esa ECOSPHERE

Sheep farming and large carnivores: What are the factors influencing claimed losses?

Géraldine Mabille,[1] Audun Stien,[1,]† Torkild Tveraa,[1] Atle Mysterud,[2] Henrik Brøseth,[3] and John D. C. Linnell[3]

[1]*Norwegian Institute for Nature Research, Department for Arctic Ecology, Framsenteret, NO-9296 Tromsø, Norway*
[2]*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway*
[3]*Norwegian Institute for Nature Research, Department of Terrestrial Ecology, P.O. Box 5685 Sluppen, NO-7485 Trondheim, Norway*

Citation: Mabille, G., A. Stien, T. Tveraa, A. Mysterud, H. Brøseth, and J. D. C. Linnell. 2015. Sheep farming and large carnivores: What are the factors influencing claimed losses? Ecosphere 6(5):82. http://dx.doi.org/10.1890/ES14-00444.1

Abstract. Large carnivore populations are recovering in many parts of the world and this generates conflicts with humans, notably in terms of livestock depredation. Governmental programs of mitigation measures and compensation for losses are often implemented to reduce conflicts, but the factors affecting losses are poorly understood. We used 11 years of data on domestic sheep (*Ovis aries*) claimed, and confirmed, to have been killed by predators in Norway to evaluate how predator density, flock management, and other environmental or habitat-related variables are related to losses. The percentage of animals claimed as lost that was found and confirmed to have been killed by large predators (i.e., the detection rate) was low, especially for sheep claimed as killed by Eurasian lynx (*Lynx lynx*), wolverine (*Gulo gulo*) and golden eagle (*Aquila chrysaetos*). Still, we generally found that similar factors predicted the number of claims and number of carcasses found across predator species. Predator density was strongly associated with losses, especially for sheep claimed as killed by brown bears (*Ursus arctos*), lynx and wolverines. Percentage of forest in the pastures, average slaughter weight of the lambs (an indicator of the forage conditions during summer) and vegetation characteristics in the spring also predicted the number of sheep claimed and found killed by lynx, wolverines and eagles. Factors related to losses due to wolves (*Canis lupus*) were harder to ascertain, possibly because of the severity of mitigation measures (e.g., electric fences) taken to protect sheep in wolf territories, a factor we were not able to include in our large scale analyses. Patrolling of the grazing area and early gathering of sheep in the autumn were not associated with a substantial reduction in losses. However, our dataset was not well suited to evaluate the efficiency of those mitigation strategies. Our findings could help develop new mitigation strategies as alternatives to predator removal where large carnivore conservation is a concern.

Key words: *Aquila chrysaetos*; *Canis lupus*; depredation; detection rates; ex post facto compensation scheme; flock management; *Gulo gulo*; *Lynx lynx*; *Ovis aries*; predator-prey interactions; Scandinavia; *Ursus arctos*.

Received 13 November 2014; revised 11 February 2015; accepted 4 March 2015; **published** 26 May 2015. Corresponding Editor: G. Chapron.

† **E-mail:** audun.stien@nina.no

Introduction

Historically persecuted and sometimes exterminated due to their impacts on livestock (e.g., Breitenmoser 1998, Linnell et al. 2010), large carnivores now benefit from increasing conservation efforts, leading to a biological recovery of their populations in many parts of Europe and

North America (Wabakken et al. 2001, Pyare et al. 2004, Sommers et al. 2010, Hebblewhite 2011). Not surprisingly, their co-occurrence with livestock in multiuse landscapes leads to losses of livestock, which can have important economic implications for farmers (Ogada et al. 2003, Treves et al. 2004, Dar et al. 2009, Ripple et al. 2014). Diverse management strategies have been implemented to mitigate losses, for example through herding, fencing, bringing livestock down from summer pastures earlier than normal, using livestock guarding dogs and translocation or killing of "problem" carnivores (Linnell et al. 1999, Stahl et al. 2001, Ogada et al. 2003, Rigg et al. 2011). Compensation schemes have also been instigated, to repay farmers for living in a carnivore-used landscape. Two main approaches exist, with payments either based on reported livestock losses (ex post facto compensation schemes, e.g., Boitani et al. 2010) or on the number of predators present and the damage they are expected to cause (performance-payment schemes, e.g., Zabel and Holm-Muller 2008). In the ex post facto compensation schemes, farmers make claims for the number of animals they believe to have lost to large carnivores and are reimbursed based on the number of animals documented as lost to carnivores (i.e., the number of carcasses found and identified by an expert as killed by carnivores). Livestock grazing pastures are often on extensive rangelands that are isolated and hard to monitor. The number of carcasses found can therefore be small relative to the number of livestock lost and the actual factors causing losses can thus be hard to ascertain (Breck et al. 2011). However, a rigorous understanding of the factors influencing losses is necessary to develop management strategies that will reduce human-carnivore conflicts (Graham et al. 2005) and mitigate the economic impacts of large carnivores.

Norwegian sheep (*Ovis aries*) farming alternates between periods when sheep are kept indoors (in winter), on infield pastures close to the farm (during early spring and late fall) and on outfield pastures consisting mainly of boreal forest or alpine tundra habitats (from May–June until September–October) (Skonhoft et al. 2010, Austrheim et al. 2011). The outfield pasture period represents a vulnerable period when the sheep generally graze freely with few fences and little supervision. Eurasian lynx (*Lynx lynx*), wolverine (*Gulo gulo*), brown bear (*Ursus arctos*), wolf (*Canis lupus*), and golden eagle (*Aquila chrysaetos*) are the main species of large predators present in Norway. They have been recovering in Scandinavia during the last 30 years (Wabakken et al. 2001, Linnell et al. 2010) and are responsible for a significant amount of depredation on free-ranging sheep. The lynx population is today managed as a game species with its population size regulated by quota hunts, while golden eagles, wolverines, brown bears and wolves are legally protected and subject to varying degrees of population regulation by licensed hunters and state game wardens (Bischof et al. 2012). The authorities may also authorize culling of specific problem individuals to prevent damage to livestock. Farmers that loose sheep due to large predators can claim for compensation of losses, and payments depend on both the number of carcasses confirmed to have been killed by large predators and a rather subjective estimate of the proportion of total (unverified) losses likely to be due to predation.

We used 11 years of data (2001–2011) on number of sheep claimed by the farmers as killed by large predators and number of sheep carcasses confirmed to have been killed by large predators to evaluate how predator density, management decisions made by the farmers and other environmental or habitat-related variables were associated with the numbers of claims and carcasses found. The management decisions included in the analysis were the number of days spent patrolling the pastures and the date when sheep were gathered in from summer pastures. The environmental and habitat-related variables examined were variables known to potentially influence depredation rates on livestock: percentage of forest in the pastures, slaughter weights of the lambs, density of alternative prey and spring conditions (e.g., Warren and Mysterud 1995, Graham et al. 2005, Odden et al. 2008, Kaartinen et al. 2009). Our analyses were run separately for 5 predator species (lynx, wolverine, bear, wolf and eagle) and for lambs vs. ewes to identify the variables related to losses in each of these predator-prey systems.

Material and Methods

Sheep data

We obtained data on the number of claims for lambs and ewes killed by large predators from 2001 to 2011 from the Norwegian Environment Agency (Miljødirektoratet). Owners report how many lambs (*Lamb*) and ewes (*Ewe*) were released on the summer pastures and how many they believe were lost to the different predator species. About 80% of the sheep that graze on outfield pastures in Norway belong to farmers that participate in the organized grazing database ("Organisert beitebruk"), which records animals grazing on spatially defined areas where farmers have grazing rights. This database contains information about when the sheep are released and taken down from the summer pastures, organization of sheep supervision, and each grazing area is mapped (Beitelagskart 2001–2011, Norwegian Forest and Landscape Institute; http://kilden.skogoglandskap.no/map/kilden). Supervision in the Norwegian context does not involve guarding or active herding, rather it represents patrolling of the grazing area to look for signs of dead or injured sheep. We used this database to extract for each municipality the mean number of days per week spent patrolling (*Patrolling*), the mean date when sheep were gathered in from summer pastures (*Gathering*), and the mean percentage of forest in the summer pastures (*Forest*, extracted from AR50 map, Norwegian Forest and Landscape Institute). Slaughter weights of lambs (*Weight*) were obtained at the farm level from the Norwegian Agricultural Authority (Statens landbruksforvaltning). Slaughtering occurs in autumn, soon after the sheep are taken down from the summer pastures and slaughter weight corresponds to ca. 40% of the weight of the live animal. We used average slaughter weights of lambs as an indicator of lamb body condition at the end of summer and thereby of the forage conditions during summer. We did not use data on slaughter weights of ewes since we had no information on the age of the slaughtered ewes, which is a strong predictor of body mass. Each farm was linked to the municipality where it was located and data was summarized at the municipality level. Because claims can be made by farmers that do not participate in the organized grazing database, and who therefore do not provide data on *Patrolling* or *Gathering*, we had missing data for some municipality-years (n = 81). We excluded those from analyses and focused on claims made in 2150 municipality-years.

Data on number and locations of sheep found killed by large predators were obtained from the central database for predator management (Rovbase 3.0, Norwegian Environment Agency). When a sheep is found dead following a predator attack; wardens from the State Nature Inspectorate register the location of the kill and conduct a field autopsy to determine the cause of mortality. The degree of confidence in the mortality cause is also registered as documented (when the cause of death cannot be confused with other causes of death), assumed (when many indices point to a given predator species being the cause of death, but where other causes cannot be excluded), unsure (when the indications are weak and can be mistaken for other indications) or unknown. We only retained data from carcasses for which the mortality cause could be documented as killed by one of our 5 predator species of interest, and that were located in a municipality where at least one compensation claim was made between 2001 and 2011. The dataset included data from 257 municipalities from 17 counties (Tables 1 and 2, Figs. 1 and 2). Descriptive statistics per county are given in Tables 1 and 2.

Predator and alternative prey data

Data on predator numbers between 2001 and 2011 were obtained from the central database for predator management (Rovbase 3.0, Norwegian Environment Agency). In Scandinavia, lynx are monitored through observations of family groups (i.e., mainly tracks in snow, but also camera trapping images and any young lynx shot or found dead) which are attributed to distinct family groups based on distance rules derived from telemetry studies of home range size and movement rates (Linnell et al. 2007). The estimates of number of family groups are supported by a snow-tracking index that involves skiing a network of 1945 transects, each 3 km in length. This method to estimate lynx population size has been validated by comparing family group counts to a population reconstruction based on harvest data by hunters (Nilsen et

Table 1. Number of sheep claimed as killed by large predators (Claim) and number sent on pastures by people making claims (Sheep) in Norway, 2001–2011. The total percentage of sheep claimed as killed by predators by people making claims (% claimed ± SE) is also given.

County	Claim	Sheep	Percentage claimed
2	5,251	58,648	9.2 ± 0.6
4	99,905	945,988	13.0 ± 0.5
5	87,477	1,086,758	7.6 ± 0.1
6	24,763	354,074	7.5 ± 0.2
7	424	3,098	13.8 ± 1.0
8	17,555	204,219	9.1 ± 0.4
9	8,760	102,634	9.5 ± 0.5
10	8,635	95,865	9.2 ± 0.5
11	1,886	35,774	7.1 ± 0.8
12	1,571	21,054	8.7 ± 0.8
14	14,695	205,428	8.0 ± 0.4
15	26,679	244,208	11.1 ± 0.5
16	49,978	662,599	9.4 ± 0.3
17	62,125	558,959	11.8 ± 0.4
18	31,427	643,380	10.9 ± 0.3
19	31,102	581,043	10.6 ± 0.2
20	13,050	124,880	10.8 ± 0.7
Total	552,625	5,928,609	9.8± 0.1

al. 2012). Wolverines are followed through the monitoring of known natal dens and an extensive search for new natal dens from the beginning of March to the summer each year (Landa et al. 1998). In recent years the annual search effort has exceeded 100,000 km of snow-scooter-based searching and the population estimates based on those den counts correspond very well with estimates from DNA sampling (Brøseth et al. 2010). Bears are followed by analyzing DNA from feces and hair samples which are collected each autumn by hunters and state wardens and which allow the minimum number of individuals alive in a given year to be estimated (Solberg et al. 2006). Wolves are mainly monitored through tracking in the snow (Liberg et al. 2012). Tracking, used in connection with radio-telemetry, permits an estimation of the minimum number of individuals, to delimit the territory utilized by each pack or scent-marking pair, and also the detection of stationary and dispersing solitary wolves. Tracking efforts are concentrated in Østfold, Akershus and Hedmark counties, where the management area for breeding wolves is located so that the estimate of wolf density was only reliable for those counties. Thus, we only included data from those counties (Wolf area; see Fig. 1) in analyses of number of sheep claimed or found to have been killed by wolf. For more details on the collection and analysis of predator data, see www.rovdata.no.

To estimate density of lynx, wolverine and bear in each municipality, we first established buffers around the point where the predators had been observed, or around the mean position for the year if a group or individual had been observed several times in a given year. For each

Table 2. Number of sheep claimed as killed by large predators (Claim) and number of sheep carcasses found (Carc.) that could be confirmed as killed by large predators (Lynx, Wolverine, Bear, Wolf, Eagle and Carnivore: unknown carnivore) in Norway, 2001–2011.

	Lynx		Wolverine		Bear		Wolf		Eagle		Carnivore	
County	Claim	Carc.	Claim	Carc.	Claim	Carc.	Claim	Carc.	Claim	Carc.	Claim	Carc.
2	4,577	60	18	0	45	0	489	39	21	0	101	0
4	12,502	610	37,606	1,112	24,571	2,075	10,927	1,670	4,665	233	9,634	64
5	23,247	314	46,022	886	8,923	434	1,950	110	3,587	56	3,748	3
6	20,661	668	961	65	898	68	4	0	947	45	1,292	0
7	419	1	0	0	0	0	0	0	4	0	1	0
8	14,431	185	140	0	832	18	295	0	1,301	7	556	2
9	2,018	29	210	7	279	1	1,515	18	2,760	31	1,978	0
10	2,395	15	218	0	530	2	1,652	29	3,134	20	706	0
11	383	33	521	20	6	0	82	0	730	35	164	1
12	187	0	609	0	0	0	0	0	680	4	95	0
14	3,476	13	7,020	260	271	22	214	0	3,351	23	363	0
15	2,598	10	22,321	326	527	24	20	0	859	27	354	0
16	6,705	118	28,488	609	8,574	699	202	24	3,559	85	2,450	8
17	22,366	674	15,399	330	14,541	1,516	224	46	5,528	133	4,067	55
18	19,611	520	31,427	823	5,806	468	85	11	7,803	135	1,526	45
19	19,573	160	31,102	333	1,837	154	121	0	8,379	83	2,601	17
20	3,889	81	5,970	74	2,343	192	0	0	433	5	415	4
Total	159,038	3,491	228,032	4,845	69,983	5,673	17,780	1,947	47,741	922	30,051	199

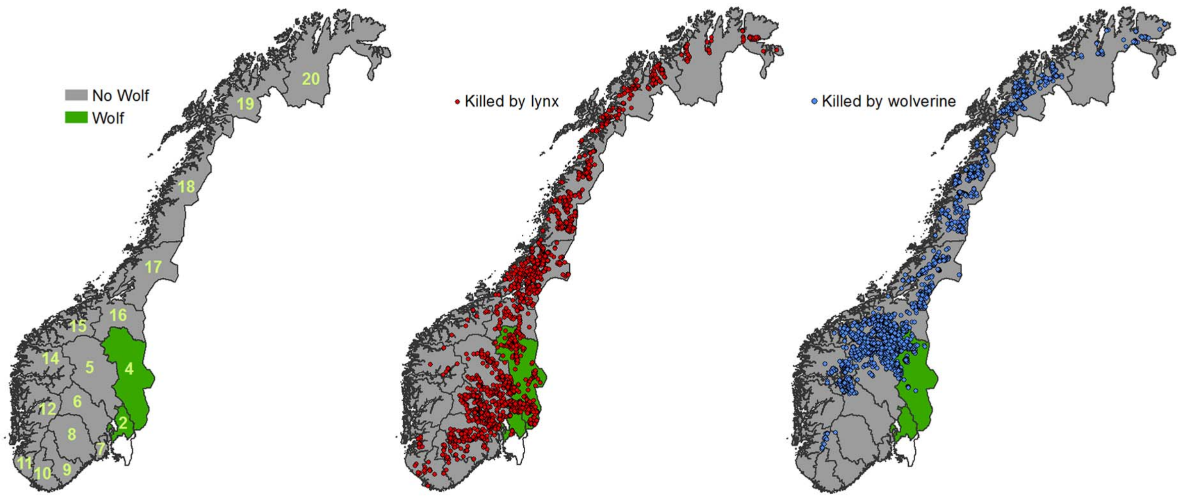

Fig. 1. Location of the different Norwegian counties considered in our analyses (left panel) and location of sheep carcasses documented to have been killed by lynx (middle panel), wolverine (right panel) in Norway, 2001–2011. Counties that appear in green are counties that were retained in analyses and where wolves were monitored. Only carcasses killed by wolves in those counties (i.e., county 2 and 4) were considered in the analyses.

species, the size of the buffer was determined using the frequency distribution of the distances between confirmed kills and predators (Appendix A) and was taken as the distance where ca. 75% of the confirmed kills were found (i.e., 30 km radii for lynx and wolverines and 20 km for bears). We then added "1 predator" (lynx, wolverine or bear) to each cell (1×1 km) covered by a buffer. We finally estimated the density of lynx, wolverine and bear as the average value of lynx, wolverine and bear cells in each municipality. Since the collection of bear feces and hair started in 2006, we could not obtain yearly estimates of bear numbers for the whole study

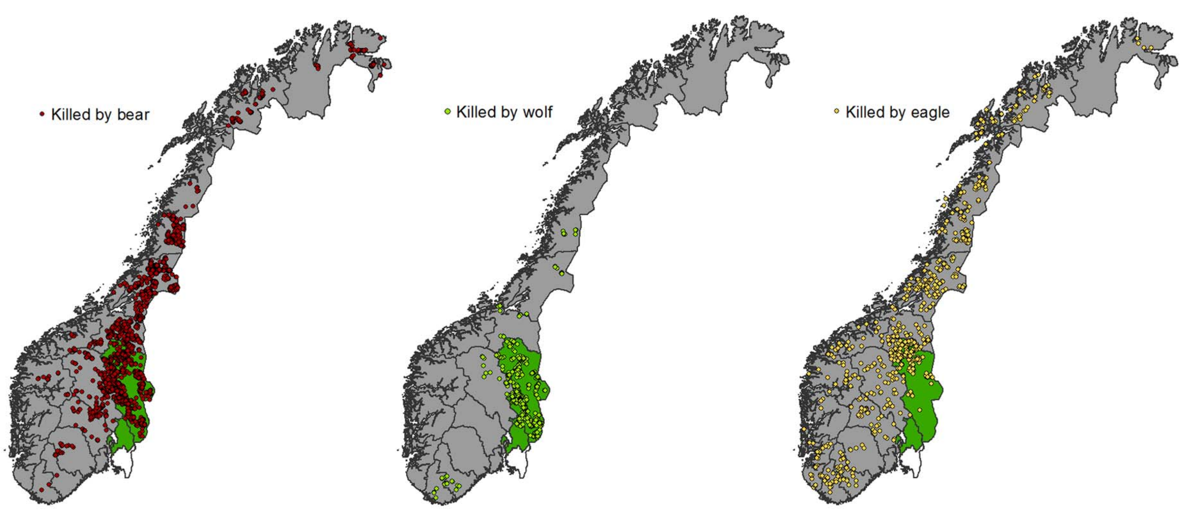

Fig. 2. Location of sheep carcasses documented to have been killed by bear (left panel), wolf (middle panel) and eagle (right panel) in Norway, 2001–2011. Counties that appear in green are counties that were retained in analyses and where wolves were monitored.

period (2001–2011). We therefore used the mean density across the available years (2006–2012) as an index of the bear density. Our estimate of bear densities therefore varies in space by municipality, but not among years. Norwegian bears are at the outskirts of a large Swedish bear population, and bear regularly turn up in the same limited areas along the border closest to the Swedish core bear areas (Aanes et al. 1996, Sagor et al. 1997) so we trust that our index based on data for 2006–2011 can be applied to estimate bear density for 2001–2011. For wolf, we used the polygons delineating the home ranges of packs and scent-marking pairs and the number of animals known to live in each group to estimate density at the municipality level. We attributed to each 1×1 km cell covered by the home range of a group, a value corresponding to the number of animals known to live in this group. We then estimated the density of wolf as the average value of wolf presence across all cells within each municipality.

Roe deer are the main wild prey for Eurasian lynx in most of Norway. We used the number of animals harvested in each municipality as an index of roe deer density (*Roe deer*). The average number of roe deer harvested each year between 1996 and 2002 was divided by the area of suitable habitat (excluding open water and alpine tundra). This type of index based on hunting statistics has been shown, in Norway, to correlate well with other indices of population abundance like number of roe deer killed in car accidents or number of sightings at feeding-sites during the winter (e.g., Grøtan et al. 2005). Averaged over all municipalities and years from the 1950s to 2005, only 28% ± 19% of the hunting quota for roe deer was harvested (Grøtan et al. 2005). Quotas were therefore unlikely to influence hunting bag. To estimate moose density, we also collected hunting statistics on moose that can be an important prey for wolves and bears. Moose density, however, was highly correlated with the percentage of forest in a municipality (*Forest*, $r = 0.59$) so we could not keep it as an explanatory variable in our models. Furthermore, we examined whether reindeer density (semi-domestic and wild) explained the number of sheep either claimed or found killed by the different predator species as reindeer can be preyed upon by all of them. We found no evidence for a relationship between reindeer density and the number of claims or the number of sheep carcasses found in a municipality. Therefore, reindeer density was not included in our final analyses.

Spring conditions

Previous studies have shown that weather in spring and the way it influences vegetation characteristics can have important impacts on lamb body weight (Nielsen et al. 2012) and sheep losses (Portier et al. 1998). We thus wanted to examine whether the temperature in May (*MayTemp*) and vegetation characteristics influenced number of claims and number of sheep carcasses killed by large predators.

We used high resolution remote sensing data (pixel width ~250 m) from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite to determine vegetation characteristics throughout Norway. The Enhanced Vegetation Index (EVI) is a MODIS product which, similar to the Normalized Difference Vegetation Index (NDVI, see Pettorelli et al. 2011 for examples of use in ecology), provides spatial and temporal comparisons of vegetation canopy greenness. We used 16 day composites (1 measure per 16-day period) of EVI for 2001–2011 (available at http://modis-land.gsfc.nasa.gov/vi.htm) and fitted a double logistic function (Beck et al. 2006) to the data available for each pixel and year (see Tveraa et al. 2013 for details on the equation used). From these smooth estimates we determined for each pixel and year the maximum EVI during the year (*mEVI*) as an index of plant productivity, the rate of increase in greening in spring (*Inc*), and the onset of spring (*Spring*) defined as the date in spring when EVI was halfway between the minimum level in winter and the maximum (*mEVI*). We then summarized those values at the municipality level using mean values of the pixels covering the municipality. *MayTemp* and *Spring* were highly correlated to the percentage of forest in a municipality ($r = 0.55$ and -0.60, respectively), while *mEVI* did not explain any variation in the number of claims and number of carcasses killed by large predators. We thus only kept the rate of increase in greening (*Inc*) to describe the spring conditions in our final analyses.

Statistical analyses

We ran 10 models to examine the relative

Table 3. Age class (Lamb, Ewe or Unknown) for the number of sheep claimed (Claim) and number of sheep carcasses found (Carcass) to have been killed by large predators (Lynx, Wolverine, Bear, Wolf, Eagle and Carnivore: unknown carnivore) in Norway, 2001–2011.

	Lamb		Ewe		Unknown	
Predator	Claim	Carcass	Claim	Carcass	Claim	Carcass
Lynx	138,881	3,036	20,157	445	NA†	10
Wolverine	197,955	4,313	30,077	511	NA†	21
Bear	32,872	877	37,111	4,792	NA†	4
Wolf	13,301	1,406	4,479	541	NA†	
Eagle	45,635	861	2,106	56	NA†	5
Carnivore	23,498	125	6,553	74	NA†	
Total	383,009	10,618	100,483	6,419	NA†	40

† Not applicable: no claims were made for sheep of unknown age class.

importance of 8 variables to explain variation in the number of lambs and ewes claimed to have been killed by lynx, wolverines, bears, wolves and eagles; and then ran 10 models to examine the importance of the same 8 variables to explain variation in the number of lambs and ewes found and confirmed to have been killed by the different predator species. The explanatory variables entered in the models were: number of sheep released on pastures by claimants (*Lamb* or *Ewe* depending on if we were running a lamb or a ewe model), predator density (*Predator*), percentage of forest in the summer pastures (*Forest*), density of roe deer (*Roe deer*), lamb slaughter weights (*Weight*), rate of increase in vegetation greening (*Inc*), number of days spent patrolling (*Patrolling*) and date when the sheep where brought down from summer pastures (*Gathering*). The number of sheep released on pastures was log-transformed before entering the models because the number of claims and carcasses found did not increase linearly with the number of sheep on pastures. The predator density was defined as the density of lynx, wolverine, bear or wolf depending on whether the model examined number of claims or carcasses killed by lynx, wolverine, bear and wolf, respectively. Since we had no estimate of eagle densities, predator density was not entered as a predictor in the analyses of claimed losses and carcasses found killed by eagles. All variables were standardized before entering the models to allow for a direct comparison of the relative effect size of the explanatory variables.

Analyses were performed using generalized linear mixed models in the glmmADMB package (Fournier et al. 2012, Skaug et al. 2013) in R with response following a negative binomial distribution and municipality included as a random factor. We also tested for the existence of spatial autocorrelation in the model residuals but never found it to be statistically significant (all at $P > 0.05$, Mantel tests on the mean residuals per municipality).

Results

In the 257 municipalities under study between 2001 and 2011, 552,625 sheep were claimed as lost to predators, which represents on average 9.8 ± 0.1% of the sheep sent on pastures by people making claims (Table 1). In the same period, 17,077 carcasses were found and confirmed to have been killed by large predators (Table 2). The number of carcasses confirmed to have been killed by lynx, wolverine, bear, wolf and eagle represented 2.2%, 2.1%, 8.1%, 11.0% and 1.9% of the number of claims made, respectively (Table 2). The number of carcasses for which mortality cause was confirmed to be predation by large predators represented 2.8% of the lambs and 6.4% of the ewes claimed to have been killed by these predators (Table 3).

The period of the summer when most sheep carcasses were found differed between the predator species responsible for the kill. The distribution of carcasses killed by lynx was fairly uniform over the period from June to October. In contrast, the number of carcasses found killed by wolverines peaked in August–September, by bears in July–August, by wolves in June–July and by eagles in June (Fig. 3).

In general, the effect size of the different predictor variables showed the same pattern in

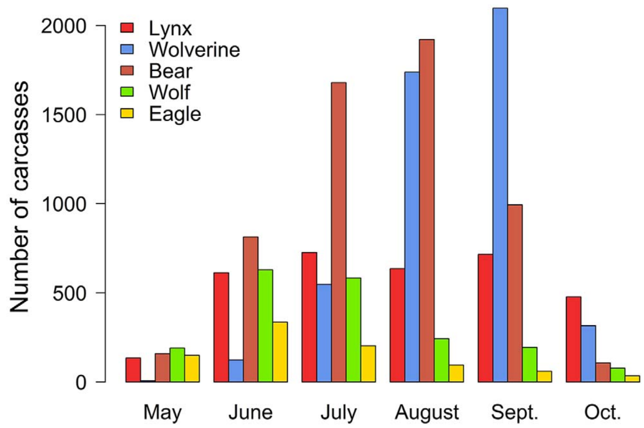

Fig. 3. Temporal changes in the number of sheep found killed (number of carcasses) by lynx, wolverine, bear, wolf, and golden eagle during the summer (May–October) in Norway, 2001–2011.

the analyses of claimed losses and carcasses found (Fig. 4). In most of the analyses the number of sheep released on outfield pastures showed a strong positive relationship to the number of sheep claimed as killed and found killed by the different predator species (Fig. 4). An exception was the number of ewe carcasses found killed by eagles but this result was based on a very small number of ewe carcasses (Table 3). Also the number of lamb and ewe carcasses found killed by wolves showed a weak relationship to the number of sheep sent on pastures by claimants.

For lynx, wolverine and especially bear, the number of claimed losses and the number of carcasses found were positively related to predator density (Fig. 4). In contrast, there was little evidence for wolf density to be related to the claimed losses or carcasses found killed by wolves. Due to no suitable eagle density data being available, the association with predator density could not be investigated for eagles.

The percentage of forest in the summer pastures was positively related to the number of lambs and ewes claimed lost and the number of lamb carcasses attributed to lynx. The percentage of forest in the summer pastures was negatively related to the number of lambs and ewes claimed lost to wolverines and lamb carcasses attributed to wolverines, and also the number of lambs claimed and found killed by eagles. The number of lambs and ewes claimed to have been killed by wolves was positively related to the percentage of forest in the pastures while the number of carcasses found killed by wolves were not (Fig. 4).

Roe deer density was negatively related to the number of sheep claimed and found killed by bears. For the main roe deer predator, the lynx, the evidence for an association between roe deer densities and claimed losses and carcasses found was weaker. Only the claimed losses to lynx showed an association to roe deer density and this association was positive (Fig. 4).

Average lamb slaughter weight was negatively and strongly related to the number of claims and carcasses attributed to wolverines. Furthermore, for wolverine, a fast increase in greening in the spring (indicative of poor forage conditions later in the season) was also associated with elevated number of claims and carcasses found. An increase in the average lamb weight and a fast increase in greening in the spring were both related to a decrease in the number of lambs claimed and found to have been killed by eagles (Fig. 4).

We found in general only minor associations between husbandry management decisions and claimed losses and carcasses found. However, a later gathering in the autumn was associated with reduced lamb loss claims and a reduced number of lamb carcasses killed by wolves, as well as a reduced number of ewe loss claims and carcasses found killed by bears (Fig. 4). For ewes killed by lynx and eagles, on the other hand, a later gathering was linked to higher numbers of

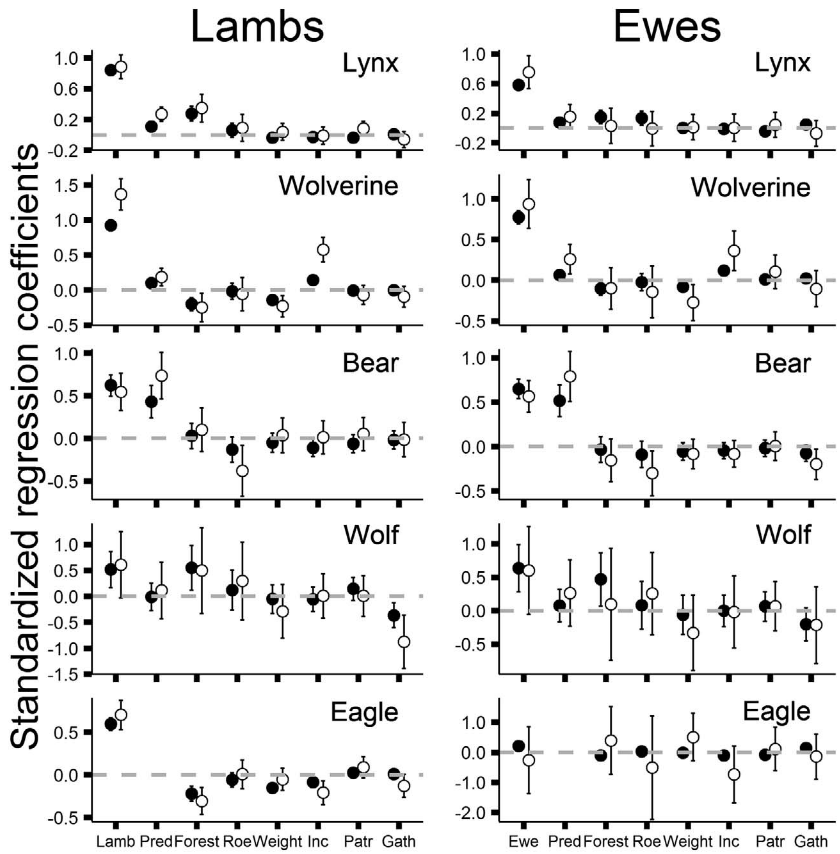

Fig. 4. Estimated effect sizes of number of sheep sent on pastures (*Lamb* on left panel and *Ewe* on right panel), predator density (*Pred*), percentage of forest in the pastures (*Forest*), roe deer density (*Roe*), lamb slaughter weights (*Weight*), rate of increase in greening (*Inc*), number of days with patrolling (*Patr*) and date when sheep were brought down from summer pastures (*Gath*) on number of sheep claimed killed by large predators (closed circles) and number of carcasses confirmed as killed by large predators (open circles) in Norway, 2001–2011. Since we had no estimate of eagle density, there was no variable describing predator density in the "eagle models". Explanatory variables were standardized to allow for a direct comparison of the effect sizes. The vertical bars show the 95% confidence intervals around the estimated coefficients.

claims (Fig. 4).

The percentage of the variance explained by the models varied greatly from case to case (Appendix B). The models that predicted the observed data best were models examining the number of sheep claimed and found to have been killed by wolverines, while models examining the number of sheep killed by wolves performed poorly. For ewes killed by eagles, the models also explained little variance but they were based on a relatively small number of claims and carcasses found (see Table 3).

Discussion

Detection rate: How does it affect claims?

The proportion of sheep claimed as lost that were found and confirmed to have been killed by large predators (i.e., the detection rate) was universally low, and including carcasses for which mortality cause could not be ascertained did not increase detection significantly (considering all carcasses found, carcasses represented 3.6%, 3.7%, 12.3%, 15.5%, and 3.7% of all sheep claimed to have been killed by lynx, wolverine, bear, wolf and eagle, respectively). Still, the detection rate was somewhat higher for ewes than for lambs, a pattern that may be due to lamb carcasses decomposing or disappearing more quickly. The detection rate was also higher for sheep killed by wolves and bears compared to lynx, wolverines or eagles. This could be the result of bears killing mostly ewes (Warren and Mysterud 1995, Knarrum et al. 2006), which seemed easier to find than lamb carcasses. Also, it could be related to the fact that wolves and bears were killing sheep mostly in counties 4, 5, 16 and 17 (Table 2) which were the counties with the highest patrolling effort (4 days or more per week on average). Finally, when bears and wolves hunt sheep, they typically scare the entire herd, which generates lots of noise from the bells from the running sheep. The change in behavior may even drive the sheep back to the farm, thereby triggering increased search effort from the owner and increasing detection rates.

Previous studies have suggested detection rates to be linked to the effort spent by the farmer to monitor livestock (e.g., Breck et al. 2011) and detection of carcasses killed by wolves was also related to the patrolling effort in our study ($P = 0.02$). For sheep killed by lynx, wolverines and eagles, detection rates were very low (ca. 1 in 50 animals claimed were found and had mortality cause ascertained) and not linked to the patrolling effort averaged at the municipality level. It may, however, be related to the effort at a finer scale (farm level).

The low detection rates render mortality cause hard to establish for producers, who are left with an "educated guess" for why their sheep disappear. Still, we found within predator species very similar patterns with respect to the factors that were correlated to the number of claims and number of carcasses found. This suggests that farmers assign mortality causes for their sheep proportionally according to the predator specific mortality cause of the carcasses found in their area or that their knowledge of their environment (e.g., composition of the predator community in the area) allows them to predict accurately the mortality causes in their flock. The large difference in detection rates between the different predator species suggests that producers do not tend to claim for sheep killed by wolves or bears unless there is good evidence for wolf or bear predation in the area. In contrast, they seem to be more ready to attribute sheep mortality to lynx, wolverines and eagles, even if the number of carcasses documented as killed is low.

Main factors affecting claims and carcasses found

Our overall estimate of the percentage of released sheep claimed as killed by predators was on average 10% (Table 1) while the overall losses (i.e., including both predator and other mortality causes) in the Norwegian sheep industry are around 6% (SLF 2009). This indicates that owners that claim predator losses experienced higher than average losses of sheep.

The number of sheep sent on pastures by claimants was generally a good predictor of the number of claims made and of carcasses found killed by large predators. There was in general a logarithmic relationship between the number of sheep sent on pastures and the number of claims/carcasses found. This may be because the predators are not able to take more sheep as more are released on pastures. Unraveling the mechanisms behind this relationship is difficult however, since it certainly originates from a mixture of factors including the functional responses of predators to different prey densities (Gervasi et al. 2014), different propensity to claim depending on the relative loss in a flock and claims being based on very low detection rates of carcasses.

Except for wolves, the density at which predators were present in the municipality was an important predictor of both the number of claims and carcasses found. The finding that losses were related to lynx, wolverine and bear densities suggests that kills are not the product of just a few "problem individuals" that specialize on sheep among the predator population (Linnell et al. 1999), but rather that sheep depredation increases with the number of lynx/wolverines/bears present in the area. The displacement or shooting of specific individuals responsible for some kills will thus probably have a limited effect on reducing losses if the overall predator population size stays at a similar size (Landa et al. 1999, Herfindal et al. 2005). For example, a recent study on wolf and livestock suggests that at least 25% of the wolf population should be harvested for the lethal control to reduce livestock depredations in western America (Wielgus and Peebles 2014) and other studies report up to 45% reduction in the predator population with limited positive effects on the prey population (Hervieux et al. 2014). Such high levels of predator removal may be in conflict with Norwegian conservation objectives. In our study wolf density failed to predict the number of sheep claimed or confirmed killed by wolves. This is probably because of all the mitigation measures taken to prevent damage from wolf in the known wolf territories (e.g., moving of sheep outside of the territories, extraordinary monitoring after predator damage, fencing, Bjøru et al. 2002) which might be efficient to prevent losses. We also only accounted for wolf packs and pairs with a known territory in our estimates of wolf density while dispersing wolves may also cause considerable losses. Since we had no data on eagle densities, we could not use eagle densities to predict losses due to eagles.

In general, the number of sheep on pastures and predator density were strong predictors of losses. However, other factors like percentage of forest in the pastures, slaughter weights of the lambs and a measure of spring plant phenology also influenced both claims and carcasses found. As we could expect from the habitat preferences of the different predator species, municipalities with a high percentage of forest in the summer pastures claimed more losses due to lynx (a forest-dwelling animal) and less losses due to eagles and wolverines, which are associated with open alpine-tundra habitats (Stahl et al. 2002, May et al. 2008). High losses of lambs and ewes claimed as being due to wolverines were also associated with low slaughter weights of the lambs, suggesting that sheep were more vulnerable to predation by wolverines when feeding conditions were poor and lamb body growth was moderate. It is notable that the association with lamb weight was also detectable for ewe losses to wolverines, even though adults are usually less susceptible to environmental variation than juveniles in long-lived species (Gaillard et al. 2000, Gaillard and Yoccoz 2003); and we thus expected poor feeding conditions to influence mainly lambs and not ewes. Interestingly, higher lamb slaughter weights were associated with a lower number of claims for lambs killed by eagles but not a lower number of lamb carcasses confirmed to be killed by eagles. This may suggest that farmers rely more on their overall knowledge of the composition of the predator community than on the available evidence concerning actual losses when making their claims of kills due to eagles. Furthermore, the farmers seemed to expect higher losses due to eagles when lambs were lighter and thereby easier to kill for a relatively small predator like the golden eagle. The rate of increase in vegetation greening also predicted losses to wolverines and eagles. Plant phenology is a major factor affecting the quality of the vegetation (Mysterud et al. 2011) and has been identified as an important determinant of habitat use and fitness of large herbivores (e.g., Albon and Langvatn 1992, Pettorelli et al. 2005). Net primary productivity has also being shown to be negatively related to livestock losses to predators (Graham et al. 2005). Spring conditions influence the start of vegetation growth and plant phenology (e.g., Langvatn et al. 1996, Nielsen et al. 2012) with a faster increase in vegetation greening being related to vegetation of lower quality at the end of the season and a decrease in lamb body growth (Pettorelli et al. 2007). A faster greening in the spring was related to more sheep losses claimed as due to wolverines and this may be linked to sheep being in poorer body condition and therefore more vulnerable in the late season when wolverines make most of their kills (Fig. 3). On the other hand, a faster greening was related to fewer losses to eagles. This may be due to the early vegetation flush making the sheep less susceptible to attacks by eagles early in the season when eagles tend to take more sheep (Fig. 3).

Roe deer density was weakly related to the number of claims and carcasses found. It mainly predicted the number of sheep found killed by bears, and to a minor degree the number of sheep claimed to have been killed by lynx. Lynx kill rates on sheep have been found to be linked to roe deer density in a complex manner, with kill rates negatively related to roe deer density on a regional scale (Odden et al. 2013, Gervasi et al. 2014), while positively linked to roe deer habitat (i.e., forest) on a local scale (Odden et al. 2008). Our study confirms the positive relationship between forest habitat and the number of lamb claims/ carcasses documented but suggests a positive, and not the expected negative, relationship between roe deer density and claims/ carcasses found. In contrast, we found that the number of sheep carcasses attributed to bears was negatively linked to roe deer density. In the absence of any direct mechanistic explanation for this result we speculate that this pattern appeared because bears are generally absent from the human dominated landscapes with high roe deer densities (Torres et al. 2011) and that this gave rise to a pattern of lower losses of sheep to bears in areas with high roe deer densities.

Management decisions: Are they ineffective to reduce losses?

We found only a weak association between husbandry management decisions and the number of claims and number of carcasses found killed by predators. When implementing mitigation measures, a key element is to understand the ecological mechanisms that drive predator conflicts with livestock. Important factors that are likely to influence losses of sheep to predators are the kill rates by the different predator species, predator densities, prey densities and the amount of time livestock is available as prey (e.g., Gervasi et al. 2012, Gervasi et al. 2014). Patrolling of pastures as it is practiced today in Norway is not expected to decrease kill rates much as it does not place any form of "barrier" between sheep and predators. Rather it is intended to reduce the uncertainty surrounding causes of mortality. However, the overall detection rate remained low for all species—with 85 to 95% of all claimed losses still being unverified. Bringing sheep down earlier from summer pastures decreases the period when sheep are exposed to predators. Owners make decisions on how to organize sheep farming based on their current knowledge of the loss situation. They can obviously adapt, as an acute response to high losses, by increasing patrolling or bringing their sheep down earlier from pastures. Our dataset only measured the result of those two processes and thereby may not be well suited to evaluate the efficiency of management decisions. For example, sheep staying later on pastures (later *Gathering*) was linked to lower lamb losses to wolf and lower ewe losses to bear (Fig. 4). Such a pattern is most likely caused by earlier gathering of the sheep having been implemented as a response to high losses in earlier years. In contrast to our results, studies undertaken at the local scale and using before-after or control-treatment designs, have shown that early gathering of the sheep and increased sheep patrolling right after severe predator damage, were efficient at reducing losses (Hansen et al. 2012, 2013).

Conclusions

Detection rates were remarkably low, making claimed losses hard to document and appropriate compensation levels difficult to determine. Increased carcass detection in ex post facto compensation schemes is important, both to improve the understanding of factors affecting losses and make compensation easier and fairer. The available data still allowed us to find a good correlation between factors affecting claims made by farmers and the number of carcasses documented to have been killed by large predators. Predator density was a strong predictor of claimed losses but other factors such as habitat type, lamb body growth and spring conditions were also good predictors. These findings could help develop new mitigation strategies as alternatives to predator removal in areas where large carnivore conservation is a concern. For example, where lynx are present, making sheep graze in open rather than forested areas could reduce losses. In a similar way, increasing lamb body size before release into summer grazing areas could help to reduce losses to wolverines. For brown bear, however, our results suggest that the only way to substantially reduce losses is through a reduction in the predator density, which may be incompatible with national and international conservation legislation, or a change in livestock husbandry towards a system based on fencing and/or shepherding methods that actively protect sheep (Rigg et al. 2011).

Acknowledgments

The study was funded by the Research Council of Norway and the Norwegian Environmental Agency. The data for brown bear, lynx and wolverine are from the Norwegian Large Predator Monitoring Program (Rovdata) financed by the Ministry of the Environment through the Norwegian Environmental Agency. We thank two anonymous reviewers for useful comments on a previous version of this manuscript.

Literature Cited

Aanes, R., J. E. Swenson, and J. D. C. Linnell. 1996. Rovvilt og sauenæring i Norge. 1. Tap av sau til rovvilt: en presentasjon av tapets omfang basert pa brukeropplysninger. NINA Oppdragsmelding, Norway.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.

Austrheim, G., E. J. Solberg, and A. Mysterud. 2011. Spatio-temporal variation in large herbivore pressure in Norway during 1949-1999: Has decreased grazing by livestock been countered by increased browsing by cervids? Wildlife Biology 17:286–298.

Beck, P. S. A., C. Atzberger, K. A. Hogda, B. Johansen, and A. K. Skidmore. 2006. Improved monitoring of vegetation dynamics at very high latitudes: A new method using MODIS NDVI. Remote Sensing of Environment 100:321–334.

Bischof, R., E. B. Nilsen, H. Brøseth, P. Mannil, J. Ozolins, and J. D. C. Linnell. 2012. Implementation uncertainty when using recreational hunting to manage carnivores. Journal of Applied Ecology 49:824–832.

Bjøru, R., D. K. Mogstad, and E. Jetne. 2002. Førebyggande tiltak mot rovviltskade på sau og rein: evaluering av tiltak og verkemiddelbruk i fylka (1998-2001). Planteforsk Tjøtta Grønn forskning, Norway.

Boitani, L., P. Ciucci, and E. Raganella-Pelliccioni. 2010. Ex-post compensation payments for wolf predation on livestock in Italy: A tool for conservation? Wildlife Research 37:722–730.

Breck, S. W., B. M. Kluever, M. Panasci, J. Oakleaf, T. Johnson, W. Ballard, L. Howery, and D. L. Bergman. 2011. Domestic calf mortality and producer detection rates in the Mexican wolf recovery area: Implications for livestock management and carnivore compensation schemes. Biological Conservation 144:930–936.

Breitenmoser, U. 1998. Large predators in the Alps: The fall and rise of man's competitors. Biological Conservation 83:279–289.

Brøseth, H., O. Flagstad, C. Wardig, M. Johansson, and H. Ellegren. 2010. Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent adult survival. Biological Conservation 143:113–120.

Dar, N. I., R. A. Minhas, Q. Zaman, and M. Linkie. 2009. Predicting the patterns, perceptions and causes of human-carnivore conflict in and around Machiara National Park, Pakistan. Biological Conservation 142:2076–2082.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods & Software 27:233–249.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toiego. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84:3294–3306.

Gervasi, V., E. B. Nilsen, J. Odden, Y. Bouyer, and J. D. C. Linnell. 2014. The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape. Journal of Zoology 292:175–183.

Gervasi, V., et al. 2012. Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore-ungulate systems in Scandinavia. Journal of Animal Ecology 81:443–454.

Graham, K., A. P. Beckerman, and S. Thirgood. 2005. Human-predator-prey conflicts: ecological correlates, prey losses and patterns of management. Biological Conservation 122:159–171.

Grøtan, V., B. E. Saether, S. Engen, E. J. Solberg, J. D. C. Linnell, R. Andersen, H. Broseth, and E. Lund. 2005. Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. Ecology 86:1472–1482.

Hansen, I., J. Odden, and J. D. C. Linnell. 2012. Evaluering og prioritering av forebyggende tiltak i rovviltregion 2. Bioforsk, Norway.

Hansen, I., J. Odden, and J. D. C. Linnell. 2013. Evaluering og prioritering av forebyggende tiltak i rovviltregion 3. Bioforsk, Norway.

Hebblewhite, M. 2011. Unreliable knowledge about economic impacts of large carnivores on bovine calves. Journal of Wildlife Management 75:1724–1730.

Herfindal, I., J. D. C. Linnell, P. F. Moa, J. Odden, L. B. Austmo, and R. Andersen. 2005. Does recreational hunting of lynx reduce depredation losses of domestic sheep? Journal of Wildlife Management 69:1034–1042.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Canadian Journal of Zoology 92:1029–1037.

Kaartinen, S., M. Luoto, and I. Kojola. 2009. Carnivore-livestock conflicts: determinants of wolf (*Canis lupus*) depredation on sheep farms in Finland. Biodiversity and Conservation 18:3503–3517.

Knarrum, V., O. J. Sorensen, T. Eggen, T. Kvam, O. Opseth, K. Overskaug, and A. Eidsmo. 2006. Brown bear predation on domestic sheep in central

Norway. Ursus 17:67–74.

Landa, A., K. Gudvangen, J. E. Swenson, and E. Roskaft. 1999. Factors associated with wolverine *Gulo gulo* predation on domestic sheep. Journal of Applied Ecology 36:963–973.

Landa, A., J. Tufto, R. Franzen, T. Bo, M. Linden, and J. E. Swenson. 1998. Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. Wildlife Biology 4:159–168.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Liberg, O., A. Aronson, H. Sand, P. Wabakken, E. Maartmann, L. Svensson, and M. Akesson. 2012. Monitoring of wolves in Scandinavia. Hystrix-Italian Journal of Mammalogy 23:29–34.

Linnell, J. D. C., H. Broseth, J. Odden, and E. B. Nilsen. 2010. Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. Environmental Management 45:1142–1154.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: Do "problem individuals" really exist? Wildlife Society Bulletin 27:698–705.

Linnell, J. D. C., et al. 2007. Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. Wildlife Biology 13:447–455.

May, R., J. van Dijk, P. Wabakken, J. E. Swenson, J. D. C. Linnell, B. Zimmermann, J. Odden, H. C. Pedersen, R. Andersen, and A. Landa. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. Journal of Applied Ecology 45:1382–1391.

Mysterud, A., D. O. Hessen, R. Mobaek, V. Martinsen, J. Mulder, and G. Austrheim. 2011. Plant quality, seasonality and sheep grazing in an alpine ecosystem. Basic and Applied Ecology 12:195–206.

Nielsen, A., N. G. Yoccoz, G. Steinheim, G. O. Storvik, Y. Rekdal, M. Angeloff, N. Pettorelli, O. Holand, and A. Mysterud. 2012. Are responses of herbivores to environmental variability spatially consistent in alpine ecosystems? Global Change Biology 18:3050–3062.

Nilsen, E. B., H. Broseth, J. Odden, and J. D. C. Linnell. 2012. Quota hunting of Eurasian lynx in Norway: patterns of hunter selection, hunter efficiency and monitoring accuracy. European Journal of Wildlife Research 58:325–333.

Odden, J., I. Herfindal, J. D. C. Linnell, and R. Andersen. 2008. Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. Journal of Wildlife Management 72:276–282.

Odden, J., E. B. Nilsen, and J. D. C. Linnell. 2013. Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. Plos One 8:e79261.

Ogada, M. O., R. Woodroffe, N. O. Oguge, and L. G. Frank. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology 17:1521–1530.

Pettorelli, N., A. Mysterud, N. G. Yoccoz, R. Langvatn, and N. C. Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society B 272:2357–2364.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Cote. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jedrzejewska, M. Lima, and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46:15–27.

Portier, C., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271–278.

Pyare, S., S. Cain, D. Moody, C. Schwartz, and J. Berger. 2004. Carnivore re-colonisation: reality, possibility and a non-equilibrium century for grizzly bears in the southern Yellowstone ecosystem. Animal Conservation 7:71–77.

Rigg, R., S. Findo, M. Wechselberger, M. L. Gorman, C. Sillero-Zubiri, and D. W. Macdonald. 2011. Mitigating carnivore-livestock conflict in Europe: lessons from Slovakia. Oryx 45:272–280.

Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:151–+.

Sagor, J. T., J. E. Swenson, and E. Roskaft. 1997. Compatibility of brown bear *Ursus arctos* and free-ranging sheep in Norway. Biological Conservation 81:91–95.

Skaug, H. J., D. A. Fournier, A. Nielsen, A. Magnusson, and B. Bolker. 2013. Generalized linear mixed models using AD Model Builder. R package version 0.7.4.

Skonhoft, A., G. Austrheim, and A. Mysterud. 2010. A bioeconomic sheep-vegetation trade-off model: an analysis of the nordic sheep farming system. Natural Resource Modeling 23:354–380.

SLF. 2009. Bedre sauehold og reduserte tap av dyr pa utmarksbeite. Rapport fra nasjonalt beiteprosjekt 2009. Erfaring ved bruk av radiobjeller. Statens landbruksforvaltning, Norway.

Solberg, K. H., E. Bellemain, O. M. Drageset, P. Taberlet, and J. E. Swenson. 2006. An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. Biological Conservation 128:158–168.

Sommers, A. P., C. C. Price, C. D. Urbigkit, and E. M.

Peterson. 2010. Quantifying economic impacts of large-carnivore depredation on bovine calves. Journal of Wildlife Management 74:1425–1434.

Stahl, P., J. M. Vandel, V. Herrenschmidt, and P. Migot. 2001. The effect of removing lynx in reducing attacks on sheep in the French Jura mountains. Biological Conservation 101:15–22.

Stahl, P., J. M. Vandel, S. Ruette, L. Coat, Y. Coat, and L. Balestra. 2002. Factors affecting lynx predation on sheep in the French Jura. Journal of Applied Ecology 39:204–216.

Torres, R. T., J. C. Carvalho, M. Panzacchi, J. D. C. Linnell, and C. Fonseca. 2011. Comparative use of forest habitats by roe deer and moose in a human-modified landscape in southeastern Norway during winter. Ecological Research 26:781–789.

Treves, A., L. Naughton-Treves, E. K. Harper, D. J. Mladenoff, R. A. Rose, T. A. Sickley, and A. P. Wydeven. 2004. Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. Conservation Biology 18:114–125.

Tveraa, T., A. Stien, B. J. Bardsen, and P. Fauchald. 2013. Population densities, vegetation green-up, and plant productivity: impacts on reproductive success and juvenile body mass in reindeer. PLoS ONE 8:e56450.

Wabakken, P., H. Sand, O. Liberg, and A. Bjarvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology 79:710–725.

Warren, J. T., and I. Mysterud. 1995. Mortality of domestic sheep in free-ranging flocks in southeastern Norway. Journal of Animal Science 73:1012–1018.

Wielgus, R. B., and K. A. Peebles. 2014. Effects of wolf mortality on livestock depredations. PLoS ONE 9:e113505–e113505.

Zabel, A., and K. Holm-Muller. 2008. Conservation performance payments for carnivore conservation in Sweden. Conservation Biology 22:247–251.

Supplemental Material

Appendix A

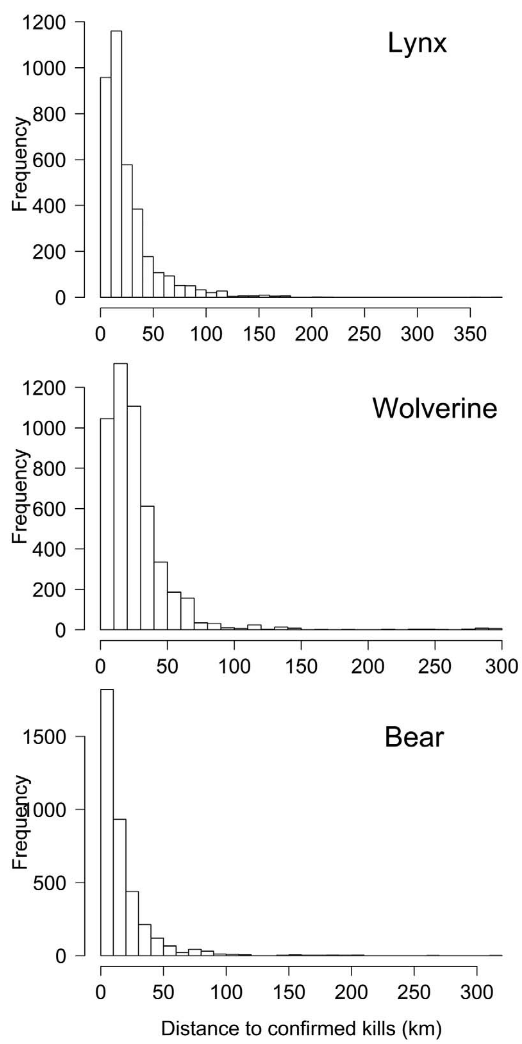

Fig. A1. Distances between predators (mean position of lynx family groups, position of wolverine dens and mean position of individual bears) and sheep carcasses found and confirmed by the State Nature Inspectorate to have been killed by lynx, wolverines and bears. We used these distributions to determine the radii of the circles where we considered the different predator species to be present (as distance where ca. 75% of the confirmed killed are found: 30 km for lynx and wolverines and 20 km for bears). The smaller radius obtained for bears is due to the fact that only reproductive females are monitored for lynx and wolverines while all individuals (males, reproductive females and non-reproductive females) are monitored for bears. Kills made by males and non-reproductive females of lynx and wolverine spread thus further from the positions of the known reproductive females.

APPENDIX B

Table B1. Overall variance explained by models presented in Fig. 4 and examining the number of sheep claimed killed by large predators (Claims) and number of carcasses confirmed as killed by large predators (Carcasses) in Norway, 2001–2011. Overall variance explained was approximated by calculating the square of the correlation between the values predicted by the model and the data observed.

	Lambs		Ewes	
Predator	Claims	Carcasses	Claims	Carcasses
Lynx	0.36	0.16	0.31	0.08
Wolverine	0.66	0.18	0.55	0.07
Bear	0.25	0.21	0.26	0.18
Wolf	0.10	0.05	0.08	0.03
Eagle	0.16	0.11	0.03	0.10