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## Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment

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**Abstract** Inter-specific competition, facilitation and predation influence herbivore assemblages, but no study has experimentally explored the interactions between large ungulates and small rodents. In a fully replicated, landscape scale experiment, we manipulated densities of domestic sheep in mountain pastures in Norway. We then determined population growth and densities of rodents by live trapping in each of the areas with different sheep densities. We found that the (summer) population growth rate and autumn density of the field vole (*Microtus agrestis*) was lower at high sheep density. This provides the first experimental evidence of negative interactions between an ungulate and small rodent species. There was no effect on the bank vole (*Clethrionomys glareolus*), whose diet differs from sheep. Sheep density, therefore, potentially alters the pattern of inter-specific population synchrony amongst voles. Our study shows that negative interactions between large ungulates and small rodents may be species-specific and negative population consequences for the rodent population appear above threshold ungulate densities.

**Keywords** *Clethrionomys glareolus* · Competition · Facilitation · *Microtus agrestis* · *Ovis aries*

### Introduction

The influence of competition, facilitation and predation on inter-specific herbivore assemblages are difficult to ascertain, resulting in considerable controversy (McNaughton 1976; Sinclair and Norton-Griffiths 1982; Sinclair 1985; Duncan et al. 1990; Fritz et al. 2002). Inter-specific competition arises whenever one species reduces shared food resources below the level that can be exploited efficiently by another species (Bell 1971; Illius and Gordon 1987; Tokeshi 1999; Murray and Illius 2000). However, by reducing plant biomass, one species may also benefit another by facilitating access to forage of a suitable height or quality (Bell 1971; McNaughton 1976; Gordon 1988; McNaughton et al. 1997), or the quality of eventual re-growth may be higher (Alpe et al. 1999; Arsenault and Owen-Smith 2002).

Most studies have explored such processes related to interactions among either ungulate (e.g., Sinclair and Norton-Griffiths 1982; Sinclair 1985) or rodent (e.g., Brown et al. 1994; Garb et al. 2000) species respectively. Few have investigated interactions between large ungulates and small herbivorous rodents. Ungulate grazing likely affects rodent populations by the same mechanisms existing between large herbivores or between different rodent species; i.e., competition, facilitation and predation. If competition is important, rodent population growth should decrease with increasing ungulate densities, given habitat and diet overlap, and given that the shared resources are in limited supply (Tokeshi 1999). Interference competition between ungulates and rodents are unlikely, while exploitation competition is likely, and more likely with increasing diet and habitat overlap. Facilitative or positive interactions are encounters between organisms that benefit at least one of the participants and do not cause harm to either (Bruno et al. 2003). Several mechanisms can account for

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this in grazing ecosystems. A recent review concludes that evidence for facilitation through stimulation of grass re-growth during the growing season appears stronger than that for increased resource access through removal of obstructing plant structures during the dormant season (Arsenault and Owen-Smith 2002, see also Gordon 1988). If plant quality/quantity increases, rodent population growth rate and density may increase with increasing ungulate density.

Scattered observational evidence in the literature from salt deserts to high arctic ecosystems report both increases (Jones and Longland 1999; Keesing and Crawford 2001) and decreases in the activity or abundance of rodents when subject to ungulate grazing (Jones and Longland 1999; Weickert et al. 2001). In some instances, respective increases or decreases depended on the habitat type (Hanley and Page 1980; Hewson 1982) or rodent species involved (Hanley and Page 1980; Jones and Longland 1999). This suggests that several mechanisms are operating within such systems and that an experimental approach beyond a comparison of “grazed versus ungrazed” is needed to test these hypotheses. Indeed, no previous study has experimentally evaluated the effect of more than one level of an ungulate density on small rodent dynamics. Other studies touch on similar issues based solely on diet overlap (Johannessen and Samset 1994; Klein and Bay 1994), which is merely an assumption for competition (de Boer and Prins 1990; Tokeshi 1999).

In a fully replicated, landscape scale (2.7 km<sup>2</sup>) experiment, we explored the causal relationship between three levels of domestic sheep densities and the population growth and density of rodents derived from live trapping. We combine live trapping with a detailed evaluation of changes in habitat features such as plant height, plant coverage and changes in abundance of main forage plants for the sheep and rodent species present. In our area, the field vole (*Microtus agrestis*) is a common species feeding mainly on grass, forbs and herbs in meadow habitats (Hansson 1983; Henttonen and Hansson 1984), while bank vole (*Clethrionomys glareolus*) eat less grass and more bilberry in less productive and abundant habitat (Hansson 1983; Henttonen and Hansson 1984). Diet and habitat overlap with sheep is thus larger in the field vole than in the bank vole.

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## Materials and methods

### Experimental design

A large enclosure covering 2.7 km<sup>2</sup> and with a total of 17.3 km of standard sheep fencing (110 cm high) was established in the summer of 2001 in Hol municipality, Buskerud county in the southern part of Norway (between 7°55′–8°00′ and 60°40′–60°45′). 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) and the soil is

moderately base-rich, especially in landscape depressions with seepage water. The enclosure is situated between 1,050 m and 1,300 m a.s.l. in an alpine environment. The lower border is close to the forest line, located in the lower alpine zone and continues up into the middle alpine zone. There are only a few scattered birch (*Betula* sp.) trees in the lowest areas. Vegetation is dominated by low shrubs interspersed with grass-dominated meadows (Rekdal 2001). Prior to fencing, there was a very low grazing pressure by domestic sheep (< 10 sheep per km<sup>2</sup>) in the area, and only occasional visits by individual or small herds of wild reindeer (*Rangifer tarandus*) in spring. Moose (*Alces alces*) can occasionally enter the area while foraging at night.

The large enclosure was split into nine treatment enclosures, hereafter referred to as sub-enclosures, so that three full replicates could be run. Altitude is a main determinant of habitat in the mountains, so each sub-enclosure was constructed such that all had a similar altitudinal range. Average size of the sub-enclosures was 0.3 km<sup>2</sup>, but there were minor size variations due to practical difficulties in putting up fencing in areas with bare rock visible.

We used a block-wise randomisation design. For each of three adjacent sub-enclosures, we randomly assigned the treatments “control” (no sheep), low and high density of sheep. In 2001, a professional grazing ecologist (Yngve Rekdal, NIJOS) mapped the vegetation of the area and assessed its value for grazing by sheep (Rekdal 2001). Based on his recommendations, we used 25 sheep per km<sup>2</sup> as low density and 80 sheep per km<sup>2</sup> as high density. This covers most of the variation in densities of sheep grazing on mountain pastures in Norway. When calculating densities, we used density relative to area of grazeable habitat, and excluded water bodies and some other habitats dominated by mosses, rocks, lichens and bogs with little or no forage. The gross densities were slightly lower; the three low and high density sub-enclosures were 19, 19 and 21 and 56, 69 and 72 sheep per km<sup>2</sup>, respectively. The distribution of main habitat types used by sheep was similar among the sub-enclosures (Rekdal 2001). All sheep were of the “Kvit norsk sau” breed (often called “Dala breed”), the most common breed in Norway (Drabløs 1997). Ewes averaged 83 kg in live weight (spring) and lambs averaged 19 kg in spring and 42 kg in autumn (A. Mysterud, unpublished data). The experiment was run three full grazing seasons (2002–2004). 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.

### Trapping of voles and observations of predators

We used live trapping of voles with Ugglan traps baited with crushed oats and apple. All traps were checked daily. In each sub-enclosure, we had eight trap sites with four traps at each site, totalling 288 traps for the

experiment. At each trap site, the four traps were spaced 10 m to north, east, south and west from the centre of the site. As many trap sites were placed in “meadow” habitat (typical field vole and sheep habitat) as in drier, less productive “shrub” habitat (typical bank vole habitat). We also avoided areas close to edges between sub-enclosures. We restricted vole trapping to the lower half of the sub-enclosure, as rodents are expected to be more common here than in the higher altitudes where vegetation is sparse and short thus providing minimum cover. Just prior to release of our sheep in June, and immediately after collection of sheep in September 2002–2004, we trapped rodents during three “trap nights” (i.e., 864 trap nights). We determined the species and sex of all individuals, marked them (toe-clipping), and noted those that were previously marked. There was not enough data from root voles (*Microtus oeconomus*) nor lemmings (*Lemmus lemmus*) for analysis, although both are common rodent species in the Norwegian mountains. In 2002, 2003 and 2004, we trapped 0, 2 and 4 least weasels (*Mustela nivalis*) and 0, 2 and 2 stoats (*Mustela erminea*), respectively. We also observed successful nesting of short eared owl (*Asio flammeus*) in 2003. Therefore, specialist rodent predators were present in the area (cf. Ims and Andreassen 2000; Gilg et al. 2003). Raw data are presented in Table 1.

#### Plant data

In 2001 (before the experiment started) and 2003, the vascular plant community, coverage and plant height were sampled within 180 plots (20 in each of the 9 sub-enclosures), each measuring 0.25 m<sup>2</sup> (Austrheim et al. 2005). Plant height was measured as height of the

dominating strata within 5 cm intervals, as there was a marked height structure of the vegetation in this alpine habitat. The plots were randomly chosen with a balanced stratified distribution among habitats and altitudinal levels, and each plot was marked physically at each corner to ensure that the exact same location is 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 m<sup>2</sup>). We analysed abundance of the sedge *Carex bigelowii*, an important food source for field vole (Hansson 1983; Henttonen and Hansson 1984) and also abundant in the area (Austrheim et al. 2005). For the bank vole, we chose bilberry (*Vaccinium myrtillus*), also common in both the diet (Hansson 1983; Henttonen and Hansson 1984) and the study area (Austrheim et al. 2005). In addition, we chose the most common grass grazed by sheep (*Deschampsia flexuosa*, A. Mysterud, unpublished data) and two of the most frequent herbs (*Solidago virgaurea*, *Geranium sylvaticum*), both of which may be important herbivore forage. Based on faeces analyses (Stewart and Stewart 1970; Takatsuki 2003), the sheep's diet consisted of 1.8% bilberry and 9.3% *Carex* spp. (A. Mysterud, unpublished data). Diet overlap thus occurred between the sheep and both rodent species, but was likely higher for field vole than for bank vole. Sheep used all available habitats, but preferred meadows (A. Mysterud, unpublished data).

#### Statistical analyses

We analysed the rodent summer population growth rates and densities using linear models, and used model

**Table 1** Descriptive statistics for the plant and rodent data analysed in this study separated on treatment and sub-enclosure (replicate). Abundance of voles for 2002–2004 is based on live capture in spring (sp) and autumn (au). For the plant species, data are given as frequencies. Sheep densities include both ewes and lambs

Treatment		Control			Low density			High density		
Sub-enclosure		A	E	G	C	D	I	B	F	H
Density of sheep per km <sup>2</sup>		0	0	0	25	25	25	80	80	80
Vascular plant cover (%)	2003	66.5	70.5	67.5	66.5	67.5	69.5	56.0	59.4	62.0
Plant height (cm)	2003	8.5	12.8	9.0	10.8	10.5	11.5	9.8	12.2	9.9
<i>C. bigelowii</i>	2003	4.0	1.2	2.6	2.5	2.9	1.6	2.4	1.6	3.2
<i>D. flexuosa</i>	2003	11.0	12.4	12.2	10.1	12.2	12.9	13.4	12.4	12.3
<i>S. virgaurea</i>	2003	1.7	7.0	1.3	1.3	2.0	4.8	2.7	1.3	2.2
<i>G. sylvaticum</i>	2003	4.3	6.3	4.7	13.0	8.8	7.8	8.0	10.3	6.0
<i>V. myrtillus</i>	2003	10.6	8.7	11.9	10.9	8.8	9.0	10.0	7.3	9.0
Field vole	2002-sp	1	0	0	1	0	0	0	0	0
	2002-au	0	0	1	2	0	0	0	0	0
	2003-sp	0	1	0	3	0	0	2	0	2
	2003-au	0	3	1	6	2	3	2	0	0
	2004-sp	1	3	1	3	0	2	7	1	0
	2004-au	2	8	2	3	10	2	10	2	0
Bank vole	2002-sp	0	0	0	0	0	0	0	0	1
	2002-au	1	4	8	0	1	1	3	1	5
	2003-sp	8	7	3	1	1	5	3	1	5
	2003-au	13	11	13	13	14	10	8	7	16
	2004-sp	5	6	6	5	11	4	6	7	11
	2004-au	17	21	18	16	25	12	14	15	10

selection with the AIC criterion to find the most parsimonious model that was subsequently used for parameter estimation (Burnham and Anderson 1998; Johnson and Omland 2004). Rodent sampling from the year 2002 was excluded from the analysis because of a population low with extremely few captures (Table 1). Analyses were performed at the level of sub-enclosure for each of the two habitats (shrub/meadow) to avoid too many missing values. In the analyses, observations with no voles both in spring or autumn were excluded when analysing growth rates, but not when analysing densities. For the remaining data, we added 1 to all observations ( $\ln[(N_{\text{autumn}} + 1)/(N_{\text{spring}} + 1)]$ ), which is the most common way to exclude the problem of log-transforming zeroes (Bjørnstad et al. 1995; Steen and Haydon 2003). The same results were found when adding 0.1 instead of 1, which indicate that our results are robust to what number is added (Steen and Haydon 2003). In 2003 and 2004, two and four bank voles and one and one field vole, respectively, were captured in more than one sub-enclosure and were only registered for analysis in the first location caught. There were not enough recaptures to perform more elaborate CMR-modelling (Lebreton et al. 1992).

We analysed vascular plant coverage (%; arcsin-sqrt-transformed), plant height (cm) and the abundance of important food plants. For the latter, we used plant (abundance) growth per plot from summer 2001 to 2003 as a response variable ( $\ln[(N_{2003} + 1)/(N_{2001} + 1)]$ ). We excluded plots in which the specific species were not recorded in either 2001 or 2003. For all plant analyses, we used linear mixed models (Lindsey 1999) with sub-enclosure as a random factor to account for multiple observations within sub-enclosures. Treatment (three levels) was entered as a factorial variable, and altitude was entered as a covariate as it certainly affects plant ecology in this alpine environment.

All analyses were performed in S-Plus version 6.2 (Crawley 2003).

## Results

Population growth rate for field vole was significantly lower for high than for low sheep density (Fig. 1, Table 2). Several models were competitive, as they differed by less than two AIC units (Appendix). However, the estimated effect of grazing was robust towards other factors included in the model since the parameter estimates for low versus high sheep density were significant for the best five models (Model 6:  $P=0.050$ ; Model 7:  $P=0.023$ , Model 9:  $P=0.043$ ; Model 10:  $P=0.046$ ; see Appendix for Model No.). Growth rate of field vole was higher in meadow than shrub habitat in 2003, but lower in meadow than shrub habitat in 2004 (i.e., a significant “year  $\times$  habitat” interaction, Table 2). Population densities of field vole were similar among treatments in spring, but lower at high than at low sheep density during autumn (Table 2). In contrast, there was no effect



**Fig. 1** The relationship between the population growth rates ( $\ln[(N_{\text{autumn}} + 1)/N_{\text{spring}} + 1]$ ) of the field vole (*M. agrestis*) and sheep density (high, low and control without sheep). The figure is predicted values ( $\pm$  SE) for the western block in 2004

**Table 2** Results from linear models with summer population growth rate ( $\ln[(N_{\text{autumn}} + 1)/(N_{\text{spring}} + 1)]$ ) and density ( $\ln$  abundance + 1) of voles within each sub-enclosure as the response, and treatment, block, year and habitat as factorial variables. Intercept is in all models the estimates value for the scrub habitat at high sheep density on the eastern block in 2003

Parameter	I.s. estimate	SE	T	P
<b>Field vole</b>				
Growth rate				
Intercept	-0.5247	0.3806	-1.379	0.184
Low vs high density	0.6410	0.3014	2.127	0.047
Control vs high density	0.2782	0.3335	0.834	0.415
Block (Mid vs east)	0.5698	0.3094	1.841	0.081
Block (West vs east)	0.0474	0.3152	0.150	0.882
Habitat	0.5509	0.3593	1.533	0.142
Year	0.6923	0.3375	2.051	0.054
Habitat $\times$ Year	-1.0981	0.4835	-2.272	0.035
Spring density				
Intercept	0.3324	0.2164	1.536	0.136
Low vs high density	-0.1155	0.1874	-0.616	0.543
Control vs high density	-0.1831	0.1874	-0.977	0.337
Block (Mid vs east)	0.0240	0.1874	0.128	0.899
Block (West vs east)	0.4719	0.1874	2.518	0.018
Habitat	-0.2441	0.2164	-1.128	0.269
Year	0.0451	0.2164	0.208	0.837
Habitat $\times$ Year	0.4301	0.3061	1.405	0.171
Autumn density				
Intercept	-0.1268	0.2535	-0.500	0.621
Low vs high density	0.5635	0.2195	2.567	0.016
Control vs high density	0.1493	0.2195	0.680	0.502
Block (Mid vs east)	0.4959	0.2195	2.259	0.032
Block (West vs east)	0.4621	0.2195	2.105	0.044
Habitat	0.1540	0.2535	0.608	0.548
Year	0.6743	0.2535	2.660	0.013
Habitat $\times$ Year	-0.4432	0.3585	-1.237	0.227
Bank vole				
Intercept	0.6606	0.2745	2.406	0.023
Low vs high density	0.3356	0.2542	1.321	0.197
Control vs high density	0.1062	0.2542	0.418	0.679
Block (Mid vs east)	0.2045	0.2542	0.804	0.428
Block (West vs east)	0.2307	0.2542	0.908	0.372
Habitat	0.1189	0.2075	0.573	0.571
Year	-0.2203	0.2075	-1.061	0.297



of sheep density on population growth of the bank vole (Table 2). The treatment effect was not included in the best model (Appendix), but we included this factor in order to estimate the effect. There was more data on bank vole than for field vole, so the lack of effect of sheep density is probably not due to poor data. However, note that the parameter estimates point to the same qualitative result for bank voles (Table 2) i.e. the highest growth rates at low sheep density and the lowest growth rates at high sheep density, with the controls in-between.

Vascular plant cover was significantly lower in high sheep density compared to control, while cover in low sheep density and control was similar (Table 3).

There was no relationship between sheep density and the height of vegetation. The abundance of *C. bigelowii* increased from 2001 to 2003 in high sheep density, but not in control. *C. bigelowii* was more common at lower elevations, and the grazing effect interacted with altitude, being more marked at lower elevations. A similar trend was seen for low sheep density (Table 3). There was no effect of sheep density on abundance of bilberry, the preferred sheep grass (*D. flexuosa*), or the two herbs (*S. virgaurea*, *G. sylvaticum*).

## Discussion

We provide the first experimental evidence of negative interactions between a large ungulate and a small rodent assemblage. The experimental design used here cannot prevent changes generated by e.g. simple demographic stochasticity. However, demographic stochasticity would be expected to yield no specific pattern in population growth or rodent density relative to sheep density, and the patterns observed are more easily interpreted in light of competition and/or facilitation processes. Indeed, high sheep density on mountain pastures reduced the summer population growth rate and hence autumn densities of the field vole. There was also lighter sheep lambs at high compared to low density (A. Mysterud, unpublished data), indicating some resource limitation for the sheep, and competition likely occurred. Indeed, a generalist herbivore (the sheep) may be competitively superior to those with a narrower diet (e.g., Latham et al. 1996; Johnson et al. 2000; Hulbert and Andersen 2001) such as voles.

**Table 3** Results from linear-mixed models (with “sub-enclosure” as random factor) describing (A) vascular plant cover and (B) height in 2003 and changes in abundance of (C) *C. bigelowii* (main field and root vole food), (D) *D. flexuosa* (main sheep forage), (E) *S. virgaurea* (preferred herb), (F) *G. sylvaticum* (preferred herb) and (G) *V. myrtilus* (main bank vole food) from 2001 to 2003 ( $\ln[(N_{2003} + 1)/(N_{2001} + 1)]$ )

Parameter	L.s. mean	SE	df	T	P
<b>A. Vascular plant cover</b>					
Intercept	1.2314	0.3216	166	3.829	0.000
High density vs Control	-0.0936	0.0318	6	-2.948	0.026
Low density vs Control	-0.0058	0.0317	6	-0.183	0.861
Altitude	-0.0002	0.0003	166	-0.793	0.429
<b>B. Height of plants</b>					
Intercept	19.2212	10.7596	166	1.786	0.076
High density vs Control	0.4992	1.2888	6	0.387	0.712
Low density vs Control	0.6662	1.2878	6	0.517	0.624
Altitude	-0.0079	0.0092	166	-0.852	0.395
<b>C. <i>C. bigelowii</i></b>					
Intercept	-4.4295	3.0981	45	-1.430	0.160
High density vs Control	11.0114	3.7393	6	2.945	0.026
Low density vs Control	8.3009	4.3243	6	1.920	0.103
Altitude	0.0036	0.0025	45	1.421	0.162
(High density vs Control) × Altitude	-0.0087	0.0031	45	-2.835	0.007
(Low density vs Control) × Altitude	-0.0067	0.0035	45	-1.885	0.066
<b>D. <i>D. flexuosa</i></b>					
Intercept	0.9977	0.8513	144	1.172	0.243
High density vs Control	0.2591	0.1820	6	1.424	0.204
Low density vs Control	0.0235	0.1809	6	0.130	0.901
Altitude	-0.0009	0.0007	144	-1.330	0.186
<b>E. <i>S. virgaurea</i></b>					
Intercept	0.4851	0.9767	31	0.497	0.623
High density vs Control	-0.2777	0.1500	6	-1.851	0.114
Low density vs Control	-0.1233	0.1556	6	-0.793	0.458
Altitude	-0.0004	0.0008	31	-0.511	0.613
<b>F. <i>G. sylvaticum</i></b>					
Intercept	-1.7674	2.3796	40	-0.743	0.462
High density vs Control	-0.3158	0.2438	6	-1.295	0.243
Low density vs Control	0.0172	0.2645	6	0.065	0.950
Altitude	0.0017	0.0020	40	0.834	0.409
<b>G. <i>V. myrtilus</i></b>					
Intercept	0.8375	0.7860	129	1.066	0.289
High density vs Control	-0.2956	0.1842	6	-1.605	0.160
Low density vs Control	-0.1005	0.1842	6	-0.546	0.605
Altitude	-0.0006	0.0006	129	-0.962	0.338

Plots in which these plants were not present in either 2001 or 2003 were excluded from the analyses

Earlier studies on the relationship between small rodents and large ungulates simply compare grazed to ungrazed plots (Hanley and Page 1980; Hewson 1982; Putman et al. 1989; Jones and Longland 1999; Keesing and Crawford 2001; Weickert et al. 2001). However, from competition theory (Tokeshi 1999), it is clearly evident that the level of grazing will determine whether or not competition (or other interaction) occurs, not just whether or not another grazing species is present. In accordance with this, we found a strong contrast in the effect between high and low density of sheep. The difference between control and low density was not significant, but since estimates for low density were actually higher than for controls (Fig. 1), facilitation of rodent populations by low levels of domestic sheep grazing cannot be rejected by our study. It has been shown that domestic sheep grazing on Iceland increased cover of the main forage plant, *C. bigelowii*, due to less competition from mosses that were destroyed by trampling (Jónsdóttir 1991). We found the same increased abundance of *C. bigelowii* under sheep grazing (Table 3). Increased tillering can increase the distribution of this forage plant, and may be a mechanism of facilitation. Increased frequency of *C. bigelowii* was strongest at high density, so evidently, at this grazing level, this possible positive effect is likely overrun by reduced standing biomass. The current study was performed during the first three grazing seasons in an area that was previously lightly grazed. We cannot exclude that future vegetation changes can also affect the relationship between sheep and voles. In any case, our results suggest a variable relationship between ungulates and voles; depending on the density of sheep as well as the diet overlap between the competing species.

We considered summer population growth of voles only. Forage may be even more limiting for voles during winter than during summer, as winter food supply was shown to limit growth in northern vole populations in Finland (Huitu et al. 2003). The time scale of our study was in the first 3 years of sheep grazing, and only minor changes to the habitat had occurred. More marked effects of heavy grazing mainly by fallow deer *Dama dama* in the New Forest, England was attributed to changes in structure and composition of the vegetation (Putman et al. 1989). Provided that predation may synchronize local abundances (Steen 1995; Ims and Andreassen 2000), our results are likely to be conservative.

Predation is known to play a major role in the cyclic dynamics of small rodent populations at northern latitudes (Hanski et al. 1991; Gilg et al. 2003). Shared predators are expected to synchronize different vole species (Hansson and Henttonen 1988). Specifically, population numbers of the two main vole species in our study—the field vole and the bank vole—have been pooled when analysing patterns of population synchrony (Ims and Andreassen 2000). In contrast,

competition is expected to more strongly affect the field vole with a more similar diet and habitat use to sheep than the bank vole. That sympatric populations of the bank vole were unaffected thus suggest competition rather than predation as the cause of this reduction in field vole densities. Our experiment was designed mainly to test whether sheep density and rodent interactions were positive or negative. However, even though the inter-specific pattern observed fit patterns expected due to competition processes, the observed pattern for our voles could also be explained by predation. Indeed, the field vole is regarded as competitively superior to (Hansson 1983) but more vulnerable to predation than the bank vole (Hanski and Henttonen 1996). The field vole may therefore be more affected by grazing related changes in cover due to their higher vulnerability, especially to predation by the mustelids that were present in our study site. Our study demonstrates that grazing may at least have a marginal effect on the pattern of synchrony among vole species. Furthermore, since the interaction negatively affects the species with the most variable dynamics (the field vole), allowing the more stable, self-regulated species to dominate (the bank vole), a somewhat less cyclic small mammal community will likely be the result of high sheep density (Hanski and Henttonen 1996).

The use of outlying pastures for domestic herbivore grazing is a controversial agricultural practice in many areas (Oesterheld et al. 1992; Simpson et al. 1998). It is well documented that large herbivores may have considerable impact on vegetation communities and ecosystem processes (Jefferies et al. 1994; Hobbs 1996; Frank et al. 1998; Augustine and McNaughton 1998; Perevolotsky and Seligman 1998; Milchunas et al. 1998; Olf and Ritchie 1998; Knapp et al. 1999). Our results demonstrate that large ungulate grazing may affect small rodent communities, depending on ungulate density and the dietary overlap. This may provide conservation and management with critical information regarding a part of the biodiversity not too often drawing the big headlines. More importantly, it sheds light on the ecological structuring of herbivore communities in general.

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## Appendix

**Table 4** Results from model selection on population growth rates in field voles and bank voles using the AIC criterion

	Model no	Treatment	Habitat	Year	Block	Treatment ×Habitat	Treatment ×Year	Treatment ×Block	Habitat ×Year	Habitat ×Block	Year ×Block	AIC	ΔAIC
Field vole	1	x	x	x	x							63.355	4.486
	2	x	x	x	x	x						63.382	4.514
	3	x	x	x	x		x					66.185	7.316
	4	x	x	x	x			x				64.858	5.989
	5	x	x	x	x				x			58.869	0.000
	6	x	x	x	x				x	x		59.322	0.454
	7	x	x	x	x				x		x	59.020	0.151
	8	x	x	x					x			60.875	2.006
	9	x										60.318	1.449
	10	x				x						59.916	1.047
	11			x	x					x		62.098	3.229
	12			x	x	x				x		60.968	2.100
	13	x	x	x	x		x		x			61.913	3.044
Bank vole	1	x	x	x	x							76.264	6.302
	2	x	x	x	x	x						78.983	9.021
	3	x	x	x	x		x					78.685	8.722
	4	x	x	x	x			x				78.636	8.673
	5	x	x	x	x				x			77.759	7.796
	6	x	x	x	x					x		79.686	9.723
	7	x	x	x	x						x	79.754	9.791
	8	x	x		x							75.636	5.673
	9	x				x						74.026	4.063
	10	x										71.175	1.212
	11		x									70.846	0.883
	12				x							69.962	0.000
	13					x						72.118	2.155
	14	x			x							71.861	1.899
	15	x	x	x	x							76.264	6.302

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