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Mortality of lambs in free-ranging domestic sheep (*Ovis aries*) in northern Norway

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Abstract

Domestic lamb mortality on an open forested and alpine summer range in the municipality of Målselv in northern Norway was investigated. Two hundred and fifty-three lambs in four of the area's six flocks were randomly fitted with mortality transmitters and monitored throughout the summer grazing season from June to September. Total losses in the six flocks were 183 (22.9%) lambs and 20 (4.2%) ewes. The carcasses of 69 lambs, 36 of which had radio-collars, and six ewes were recovered. Of the collared lambs, eight (22%) died as a result of disease and 27 (75%) were killed by predators. Implicated predators included red fox *Vulpes vulpes*, lynx *Lynx lynx*, golden eagle *Aquila chrysaetos* and wolverine *Gulo gulo*. Diseased animals included those diagnosed with pasteurellosis, disrupted intestinal functions and advanced coccidiosis. The remains of one lamb were too decomposed for necropsy, though there was no evidence that it had been attacked by a predator. Factors associated with losses were identified using logistic regression. Age of lamb at time of release on the summer range and age of dam were statistically associated with lamb losses ($P < 0.05$). Mortality was higher among older lambs and those of year-old ewes. Parameters commonly associated with lamb size and growth were not statistically associated with mortality. The negative association between lamb mortality and age of dam may be related to the quality of maternal care provided by ewes of different ages, particularly vigilance in the habitat of predators. Similarly, the positive association between mortality and age of lamb may be related to changing lamb behaviour, specifically increased distance from ewe, as lambs grow older and more independent. Predators, when present, are a major cause of mortality in free-ranging lambs, as in most wild ungulates.

Key words: *Ovis aries*, predation, wolverine, forest, alpine, grazing

INTRODUCTION

The alpine regions of Norway provide summer grazing for most of the country's one million ewes and their lambs. In many areas, sheep are released in early summer directly onto the range from valley farms, and graze freely up through the coniferous and birch *Betula odorata* forests and onto alpine heaths and meadows. The amount of time spent in the forest on the way to the alpine areas can vary from a few days to several weeks, depending presumably on ambient temperature, which influences snowmelt and forage plant development (Warren & Mysterud, 1991). Similar upslope movements along this phenological gradient have also been described in red deer *Cervus elaphus* (Albon & Langvatn, 1992).

In a mountainous region in Troms county in northern Norway, and increasingly also in other parts of the country, where sheep follow this gradient from lower to higher elevations, lamb mortality is chronically high. Wolverine *Gulo gulo* is believed to be responsible for most of these losses, though red foxes *Vulpes vulpes*, lynx *Lynx lynx* and golden eagles *Aquila chrysaetos* are also present and may kill lambs. The habitat preferences of at least the largest of these predators (wolverine and lynx) however, are quite different (Kjørstad *et al.*, 1998; Landa *et al.*, 1998). Sheep exploiting an altitudinal gradient through varying vegetation profiles will thus transverse the habitats of different potential predators during the grazing season.

Determining the extent to which the different predators are responsible for lamb mortality is usually quite difficult. The extensive nature of the grazing system combined with effective renovation by scavengers hinders recovery of carcasses. Disease and accidents may also contribute to high mortality in the region, though the extent to which these factors play a part is also uncertain.

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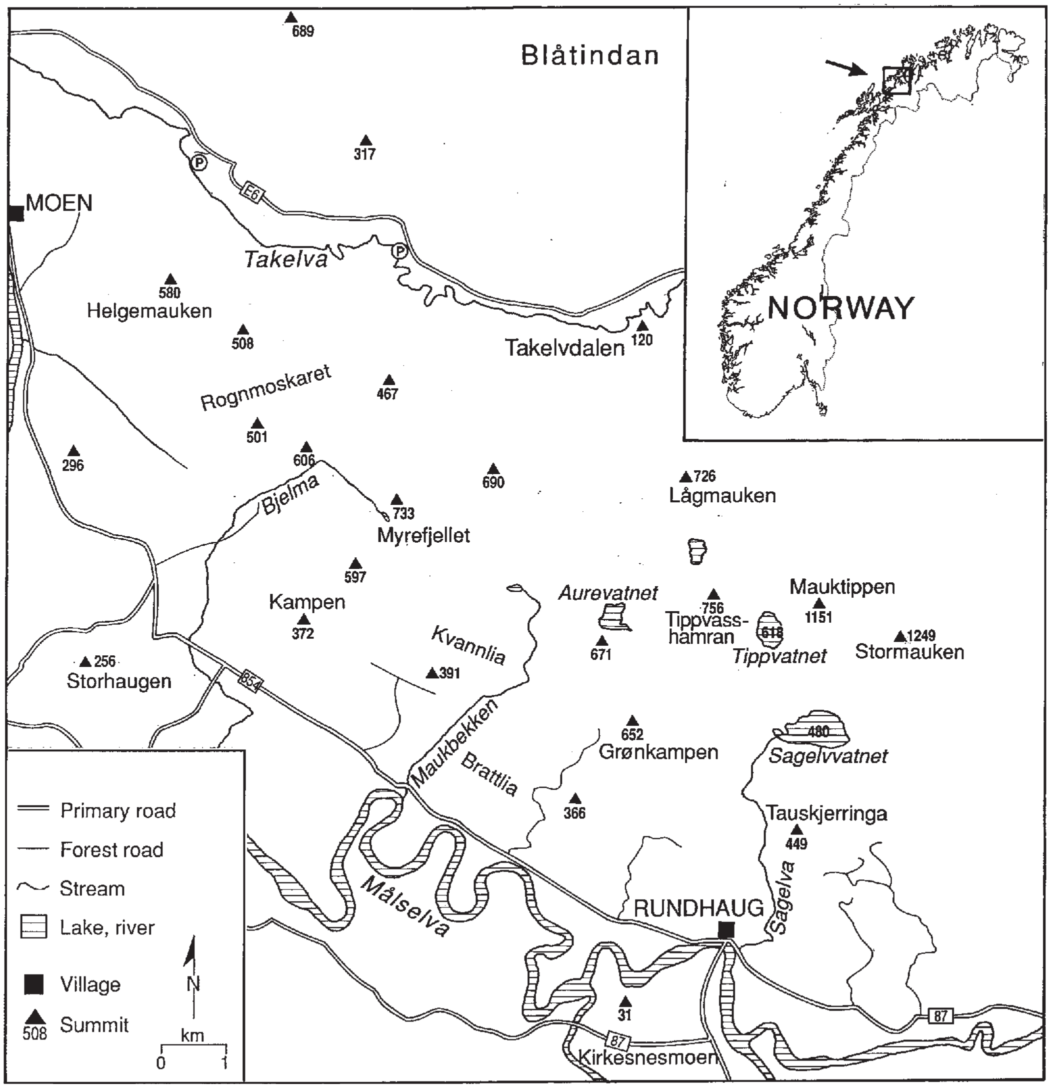

Fig. 1. Map of the study area in the municipality of Målselv in northern Norway.

By randomly collaring lambs with radio-transmitters, mortality on the summer range could be monitored, and causes of death revealed and quantified. This paper describes the causes of death among lambs as well as the temporal and spatial distribution of carcasses in four flocks of sheep on a forested/alpine summer range in northern Norway. Factors associated with lamb mortality on the open summer range are identified using logistic regression, and these are discussed, especially with respect to the region's predators.

MATERIALS AND METHODS

Study area

This study was conducted in the municipality of Målselv, in Troms county, northern Norway. The area of *c.* 110 km^2 lies between the Målselv and Takelv valleys (Fig. 1). The region is mountainous and lies near the coast. The altitudinal gradient is therefore considerable, ranging from 40 to 1250 m, though most of the actual grazing area is rolling forested terrain and alpine plateau between 300 and 800 m. A few small lakes and ponds dot the area, and bogs are common both above and below the treeline.

Climate in the region is semi-continental with cold winters and cool summers (Nordisk Ministerråd, 1984). Winter snow pack can be substantial, especially in the higher elevations. Average January and July temperatures at the nearest weather station (Bardufoss, 10 km from study area) are -10.3° and $13\,^\circ$C, respectively. Average annual precipitation is 652 mm.

The study area lies within the sub-maritime birch/pine (*Betula odorata*/*Pinus sylvestris*) vegetation region (Nordisk Ministerråd, 1984). These two species occur in mixed stands in the valleys and lower slopes. Further upslope, birch occurs in pure stands up to the climatic treeline. Understorey vegetation is often a luxuriant mixture of shrubs such as blueberry *Vaccinium myrtillus*, large ferns *Dryopteris* spp. and forbs such as crane's bill *Geranium sylvaticum*, cow wheat *Melampyrum* spp. and chickweed wintergreen *Trientalis europea*. Alpine vegetation varies from lichen *Cladonia* spp. on dry, exposed ridges to hairgrass *Dechampsia flexuosa*, cowberry *Empetrum hermaphroditum*, blueberry and dwarf birch *Betula nana* on sites with a stable winter snowpack.

Elk *Alces alces* are common in the valleys and on the forested slopes, and roe deer *Capreolus capreolus* also occur, though in small numbers. In addition to resident populations of red fox, lynx, golden eagle and wolverine, transient individuals of both brown bear *Ursus arctos* and wolf *Canis lupus* may also occur. Several avian scavengers are common, such as the raven *Corvus corax* and white-tailed sea eagle *Haliaetus albicilla*.

Six flocks of sheep totalling over 1200 animals graze in the study area from the beginning of June until mid-September. In addition, domestic reindeer may graze in the central and eastern parts of the area from November to May.

Radio-tracking and carcass recovery

Just before release onto their summer range, 236 lambs in 4 of the area's 6 flocks of sheep were randomly chosen and fitted with silent mortality transmitters. These transmitters are activated after 2–3 h absence of movement, allowing carcasses to be quickly located. The telemetry equipment used has been described in detail by Mysterud & Warren (1991). The 4 flocks were chosen from the 6 in this area with respect to their expected distribution on the range to aid accurate radio-tracking. Subsequent regression analysis of the data (described below) includes only parameters from the 4 flocks with mortality transmitters.

Sheep in the 4 flocks, 719 lambs and 426 ewes, primarily of the Steigar breed, were released gradually (over *c*. 1 week) onto the range in the forested valley on the north side of Målselva (Fig. 1), and allowed to graze freely until they were herded and brought down from their alpine range in mid-September. Monitoring of the area for activated transmitters began when the first animals were released, and tracking continued throughout the summer from several points along the roads in the Målselv and Takelv valleys, as well as on foot within the grazing area itself.

Upon discovery, lamb carcasses and the surrounding site were examined according to standardized procedures used in previous studies (e.g. Warren & Mysterud, 1995). Carcasses lacking an obvious cause of death were immediately sent to the nearest veterinary laboratory for pathological necropsy. Lambs killed by predators were examined either in the field or at the study's field station. When possible, fresh predator-killed lambs were also sent to the veterinary laboratory after field examination. Shed radio-collars, as well as those recovered from lamb carcasses were subsequently placed on unreleased lambs early in the season, or on unmarked lambs captured in the field. The total number of lambs collared during the grazing season was 253.

Flock demography and regression model

From birth until their release onto the open range, several standard husbandry parameters were recorded for all animals. Lambs were weighed within 24 h of birth in April and May, and again just before their release in early June. These 2 weights were modelled as separate variables, and were also used to calculate a spring growth rate (g/day). The age of the lambs at release, age of dam, sex and litter size were also recorded. These were used as independent variables in developing a logistic regression model:

$$\pi(x) = e^{ß_o + ß_1 x_1 + \ldots ß_i x_i} / 1 + e^{ß_o + ß_1 x_1 + \ldots ß_i x_i} \quad [1]$$

where $\pi(x)$ is the logistic regression function, which in this context states P(mortality | the independent variable x), $ß_o$ is a constant and $ß_1 \ldots ß_i$ are the regression coefficients for the independent variables $x_1 \ldots x_i$ (see Trexler & Travis, 1993).

Model development was guided by Hosmer & Lemeshow (1989) and by previous mortality studies (Malmberg, 1994; Warren & Mysterud, 1995). Preliminary analysis revealed that linearity in the logit could not be assumed for birth weight and age of dam. These parameters were subsequently grouped and modelled using categorical dummy variables, as were sex and treatment (i.e. radio-collared/non-collared). Litter size, weight and age upon release and spring growth rate displayed satisfactory logit linearity and were modelled as continuous variables.

Initially, univariate models were developed for each independent variable. Those judged to be at least weakly associated with lamb mortality (Wald test (W), $P < 0.25$) were the subsequent building blocks for the multivariable model. Further model development was conducted using 'manual' forward step-wise regression, whereby the individual contribution of each new variable was evaluated using a Wald test (W). Variables with $P < 0.1$ were retained in the multivariable main effects model (see Hosmer & Lemeshow, 1989). On completion of the main effects model, the contribution of biologically plausible interactions was evaluated. Interactions contributing significantly to the main effects model (G-test, $P < 0.1$) were included in the final model. Goodness-of-fit of the final model was assessed using the Hosmer–Lemeshow statistic $\hat{C}$ Model development and evaluation was done using the LOGIT module of SYSTAT (Steinberg & Colla, 1991).

RESULTS

Carcass recovery and causes of death

Forty-seven of the 263 (17.9%) radio-collared lambs died during the grazing season. Of these, 36 were recovered. The remaining 11 were not recovered, presumably because of equipment failure. It is assumed,

Table 1. Number of ewes and lambs released and lost on the open range in the six flocks in the Målselv grazing area. Radio-collared lambs were in flocks I–IV

	Animals released		Animals lost		Loss (%)	
Flock	Ewes	Lambs	Ewes	Lambs	Ewes	Lambs
I	100	173	3	25	3.0	14,5
II	162	268	4	61	2.5	22.8
III	118	188	5	39	4.2	20.7
IV	46	90	3	17	6.5	18.9
V	15	22	0	6	0.0	27.3
VI	37	59	5	35	13.5	59.3
Total	478	800	20	183	4.2	22.9

however, that collar failure occurred randomly with respect to cause, time and location of death. Additional, non-collared carcasses were also recovered. Sixty-nine of the 800 (8.6%) (collared and non-collared) lambs and six of the 478 (1.3%) ewes in the six flocks were recovered during the grazing season, including one severely injured lamb that survived an attack by wolverine, but which was subsequently destroyed by project workers. In addition to the recovered animals, 114 lambs and 14 ewes died on the summer range. Thus, total losses in the six flocks were 183 (22.9%) lambs and 20 (4.2%) ewes (Table 1).

Among the 36 recovered radio-collared lambs in the four flocks, eight (22%) died as a result of disease and 27 (75%) were killed by predators. Among the latter, two (6%) were killed by red fox, five (14%) by golden eagle, three by lynx (8%) and 17 (47%) by wolverine. Among the diseased animals, five (14%) were diagnosed with pasteurellosis, one (3%) had disrupted intestinal functions, and one (3%) had advanced coccidiosis. The remains of one (3%) lamb were too decomposed for necropsy, though there were no signs by which to implicate a predator.

Temporal and spatial distribution

The temporal distribution of the 36 recovered radio-collared carcasses was uneven. The first carcasses were recovered almost immediately after the sheep were released on to the range, and 21 dead lambs were recovered by the beginning of July. During mid-season, 6–8 weeks after release, no carcasses were found, while 15 carcasses were recovered in August and September (Fig. 2).

Causes of death were also unevenly distributed in time. Diseased animals succumbed mostly in the first half of the grazing season, while 14 of the 15 lambs recovered in the second half of the season were killed by predators (Fig. 2). Red fox was responsible for the first predator kills, followed by lynx and golden eagle. Wolverine was the sole predator responsible for lamb kills in late season.

Carcasses were located in all parts of the grazing area, though most were recovered in the south-eastern and south-central parts of the range around Sagelvvatnet and Kvannlia, respectively (Fig. 3). Fox and lynx kills were made mostly on the forested slopes above the site from which the sheep were released. Eagle kills were made just as the sheep emerged above the birch forest, and were often associated with locally rugged terrain. Wolverine kills were located especially in the eastern half of the area, while sheep grazed primarily above the treeline.

The use of predator-killed animals by the perpetrators themselves varied greatly, but was generally low, especially among wolverine-killed animals. Decapitated carcasses were common, the occurrence of which increased towards the end of the season. Foxes, lynx and eagles used carcasses to a greater extent. Scavenging by golden eagles, white-tailed sea eagles and other raptors as well as by ravens was common and often extensive.

Twelve predator-killed lambs were examined at the veterinary laboratory to evaluate overall condition. One of these was too decomposed for further necropsy. Among the remaining 11, no specific signs of disease,

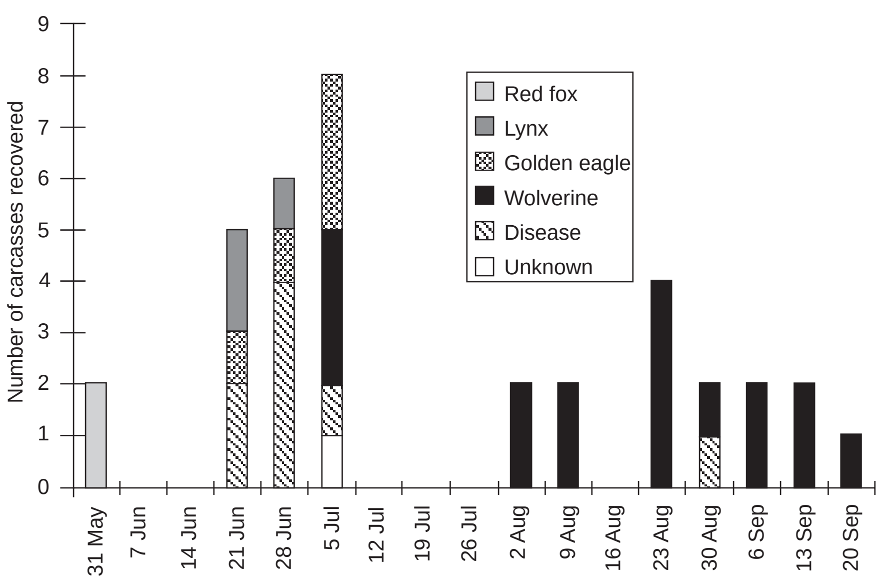

Fig. 2. Temporal distribution of recovered carcasses by cause of death.

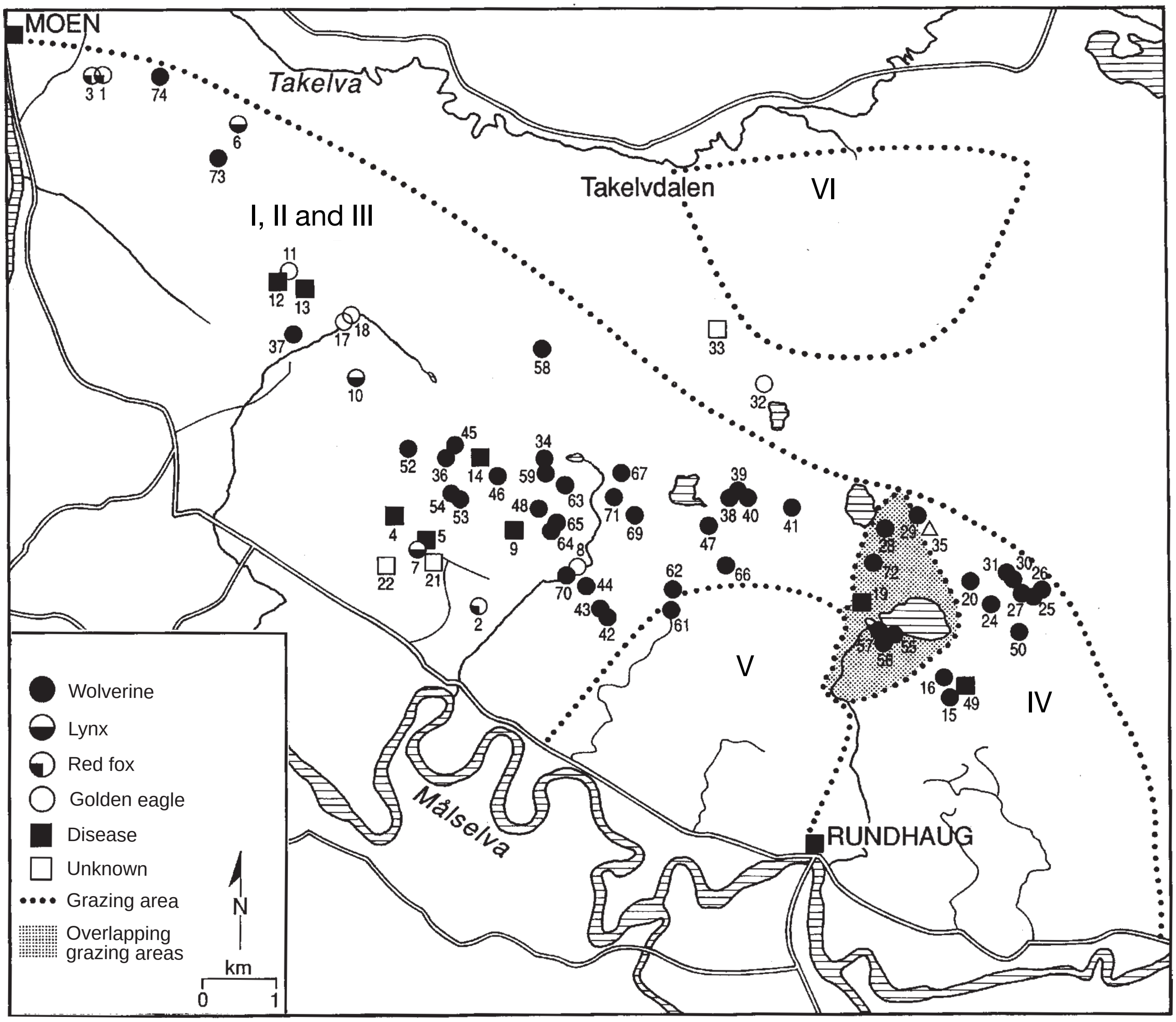

Fig. 3. Spatial distribution of recovered carcasses by cause of death, numbered in chronological order of recovery. Map shows also principle grazing areas of the study's six flocks.

parasite burden or reduced physical or physiological condition were found.

Initially, each independent variable was modelled individually. Birth weight, age of dam, age at release and spring growth rate were subsequently included in the multivariate model ($P < 0.25$). Use of these in the forward step-wise regression yielded the 'main effects' model, in which only two variables were retained: ewe age and age at release (Table 2). The interactions between ewe age and age at release was considered, but did not contribute significantly to the model (P=0.88). The resulting model of the main effects of lamb mortality (Table 2) fit the data well ($\hat{C} = 1.43$, d.f. = 3, $P = 0.70$).

With lamb mortality in the four radio-collared flocks well over 10% (19.7%), the approximate likelihood (unlikelihood) of mortality among lambs with a given value of independent variable x is better assessed by converting the odds ratio associated with variable x to relative risks (RR):

$$RR = \Psi / (1 + ((\Psi - 1)R_o)) \qquad [2]$$

where R_o is mortality in the reference group. Thus, a given lamb of a yearling ewe ran a 70% higher risk (i.e. $RR = 1.70$) of succumbing during the grazing season than a given reference lamb with a 2- to 5-year-old ewe. The lambs of older ewes, however, ran only 74% as great a risk ($RR = 0.74$) of mortality as those in the reference group. Lambs that were older upon release on to the range ran a higher relative risk of mortality than did younger lambs; each additional day of age was associated with a 4% increase ($RR = 1.04$) in the relative risk (Table 2).

DISCUSSION

Causes and distribution of mortality

Lambs died throughout the season, though cause of death varied. Lambs seem most susceptible to disease in the first part of the season. Upon release on to the

Table 2. Multivariate model of lamb mortality (main effects model). β, estimated coefficient; SE, standard error; Ψ, odds ratio; 95% confidence interval; *RR*, relative risk; *W*, Wald test statistic; *P*-value

Variable	β	SE	Ψ	95% CI	*RR*	*W*	*P*
Constant	−2.74	0.68	–	–	–	–	–
Ewe age 1 year	0.59	0.23	1.80	2.84 1.70	1.70	2.52	0.01
Ewe age 3 years	−0.34	0.28	0.72	1.25 0.41	0.74	−1.18	0.24
Age at release	0.05	0.02	1.05	1.09 1.01	1.04	2.34	0.02

range, lambs (and their ewes) must quickly make the transition from grazing contained, managed home pastures to searching for much more varied and patchy forage plants in the forest. Animals must travel farther in search of forage, be more vigilant and endure the elements. Lambs unable to keep pace with their ewes, and perhaps already having contracted an infection before release, can become weak and succumb. At the same time, lamb growth rate is greatest early in the season. Most lambs grow quickly during this period, becoming more mobile and perhaps clearing a neonatal threshold. Disease seems to become less important as the season progresses and lambs become more robust. A similar mortality pattern has been described among wild ungulates (reviewed by Linnell, Aanes & Andersen, 1995). The diseases reported here are common among free-ranging flocks in Norway (Mysterud & Warren, 1991), and losses attributed to disease, about 20% of the total loss, are comparable to those in similar studies elsewhere (Warren, Mysterud & Hasvold, 1998).

While diseased lambs succumbed mostly in early season, predation was prevalent throughout the summer, and predators accounted for three-quarters of the total lamb mortality. While quite high, such high losses to predators are not unprecedented; predator-related mortality in both wild and domestic ungulates is often considerable (Bjärvall *et al*., 1990; Linnell *et al*., 1995). Four predator species were implicated in connection with lamb losses. Though certain factors may influence an individual's susceptibility to predation once a predator is encountered (Warren & Mysterud, 1995), the chances of encountering a particular predator species will vary with habitat. Shortly after the sheep were released, red foxes made the first registered kill. Early losses to foxes are common in much of Norway (Malmberg, 1994). Early in the season, lambs are small and graze just upslope from their release site. Foxes, which are tolerant of human activity, frequent the valleys and lower slopes and are therefore likely to be the first predator encountered by the young lambs.

Three weeks later and further upslope, the first lynx kill was located. Predation by lynx can lead to substantial losses, and has been linked to high mortality among both domestic lambs and reindeer calves farther south in Norway (Mysterud & Warren, 1991; Kjelvik *et al*., 1998). Only three lynx kills were recorded in this study. These carcasses were recovered within a period of 4 days, and exclusively in the mostly forested western half of the study area.

Shortly after the first lynx kill was discovered, as the sheep grazed in the more open birch forest and in more precipitous terrain, golden eagles began taking sheep. Five eagle-killed lambs were recovered between the end of June and the beginning of August. Golden eagles were also observed regularly throughout August and September, though they were not implicated in any lamb kills in the second half of the season. Use of abundant carrion by eagles in the latter part of the summer (as the result of wolverine predation) probably reduced or even eliminated their need to make additional kills.

Predation by wolverine was the single most important cause of death among lambs in the study area, accounting for nearly half of the total lamb mortality. Wolverine tracks were first seen in the snow just below the treeline in early June, in the south-eastern part of the study area. The first wolverine kills were recorded in the beginning of July. It was not until the beginning of August, however, that wolverines consistently took lambs in the study flocks. Predation continued throughout the study area as long as sheep were on the range.

Wolverines are opportunistic and respond to abundant and easily captured prey (Magoun, 1987). Though present, wolverine did not consistently exploit sheep, however, until later in the season when the sheep began grazing on the alpine portions of the range. The younger, smaller lambs were even more vulnerable while grazing in the forest (e.g. Festa-Bianchet, Urquhart & Smith, 1994), though, with the exception of the very first kills, wolverine apparently ventured little below the treeline after sheep earlier in the season.

Alternatively, it is possible that wolverines began taking lambs early in the season, but in the north-eastern part of the study area, in one of the flocks not fitted with radio-transmitters. A den, located on the steep north face of Stormauken (H. Utby, pers. comm.), could have limited early summer excursions to this area (Magoun & Copeland, 1998; Warren *et al*., 1998). Indeed, lamb losses were greatest (35 of 59 lambs, 59.3%) in the flock north of Stormauken. The timing of these losses, however, is uncertain.

Reproduction among wolverines in the study area had been suspected since the late 1980s. Chronically high lamb losses and frequent observations of wolverines and of tracks seemed to indicate resident individuals. Reproduction was subsequently confirmed when two wolverines were shot; the first in the beginning of August on the south slope of Stormauken, just north of Sagelvvatn, and the second in the beginning of September north-west of Stormauken. Both were judged to be current-year offspring, and their removal had no apparent effect on lamb losses during the remainder of the grazing season.

The number of lambs killed in the latter part of the summer far exceeded that which was necessary to meet short-term food requirements of the wolverines. On at least three occasions, two to five lambs (radio-collared and uncollared) were killed within a single day. Once, three intact carcasses were found by Sagelvvatn within a radius of 100 m. Such behaviour is well described for mustelids and other carnivores (Mysterud, 1980; Jedrezejwksa & Jedrezejwksa, 1989). The wolverine, a generalist and a relatively poor hunter, apparently exploits the opportunity to fell readily available and easily killed prey (*sensu* Oksanen, Oksanen & Fretwell, 1985). It can be argued that this short-term surplus could be later used by the predator itself or by its conspecifics. While our prompt confiscation of discovered lambs (collared and uncollared) rendered at least part of this surplus unavailable, it is likely, however, that the extensive use of carrion by golden eagles (at least two), sea eagles (at least two), and especially by ravens (perhaps as many as 50) also precluded subsequent use by wolverines.

There was no evidence that the lambs killed by wolverines were in poorer physical condition. Of the 10 wolverine-killed lambs sent in for pathological examination, none was found to be in a compromised condition.

In summary, a mid-season pause in lamb mortality divided the summer into two distinct periods with respect to causes of death. All but one of the diseased animals, and lambs killed by four different predators (red fox, lynx, golden eagle and wolverine) were recovered in the first half of the season. In the latter part of the summer, however, wolverines alone were responsible for the loss of most (14 of 15) of the radio-collared lambs. The observed pattern in the losses to the different predator species is probably the result of the tracking and use of forage plants by sheep along a phenological gradient from the valley and lower slopes to the alpine heath (e.g. Warren & Mysterud, 1991; Albon & Longvatn, 1992), which subsequently leads them through, if only temporarily, the preferred habitats of different species within the predator guild.

Studies describing lamb, fawn and calf mortality among domestic and wild ungulates have documented the vulnerability of the young, particularly immediately following birth. Thus, factors such as birth weight, parturition date and perinatal weather conditions are often shown to influence neonatal mortality (Petersson & Danell, 1985; Linnell *et al.*, 1995). In the current study, however, birth weight, litter size and growth rate (from birth to release) were not significantly associated with lamb mortality. The significance of these factors is ambiguous also in other mortality studies, including those conducted in Norway using the same methods as described here (Malmberg, 1994; Warren & Mysterud, 1995). Such ambiguity may reflect the highly varied environmental conditions, with respect to weather, predators and topography encountered by sheep on the open range. Juveniles remain vulnerable several weeks postpartum, however, especially on ranges with predators (Linnell *et al.*, 1995).

In several species, and not just in ungulates, age of dam seems to influence offspring survival (Linnell *et al.*, 1995; Melting, Eggen & Kvam, 1998); younger mothers are poorer mothers, and in the current study, mortality was higher among the lambs of year-old ewes. Presumably, year-old mothers are still investing in their own growth and development at a cost that is borne by their offspring (Birgersson, 1997). The effects of age of dam on offspring mortality may be also related to factors not directly connected to resource (nutrient/energy) allocation and growth. Especially in an environment where predation is prevalent, ewe age and thereby level of experience and vigilance may also influence lamb vulnerability. The distance maintained between ewe and lamb decreases with ewe age (Hewson & Verkaik, 1981), which could afford lambs greater protection against predators. This argument has also been put forward to explain similar results in mortality studies in which bears were the main predator (Mysterud, 1974; Warren & Mysterud, 1995).

Distance between dam and offspring may be affected not only by age of ewe, but also by the lamb's age and activity level. As lambs begin venturing from their dams, concurrently for example with less frequent suckling (Festa-Bianchet, 1988), they may become more vulnerable to predation. This could explain perhaps the unexpected result that the relative risk of mortality increased with age upon release onto the summer range. Gluesing & Balph (1980) showed that the amount of time spent at various activities changes as lambs grow older. In their study, lambs grazed more and rested less with age, and within litters the more active lamb was the most susceptible to predation. A higher activity level among male white-tailed deer fawns has also been suggested to place them at higher risk (than females) of detection by predators (Schwede, Heindrichs & Wemmer, 1992).

There was no difference between surviving and lost lambs with respect to their release weights. Size (weight), a commonly used indicator of condition and vulnerability, was thus not statistically associated with lamb mortality. It is important to recall, however, that 75% of the total lamb losses was the result of predation. In such environments, age-related behaviour such as level of activity (especially among lambs) and vigilance (especially among their ewes), rather than the lamb's size, may be a more important factor associated with lamb survival.

In this study, free-ranging sheep were preyed upon by four species of endemic predators. This situation is similar to that in other parts of Norway, and perhaps in the future in other parts of Europe. Often, factors associated with higher domestic lamb mortality are similar to those found also in wild ungulate (and to some extent most mammal) populations (Caughley, 1966). Identifying factors associated with mortality on the open range is complicated, however, by the diversity of habitats and topography used by free-ranging animals, and where several predator species are encountered.

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