Høgskolen i Telemark

Studies on herbivore winter distribution and lamb loss in Hallingdalen, south-east Norway

Paper 1
Winter distribution of cervids and mountain hare in relation to topography and snow depth
Pål Andreas Hoel og Raymond Hermansen

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Lamb loss in relation to roe deer density in south-east Norway
Raymond Hermansen og Pål Andreas Hoel

Avdeling for allmennvitenskaplige fag
Hallvard Eikas plass, 3800 Bø

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FORORD

Denne mastergradsoppgaven har vært gjennomført på oppdrag fra Norsk Institutt for Naturforskning (NINA) og har vært et samarbeid mellom NINA og avdeling for allmennvitenskapelige fag, institutt for natur-, helse- og miljøvernfag ved Høgskolen i Telemark, Bø. Prosjektet har vært en del av det pågående skandinaviske forskningsprosjektet på gaupe, Scandlynx. Feltarbeid, analyser og skriving av oppgaven har vært likt fordelt mellom begge studenter. Oppgaven består av to artikler som omhandler hvert sitt tema. Begge artiklene er skrevet på engelsk. Når det gjelder formatering av tekst, figurer og tabeller har vi valgt å følge retningslinjene til Journal of Wildlife Management. Vi vil gjerne takke John Odden og John Linnell ved NINA for samarbeidet og for verdifulle kommentarer samt veileder Howard Parker ved Høgskolen i Telemark, Bø for god veiledning i skriveprosessen av denne oppgaven.

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Winter distribution of cervids and mountain hare in relation to topography and snow depth

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ABSTRACT Winter distribution of roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), moose (*Alces alces*), and mountain hare (*Lepus timidus*) was studied in relation to topographic variables and snow depth in the Hallingdalen valley, Norway. Snow depths on the study area were positively correlated with elevation, when both snow depth and variation in snow depth increased with increasing elevation. Herbivore distribution was based on pellet-group counts on 1,416 plots made during spring and early summer. The strongest determinant of winter distribution of roe deer, red deer and moose was decreasing elevation and decreasing snow depth. Roe deer and moose preferred gentler slopes (0–20°) than red deer (20–30°). Moose preferred southern and western exposures, while red deer selected east-faced areas. Mountain hare did not select for elevation or slope, but preferred greater snow depth and southern exposures. Digital density maps provided an intuitive sense of the different species winter distribution.

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Topography and snow depth are important factors determining winter distribution and density of cervids in European forests and mountain habitats, especially for roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) that have high foot-loading and are short legged, and are therefore most sensitive to snow depth (Mysterud 1999, Pompilio and Meriggi 2001, Homolka and Heroldova 2003, Palmer and Truscott 2003, Luccarini et al. 2006), but moose (*Alces alces*) are also sensitive to some extent (Poole and Stuart-Smith 2006). Typically, migratory cervids in the temperate region choose a lower elevation winter range than in summer to avoid deep snow (Mysterud 1999). Mysterud (1999) demonstrated that roe deer conformed to the usual pattern of temperate cervids with migration to lower altitudes during winter. Ramanzin et al. (2007) found that migratory roe deer used lower elevation in winter, while stationary roe deer had both summer and winter ranges approximately at the same elevation. Luccarini et al. (2006) showed that both migratory and stationary red deer used lower altitudes during winter, and Latham et al. (1997) found that red deer density correlated negatively with snow depth. Poole and Stuart-Smith (2006) concluded that the strongest determinant of late winter range for moose at the landscape scale was decreasing elevation and believed elevation to be a surrogate for snow dept, which is probably the primary causative factor influencing late-winter distribution of moose.

Abruptness and directions of slopes may also have an influence on cervid winter distribution. At northerly latitudes snow will melt faster on southerly exposures, increasing access to forage and decreasing costs of locomotion (Parker et al. 1984). Pépin et al. (2008) demonstrated that red deer changed from south and south-west aspects in summer to southerly and easterly aspects in winter, and used steeper slopes in winter than summer. Schmidt (1993)

showed that non-supplementary fed and stationary red deer selected southern exposures in winter, and concluded that this behaviour was to reduce energy costs of thermoregulation due to cold winds. Poole and Stuart-Smith (2006) found that moose selected areas of gentler slopes and with higher solar insolation. Little use of slopes <30% and selection for southern and western exposures are also reported by Matchett (1985) and Langley (1993).

In contrast to cervids, mountain hare (*Lepus timidus*) winter distribution is rarely hampered by deep snow because they feed on deciduous shrubs, shots and twigs available above snow cover (Angerbjörn and Flux 1995). Mountain hares move and forage above snow cover (Hiltunen and Kauhala 2006) and increasing snow levels can thereby aid hare foraging by enabling them to reach previously unbrowsed levels in the shrub layer. Mountain hare distribution in relation to topography has not been widely studied.

In this study, we relate roe deer, red deer, moose, and mountain hare winter distribution based on pellet-group counts to topography and snow depth. We predicted a negative relationship between roe deer, red deer, and moose pellet-group density and altitude and snow depth. Further, we predicted that roe deer and moose selected southerly exposures and gentler slopes, and that red deer selected steeper slopes and south- and east-faced slopes. Lastly, we predicted a positive relationship between pellet-group density and snow depth for mountain hares.

STUDY AREA

The study was carried out in a 995 km^2 area located in the Hallingdalen valley, south-east of Norway, within the 4 municipalities of Nes, Gol, Ål and Hol (Fig.1). Average coordinates were between 67°11'02'' and 67°36'00'' N and 04°51'01'' and 05°13'00'' E. The terrain is steep, rising from the Hallingdalen River at about 150 m above sea level (a.s.l.) to 800–1,100 m a.s.l. on both sides of the valley. The boreal vegetation in the valley is varied and

dominated by Scots pine (*Pinus sylvestris*), Norwegian spruce (*Picea abies*), and birch (*Betula pubescens*) along the valley sides. Other common tree species are Eurasian aspen (*Populus tremula*), goat willow (*Salix caprea*), and European rowan *(Sorbus aucuparia)*. Mountain birch (*Betula tortuosa*) dominates at timberline. Small farms and cultivated areas dominate along the valley floor.

During the study, densities of roe deer, red deer, moose, and mountain hare in the valley were unknown. However, the impression locally was that roe deer densities were low, red deer low but expanding, hares "normal" (which is quite low), and moose relatively high. The main predator on roe deer in the winter is the Eurasian lynx (*Lynx lynx*) (Odden et al. 2006, Ratikainen et al. 2007). Red fox *(Vulpes vulpes)* can prey on roe deer fawns in spring and summer (Panzacchi et al. 2007) and adult roe deer in severe winters (Cederlund and Lindstrom, 1983). Lynx (Odden et al. 2006) and red fox (Dell'Arte et al. 2007) also prey on hares, while most moose and red deer succumb to hunting. Mean monthly temperature varied from –10°C in February to +5°C in April (Norwegian Meteorological Institute 2007).

METHODS

Pellet-group counts

We used the faecal pellet-group counting method (Mayle et al. 1999) to estimate cervid and mountain hare distribution as the method has been shown to provide reliable results in population studies of roe deer and red deer (Hemami et al. 2005, Prokesova et al. 2006, Borkowski and Ukalska 2007, Forsyth et al. 2007), moose (Forbes and Theberge 1993, Härkönen and Heikkilä 1999), and hares (Newey et al. 2003, Homyack et al. 2006, Shimano et al. 2006, Karmiris and Nastis 2007). Field work took place in late May and early June 2007, just after the snow melt but before significant vegetation growth. We used a stratified random sampling model together with the standing-crop method for pellet-group counting

(Mayle et al. 1999). The standing-crop method is more applicable than the clearance plot method in areas where densities are low, or where the disappearance rate of pellet-groups is high. This is because the standing-crop method allows more time for the accumulation of pellet-groups (Mayle et al. 1999), and is more applicable if the persistence time for pellets is poorly known (Hemami et al. 2005). In our study area the persistence time for pellets was unknown, and the density of pellet-groups low, especially for roe deer and red deer. Therefore we used the standing-crop method.

A total of 50 1x1 km grid cells were randomly chosen throughout the study area. Within the 1x1 km routes we counted pellet-groups along triangular transects, starting in one corner of the 1x1 km grid cell. We navigated to the start of each triangular transect using a hand held Global Positioning System (GPS). Start and end coordinates of each line in the triangle were stored in the GPS beforehand, and we went from the start point to the end point in a straight line. The total length of each triangular transect was 3.24 km. Along each transect we counted the number of pellet-groups in circular plots of 12.56 m^2 spaced at approximately 100 m intervals (i.e., 30 plots/transect). We did not count pellet-groups in plots located on agricultural land or in urban areas. The total number of plots inspected was 1,416. If half or more of the pellets in a group located along a plot edge were lying within the plot, we included it to the count (Härkönen and Heikkilä 1999, Prokesovà et al. 2006). When searching for pellets we pushed aside growing vegetation (Forsyth et al. 2007), primarily blueberry (*Vaccinium myrtillus*) and mountain cranberry (*Vaccinium vitis-idaea*).

We counted pellet-groups from roe deer, red deer, moose, and mountain hare. According to Dzieciolowski (1976), the persistence time of red deer faeces is 3 months in winter. Previous studies of roe deer (Welch et al. 1990) and brown hare (Karmiris and Nastis 2007) habitat selection have used a 3-month pellet-group accumulation interval. Härkönen and Heikkilä (1999) used the accumulation times of 210 to 240 days for moose. Based on

these studies, we assumed the pellet-groups counted in our study to have been accumulated from January to May. We considered it a pellet group if there were assemblages of 2 or more single pellets for roe deer and red deer, 5 or more single for moose, and 1 or more for mountain hare. Sometimes it was difficult to determine whether the pellets in a group had originated from 1 or more defecation event, especially for mountain hare. In these cases we allowed for colour, size, and distance between the pellet-groups.

Snow depth data collection

To collect data on snow depth, we sent our sample plots with exact coordinates (WGS 84, UTM zone 33N) to the Norwegian Water Resources & Energy Directorate (NVE). Snow depth estimations are based on a precipitation/degree-day type model. The snow model is based on daily input of temperature and precipitation data (adjusted for altitude), distributed in a 1x1 km resolution grid. In the estimations, changes in snow depth due to melting, new snowfall, and snow age are taken into account (Engeset et al. 2004). Snow depth data stored in grids can be used to calculate plot values, and from NVE we obtained mean snow depths for January, February, March, and April for all our sample plots ($n =1416$). When data on snow depth are stored in grids with 1x1 km grid cells all sample plots within the same 1x1 km grid cell will have the same mean snow depth for each month. Therefore we calculated mean altitude for each different value for snow depth ($n =166$) from a Digital Elevation Model (DEM).

Using correlation analyses, we examined the strength with which two sets of measurements have a positive or negative linear association (Ennos 2007). Because snow depth data did not follow the requirements for normal distribution, we used Spearman's correlation analyses to determine whether snow depth was associated with elevation, and created scatter diagrams to illustrate these relationships for the months of January to April, 2007.

Topographic variables

We calculated the topographic variables from a 25x25 m USGS DEM, using ArcGIS 9, ArcMap version 9.2. To cover the study area we put together 4 100x100 km DEMs, using mosaic to new raster with the mosaic method blend and the mosaic colormap mode match. We created a minimum convex polygon from the sample plots to create a study area polygon, and then clipped the mosaic DEM by this polygon to a study area density map DEM. We made slope and aspect grids from the study area density map DEM using the spatial analyst in ArcMap version 9.2. Then we divided the aspect grid into 4 category grids (north, east, south, and west). For each sample plot we calculated elevation and elevation^2 from the study area DEM, slope from the slope grid, and aspect categories from the aspect grid, and used the values from these variables in the statistical analyses together with the number of pellet-groups found. Elevation values are in meters (m), and slope and aspect values in degrees (°).

Density maps and statistical calculation

Using the pellet-groups method, densities of cervids and hares are usually reported as density of pellet-groups per area (usually per km^2) (Härkönen and Heikkilä 1999, Hemami et al. 2005, Prokesovà et al. 2006). In lieu of calculating real densities for the species represented in our study, we worked out digital density maps, one map for each species pellet-group (roe deer, red deer, moose, and mountain hare). We made the digital density maps in order to make intuitive sense of the different species' winter distribution in our study area.

Generalized linear models (GLMz) were introduced by Nelder and Wedderburn (1972), and extend the general linear model by removing the strict assumptions of normality, linearity, and constant variance (Norusis 2007). The GLMz assume that the value of an observation Y is given by a function of a linear combination of explanatory variables X_1, X_2 …Xp (Manly et al. 2002). Since our pellet-count data is Poisson distributed, we followed a log-linear model, using a GLMz with Poisson distribution and log link function. The number

of pellet-groups for each species is the dependent variable in the GLMz, while elevation, elevation^2, slope, and aspect category are the explanatory variables. In the GLMz model we included main effects of species, elevation, elevation^2, aspect category, and slope as well as interactions between species, elevation, aspect category, and slope. The interaction between species and elevation^2 was not significant, meaning that all species have the same shape on the curve of pellet-groups in relation to altitude. But there can still be a difference in what altitude the different species prefer. Therefore we excluded the interaction between species and elevation^2 (since it was not significant), but included main effects of elevation^2 in our model. When the test of model effects (Table 1) was significant for all factors, we completed the test. Together with the parameter estimates (β) from the GLMz (Table 2) we used elevation, slope, and aspect category grids in the raster calculator in ArcMap version 9.2, to compute the density maps for each species. The formulas we used in the raster calculator are as follows:

Roe deer

(Intercept) + Roe deer + (Aspect north + Roe deer*Aspect north) x aspect north grid + (Aspect east + Roe deer*Aspect east) x aspect east grid + (Aspect south + Roe deer*Aspect south) x aspect south grid + (Elevation + Roe deer*Elevation) x elevation grid + (Elevation^2 x elevation grid^2) + (Slope + Roe deer*Slope) x slope grid

Red deer

(Intercept) + Red deer + (Aspect north + Red deer*Aspect north) x aspect north grid + (Aspect east + Red deer*Aspect east) x aspect east grid + (Aspect south + Red deer*Aspect south) x aspect south grid + (Elevation + Red deer*Elevation) x

elevation grid + (Elevation^2 x elevation grid^2) + (Slope + Red deer*Slope) x slope

grid

Moose

(Intercept) + Moose + (Aspect north + Moose*Aspect north) x aspect north grid +

(Aspect east + Moose*Aspect east) x aspect east grid + (Aspect south +

Moose*Aspect south) x aspect south grid + (Elevation + Moose*Elevation) x

elevation grid + (Elevation^2 x elevation grid^2) + (Slope + Moose*Slope) x slope grid

* = interaction

For mountain hare, the formula is slightly different, because hare is included in the intercept in the GLMz. Therefore, the formula for brown hare is as follows:

Intercept + (Aspect north x aspect north grid) + (Aspect east x aspect east grid) +

(Aspect south x aspect south grid) + (Elevation x elevation grid) + (Elevation^2 x

elevation grid^2) + (Slope x slope grid)

In our study, we wanted to check for relations between pellet-groups, the topographic variables and snow depth. We used Spearman's correlation to evaluate relations between pellet-groups and elevation, slope, and mean snow depth for January, February, March, and April. Chi-square tests can be used to test for whether species are using habitat characters differently (Manly et al. 2002). We used the chi-square test to check for differences between pellet-groups in the different aspect and slope categories, with pellet-groups from roe deer, red deer, moose, and mountain hare as weighted cases before conducting the test. We computed the test for each species separately. To compute statistics we used the statistical

package SPSS 15.0 for Windows. We worked out density maps in ArcGIS 9, ArcMap version 9.2, scatter diagrams in SPSS 15.0 for Windows, and histograms in Microsoft Office Excel 2003.

RESULTS

Snow depth

Mean snow depth in cm ($\pm$ SD) on the study area in 2007 was 35.97 $\pm$ 32.48, 51.54 $\pm$ 39.01, 60.81 $\pm$ 45.78, and 45.42 $\pm$ 48.83 in January, February, March, and April respectively ($n =$ 166). Snow depth was strongly correlated with elevation (January: $r_S = 0.865$, February: $r_S = 0.873$, March: $r_S = 0.884$, April: $r_S = 0.898$, $P \leq 0.01$). Scatter diagrams show that both snow depth and variation in snow depth increase with increasing elevation (Fig. 2).

Pellet-groups and relations to topography and snow depth

We found a total of 29, 26, 408, and 468 pellet-groups from roe deer, red deer, moose, and mountain hare respectively in the 1,416 plots investigated.

The pellet-groups from roe deer did not differ significantly between aspect categories (Fig. 3A, Table 3). Roe deer preferred gentler slopes (10–20°) (Fig. 3 B) when pellet-groups differed between slope categories (Table 3). Most roe deer pellet-groups were found at lower elevations and were negatively correlated with elevation (Table 4). Roe deer pellet-groups were also negatively correlated with mean snow depth for January, February, March, and April (Table 4). Winter distribution of roe deer based on the pellet-group counts is shown in the roe deer density map (Fig. 4).

Red deer had the highest frequencies of pellet-groups on east faced exposures, and steeper slopes (20–30°) (Fig. 3 A, B). Pellet-groups differed significantly between the aspect categories (Table 3) and were positively correlated with slope (Table 4). Red deer pellet-

groups were also negatively correlated with mean snow depth (Table 4). Winter distribution of red deer based on the pellet-group counts are shown in the red deer density map (Fig. 5).

Moose had the highest frequencies of pellet-groups on south and west faced exposures and on gentler slopes (0–10°) (Fig. 3 A, B) when pellet-groups differed significantly between both aspect categories and slope categories (Table 3). Moose pellet-groups were negatively correlated with both elevation and mean snow depth for January, February, March, and April (Table 4). Winter distribution of moose based on pellet-group counts is shown in the moose density map (Fig. 6).

We found the highest frequency of mountain hare pellet-groups on southern exposures (Fig. 3 A). Pellet-groups differed significantly between the aspect categories (Table 3). Mountain hare pellet-groups were positively correlated with mean snow depth (Table 4). Winter distribution of mountain hare based on pellet-group counts is shown in the mountain hare density map (Fig. 7).

DISCUSSION

We counted pellet-groups only at altitudes from 150–1,100 m a.s.l. Our density maps, however, indicate low densities for each species above 1,100 m. This information should be disregarded as we lack data above this altitude.

As we predicted, the frequency of roe deer pellet-groups showed a negative association with elevation and mean snow depth for the 4 winter months (January, February, March, and April). Likewise, Mysterud et al. 1997 showed that roe deer used areas at lower altitudes during winter to find winter areas with shallower snow depth. Increasing snow depth lowers the opportunity to forage, increases costs of movement (Parker et al. 1984), mortality and vulnerability to predation (Cederlund and Lindström 1983). In contrast, the distribution of roe deer pellet-groups did not differ between aspect categories. Therefore we cannot conclude

that most roe deer pellet-groups were more prevalent on south faced areas as predicted. Further research involving larger sample sizes is likely necessary to test this hypothesis with any confidence.

The frequency of red deer pellet-groups, as predicted, was highest at lower elevations and lower mean snow depths, confirming results from other studies (Latham et al. 1997, Luccarini et al. 2006, Pépin et al. 2008). The selection for steeper slopes, eastern exposures and lower altitudes during winter can be explained by less snow (Pépin et al. 2008), lower wind velocities (Schmidt 1993), and more available winter forage (Garrott et al. 1987) in these areas. As was the case with roe deer pellet-groups, correlations were weak, possibly due to small sample sizes.

With the highest frequency of pellet-groups recorded on southern and western exposures, and with negative correlations with elevation and mean snow depth, our results support that moose prefer habitats at lower elevations and snow depths during winter. Lower snow depths will reduce decrease in autumn body mass (Hjeljord and Histøl 1999) and energy costs of locomotion, increase forage availability (Parker et al. 1984), positively affecting moose density in areas with shallower snow.

Following our predictions, mountain hare were not affected by topography or snow depth in the same way as the cervids, though we did find a preference for southern exposures. Mountain hare followed our hypothesis, that pellet-groups were positively correlated with mean snow depth. This is probably because on areas with greater snow depth and increasing variation in snow depth, hares are able to forage over a greater vertical distance in the shrub layer, thereby leaving more pellets on the ground after snow melt.

The pellet-group sampling scheme we employed, using circular plots spaced at 100 m intervals, enabled us to effectively sample a large area. However, based on the low pellet-group densities we encountered, a future sampling of the study area might benefit by a

modified sampling design. Predicting that most pellet-groups will be found at lower elevations and lower snow depths, counting the number of pellet-groups in transverse line transects, e.g. in 1–2 m wide strips (Härkönen and Heikkilä 1999, Acevedo et al. 2005, Hemami et al. 2005) should be a more applicable method. Other potentially beneficial modifications of the sampling scheme might include shorter distance between plots, e.g. plots spaced at 20 m intervals (Härkönen and Heikkilä 1999) and a shorter distance between transects, though these modifications would likely increase costs.

Accumulation periods and defecation rates for the different species pellet-groups were unknown in our study area. Therefore predictions were based on information from other studies (Dzieciolowski 1976, Welch et al. 1990, Härkönen and Heikkilä 1999, Karmiris and Nastis 2007) conducted in different habitats and under different conditions than our own. We suggest that investigations of pellet-group accumulation time and defecation rates will be carried out prior to new studies in the area. We also suggest the use of clearance plot method for pellet-group counting, with e.g. a 3-month pellet-group accumulation period (Welch et al. 1990, Karmiris and Nastis 2007).

MANAGEMENT IMPLICATIONS

The management of cervid populations in Norwegian valleys is contingent upon forestry developmental practices in these key habitats that provide both food and shelter during severe winters with deep snow. Forest areas at lower elevations should therefore be prevented from development, while a heterogeneous pattern of forest composition should attempted, as this seems to have an influence on the distribution and population density of both roe deer (Saïd and Servanty 2005) and moose (Maier et al. 2005). High densities of especially roe deer should also provide suitable prey for the Eurasian lynx, an important natural predator in the

boreal forest of south-eastern Norway (Odden et al. 2006), and in turn lead to reduced

predation on domestic animals during grazing season.

LITERATURE CITED

Acevedo, P., M. Delibes-Mateos, M. A. Escudero, J. Vicente, J. Marco, and C. Gortazar.

    2005. Environmental constraints in the colonization of roe deer (*Capreolus capreolus*

    Linnaeus, 1958) across the Iberian Mountains, Spain. Journal of Biogeography

    32:1671–1680.

Angerbjörn, A., and J. E. C Flux. 1995. *Lepus timidus*. Mammalian Species 495:1–11.

Borkowski, J., and J. Ukalska. 2007. Winter habitat use by red and roe deer in pine-dominated

    forest. Forest Ecology and Management 255:468–475.

Cederlund, G., and E. Lindstrom. 1983. Effects of severe winters and fox predation on roe

    deer mortality. Acta Theriologica 28:129–145.

Dell'Arte, G. L., T. Laaksonen, K. Norrdahl, and E. Korpimäki. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecologica 31:276–281.

Dzieciolowski, R. 1976. Roe deer census by pellet-group counts. Acta Theriologica 21:351–358.

Engeset, R., O. E. Tveito, H.- C. Udnæs, E. Alfnes, Z. Mengistu, K. Isaksen, and E. J. Førland. 2004. Snow map validation for Norway. Proceedings XXIII Nordic Hydrological Conference 2004, 8-12 August 2004, Tallinn, Estonia. NHP report 48:122–131.

Ennos, R. 2007. Statistical and Data Handling Skills in Biology. Second edition. Pearson Education Limited, Harlow, England.

Forbes, G. J., and J. B. Theberge. 1993. Multiple landscape scales and winter distribution of moose (Alces alces) in a forest ecotone. Canadian Field-Naturalist 107:201–207.

Forsyth, D. M., R. J. Barker, G. Morriss, and M. P. Scroggie. 2007. Modeling the Relationship Between Fecal Pellet indices and Deer Density. Journal of Wildlife Management 71 (3):964–970.

Garrott, R. A. G, G. C. White, R. M. Bartman, L. H. Carpenter, and A. W. Allredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634–643.

Hemami, M. R., A. R. Watkinson, and P. M. Dolman. 2005. Population densities and habitat associations of introduced muntjac *Muntiacus reevesi* and native roe deer *Capreolus cadreolus* in a lowland pine forest. Forest Ecology and Management 215:224–238.

Hiltunen, M., and K. Kauhala. 2006. Selection of sampling stand habitats by the mountain hare (*Lepus timidus*) during winter. Mammalian Biology 70:183–189.

Hjeljord, O., and T. Histøl. 1999. Range-body mass interactions of a northern ungulate - a test of hypotheis. Oecologica 119:326–339.

Homolka, M., and M. Heroldová. 2003. Impact of large herbivores on mountain stands in the Beskydy Mountains. Forest Ecology and Management 181:119–129.

Homyack, J. A., D. J. Harrison, J. A. Litvaitis, and W. B. Krohn. 2006. Quantifying Densities of Snowshoe hare in Maine Using Pellet Plots. Wildlife Society Bulletin 34 (1):74–80.

Härkönen, S., and R. Heikkilä. 1999. Use of pellet group counts in determining density and habitat use of moose *Alces alces* in Finland. Wildlife Biology 5:233–239.

Karmiris, I. E., and A. S. Nastis. 2007. Intensity of livestock grazing in relation to habitat use by brown hares (*Lepus europaeus*). Journal of Zoology 271:193–197.

Langley, M. A. 1993. Habitat selection, mortality and population monitoring of Shiras moose in the North Fork of the Flathead River valley, Montana. M.SC. thesis, University of Montana, Missoula.

Latham, J., B. W. Staines, and M. L. Gorman. 1997. Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. Journal of Zoology, London 242:681–704.

Luccarini, S., L. Mauri, S. Ciutu, P. Lambertini, and M. Apollonio. 2006. Red deer (*Cervus elaphus*) spatial use in the Italian Alps: home range patterns, seasonal migrations, and effects of snow and winter feeding. Ethology, Ecology & Evolution 18:127–145.

Maier, J. A. K., J. M. Ver Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research 35:2233–2243.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Second edition. Resource selection by animals. Statistical design and analysis for field studies. Second Edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Matchett, M. R. 1985. Habitat selection by moose in the Yaak river drainage, northwestern Montana. Alces 21:161–189.

Mayle, B. A., A. J. Peace, and R. M. A. Gill. 1999. How many deer? A field guide to estimating deer population size. Forestry Commision, Edinburgh, Scotland.

Mysterud, A., B. H. Bjørnsen, and E. Østbye. 1997. Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway. Wildlife Bilology 3:27–33.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology, London 247:479–486.

Nelder, J. A., and R. W. M. Wedderburn. 1972. Generalized linear models. Journal of the Royal Statistical Society 135:370–384.

Newey, S., M. Bell, S. Enthoven, and S. Thirgood. 2003. Can distance sampling and dung plots be used to assess the density of mountain hare *Lepus timidus*? Wildlife Biology 9:185–192.

Norusis, M. J. 2007. SPSS 15.0 Advanced Statistical Procedures Companion. Prentice Hall Inc., New Jersey, USA.

Norwegian Meteorological Institute. 2007. Home page at http://met.no/index.shtml.

Odden, J., J. D. C Linnell, and R. Andersen. 2006. Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. European Journal of Wildlife Research 52 (4):237–244.

Palmer, S. C. F., and A. - M. Truscott. 2003. Seasonal habitat use and browsing by deer in Caledonian pinewoods. Forest Ecology and Management 174:149–166.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditure for locomotion by mule deer and elk. Journal of Wildlife Management 48:474–488.

Panzacchi, M., J. D. C. Linnell, G. Serrao, S. Eie, M. Odden, J. Odden, and R. Andersen. 2007. Evaluation of the importance of roe deer fawns in the spring–summer diet of red foxes in southeastern Norway. Ecological Research. DOI 10.1007/s11284-007-0452-2.

Pépin, D., C. Adrados, G. Janeau, J. Joachim, and C. Mann. 2008. Individual variation in migratory and explanatory movements and habitat use by adult red deer (*Cervus elaphus* L.) in a mountainous temperate forest. Ecological Research. DOI 10.1007/s11284-008-0468-2.

Pompilio, L., and A. Meriggi. 2001. Modelling wild ungulate distribution in Alpine habitat: a case study. Italian Journal of Zoology 68:281–289.

Poole, K. G., and K. Stuart-Smith. 2006. Winter habitat selection by female moose in western interior montane forests. Canadian Journal of Zoology 84:1823–1832.

Prokesovà, J., M. Barancekova, and M. Homolka. 2006. Density of red deer and their distribution in relation to different habitat characteristics in a floodpain forest. Folia Zoologica 55 (1):1–14.

Ramanzin, M., E. Sturaro, and D. Zanon. 2007. Seasonal and home range of roe deer (*Capreolus capreolus*) in the Italian eastern Alps. Canadian Journal of Zoology 85:280–289.

Ratikainen, I., Panzacchi M., Mysterud A., Odden J., Linnell J. & Andersen R. 2007. Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. Journal of Zoology 273:192–199.

Saïd, S., and S. Servanty. 2005. The influence of landscape structure on female roe deer home-range size. Landscape Ecology 20:1003–1012.

Schmidt, K. 1993. Winter ecology of nonmigratory Alpine red deer. Oecologica 95:226–233.

Shimano, K., H. Yatake, M. Nashimoto, S. Shiraki, and R. Matsuki. 2006. Habitat
    Availability and Density estimations for the Japanese Hare by Fecal Pellet Counting.
    Journal of Wildlife Management 70 (6):1650–1658.

Welch, D., B. W. Staines, D. C. Catt, and D. Scott. 1990. Habitat usage by red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer in a Scottish Sitka spruce plantation.
    Journal of Zoolgy, London 221:453–476.

FIGURE CAPTIONS

Figure 1. The 995 km^2 study area (shaded) in the Hallingdalen Valley, south-east Norway (small map).

Figure 2. Scatterplott of the relations between snow depth (n = 166) and elevation in a) January, b) February, c) March, and d) April 2007 on the study area in the Hallingdalen valley, south-east Norway. The dots represent mean snow depth in cm.

Figure 3. The number of pellet-groups found for roe deer, red deer, moose, and mountain hare within aspect and slope categories. Aspect category 1 = north, 2 = east, 3 = south, 4 = west. Slope category 1 = 0–10°, 2 = 10–20°, 3 = 20–30°, 4 = >30°.

Figure 4. Roe deer density map from the study area in the Hallingdalen valley, south-eastern Norway.

Figure 5. Red deer density map from the study area in the Hallingdalen valley, south-eastern Norway.

Figure 6. Moose density map from the study area in the Hallingdalen Valley, south-eastern Norway.

Figure 7. Mountain hare density map from the study area in the Hallingdalen Valley, south-eastern Norway.

Figure 1
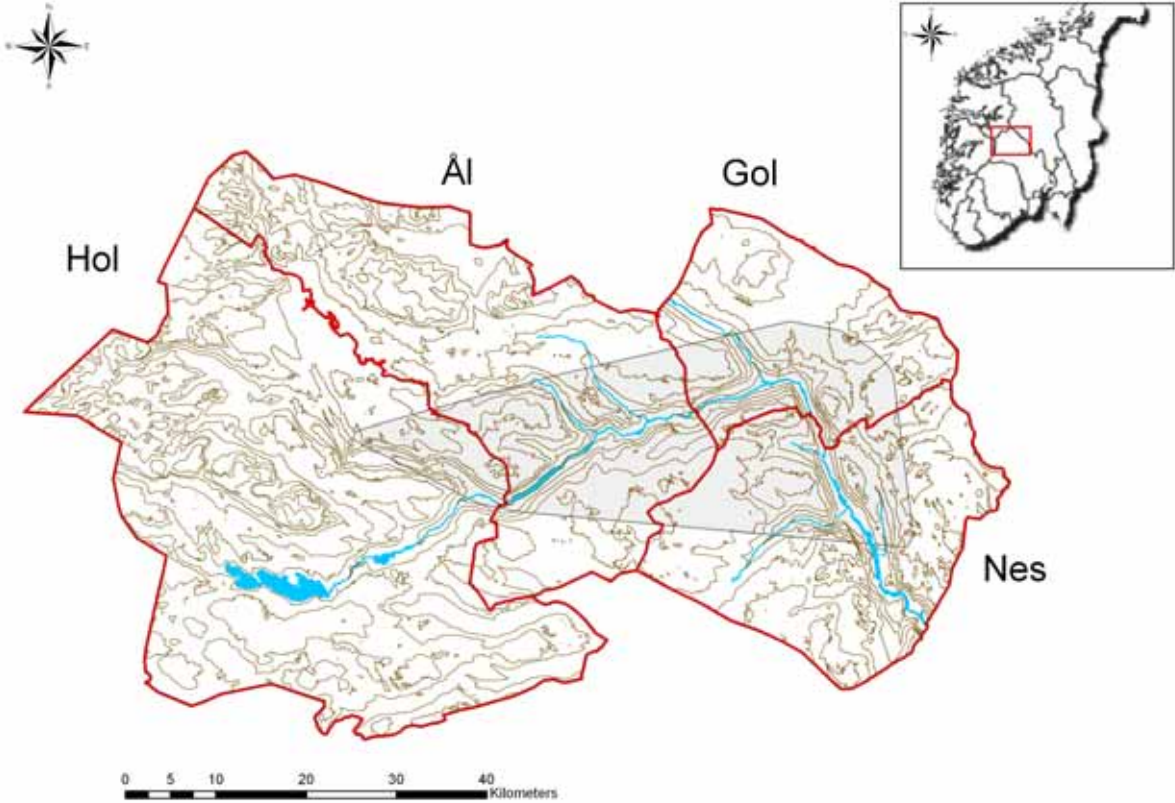
Figure 2
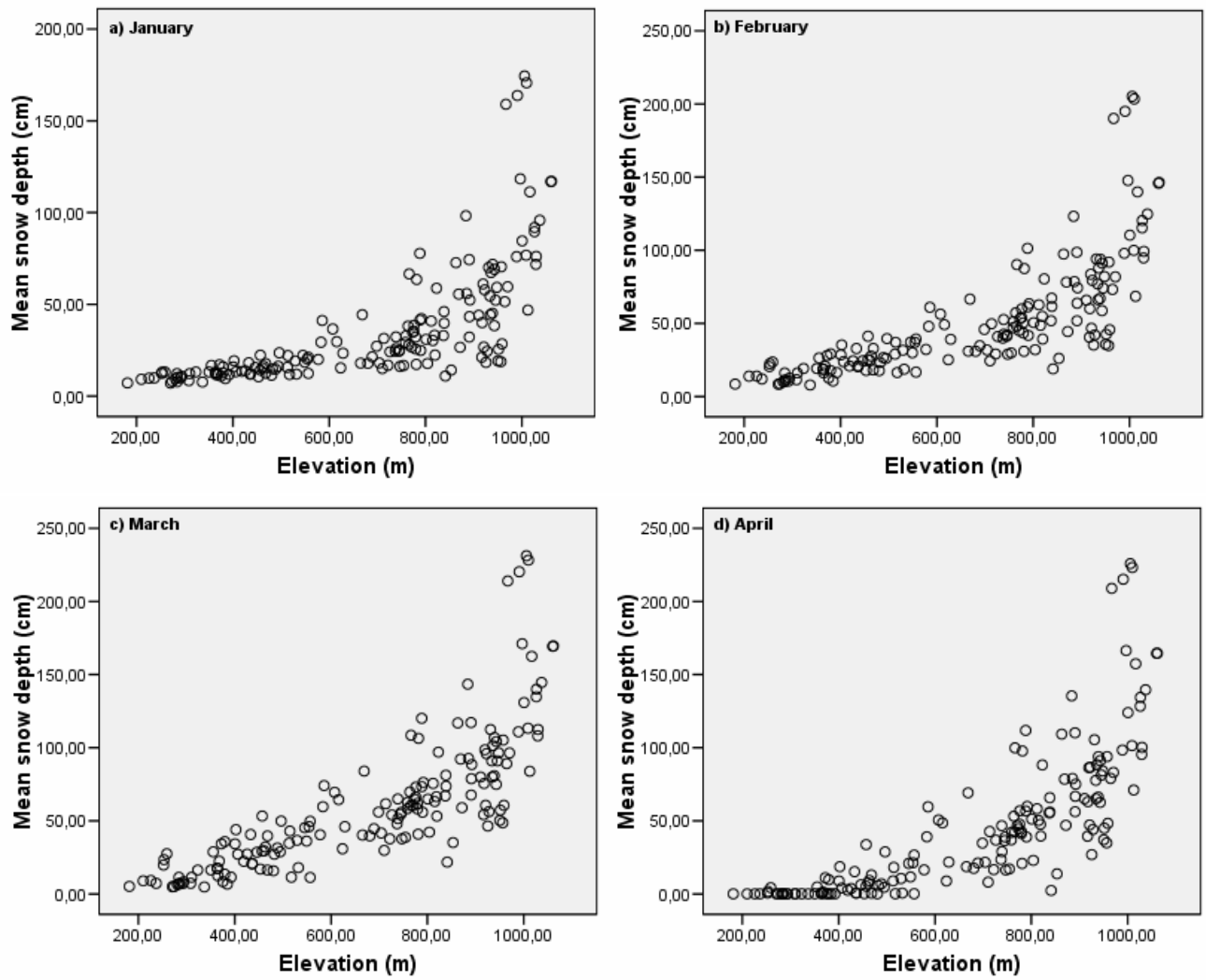
Figure 3

a) Selection of aspect categories
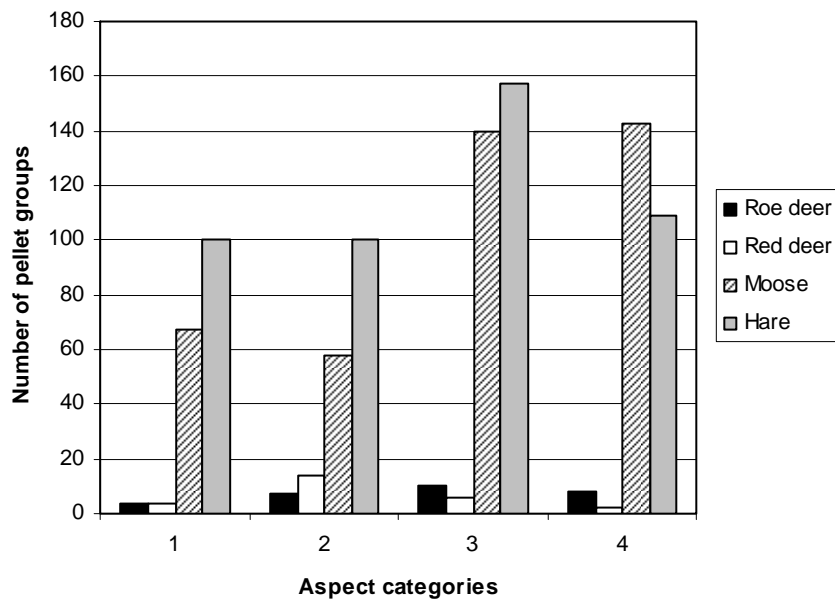
b) Selection of slope categories
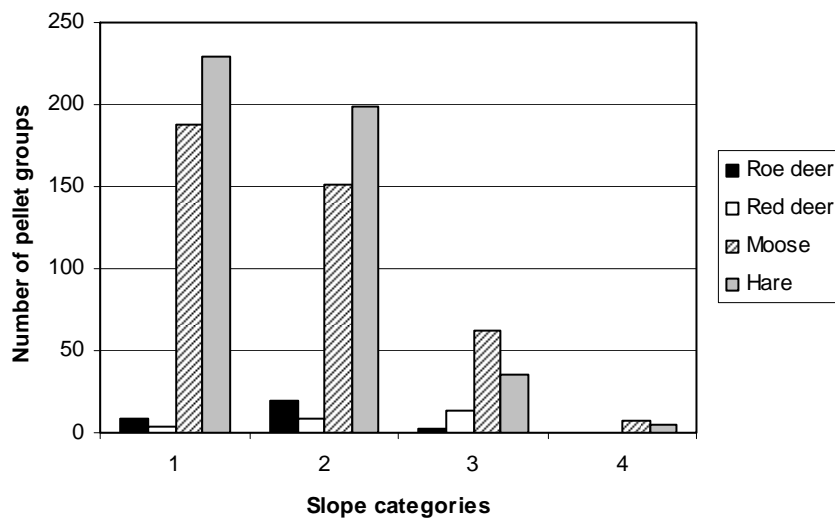
Figure 4

Roe deer density map

Figure 5

Figure 6
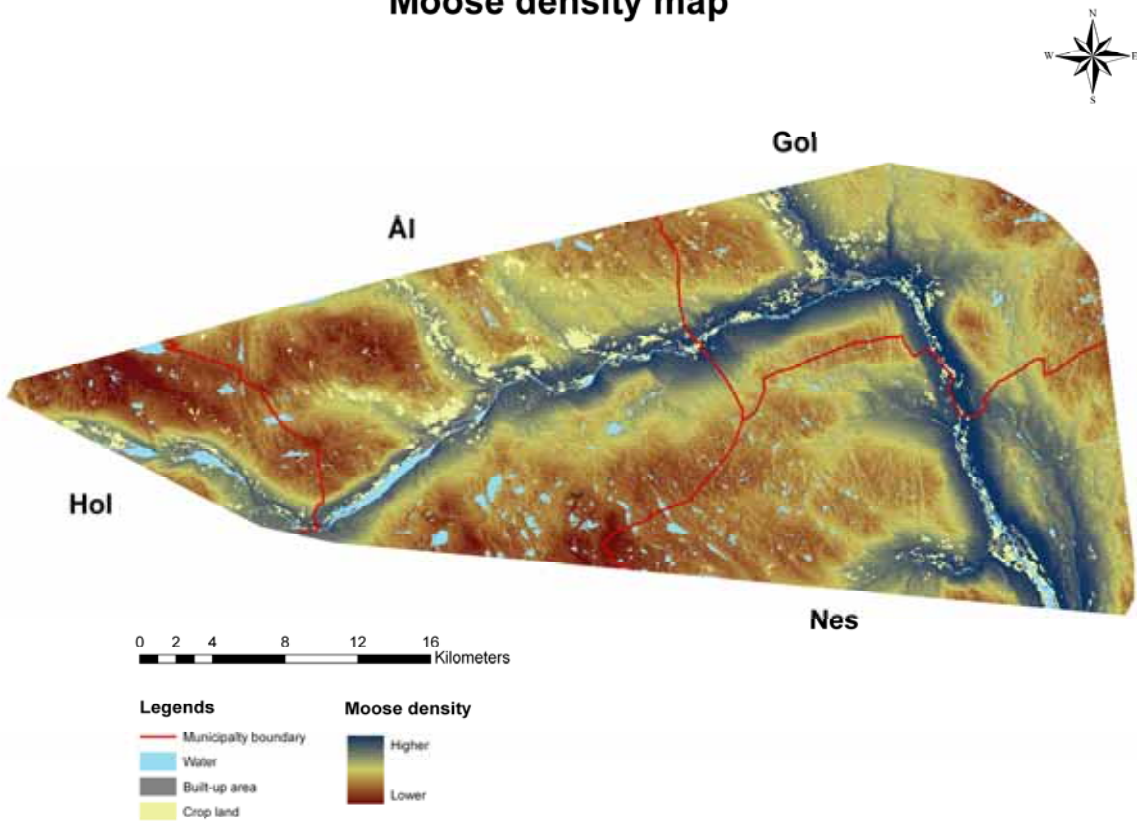
Moose density map

Figure 7

Mountain hare density map
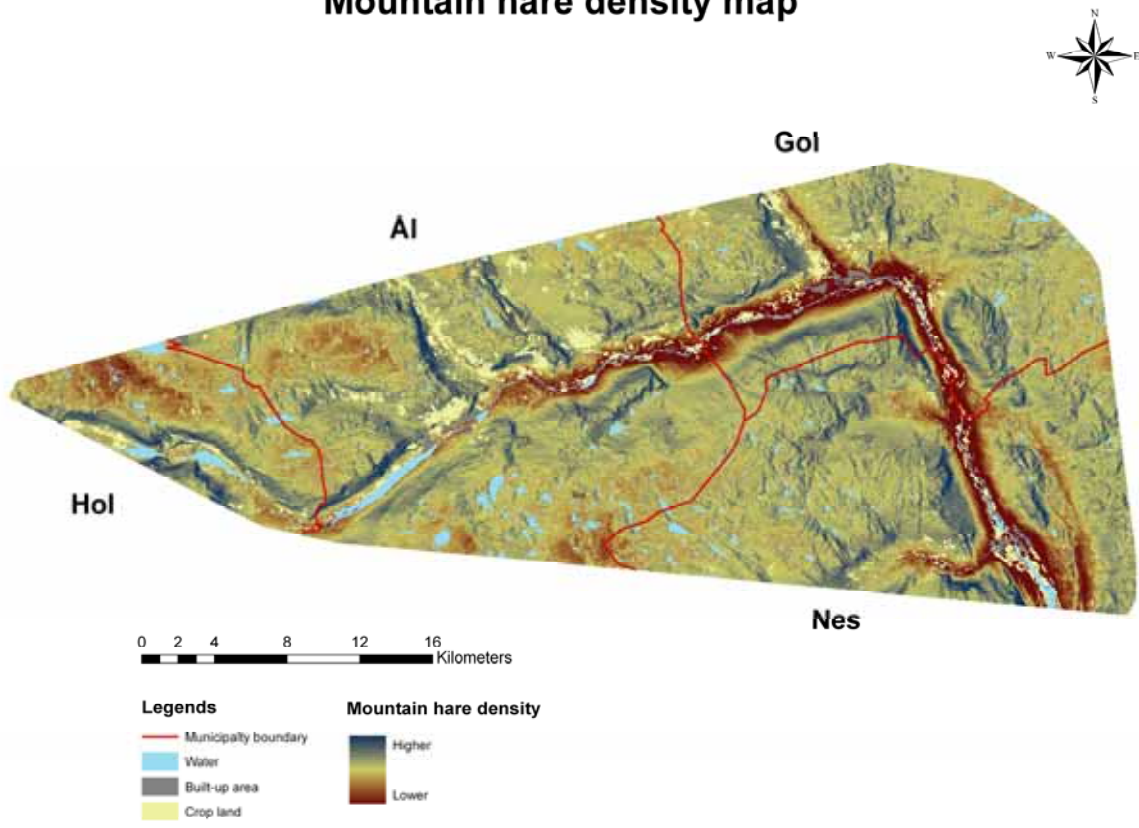
Table 1. Test of model effects from the generalized linear model.

Source	Type III		
	Wald Chi-Square	df.	Sig.
(Intercept)	177.131	1	0.000
Species	86.840	3	0.000
Elevation	25.597	1	0.000
Elevation^2	42.548	1	0.000
Slope	22.719	1	0.029
Aspect category	8.999	3	0.000
Species*Elevation	109.266	3	0.000
Species*Slope	22.882	3	0.000
Species*Aspect category	65.909	9	0.000

Dependent Variable: Pellets.

Model: (Intercept), Species, Elevation, Elevation^2, Aspect category, Slope, Species*Elevation, Species*Aspect category, Species*Slope.

Table 2. Parameter estimates from the generalized linear model. Dependent Variable: Pellets. Model: (Intercept), Species, Elevation, Elevation^2, Aspect category, Slope, Species* Elevation, Species*Aspect category, Species* Slope.

Parameter	β	Std. Error	95% Wald Confidence Interval		Hypothesis test		
			Lower	Upper	Wald Chi-Square	df.	Sig.
(Intercept)	−3.310	0.2854	−3.869	−2.750	134.522	1	0.000
Roe deer	0.488	0.5844	−0.657	1.633	0.697	1	0.404
Red deer	−5.141	0.8981	−6.902	−3.381	32.768	1	0.000
Moose	1.820	0.2385	1.353	2.288	58.244	1	0.000
Hare	0^a	.	.	.	.	.	.
Elevation	0.006	0.0008	0.004	0.007	52.150	1	0.000
Elevation^2	3.746E-6	5.7435E-7	−4.872E-6	−2.621E-6	42.548	1	0.000
Slope	0.015	0.0058	0.004	0.026	6.688	1	0.010
Aspect north	0.111	0.1108	−0.106	0.328	1.003	1	0.317
Aspect east	0.317	0.1111	0.099	0.534	8.116	1	0.004
Aspect south	0.076	0.0995	−0.119	0.271	0.577	1	0.448
Aspect west	0^a	.	.	.	.	.	.
Roe deer*Elevation	−0.005	0.0008	−0.006	−0.003	39.972	1	0.000
Red deer*Elevation	3.426E-5	0.0008	−0.001	0.002	0.002	1	0.965
Moose*Elevation	−0.002	0.0003	−0.003	−0.002	84.879	1	0.000
Hare*Elevation	0^a	.	.	.	.	.	.
Roe deer*Slope	−0.012	0.0220	−0.055	0.031	0.303	1	0.582

Table 2. Continued.

Parameter	β	Std. Error	95% Wald Confidence Interval		Hypothesis test		
			Lower	Upper	Wald Chi-Square	df.	Sig.
Red deer*Slope	0.084	0.0179	0.049	0.119	21.772	1	0.000
Moose*Slope	0.004	0.0081	−0.012	0.020	0.226	1	0.634
Hare*Slope	0[a]	.	.	.	.	.	.
Roe deer*Aspect north	−0.541	0.5020	−1.524	0.443	1.159	1	0.282
Roe deer*Aspect east	−0.448	0.4328	−1.297	0.400	1.073	1	0.300
Roe deer*Aspect south	−0.079	0.3909	−0.845	0.687	0.041	1	0.839
Roe deer*Aspect west	0[a]	.	.	.	.	.	.
Red deer*Aspect north	0.789	0.6990	−0.581	2.159	1.276	1	0.259
Red deer*Aspect east	1.952	0.6177	0.741	3.162	9.985	1	0.002
Red deer*Aspect south	0.784	0.6583	−0.506	2.075	1.419	1	0.234
Red deer*Aspect west	0[a]	.	.	.	.	.	.
Moose*Aspect north	−0.677	0.1617	−0.994	−0.361	17.558	1	0.000
Moose*Aspect east	−0.999	0.1672	−1.327	−0.672	35.750	1	0.000
Moose*Aspect south	−0.336	0.1374	−0.605	−0.067	5.986	1	0.014

Table 2. Continued.

Parameter	β	Std. Error	95% Wald Confidence Interval		Hypothesis test		
			Lower	Upper	Wald Chi-Square	df.	Sig.
Moose*Aspect west	0[a]	.	.	.	.	.	.
Hare*Aspect north	0[a]	.	.	.	.	.	.
Hare*Aspect east	0[a]	.	.	.	.	.	.
Hare*Aspect south	0[a]	.	.	.	.	.	.
Hare*Aspect west	0[a]	.	.	.	.	.	.
(Scale)	0.635[b]						

[a] Set to zero because this parameter is redundant.

[b] Computed based on the deviance.

Table 3. Chi-square test for differences between aspect and slope categories. Roe deer, red deer, moose, and mountain hare pellet-groups are used as weighted cases.

Habitat characters	Roe deer		Red deer		Moose		Hare	
	χ^2	Asymp. Sig.	χ^2	Asymp. Sig.	χ^2	Asymp. Sig.	χ^2	Asymp. Sig.
Aspect category	2.586	0.460	12.769	0.005	61.627	0.000	19.236	0.000
Slope category	15.379	0.000	5.846	0.054	200.216	0.000	329.368	0.000

Table 4. Correlation between roe deer, red deer, moose, and mountain hare pellet-groups, and different habitat characters.

Habitat characters	Roe deer		Red deer		Moose		Hare	
	r_S	*P*	r_S	*P*	r_S	*P*	r_S	*P*
Elevation	−0.098	**	−0.037	ns	−0.128	**	0.086	**
Slope	0.050	ns	0.087	**	0.072	**	0.027	ns
Mean snow depth January	−0.079	**	−0.061	*	−0.148	**	0.095	**
Mean snow depth February	−0.080	**	−0.057	*	−0.150	**	0.096	**
Mean snow depth March	−0.084	**	−0.057	*	−0.151	**	0.099	**
Mean snow depth April	−0.088	**	−0.060	*	−0.149	**	0.098	**

r_S: Spearman's correlation coefficient; *P*: probability; ns: not significant; *: $p < 0.05$; **: $p < 0.01$.

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Lamb loss in relation to roe deer density in south-east Norway

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ABSTRACT We studied lamb loss in relation to density of roe deer in the Hallingdalen

valley, south-east Norway. Average loss of lambs in 13 grazing regions was 4.7%. Loss of

lambs showed a positive linear relationship to density of roe deer and there was no relation

between lamb loss and sheep density. Our results suggest that the probability of lamb dying

during summer grazing is minor where the density of roe deer is low, which indicates that the

loss of lamb is mostly caused by lynx on our study area, and that lynx kill most lambs

incidentally while hunting roe deer.

KEY WORDS sheep, lamb loss, *Capreolus capreolus*, grazing area, lynx, Norway.

In Norway, 53,000–59,000 of 2.0–2.5 million free-ranging sheep were lost each year from

2003–2006 (Norwegian Directorate for Nature Management 2007). Free-ranging sheep in

Norway are rarely guarded (Linnell et al. 1999) and like roe deer (*Capreolus capreolus*) their

numbers have increased markedly during the last century (Sunde et al. 2000, Moa et al. 2006).

However, sheep and roe deer tend to select different habitats. While sheep prefer young forest

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stands of low site quality, roe deer tend to select habitats with higher average availability of herbs, and particularly those with good canopy cover (Mysterud et al. 1999). Compared to roe deer and other wild ungulates, sheep have poorly developed anti-predator behaviour (MacCracken and Hansen 1987, Linnell et al. 1999, Sacks and Neale 2002).

The loss of lambs in Norway is mainly caused by Eurasian lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) (Odden et al. 2002). In our study area lynx are the main large predator, while wolverines are absent. Lambs are only seasonal prey to lynx in Norway, and apparently are mainly killed incidentally by lynx when encountered during other activities (Odden et al. 2008). Far more lambs are killed than are eaten implying that much of the observed depredation is a form of surplus killing. Today the primary prey of lynx in south-east Norway is roe deer, even in areas where their densities are low (Andersen et al. 2005, Odden et al. 2006).

According to optimal foraging theory (OFT) (MacArthur and Pianka 1996), foraging carnivores should exploit habitat patches containing the most abundant and thus most accessible prey, unless their movements are constrained by other factors (Sandell 1989). However, do predators behave according to OFT, or do they instead kill sheep encountered by chance during e.g. hunting wild prey and territory maintenance? Several studies have addressed this question and concluded that depredation rate on sheep was not related to sheep abundance nor sheep dispersion in lynx home ranges (Stahl et al. 2002, Moa et al. 2006, Odden et al. 2008). However, Mech (1988), Mereggi et al. (1996), and Gula (2008), found a higher use of livestock by wolves (*Canis lupus*) in areas with very low densities of wild ungulates. Likewise, Mereggi and Lovari (1996) suggested that a simultaneous reintroduction of several wild ungulate species is likely to reduce predation on livestock, and has often been advocated as a means of reducing attacks on livestock (Tassi 1976, Boscagli 1985). However Linnell et al. (1996) commented that carnivore populations may also increase as a result.

There is reason to believe that lynx are primarily hunting for wild prey, especially roe deer, and that the killing of sheep is a secondary occupation (e.g. Grosjean 1992, Linnell et al. 1999, Odden et al. 2002, Stahl et al. 2002, Moa et al. 2006, Odden et al. 2006). Both Stahl et al. (2001) and Odden et al. (2008) support this hypothesis and found that depredation hot-spots were most likely to occur in areas with high roe deer densities.

The aims of our study were (i) to examine the relationship between density of roe deer and loss of lambs and (ii) the density of sheep and loss of lambs. Since the density of roe deer in our study area is low (Hoel and Hermansen 2008) and lynx are the main predator on roe deer here, we predicted a positive relationship between roe deer density and loss of lambs. Odden et al (2008) found no relationship between the density of sheep and loss of lambs, therefore we predicted the same result in our study.

STUDY AREA

The study was carried out on 5,072 km^2 located in the Hallingdalen valley, south-east Norway, in the municipalities of Flå, Nes, Gol, Ål and Hol (Fig.1). Average coordinates were between 66°84'53'' and 67°54'83'' N, and 04°14'67'' and 05°46'59'' E. The Hallingdalen River runs south-east along the valley bottom at about 150 m above sea level (a.s.l.). The valley sides are steep, timberline occurs at approximately 1000 m a.s.l. The boreal vegetation in the valley is varied and dominated by Scots pine (*Pinus sylvestris*), Norwegian spruce (*Picea abies*), and birch (*Betula pubescens*). Other common tree species are Eurasian aspen (*Populus tremula*), goat willow (*Salix caprea*), and European rowan *(Sorbus aucuparia)*. Mountain birch (*Betula tortuosa*) dominates at timberline. Small farms and cultivated areas dominate along the valley floor. The grazing land within the study area was divided into13 regions.

According to local landowners and hunters the density of roe deer in the area has been low for many years. Sheep range unattended in the forest and lower alpine zones from May to September (Odden et al. 2008). Annually about 320,000 sheep graze the area producing 580,000–615,000 lambs. The mean density of sheep was 19 per km^2 (The Norwegian Forest and Landscape Institute 2008).

METHODS

We constructed a roe deer density map by counting pellet-groups inside the study area (Hoel and Hermansen 2008). We extrapolated this density map to the 5,072 km^2 study area and used it in our analysis. We obtained data on lamb losses from The Norwegian Forest and Landscape Institute (2008). To extract the data we needed for loss of lambs from 2005–2007 we used ArcGIS 9, ArcMap version 9.2, to clip the grazing areas by a study area polygon. Since the roe deer density map was in raster format, we changed the clipped grazing area polygon into raster format by using the function polygon to raster, to prepare for extraction. Finally we extracted the mean density of roe deer from each grazing area by using zonal statistic in ArcMap version 9.2. We also used the data from The Norwegian Forest and Landscape Institute (2008) to calculate the mean density of sheep in our study. These data were stored in databases together with the number and percentage of sheep and lambs released and lost at pasture.

To stabilize the variance of the lamb loss data and to prepare for a best possible regression model, we took the square root of the proportion of lamb loss values before accomplishing an arcsin-transformation. We used multiple linear regressions (Ennos 2007) to investigate whether lamb loss showed a relation to roe deer density, or density of sheep. In the regression analysis we used a stepwise method with the arcsin value for lamb loss as a

dependent variable and the densities of roe deer and sheep as independent variables in the statistical package SPSS 15.0 for Windows.

RESULTS

The mean loss of lambs from 2005–2007 on the 13 grazing areas was at 0.047 (4.7%) (min. = 0.015, max. = 0.113), or a mean of 143 lambs lost (min. = 16, max. = 447) per grazing area, when mean number of lambs released per grazing area was 3,163 (min. = 1,011, max. =10,060). Lamb loss was positively related to roe deer density (Fig.1), but not to the density of sheep ($\beta = -0.220$, $t = -1.008$, df = 12, $P = 0.337$).

DISCUSSION

As predicted, roe deer density and lamb loss were positively related. The fact that we found no relationship between loss of lambs and density of sheep strengthens the relation between roe deer density and lamb loss. These results indicate no casual relationships, only that a lower probability of lamb loss occurs in areas of low roe deer density. However, since the lynx is the main predator on lambs in our study area, we tend to agree with the conclusion arrived at by Stahl et al. (2002), Moa et al. (2006) and Odden et al. (2008), that there appears to be no relationship between sheep depredation rate and sheep abundance, which in turn suggests that lynx did not show a selection for sheep grazing areas. Likewise, our results are comparable with those of Stahl et al. (2001) and Odden et al. (2008), that predation on livestock by lynx will most likely occur in areas with high roe deer densities. A study on lambs with mortality transmitters, on a neighbouring study area, showed that 93.1% of lambs lost on summer range were killed by lynx (Hansen 2007).

According to Mech (1988), Mereggi et al. (1996) and Gula (2008), low densities of wild ungulates can lead to higher depredation on livestock by wolves. Likewise, higher

densities of wild ungulates should produce the opposite effect. Higher densities of roe deer could conceivably reduce the distance travelled by hunting lynx and thereby the rates of encounter with and attacks on sheep. Though roe deer and lynx may simply be selecting the same habitats for unrelated reasons, it seems more likely that their concurrent use of habitat is the result of their strong predator-prey relationship (Moa et al. 2006, Odden et al. 2008).

One obvious source of error in our study involves the discrepancy between the time of year when roe deer density was calculated (winter) and when lamb loss occurs (summer and autumn). Though we have no information on how the distribution of roe deer changes from winter to summer in our study area, the typical pattern is to use slightly higher elevations during summer (Mysterud 1999).

MANAGEMENT IMPLICATIONS

To reduce the loss of free-ranging lambs in Norway we agree with Odden et al. (2008) that management practices should concentrate livestock into smaller patches of habitat less preferred by roe deer and lynx. The best solution might be to graze sheep in electric fence enclosures or, when possible, on grazing areas above tree-line that lynx seldom frequent (Odden et al. 2008).

ACKNOWLEDGEMENTS

LITERATURE CITED

Andersen, R., J. Odden, J. D. C. Linnell, M. Odden, I. Herfindal, M. Panzacchi, Ø. Høgseth,
    L. Gangås, H. Brøseth, E. J. Solberg, and O. Hjeljord. 2005. Gaupe og rådyr i Sørøst-
    Norge. Oversikt over gjennomførte aktiviteter 1995–2004. NINA Rapport 29:43.

Boscagli, G. 1985. Il lupo. Lorenzini, Udine.

Ennos, R. 2007. Statistical and Data Handling Skills in Biology. Second edition. Pearson
    Education Limited, Harlow, England.

Grosjean, D. 1992. The impact of lynx on livestock. The Situation, Conservation Needs and
    Reintroduction of the Lynx in Europe, 17–19 oct. 1990. Neuchatel Fac. Des letters,
    Council of Europe, Strasbourge, France. Environmental Encounters 11:69–73.

Gula, R. 2008. Wolf Depredation on Domestic Animals in the Polish Carpathian Mountains.
    Journal of Wildlife Management 72(1):283–289.

Hansen, I. 2007. Tapsårsaker hos lam i Ørpen-Redalen beiteområde, Krødsherad 2007.
    Bioforsk Rapport 2(165):28.

Hoel, P. A., and R. Hermansen. 2008. Winter distribution of cervids and mountain hare in
    relation to topography and snow depth. M.SC. thesis, Telemark University College,
    Norway.

Linnell, J. D. C., M. E. Smith, J. Odden, P. Kaczensky, and J. E Swenson. 1996. Carnivores
    and sheep farming in Norway. 4. Strategies for the reduction of carnivore livestock
    conflicts: a review. NINA Oppdragsmelding 443:1–108.

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

MacArthur, R. H., and E. R. Pianka. 1996. On optimal use of patchy environment. American
    Naturalist 100:603–609.

MacCracken, J.G., and R. M. Hansen. 1987. Coyote feeding strategies in southeastern Idoha: Optimal foraging by an opportunistic predator? Journal of Wildlife Management 51:278–285.

Mech, L. D., S. H. Fritts, and W. J. Paul. 1988. Relationship between winter severity and wolf depredation on domestic animals in Minnesota. Wildlife Society Bulletin, 16:269–272.

Mereggi, A., A. Brangi, C. Matteucci, and O. Sacchi. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. Ecography 19:287–295.

Meriggi, A., and S. Lovari. 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? Journal of Applied Ecology 33:1561–1571.

Moa, P. F., I. Herfindal, J. D. C. Linnell, K. Overskaug, T. Kvam, and R. Andersen. 2006. Does the spatiotemporal distribution of livestock influence forage patch selection in Eurasian lynx? Wildlife Biology 12:63–70.

Mysterud, A. 1999. Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. Journal of Zoology, London 247:479–486.

Mysterud, A., P.K. Larsen, R.A. Ims, and E. Østbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can. J. Zool. 77:776–783.

Norwegian Directorate for Nature Management. 2007. Homepage at http://www.dirnat.no. Accessed 15 Feb 2008.

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(1):276–282.

Odden, J., J. D. C. Linnell, P. F. Moa, I. Herfindal, T. Kvam, and R. Andersen. 2002. Lynx predation on domestic sheep in Norway. Journal of Wildlife Management 66:98–105.

Odden, J., J. D. C. Linnell, and R. Andersen. 2006. Diet of Eurasian lynx, *Lynx lynx*, in the

    boreal forest of south–eastern Norway: the relative importance of livestock and hares at

    low roe deer density. European Journal of Wildlife Research 52:237–244.

Sacks, B. N., and J. C C. Neale. 2002. Foraging strategy of a generalist predator toward a

    special prey: coyote predation on sheep. Ecological Applications 12:299–306.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. - In:

    Gittelman, J.L. (Ed.); Carnivore behaviour, Ecology, and Evolution. Cornell University

    Press, New York, 164–182.

Stahl, P., J. M. Vandel, V. Herrenschmidt, and P. Migot. 2001. Predation on livestock by an

    expanding reintroduced lynx population: long term trend and spatial variability. Journal

    of Applied Ecology 38:674–687.

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.

Sunde, P., T. Kvam, J. P. Bolstad, and M. Bronndal. 2000. Foraging of lynx in a managed

    boreal-alpine environment. Ecography 23:291–298.

Tassi, F. 1976. La reintroduzione degli ungulati nell`Appennino Centrale. Camerino and

    Roma. SOS Fauna: animali in pericolo di estinzione:557–601.

The Norwegian Forest and Landscape Institute. 2008. Home page at

http://www.skogoglandskap.no

FIGURE CAPTIONS

Figure 1. The study area (5,072 km^2) in south-east Norway (small map) where data on lamb loss was collected.

Figure 2. Regression (Y = 0.322 + (0.012 × 3.233) of the proportion of lambs lost on roe deer density in 13 grazing regions in the Hallingdalen valley, south-east Norway, 2005–2007.
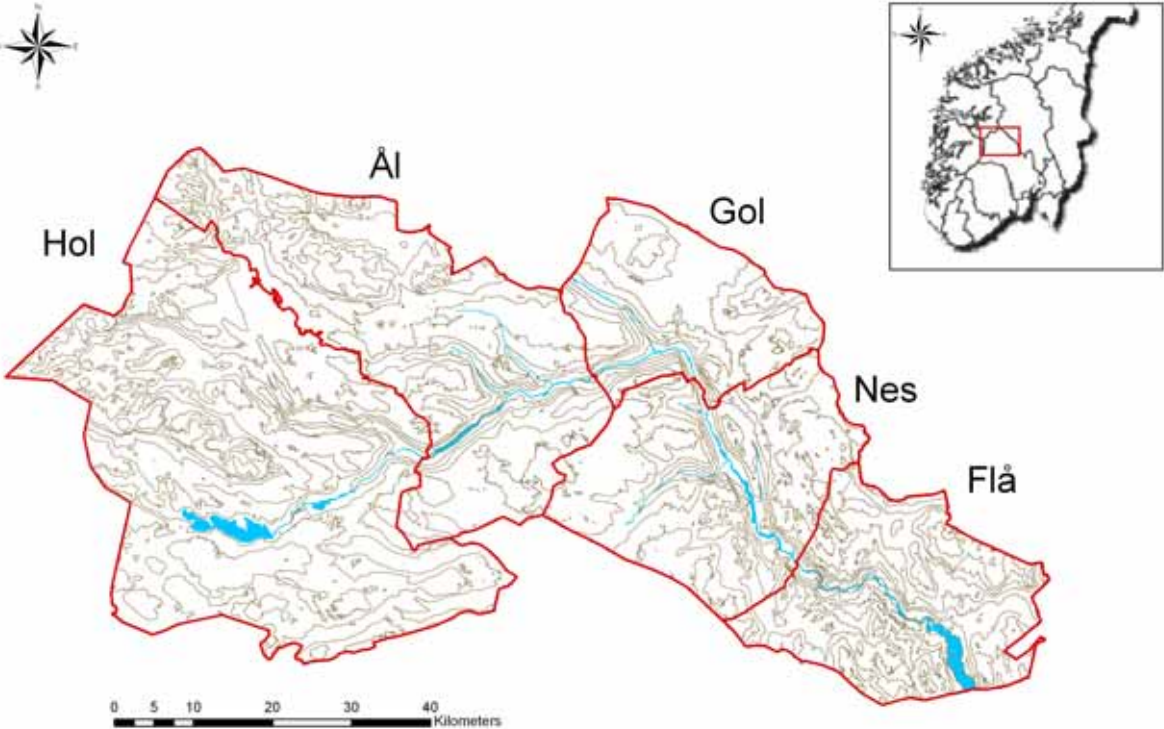
Figure 1

Figure 2