denning activity was recorded in the area.

#### Discussion

##### RELATIONSHIP BETWEEN THE NUMBER OF GRAZING SHEEP AND LOSSES

There was a positive linear relationship between the overall number of sheep grazing in the area and the number lost on the summer range. This supported the hypothesis that an increase in the number of sheep in grazing areas containing a stable wolverine population would lead to higher losses, but not proportionally higher losses. Few studies exist that consider livestock losses over a relatively long period.

**Table 3.** Relationship between number of wolverines killed and percentage sheep losses in subsequent years on the Snøhetta plateau during 1979–93 (Spearman rank-test, two-tailed)

|             |       | Within same year | 1 year after | 2 years after |
|-------------|-------|------------------|--------------|---------------|
| Ewes        | $r_s$ | 0.08             | 0.08         | −0.12         |
|             | $n$   | 15               | 14           | 13            |
|             | $P$   | 0.77             | 0.78         | 0.70          |
| Lambs       | $r_s$ | −0.55            | −0.30        | 0.02          |
|             | $n$   | 15               | 14           | 13            |
|             | $P$   | 0.034            | 0.30         | 0.94          |
| Total sheep | $r_s$ | −0.54            | −0.35        | −0.01         |
|             | $n$   | 15               | 14           | 13            |
|             | $P$   | 0.038            | 0.23         | 0.99          |

**Table 4.** Variability in sheep losses within municipalities where wolverines were being killed during the study period. The percentage losses are mean values from years with and without killing of wolverines (predation control). Standard deviation in parentheses (Mann–Whitney *U*-test, 1 d.f., two-tailed)

| Municipality |       |          | Same year | Year after | Two years after | Percentage loss in years without predation control | Percentage loss in years with predation control |
|--------------|-------|----------|-----------|------------|-----------------|----------------------------------------------------|-------------------------------------------------|
| Lesja        | Total | <i>P</i> | 0.50      | 0.74       | 0.86            | 4.8 (1.4)                                          | 5.2 (0.6)                                       |
|              |       | <i>U</i> | 11.0      | 13.0       | 14.0            |                                                    |                                                 |
|              | Ewes  | <i>P</i> | 0.74      | 0.86       | 0.86            | 2.0 (0.5)                                          | 2.0 (0.3)                                       |
|              |       | <i>U</i> | 13.0      | 14.0       | 14.0            |                                                    |                                                 |
|              | Lambs | <i>P</i> | 0.40      | 0.74       | 0.99            | 7.2 (0.8)                                          | 6.5 (1.8)                                       |
|              |       | <i>U</i> | 10.0      | 13.0       | 15.0            |                                                    |                                                 |
| Oppdal       | Total | <i>P</i> | 0.09      | 0.14       | 0.69            | 5.4 (1.5)                                          | 3.6 (0.6)                                       |
|              |       | <i>U</i> | 3.0       | 4.0        | 9.0             |                                                    |                                                 |
|              | Ewes  | <i>P</i> | 0.39      | 0.99       | 0.32            | 1.7 (0.3)                                          | 1.5 (0.4)                                       |
|              |       | <i>U</i> | 8.0       | 12.0       | 6.0             |                                                    |                                                 |
|              | Lambs | <i>P</i> | 0.09      | 0.14       | 0.69            | 7.8 (2.5)                                          | 5.0 (0.7)                                       |
|              |       | <i>U</i> | 3.0       | 4.0        | 9.0             |                                                    |                                                 |
| Sunndal      | Total | <i>P</i> | 0.43      | 0.54       | 0.83            | 5.0 (2.5)                                          | 4.0 (0.2)                                       |
|              |       | <i>U</i> | 7.0       | 8.0        | 9.0             |                                                    |                                                 |
|              | Ewes  | <i>P</i> | 0.43      | 0.17       | 0.66            | 2.1 (0.7)                                          | 1.6 (0.0)                                       |
|              |       | <i>U</i> | 7.0       | 4.0        | 8.0             |                                                    |                                                 |
|              | Lambs | <i>P</i> | 0.43      | 0.49       | 0.67            | 6.8 (3.5)                                          | 5.6 (0.2)                                       |
|              |       | <i>U</i> | 7.0       | 8.0        | 8.0             |                                                    |                                                 |
| Total area   | Total | <i>P</i> | 0.038     | 0.11       | 0.48            | 6.0 (0.8)                                          | 5.4 (1.2)                                       |
|              |       | <i>U</i> | 10.0      | 12.0       | 16.0            |                                                    |                                                 |
|              | Ewes  | <i>P</i> | 0.64      | 0.95       | 0.32            | 2.2 (0.4)                                          | 1.9 (0.3)                                       |
|              |       | <i>U</i> | 24.0      | 24.0       | 17.0            |                                                    |                                                 |
|              | Lambs | <i>P</i> | 0.028     | 0.14       | 0.57            | 8.6 (1.2)                                          | 7.8 (2.0)                                       |
|              |       | <i>U</i> | 9.0       | 13.0       | 14.0            |                                                    |                                                 |

Boggess, Andrews & Bishop (1978) and Clevenger, Campos & Hartasánchez (1994) suggested that livestock losses were a function of availability of livestock, rather than abundance of predators, which agrees with our results. Werner & Hall (1974) put forward an optimal model where a predator takes each prey item in direct proportion to the number present within its field of vision. The percentage losses of lambs and ewes should therefore be equal. Based on documented cases, however, our results showed that lambs were six times more likely to be

killed by wolverines than ewes. Because ewe carcasses are more easily found than lamb carcasses, the actual difference is probably even greater. One of the preconditions of the Werner & Hall (1974) model, and of classical foraging models, is that the time it takes to capture a prey, kill it and eat it is constant, and the energy cost should be identical irrespective of the size of the prey (Krebs & Davies 1991). The wolverine is not an efficient hunter of large prey (Landa *et al.* 1997). Lambs are inexperienced and smaller than adult ewes, and are there-

**Table 5.** Relationship between the number of recorded wolverine cubs (May–September) and loss of sheep within the cub-rearing areas during 1979–93 (Spearman rank-test, two tailed)

|       |                      |  | All areas combined | Cub-rearing area 1 | Cub-rearing area 2 | Cub-rearing area 3 |
|-------|----------------------|--|--------------------|--------------------|--------------------|--------------------|
| Ewes  | <i>r<sub>s</sub></i> |  | 0.41               | 0.38               | −0.22              | 0.17               |
|       | <i>n</i>             |  | 15                 | 12                 | 13                 | 14                 |
|       | <i>P</i>             |  | 0.13               | 0.22               | 0.48               | 0.57               |
| Lambs | <i>r<sub>s</sub></i> |  | 0.49               | 0.10               | −0.29              | 0.45               |
|       | <i>n</i>             |  | 15                 | 12                 | 13                 | 14                 |
|       | <i>P</i>             |  | 0.06               | 0.76               | 0.34               | 0.11               |
| Total | <i>r<sub>s</sub></i> |  | 0.53               | 0.15               | −0.24              | 0.43               |
|       | <i>n</i>             |  | 15                 | 12                 | 13                 | 14                 |
|       | <i>P</i>             |  | 0.044              | 0.64               | 0.42               | 0.13               |

fore probably easier to kill (Mortensen 1990). Thus, our results agree with many predation studies that show a greater vulnerability of newborn and young prey (Mech 1970). Our results probably deviate from the model of Werner & Hall (1974) because wolverines are more efficient in catching lambs than ewes.

#### ANNUAL DIFFERENCES IN LOSSES

During the study period we found no variation in the annual percentage losses on the Snøhetta plateau. Other investigations have shown that the climate at different times during the grazing season may have an effect on the survival of lambs, and that this created annual variations in losses (Douglas & Leslie 1986; Warren & Mysterud 1990). The Snøhetta plateau is relatively large, with climate conditions varying from coastal to continental. Perhaps weather variations do not affect the entire area equally.

#### DIFFERENCES IN VULNERABILITY AMONG SHEEP BREEDS

The four most numerous of the 13 sheep breeds grazing on the Snøhetta plateau in 1989–93 were selected for analysis, to ensure that the breeds analysed were evenly spread over the study area. The Norwegian short-tailed and Norwegian fur-bearing breeds experienced lower losses to wolverines than the Dala breed. Pedersen (1993) found that the social bond between ewes and lambs on summer range was higher for the short-tailed than the Dala breed. The activity level of short-tailed lambs was higher after birth, and they also showed a greater increase in weight between birth and release on to the grazing range, from release to autumn weighing, and in the total weight increase during the period from birth to autumn. Differences in behaviour among breeds, in addition to differences in breed composition of flocks, may explain the variation in losses between co-operatives and grazing areas in our investigation.

#### WOLVERINE PREDATION AND THE NUMBER OF COMPENSATED SHEEP

Applications for compensation for the loss of sheep and lambs increased after protection was enacted. Our investigation revealed no relationship between the numbers of wolverines and compensated ewes or lambs on the Snøhetta plateau. The willingness to award compensation has varied in accordance with the guidelines given by national authorities. This may have affected the relationship between compensated livestock and the wolverine population. Wolverine population censuses on the Snøhetta pla-

teau are carried out in winter (Landa *et al.* 1998c). Tracking in winter only records wolverines that are 1 year old or older. Hence the number of wolverines may vary considerably between winter and summer when the sheep are grazing, which would increase the variance in this comparison. A 15-year investigation by Boggess, Andrews & Bishop (1978) found no relationship between the numbers of coyotes or dogs and the amount of predation on livestock, although other studies have shown a positive relationship between coyote numbers and sheep loss (Nass, Lync & Theade 1984).

Generally, only a limited proportion of the lost animals are found (Myrberget & Grotnes 1969; Brøderud, Kvam & Sørensen 1982) and still fewer are found in such a state that it is possible to determine the cause of death with certainty (Myrberget & Grotnes 1969; Brøderud, Kvam & Sørensen 1982). In an intensive study with radio-marked lambs, the cause of death could not be determined for 40% of the lost lambs that were found, and 10% of the lost lambs were not found at all (Mysterud *et al.* 1993). In recent years, 10–20% of the lambs lost on the Snøhetta plateau have been found, and 50–85% of these had been killed by wolverines (Børset 1995; Mortensen 1995). Some animals 'disappear' because the wolverine hoards them in such a way that they are not found (Haglund 1966; Bjärvall, Franzén & Nilsson 1978). In doubtful cases, where it is only possible to determine that a predator has killed the sheep, compensation is given without specifying which predator is responsible. Consequently, the number of compensated animals and the total losses do not necessarily give an accurate picture of how many sheep are taken by wolverines.

#### SHEEP LOSSES AFTER KILLING OF WOLVERINES

Several studies of livestock losses following the removal of predators have been undertaken. Bjorge & Gunson (1985) found that the extermination of wolves *Canis lupus* from an area in Alberta, Canada, quickly led to re-establishment of wolves from neighbouring areas. The extermination of wolves reduced livestock losses for 2 years. Reynolds, Goddard & Brockless (1993) found that foxes became re-established in the course of the same season that foxes were removed from an area. Also, Sagør, Swenson & Røskaft (1996) found that the killing of brown bears in two areas in Norway did not reduce the losses of sheep in the following year. Our investigation showed a reduction in the percentage losses of lambs the same year as the killing of wolverines took place, but not the succeeding year. The reason for this may be that mostly single individuals were killed on the Snøhetta plateau, whereas in Bjorge & Gunson's (1985) investigation

the wolf population was locally exterminated. Because wolverines can roam over long distances (Hornocker & Hash 1981), the potential for their re-establishment is relatively large (Landa *et al.* 1998b). Our results therefore support the hypothesis that the killing of 'problematic wolverines' leads to a reduction in sheep losses, but only in the short term. When re-establishment takes place, it must be expected that losses will return. Thus, local extermination only gives a short-term effect, unless the exterminated population is isolated.

#### RELATIONSHIP BETWEEN SHEEP LOSSES AND WOLVERINE REPRODUCTION

This study revealed a positive relationship between the number of young wolverines reared successfully and both the losses of lambs and the total losses within the combined cub-rearing areas. Sheep are released on mountain ranges in June and graze unattended until the beginning of September, when they are collected. Most documented wolverine predation occurs during the last few weeks of the grazing period (Børset 1995; Mortensen 1995). The onset of sheep predation occurs at a time when the wolverine's caching behaviour (Haglund 1966) is expected to increase before winter. However, no relationship between losses during the autumn and the number of wolverine litters reared successfully the following winter have been found so far (Landa *et al.* 1997), suggesting that sheep are not an important or required prey for wolverines.

The oestrous season of wolverine females coincides with the cub-rearing period, which means that both males and subadults from previous litters visit the cub-rearing area (Rausch & Pearson 1972; Magoun 1985; Banci & Harestad 1988). The area used by wolverine females is significantly smaller when they have dependant cubs (Magoun 1985). This probably results in the denning areas containing most wolverines. This may explain why there was a link between the rearing of young wolverines and sheep losses in the denning areas as a whole. The results provide support for the hypothesis that there are higher sheep losses in wolverine denning areas. The investigation has not, however, clarified which particular types of wolverines take more sheep than others. Increased loss in the autumn in the years when many wolverine cubs are produced may suggest that cubs take part in predation on lambs just before attaining independence from their mothers. Thus, lambs might be important and easy prey for the young, newly independent wolverines facing their first winter and a life as solitary individuals.

#### MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Co-existence of wolverines and unguarded sheep without some depredation appears to be impossible. Limited losses may be acceptable for conservation purposes, but extensive damage can hardly be tolerated. The present management practices, with licensed hunting during winter and control measurements during the summer, on such a small wolverine population has to be questioned in the context of conservation of wolverines (Landa, Lindén & Kojola 1999). In areas where sheep farming occurs in wolverine habitat, this study has shown that control efforts have no long-term effects in reducing losses.

We recommend that less susceptible sheep breeds be used in wolverine areas to reduce losses to wolverines. Reduction in losses could also be achieved by removing sheep from areas where wolverine offspring are reared. Collecting and removing sheep from pasture before the onset of the period of major wolverine predation in late August will also reduce sheep losses. Economic incentives to encourage farmers to adopt forms of livestock husbandry that are compatible with wolverines in important wolverine habitat may be necessary for successful wolverine conservation.

In areas where wolverine populations are viable, it would be advantageous if control actions were designed as experiments to document better the effects of removal of different categories of wolverines on reduced sheep losses.

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