

The effect of domestic sheep on forage plants of wild reindeer; a landscape scale experiment

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Abstract Domestic herbivores often compete with wildlife for limited resources, and on longer time-scales, grazing may also increase or decrease coverage of important food plants to wildlife affecting the threshold density for when competition can be expected. In Norway, there are growing concerns about the effect of releasing 2.1 million domestic sheep (*Ovis aries*) for summer grazing into areas hosting wild populations of alpine reindeer (*Rangifer tarandus*). We quantified the effect of sheep grazing (0, 25 and 80 sheep/km²) on the development in coverage and abundance of plants known to be important in the diet of reindeer during summer (vascular plants) and winter (lichens) within a fully replicated, landscape scale (2.7 km²) experiment. From 2001 to 2005, the sedge, *Carex bigelowii*, increased while the herb *Solidago virgaurea* decreased in frequency at high density of sheep relative to controls (both marginally non-significant). There was no marked development in *Deschampsia flexuosa*, *Salix herbacea* or *Hieracium alpinum* that could be related to sheep grazing intensity. Lichen coverage and height both decreased at high density of sheep from 2002 to 2005. Effects of low grazing intensity were closer to controls than to high grazing intensity. Our study highlights that high sheep grazing intensity induce

changes to the plant community that, at the same time, can improve the summer habitat and detriment the winter habitat to reindeer. Many wild reindeer populations are fragmented and may thus be limited by either summer or winter range. The effect of sheep grazing is predicted to vary accordingly. However, currently, we have limited ability to quantify how much this explicitly means in terms of increased or reduced carrying capacity for reindeer.

Keywords Domestic-wildlife conflict · Ecosystem function · Grazing facilitation · Inter-specific competition · Lichens

Introduction

Among large herbivores, exploitation competition is regarded as the most important mechanism of interaction (Bell 1971; Illius and Gordon 1992; Murray and Illius 2000). Competition arises when sympatric herbivores overlap in diet within the same habitats, and when the shared resources are in limited supply (reviews in Putman 1996; Latham 1999). Domestic herbivores are helped through the winter season, and often stocked at high densities during summer, increasing the likelihood of competition with wildlife (Oesterheld et al. 1992). For example, cattle grazing increased home range size (Loft et al. 1993), changed habitat selection (Kie et al. 1991; Loft et al. 1991) and reduced predator cover (Loft et al. 1987) for mule deer (*Odocoileus hemionus*), suggesting competition between the two species. These are immediate responses. On longer time-scales, herbivores also may have an impact on their own food resources (reviews in Jefferies et al. 1994; Hobbs 1996; Augustine and McNaughton 1998). Therefore, if grazing increases or decreases biomass

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of important food plants in the long-term, this may, in the long-term, either decrease or increase the likelihood of competition at given density levels, but few studies have explicitly addressed this from an animal-competition perspective.

In Norway, there are currently 26 populations of wild alpine reindeer (*Rangifer tarandus*) (Bråtå 2003; Andersen and Hustad 2005). There are growing concerns regarding their long-term persistence due to a number of anthropogenic influences and fragmentation of winter and summer grazing areas (e.g., Vistnes et al. 2001). In this study, we address the potential role of releasing 2.1 million domestic sheep (*Ovis aries*) into outlying Norwegian pastures every year for summer grazing. The alpine zone constitutes 50% of the land area of Norway, and most sheep graze in the alpine areas that are also prime reindeer habitat. It is well known from many areas of the world that sheep grazing may affect coverage of vascular plants (Bowns and Bagley 1986; Miller et al. 1999; Cingolani et al. 2005; Austrheim et al. 2007), but empirical studies addressing the specific role of sheep grazing for reindeer-feeding plants have never been performed. Dietary overlap is fairly high between sheep and reindeer (Skogland 1984; Mysterud 2000). A rather unique feature of reindeer is the extensive use of lichens for winter forage (Gaare and Skogland 1975). Indeed, by far, the largest reindeer population in Norway on Hardangervidda is managed based on lichen as a limiting resource. Sheep do not eat lichens, but lichen heaths are a selected vegetation type for resting (Kausrud et al. 2006). It has therefore been suggested that sheep trampling during dry weather may severely reduce lichen coverage (Holand et al. 1999), but this has never been quantified.

We here, as part of a fully replicated, landscape scale (2.7 km²) experiment assessing ecosystem impact of sheep, determine the causal relationship between three levels of domestic sheep densities (none, low and high density) and the development in coverage and abundance of plants known to be important in the diet of reindeer during summer (vascular plants) and winter (lichens).

Materials and methods

Study area

The study area is located in Hol municipality, Buskerud county in the southern part of Norway (between 7°55'–8°00' and 60°40'–60°45') in the mountains near the lake Strandavatnet (Mysterud and Austrheim 2005). Hol has a sub-continental alpine climate with moderate to low annual precipitation (7–800 mm, Førland 1993). The bedrock consists of metaarkose (Sigmond 1998). The soil is

moderately base-rich, especially in landscape depressions with seepage water. The lower part of the study site is in the lower alpine zone close to the forest line, with only a few scattered birch (*Betula pubescens*) trees in the lowest areas. The area just barely extends into the middle alpine zone characterised by a displacement of the dwarf-shrub *Vaccinium myrtillus* (Moen 1998). Vegetation is dominated by low shrubs interspersed with grass-dominated meadows (Rekdal 2001). The area is rich in vascular plant species, a total of 104 species were recorded in 180 plots (each of 0.25 m²) and herbs dominate (53%; see section “Vascular plant coverage” below for how this was quantified; Austrheim et al. 2005). Total standing crop for dwarf shrubs and grassland communities was 207.6 and 100.2 g/m² dry weight, respectively. Dwarf shrub communities are dominated by woody species (85%) such as *V. myrtillus*, *Empetrum nigrum* and *Phyllodoce caerulea*, while graminoids (6%), bryophytes and lichens (8%) and herbs (1%) are rarer. Annual production of graminoids and herbs are 13.1 and 1.3 g/m² respectively. Grasslands are dominated by graminoids (47%) such as *Carex bigelowii* and *Deschampsia flexuosa*, woody species (31%), herbs (12%) and bryophytes and lichens (9%). Annual production of graminoids and herbs are 47.3 and 12.1 g/m², respectively.

Before the study was initiated, there was a very low grazing pressure by domestic sheep (<10 sheep per km²) in the area. Moose (*Alces alces*) have been observed to occasionally enter the area while foraging at night.

Hol municipality is part of the Nordfjella reindeer management area, forming the northern extension of the Hardangervidda plateau, which is the largest reindeer area in Norway (Andersen and Hustad 2005). The study area is known historically to be visited by individual or small herds of wild reindeer in spring. However, there was only one observation of reindeer during the entire study period, suggesting that the flocks were favouring other areas at this time. Common to both Hardangervidda and Nordfjella (as well as several other regions) is that lichen heaths are considered a limiting resource and what the management uses for setting hunting quotas (Gaare and Hansson 1989; Andersen and Hustad 2005).

Experimental design

This study is part of a project working broadly with ecosystem impact of domestic sheep grazing (Steen et al. 2005; Mysterud et al. 2005; Evju et al. 2006; Loe et al. 2007). In the summer of 2001, we established a large enclosure covering 2.7 km² and with a total of 17.3 km of standard sheep fencing (110 cm high). We split the large enclosure into nine compartments, hereafter referred to as sub-enclosures. Each sub-enclosure was constructed to span a similar altitudinal range, extending from 1050 m to

1300 m a.s.l. (Myrsterud et al. 2007). The distribution of main habitat types used by sheep was also similar among the sub-enclosures (Rekdal 2001). Average size of the sub-enclosures was 0.3 km², but some variation was unavoidable due to practical difficulties in putting up fencing in areas with bare rock visible.

We used a block-wise randomization design with three blocks (i.e., three replicates). For each of the three adjacent sub-enclosures, we randomly assigned the treatments “control” (no sheep), low and high density of sheep. As “low density”, we used 25 sheep per km², while what we refer to as “high density” is 80 sheep per km². These levels were chosen after a grazing ecologist had mapped the vegetation of the area in 2001 and assessed its grazing value for sheep (Rekdal 2001). We calculated density relative to area of grazeable habitat, and thus excluded water bodies and some other habitats dominated by mosses, lichens, bedrock and stones with little or no forage (Myrsterud and Austrheim 2005). A review of studies from North America concluded that a low grazing pressure corresponded to an average utilization of individual plants of 32% of the most important forage plants, moderate grazing corresponded to 43% and heavy grazing corresponded to 57% (Holechek et al. 1999). Based on frequency of herbs eaten, the low density and high density corresponds to low and moderate grazing pressures (Evju et al. 2006). Our density levels span the most typical densities of sheep on alpine pastures in Norway today. Grazing pressures in Norway are typically less intensive than, for instance, in Scotland (Simpson et al. 1998, see discussion in Loe et al. 2007).

All sheep were of the “Kvit norsk sau” breed, the most common breed in Norway (Myrsterud and Austrheim 2005). Ewes averaged 83 kg in live weight (spring) and lambs averaged 19 kg in spring and 42 kg in autumn. The experiment was run for four full grazing seasons (2002–2005). The grazing season was from the last week of June through the last week of August or first week of September and similar to the season for free ranging sheep in mountain regions in southern Norway (Myrsterud and Austrheim 2005). A detailed account of sheep diet, space and habitat use is presented elsewhere (Kausrud et al. 2006; Myrsterud et al. 2007).

Vascular plant coverage

In 2001 (summer before the experiment started), the frequency of vascular plants were sampled within 180 plots (each 0.25 m²), with 20 plots in each of the nine sub-enclosures (Austrheim et al. 2005). We reanalysed the plots in 2005. Plots were randomly chosen with a balanced stratified distribution among habitats and altitudinal levels. Each plot was marked physically at each corner to ensure

Table 1 An overview of raw data (as %) per replicate, i.e. the nine sub-enclosures (A–I), for the three treatments no, low and high density of sheep on alpine ranges in the Nordfjella reindeer area, Norway

| Sub-enclosure | Year | Low density of sheep (25/km ²) | | | | | | | | | High density of sheep (80/km ²) | | | | | | | | |
|---------------------------------|------|--|-------|-------|-------------|-------|-------|-------|-------------|-------|---|-------|-------------|--|--|--|--|--|--|
| | | A | E | G | Mean(SE) | C | D | I | Mean(SE) | B | F | H | Mean(SE) | | | | | | |
| <i>Carex bigelowii</i> (%) | 2001 | 28.13 | 8.14 | 13.76 | 16.67(4.12) | 16.26 | 16.88 | 10.32 | 14.48(3.76) | 15.63 | 7.20 | 18.76 | 13.86(4.05) | | | | | | |
| | 2005 | 25.63 | 6.57 | 13.13 | 15.11(3.88) | 15.64 | 17.82 | 9.07 | 14.17(3.68) | 15.95 | 11.8 | 21.57 | 16.46(4.30) | | | | | | |
| <i>Deschampsia flexuosa</i> (%) | 2001 | 43.14 | 60.34 | 68.15 | 57.21(5.08) | 53.77 | 71.59 | 65.95 | 63.77(4.67) | 64.70 | 67.22 | 58.15 | 63.35(5.02) | | | | | | |
| | 2005 | 51.88 | 57.19 | 66.25 | 58.44(5.21) | 62.19 | 76.25 | 70.31 | 69.58(4.47) | 68.13 | 65.00 | 60.94 | 64.69(5.05) | | | | | | |
| <i>Solidago virgaurea</i> (%) | 2001 | 1.57 | 3.76 | 4.39 | 3.24(1.09) | 1.26 | 2.20 | 6.26 | 21.88(4.47) | 5.63 | 4.08 | 5.63 | 32.61(5.73) | | | | | | |
| | 2005 | 3.13 | 4.38 | 5.95 | 4.49(1.38) | 1.57 | 2.20 | 5.64 | 23.55(4.75) | 3.76 | 2.83 | 6.57 | 32.71(5.67) | | | | | | |
| <i>Hieracium alpinum</i> (%) | 2001 | 12.51 | 5.63 | 2.20 | 6.78(1.99) | 2.20 | 5.64 | 4.07 | 3.97(1.33) | 4.69 | 1.57 | 3.13 | 3.13(0.90) | | | | | | |
| | 2005 | 5.00 | 8.45 | 2.51 | 5.32(1.56) | 3.13 | 4.69 | 3.44 | 3.75(1.29) | 3.14 | 0.63 | 3.45 | 2.40(0.76) | | | | | | |
| <i>Salix herbacea</i> (%) | 2001 | 41.88 | 20.95 | 33.76 | 32.20(5.20) | 25.33 | 19.70 | 20.63 | 3.24(1.24) | 37.20 | 22.51 | 38.13 | 5.11(1.35) | | | | | | |
| | 2005 | 43.76 | 20.64 | 37.83 | 34.07(5.29) | 27.20 | 20.02 | 23.44 | 3.13(1.16) | 36.26 | 23.44 | 38.44 | 4.38(1.30) | | | | | | |
| Lichen coverage (%) | 2002 | 70.00 | 67.00 | 69.00 | 68.67(1.53) | 61.00 | 70.00 | 68.00 | 66.33(1.79) | 59.00 | 66.50 | 71.50 | 65.67(1.82) | | | | | | |
| | 2005 | 75.00 | 70.00 | 68.50 | 71.17(1.45) | 65.50 | 68.00 | 72.00 | 68.50(1.66) | 59.00 | 57.50 | 69.50 | 62.00(2.24) | | | | | | |
| Lichen height (cm) | 2002 | 3.55 | 3.55 | 4.05 | 3.72(0.12) | 3.10 | 2.95 | 3.75 | 3.27(0.13) | 3.50 | 3.20 | 3.45 | 3.38(0.11) | | | | | | |
| | 2005 | 4.10 | 3.80 | 4.25 | 4.05(0.13) | 4.00 | 2.90 | 3.70 | 3.53(0.14) | 3.50 | 2.85 | 3.25 | 3.20(0.11) | | | | | | |

Note that it is the change from 2001/02 until 2005 that is the pattern of interest, as the treatment was initiated in 2002

that the exact same location was found for consecutive samples. Quadrats with more than 10% cover of bedrock and stones combined were excluded. Plant species abundance in each plot is based on presence–absence within 16 subplots (0.0156 m²); thus the percentage coverage of a given species is 0% if not found in any of the 16 subplots and 100% if found in all 16 subplots.

There are remarkably few studies reporting diet of reindeer in Norway. The only study we are aware of is from Hardangervidda and is based on esophageal fistula and rumen samples (Gaare and Skogland 1975; Skogland 1980). Based on this and what is available in our study area (Austrheim et al. 2005), we identified important plant species or groups of summer forage to reindeer. The quantitatively most important and often also selected are the graminoids *D. flexuosa* and *C. bigelowii* followed by *Salix herbacea* (Skogland 1980: p. 89). Herbs make up a smaller proportion of the diet. However, since herbs are less tolerant to sheep grazing (Bowns and Bagley 1986), we also included two fairly common and selected herbs, *Hieracium alpinum* and *Solidago virgaurea*, to obtain a comparison with the more grazing tolerant sedges. A much wider description of both bryophyte and vascular plant diversity responses to sheep grazing irrespective of functional role to reindeer is presented elsewhere (Austrheim et al. in prep.). Nomenclature for vascular plants follows Lid and Lid (1994).

Lichen coverage

Within each of the nine sub-enclosures, one transect, 20 m long, was established at high (~1200 m a.s.l.) and low (~1100 m a.s.l.) altitude. The closest lichen heath to the specific altitude was chosen, all being a minimum of 30 m from fences. Within each transect, we randomly placed five squares (each 0.25 m²). Squares with less than 50% of lichen cover were rejected and we repeated randomization until five squares fitted these restrictions. We measured lichen height and cover based on four measurements at each square and noted the dominant species. Only fruticose and foliose lichens were included; i.e. crustose lichens were not considered. All plots were first analysed on the first week of August 2002 and reanalysed on mid-August in 2005, i.e. so that three full years of trampling was done. All transects were marked with sticks and all plots started at the exact same distance from the stick in both years. Cladonia lichens are the most used group of wild reindeer (Gaare and Skogland 1975). Nomenclature for lichens follows Holien and Tønsberg (2006).

Statistical analyses

As we have a fully replicated experiment, we used design-based inference. For vascular plants, response variable was

$\log(\text{frequency}_{\text{year}2005+1}/\text{frequency}_{\text{year}2001+1})$ at the plot level, i.e. change in frequency from 2001 to 2005. As a predictor, we only entered the treatment effect. We used linear mixed effects models (LME) with a random effect that reflected the block-wise randomization design, i.e. sub-enclosure ($n=9$) nested within block ($n=3$). For lichen coverage (arcsinsqrt transformed) and height, we entered also “year” and the interaction term “year×treatment”, the latter being the factor of interest. As a random term, we

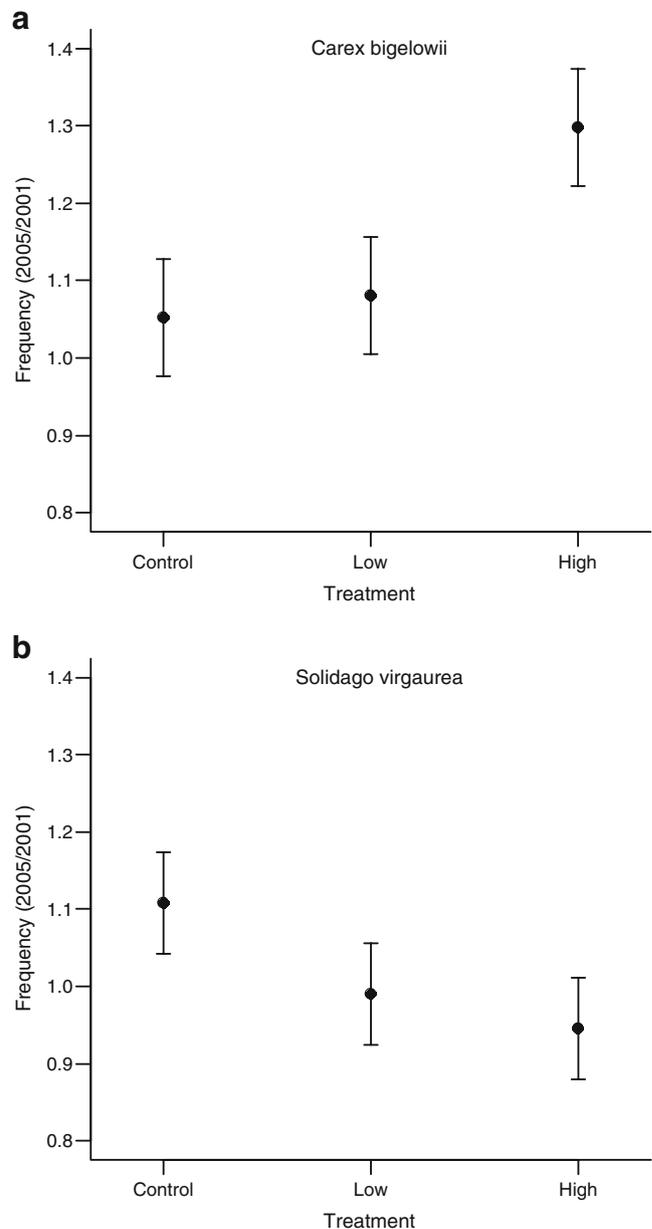


Fig. 1 The estimated (\pm SE) change in frequency of two forage plants important to reindeer during summer, **a** the sedge *C. bigelowii* and **b** the herb *S. virgaurea* from year 2001 to 2005 under different experimental sheep grazing regimes; *control* (no sheep), *low density* (25 sheep/km²) and *high density* (80 sheep/km²) of sheep on alpine pastures in Hol, Norway. A value of 1 indicates a stable population. Values are predictions from an ordinary linear model

Table 2 The development of the frequency of plants common in the summer diet of reindeer in Hol, Norway from 2001 to 2005 under three levels of sheep grazing intensity (high, low and control)

| Parameter | Estimate | SE | df | t | P (LME) |
|--------------------------------------|----------|--------|-----|--------|------------|
| <i>Carex bigelowii</i> | | | | | |
| Intercept | -0.0361 | 0.0395 | 171 | -0.916 | 0.361 |
| Treatment (high density vs. control) | 0.150 | 0.0557 | 4 | 2.687 | 0.055 |
| Treatment (low density vs. control) | 0.0334 | 0.0557 | 4 | 0.600 | 0.581 |
| <i>Deschampsia flexuosa</i> | | | | | |
| Intercept | 0.0159 | 0.0607 | 171 | 0.261 | 0.794 |
| Treatment (high density vs. control) | 0.0082 | 0.0730 | 4 | 0.112 | 0.916 |
| Treatment (low density vs. control) | 0.121 | 0.0730 | 4 | 1.656 | 0.173 |
| <i>Solidago virgaurea</i> | | | | | |
| Intercept | 0.0685 | 0.0322 | 171 | 2.129 | 0.035 |
| Treatment (high density vs. control) | -0.1197 | 0.0455 | 4 | -2.631 | 0.058 |
| Treatment (low density vs. control) | -0.0731 | 0.0455 | 4 | -1.608 | 0.183 |
| <i>Hierarcium alpinum</i> | | | | | |
| Intercept | -0.0688 | 0.0768 | 171 | -0.896 | 0.372 |
| Treatment (high density vs. control) | 0.0268 | 0.1086 | 4 | 0.247 | 0.817 |
| Treatment (low density vs. control) | 0.0393 | 0.1086 | 4 | 0.362 | 0.736 |
| <i>Salix herbacea</i> | | | | | |
| Intercept | 0.0481 | 0.0307 | 171 | 1.564 | 0.120 |
| Treatment (high density vs. control) | -0.0494 | 0.0432 | 4 | -1.143 | 0.317 |
| Treatment (low density vs. control) | -0.0263 | 0.0432 | 4 | -0.609 | 0.575 |

Data derive from a block-wise randomization experiment and estimates are from linear mixed effects models (LME) reflecting this design; random effect is sub-enclosure (n=9) nested within block (n=3)

used “transect” nested within “sub-enclosure” nested within “block”. For figures, we used predicted values from linear models (LM), due to the difficulty of obtaining SE with LME. Analyses were done in S-Plus vs. 6.2 (Crawley 2002). We always report differences between levels with “Treatment” contrasts enabling easier interpretation of estimated effect. In our case we compared “the high density treatment to the

control treatment” and “the low density treatment to the control treatment” (so the estimate is how much the high/low density treatment differ from the control treatment).

Results

An overview of the raw data is given in Table 1. The sedge *C. bigelowii* increased and the herb *S. virgaurea* decreased

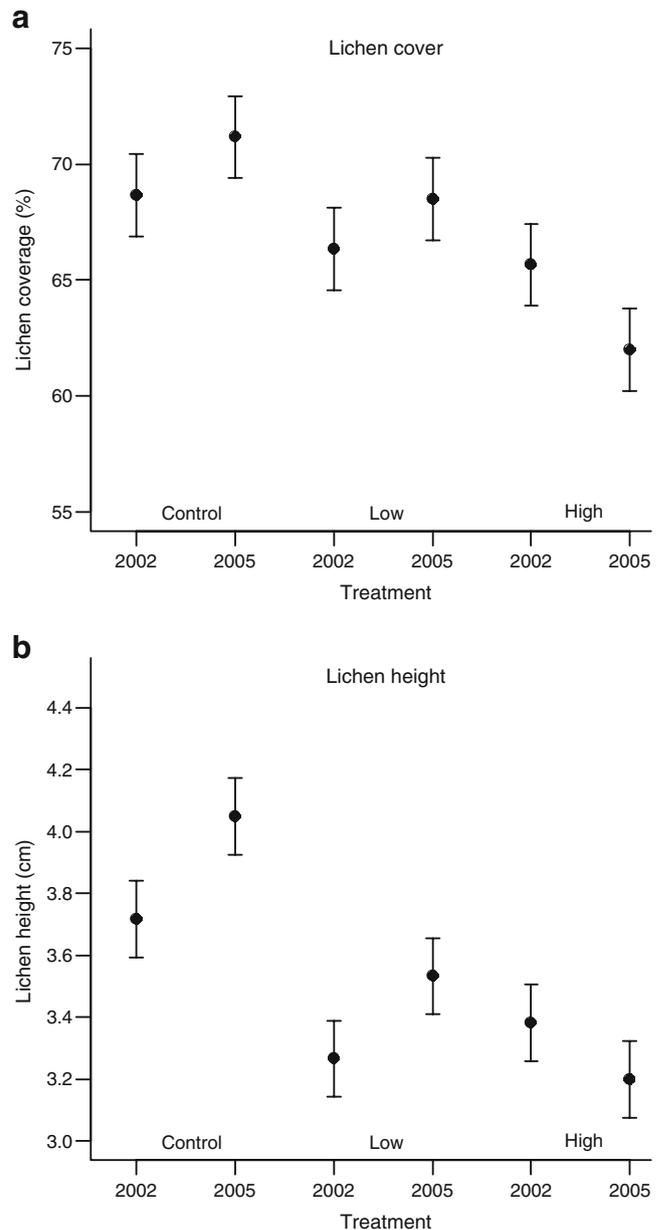


Fig. 2 The change in **a** coverage and **b** height of lichens, which are important to reindeer during winter, from year 2002 to 2005 under different experimental sheep grazing regimes; control (no sheep), low density (25 sheep/km²) and high density (80 sheep/km²) of sheep on alpine pastures in Hol, Norway. Values are predictions from an ordinary linear model

in frequency (both marginally non-significant) from 2001 to 2005 at high density of sheep relative to controls, while there was no difference between low density of sheep and controls without sheep (Fig. 1, Table 2). There was no marked development in *D. flexuosa*, *S. herbacea* or *H. alpinum* that could be related to sheep grazing intensity. *Cetraria nivalis* dominated 60% of the plots, while *Cladonia arbuscula* were dominant in 13%. Lichen coverage and height both decreased at high density of sheep from 2002 to 2005 (Fig. 2, Table 3), while the pattern over time was opposite for areas used as controls or with a low density of sheep.

Discussion

We have performed the first fully experimental evaluation of sheep grazing effects on reindeer summer and winter forage plants. There was a negative impact of high sheep density likely due to trampling on lichen height and coverage, although the estimated effect was small for the time period considered (Fig. 2). Also, effects of sheep grazing on vascular plants were evident. The sedge *C. bigelowii* increased in frequency, while the herb *S. virgaurea* declined in frequency over 4 years of high level of sheep grazing. Thus, favoured grazing plants of reindeer during summer may both decrease and increase in abundance due to sheep grazing, though those most likely quantitatively important increased. Indeed, high grazing pressure both by semi-domestic reindeer (Bråthen et al. 2007) and sheep (Bowns and Bagley 1986) reduce the amount of preferred herbs while the relative proportions of graminoids (more bulk food; Kausrud et al. 2006) increase.

Sheep grazing nevertheless contributes to the maintenance of graminoid and herb dominated vegetation (i.e., grasslands), a habitat currently decreasing in Scandinavia due to progressed forest succession in subalpine and low alpine environment with decreased land use impact and possibly rise in temperature (Linkowski and Lennartsson 2005).

Effect on summer forage

Skogland (1984) noted regarding sheep and reindeer that “a moderately heavy, interspecific, grazing pressure maintains a higher production of vascular plant leaf-tissue in a successional stage that is beneficial to both species”. We here provide experimental evidence for another potentially positive effect to reindeer, that the sedge, *C. bigelowii*, increased in frequency with a high density of sheep, being only moderately used by sheep (*Carex* spp. averages 9.0% in diet; Kausrud et al. 2006). *Deschampsia caespitosa* and *D. flexuosa* are selected by reindeer during summer and together with *Carex* spp., make up a large proportion of the diet during summer (Gaare and Skogland 1975). We found here no effect of sheep grazing on abundance of *D. flexuosa*, despite this being the quantitatively most important food to sheep (averaging 33.7% of their diet, Kausrud et al. 2006). In a nutrient-poor alpine ecosystem, the Setesdal Vesthei, a smaller enclosure experiment documented that *D. flexuosa* was clearly reduced due to sheep grazing (Austrheim et al. 2007). It is well known that impact of the same grazer may vary between ecosystems depending on nutritional resource levels in soil (Bjor and Graffer 1963; Proulx and Mazumder 1998), so this positive effect of sheep on sedges may be ecosystem-dependent. Also, the herbs (in our case *S. virgaurea*) may decrease in

Table 3 The development of the coverage and height of lichens, a key component the winter diet of reindeer, in Hol, Norway from 2001 to 2005 under three levels of sheep grazing intensity (high, low and control)

| Parameter | Estimate | SE | df | t | P (LME) |
|---|----------|--------|-----|--------|---------|
| A. Lichen coverage | | | | | |
| Intercept | 0.9799 | 0.0291 | 159 | 33.640 | <0.001 |
| Treatment (high density vs. control) | -0.0316 | 0.0412 | 4 | -0.767 | 0.486 |
| Treatment (low density vs. control) | -0.0235 | 0.0412 | 4 | -0.571 | 0.598 |
| Year (2005 vs. 2002) | 0.0281 | 0.0233 | 159 | 1.207 | 0.229 |
| Treatment (high density vs. control)×Year (2005 vs. 2002) | -0.0662 | 0.0329 | 159 | -2.014 | 0.046 |
| Treatment (low density vs. control)×Year (2005 vs. 2002) | -0.0053 | 0.0329 | 159 | -0.160 | 0.873 |
| B. Lichen height | | | | | |
| Intercept | 3.7167 | 0.2212 | 159 | 16.802 | <0.001 |
| Treatment (high density vs. control) | -0.3333 | 0.2510 | 4 | -1.328 | 0.255 |
| Treatment (low density vs. control) | -0.4500 | 0.2510 | 4 | -1.793 | 0.148 |
| Year (2005 vs. 2002) | 0.3333 | 0.1441 | 159 | 2.313 | 0.022 |
| Treatment (high density vs. control)×Year (2005 vs. 2002) | -0.5167 | 0.2038 | 159 | -2.535 | 0.012 |
| Treatment (low density vs. control)×Year (2005 vs. 2002) | -0.0667 | 0.2038 | 159 | -0.327 | 0.744 |

Data derived from a block-wise randomization experiment and estimates are from linear mixed effects models (LME) reflecting this design; random effect is transect line ($n=18$) nested within sub-enclosure ($n=9$) nested within block ($n=3$)

availability due to sheep grazing, potentially negatively impacting reindeer. Indeed, flowering by herbs was much reduced even at low sheep density (Evju et al. 2006). *S. herbacea* seem more important to reindeer than sheep. Average use in our area is <2%, while other *Salix* spp. average 14.8% (Kausrud et al. 2006). However, in another study of sheep in Central-Norway, *S. herbacea* was found to be an important forage for sheep (Skarpe et al. 2005). We thus cannot exclude a larger effect on *S. herbacea* in other areas.

Effect on winter forage

Lichens constitute <1% of the sheep diet in the study area, while sheep used 9.6% of the resting time and 4.6% of the grazing time in lichen heaths (Kausrud et al. 2006). The effect of sheep on lichen is therefore due to trampling effects. It is well known that trampling can be a factor affecting the ecosystem (Cumming and Cumming 2003; Hobbs and Searle 2005). There was indeed a measurable effect of sheep trampling on lichen coverage and height over only 3 years of trampling. The estimated effect was rather small (Fig. 2). Note, however, that there was an increase in lichen in controls and at low sheep density, likely due to succession after a history of heavy reindeer grazing in the 1980s (Gaare 1986). Due to the relatively short duration of our study (3 years), an important question is whether these trampling effects are just a start and will continue, or if they are likely to level out? The latter is likely if the same paths are used also in the future. The trampling effects could be easily spotted mainly as specific trails either towards resting sites, salt licks (one in each sub-enclosure) or just passing over this habitat. The long-term effects remain to be quantified. The more important vegetation types to sheep are meadows that, in our area, are used about three times more than expected from availability (Kausrud et al. 2006). The trampling effect on mosses in more selected vegetation types for sheep is likely more important for ecosystem function, as this may shift the competitive balance towards grasses and sedges (Jónsdóttir 1991; Austrheim et al. 2007).

Conclusion

Our study highlights that high sheep grazing intensity induce changes to the plant community that, at the same time, can improve the summer habitat and detriment the winter habitat to reindeer. Many wild reindeer populations are fragmented so that limitation may be either summer or winter range; i.e. high sheep densities could impose negative effects in regions where reindeer are limited by the availability of lichens, while the same sheep densities might positively affect summer grazing resources if this is the limitation in other areas. With the current knowledge, we

cannot say how much a specific percent reduction/increase in coverage of a certain forage plant means in terms of reduced/increased capacity for reindeer in specific numbers for a given mountain range. Indeed, we are unaware of any such studies on a cervid having such a level of detail. Clearly, this is a considerable challenge to be met in future research for plant–herbivore dynamics in general.

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