Effects of reducing sheep grazing in the Scottish Highlands

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Abstract

The effects of reducing sheep grazing on upland vegetation and wild herbivores was studied at 11 sites in the Scottish Highlands. Areas where sheep had been removed for periods of up to 25 years were compared with areas where stocking rates had remained unchanged. At 5 sites, removal of sheep was associated with taller vegetation and more signs of vole activity. While the removal of sheep appeared to have resulted in relatively few changes in floristic composition at these sites, patches of dwarf shrub-dominated vegetation tended to be larger and patches of grassland to be smaller where sheep had been removed. One previously open site was being invaded by birch woodland after sheep removal. At the remaining 6 sites removal of sheep appeared to have had little or no effect on vegetation or on wild herbivore activity. This was probably due to an increase in grazing by red deer, along with continued heather burning, at these sites. It is concluded that sheep removal is only likely to cause significant changes in vegetation composition and structure in the Scottish Highlands where red deer numbers are low and heather burning infrequent. When this occurs, vole numbers are likely to increase.

Key Words: sheep, red deer, sward structure, heather burning, voles.

The management of sheep plays an important role in the rangelands of upland Britain (Sydes and Miller 1988). This is because much upland vegetation in Britain is in a state of dynamic balance between graminaceous vegetation, dwarf shrubs, scrub and woodland, and grazing is crucial in helping to maintain this balance (Miles 1988). While the impacts of sheep grazing on the main successional pathways for upland vegetation are broadly known (Tansley 1939, Ratcliffe 1959, Miles et al. 1978), the effects of reducing sheep grazing on upland vegetation in Britain have largely been investigated using small fenced enclosures,

from which wild herbivores have usually been excluded (Jones 1967, Rawes 1981, Grant et al. 1985, Marrs et al. 1988). It may be misleading to use these findings to predict the effects of sheep removal on unfenced rangeland. Few grazing studies have been carried out on large enclosures or on open hillsides in upland Britain (Ball 1974, Welch 1984a) and none have assessed the effects of sheep grazing on wild herbivores. The aim of this study was to assess what effects there might be on common semi-natural upland vegetation communities and on the main wild vertebrate herbivores associated with them, when sheep were removed from large tracts of rangeland in the Scottish Highlands.

Methods

Since large-scale experimental manipulation of grazing is difficult and some changes take many years to develop (Miles et al. 1978, Marrs et al. 1988), a comparative survey approach was used at 11 study sites in the Scottish Highlands. At each site, floristic composition, vegetation structure and signs of herbivore activity on unimproved rangeland where sheep stocks had been maintained continuously (referred to as control areas) were compared with nearby areas which had formerly been stocked at similar rates, but where sheep had been removed for between 1 and 25 years (reduced-sheep areas).

Site Selection

Sites (Table 1) were selected to include the most common upland plant communities, to encompass a variety of management regimes (i.e., grazing intensity, frequency of heather burning) and to be large enough for assessing the effects of any grazing-induced vegetation changes on the main wild vertebrate herbivores (red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, voles *Microtus* spp., mountain hares *Lepus timidus*, rabbits *Oryctolagus cuniculus* and red grouse *Lagopus lagopus scoticus*). As there are pronounced latitudinal variations in the composition of rangeland vegetation across the Scottish Highlands, related to the marked climatic gradient (Birse 1971, Nolan and Robertson 1987), sites were distributed within 3 broad bioclimatic regions—west (mild and wet), north (cool and wet) and east (cool and dry). Eleven paired sites were selected on soil and vegetation types typical of the bioclimatic regions (Fig. 1). Each site was roughly rectangular in plan, covered an area of between 30 and 100 ha and was divided evenly between control and reduced-sheep areas.

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Table 1. Site descriptions.

	National Grid Reference	Area	Altitude	Year of sheep removal	Stocking Rate		Vegetation types (codes for equivalent National Vegetation Classification communities, after Rodwell (1991))
					Sheep	Red Deer	
(animal per hectare)							
WEST							
1.Coire Croe	NN256068	72	350-550	1988	1.5	0	Meadow-grass & <i>Nardus</i> grassland (U4, U5), <i>Vaccinium</i> heath (U16), rush pasture (M23)
2. Glasdrum	NM995461	33	300-500	1987	0.6	0	Bent-fescue & flushed grassland (U4 U5), bracken (U20),dry heather moor (H14), rush pasture (M23)
3. Glen Branter	NS078959	37	420-480	1984	1.0	0	Grassland (U4), wet heather moor (M19), <i>Juncus squarrosus</i> heath (U6), blanket bog (M20)
4. Coire Circe	NN013455	33	200-350	1968	0.5	0.5	Dry & flushed grassland (U4, M25), birch woodland (W4), dry & wet heather moor (H10, M16)
NORTH							
1. Inchnadamph	NC251230/ NC266209	80	100-300	1987	1.0	1.5	Bent-fescue & base-rich grassland (U4, CG10, CG13) dry & wet heather moor (H14, M15, M16)
2. Glen Carron	NH082527/ NH082514	78	160-300	1984	0.5	1.5	Grassland (U4), dry & wet heather moor (H14, M15, M16), blanket bog (M21)
3. Drumrunie	NC1174060	76	130-270	1984	0.1	0.1	Grassland (U20), dry & wet heather moor (H14, M15, M16), blanket bog (M21)
4. Achnasheen	NH082527/ NH175581	73	180-240	1964**	0.5	1.5	Grassland (U4), dry & wet heather moor (H14, M15, M16), blanket bog (M18, M21)
EAST							
1. Glen Moy	NO401671	107	320-420	1987*+	1.5	3.0	Dry & flushed grassland (U4, M25), dry & wet heather moor (H10, H12), rush pasture (M23)
2. Glen Dye	NO626838	80	200-325	1980*+	2.2	3.0	Dry heather moor (H10, H12), bracken (U20), grassland (U4), rush pasture (M23)
3. Glen Tanar	NO416939	81	450-550	1970*	0.5	2.0	Dry heather moor (H10, H14), flushed grassland (U6), rush pasture (M23)

+grazing reduced from all year to summer only.

*heather burning carried out every 8-12 years on both reduced-sheep and control areas.

** heather burning carried out every 8-12 years on the reduced-sheep part of the site only.

Aerial photographs at scales between 1:10000 to 1:25000, taken as close as possible to the date when sheep were removed, were examined to check that there were no differences in the appearance of the vegetation between each paired control and reduced-sheep area. Comparability of soils, parent materials, underlying geology, and physiography were assessed during site inspections by soil surveys who dug trial soil pits and examined auger samples taken from below the main vegetation types at each site. Details of current and past management practices (Table 1) were obtained from farmers, gamekeepers, estate managers, and land owners. A number of potential paired sites were rejected at this stage, because reduced-sheep and control areas were too dissimilar.

Sampling Procedure

At each site broad vegetation types were first defined, using the cover of a number of common upland plant species (Table 2).

Detailed quantitative descriptions of the vegetation structure within each vegetation type, along with assessments of activity by grazing animals were carried out in 2 m radius circular plots. This plot size and shape was chosen to obtain an adequate sample of vegetation and ungulate dung (Batchelor 1973), while being small enough to allow estimation of the main structural components of the vegetation by eye. Plots were located by constrained random sampling, along parallel transects, which approximately followed the contours of the hillside. The approximate starting point of each transect was chosen to ensure adequate coverage of the whole site, while the exact starting point was determined by taking a random number of paces from the lower site boundary or the previous transect. Floristic composition in each circular plot was assessed using a randomly placed 1 m² quadrat. Between 6 and 18 plots were sampled within each vegetation type on both the reduced-sheep and control areas at each site, except in a few cases where only 4 or 5 plots could be sampled due to a vegeta-

Fig. 1. Location of the study sites and the main bioclimatic zones.

tion type having a very limited extent. Each site was sampled once in early summer 1989 and again in early summer 1990.

Floristic Composition of Vegetation

Species composition was recorded in the 1 m² quadrat within each circular plot. Nomenclature followed Clapham et al. (1987) for vascular plants and Smith (1978) for mosses, although species in some genera (e.g. *Festuca* spp., *Carex* spp.) were not distinguished if they were difficult to identify when heavily grazed (Table 3). At each site the number of plant species in the reduced-sheep area was compared with that in the control area by taking an equal number of plots differed from each vegetation type and using chi-square tests; where the number of plots between the 2 areas, excess samples were chosen randomly and excluded. Cover estimates for all species present were made on the Domin scale (Kershaw and Looney 1985). Cover estimates were grouped by site and vegetation type; because these data were obtained using an ordinal scale, it was often not possible to transform them into a normal distribution. Therefore differences between control and reduced-sheep areas for each vegetation type, on each site, were examined using the Mann-Whitney U statistic given in the SAS NPARIWAY procedure (SAS 1982).

Sward Structure

The identity, arrangement and height of the sward components in the 2 m radius circular plots were described quantitatively using 9 vegetation layer classes (trees and shrubs, ferns, rushes, dwarf shrubs, grasses, herbs, mosses, algae, and litter). The extent of each distinct 'combination' of the layer classes was estimated and the height of each layer within each combination measured (Grant 1993). Bar diagrams were used to show the mean extent of

vegetation layers at selected height intervals, for reduced-sheep and control areas at each site. The extent of a vegetation layer within an individual vegetation type was often not normally distributed and difficult to transform to normality. Therefore differences in the extent of the most common layer combinations at each site, within each vegetation type, were again compared using Mann-Whitney U-tests. The height of structural layers was, however, normally distributed. The height of individual structural layers in each plot was calculated by weighting the measured height according to the extent of the layer combination in which the layer occurred and differences between reduced-sheep and control plots were examined using t-tests. The mean height of the overall sward in each plot was calculated in a similar way, using the height of the uppermost layers(s).

The patch size of the various types was measured by walking 2 sets of transects at each site (Phillips 1989, Grant 1993) in summer 1990. Transects were aligned along compass bearings which ran parallel and perpendicular to the contours. The number of paces taken to cross each patch was recorded, converted to metres and corrected for slope. The data were generally skewed, most vegetation types consisting of a few large patches and many small ones and so were normalized using a log transform (base *e*). The transformed data were then examined using the SAS General Linear Model (GLM) procedure (SAS 1982) to do a two-way analysis of variance with interactions. Patch sizes from the 2 sets of transects (termed 'length' along the contours and 'breadth' across the contours) were modeled separately, using vegetation type and grazing regime (reduced-sheep versus control) as class variables, with a vegetation type $\times$ grazing regime interaction term, for each site.

Table 2. Key to the vegetation types used in the study.

Vegetation Type	Cover of Key Species/Genera
Grassland	>50% Graminoids <20% Dwarf shrub <20% <i>Sphagnum</i> spp.
Base-rich grassland	as grassland but with: >20% <i>Thymus drucei</i> , <i>Lotus corniculatus</i> or <i>Dryas octopetala</i>
Bracken	as grassland but with: >10% <i>Pteridium aquilinum</i>
Dry heather moor	>20% Dwarf shrub <20% <i>Sphagnum</i> spp., <i>Scirpus cespitosus</i> or <i>Molinia caerulea</i>
Wet heather moor	>20% Dwarf shrub >20% <i>Sphagnum</i> spp., <i>S. cespitosus</i> or <i>M. caerulea</i>
<i>Juncus squarrosus</i> heath	>30% <i>J. squarrosus</i> <20% <i>Sphagnum</i> spp. <20% <i>Eriophorum</i> spp.
Blanket bog	>20% <i>Sphagnum</i> spp. <20% Dwarf shrub >10% <i>Eriophorum</i> spp.
Flushed grassland	>20% <i>Sphagnum</i> spp. or >50% <i>Carex</i> spp., <i>M. caerulea</i> or <i>Myrica gale</i>
Rush pasture	>30% <i>Juncus</i> spp. >20% <i>Sphagnum</i> spp.

Table 3. Median cover scores (Domin scale) for the main plant species on the control area of each site. Suffix indicates where the cover on the reduced-sheep treatment was significantly greater (+) or less (-) in one or more vegetation types; Mann-Whitney U-test, $P < 0.05$.

Species	Bioclimatic zone Site	West				North			East			
		1	2	3	4	1	2	3	4	1	2	3
Dwarf shrubs												
<i>Calluna vulgaris</i> L. Hull			1 ⁺	9	8 ⁺	9	6	8	6	9 ⁺	9	6
<i>Erica cinerea</i> L.			5		4 ⁻			4	3		1	
<i>Erica tetralix</i> L.				2		3	5 ⁻	5	5 ⁺			
<i>Vaccinium myrillus</i> L.		9 ⁺	5	6	4					5		2
Grasses & sedges												
<i>Agrostis</i> L.		7	5	8 ⁻	4 ⁻	6 ⁺		2 ⁻	0 ⁺	5	6	
<i>Anthoxanthum odoratum</i> L.		8 ⁻	6	6	2	5				2	4	
<i>Carex</i> L.		5 ⁻	5 ⁺	1	2	4	5 ⁺	3	5	4	2	2 ⁺
<i>Deschampsia flexuosa</i> (L.) Trin.		5 ⁻	4	5 ⁺	0 ⁺	4	0 ⁺		0 ⁺	5 ⁻	3	3
<i>Festuca</i> L.		6	8	5	8 ⁻		0 ⁻	0 ⁻			5	
<i>Molinia caerulea</i> (L.) Moench.					3	3 ⁻	6 ⁻	5	6 ⁻			
<i>Nardus stricta</i> L.		8	8	5	4 ⁻		2		2 ⁺	7	3	5
Rushes												
<i>Eriphorum angustifolium</i> Honckeney		0 ⁺		5		2	3	3	3			
<i>E. vaginatum</i> L.				7 ⁺			7	8	7			
<i>Juncus squarrosus</i> L.		7	5 ⁺	4						4 ⁻	3 ⁻	5
<i>Luzula</i> D.C.		2 ⁻	2 ⁺	4						3	5	
<i>Scirpus caespitosus</i> L.					5 ⁻	5	8 ⁺	8 ⁻	8			
Herbs												
<i>Galium saxatile</i> (L.) Hudson		6	5		3 ⁺	4	0		9	5	5	
<i>Narthecium ossifragum</i> L.				2	4 ⁻	5	7	4	7 ⁺	7		
<i>Polygala serpyllifolia</i> Weihe			3		3 ⁻	1 ⁻	2					
<i>Potentilla erecta</i> (L.) Rauschel		7	8		6	5	1	3	2 ⁺	3	2	
Ferns												
<i>Pteridium aquilinum</i> (L.) Kuhn			8			7		7			8	
Mosses												
<i>Hylocomium splendens</i> (Hedw.) Br. Eur.			7		3	5			5			
<i>Hypnum cupressiforme</i> Hedw.		6	7 ⁻	5	3 ⁻	3		2	6	5	5	7
<i>Pleurozium schreberi</i> (Brid.) Mitt.			1	5						4		
<i>Polytrichum</i> Hedw.		4	4	5 ⁺								
<i>Racomitrium lanuginosum</i> (Hedw.) Brid.		8				3 ⁻	5	0 ⁺	5 ⁻			
<i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.		1 ⁺			2			3				
<i>R. squarrosus</i> (Hedw.) Warnst.		8 ⁻	6	5	3	4 ⁺	4	2 ⁺	5	5	5	3
<i>Sphagnum</i> L.		1 ⁺		7 ⁻	8		8 ⁺	6 ⁻	3 ⁻	3		2
Lichens												
<i>Cladonia</i> (Hill) Web.				3		3	2	0 ⁺	3 ⁻			3 ⁻

Herbivore Dung

Use of plots by sheep, red deer, and roe deer was assessed from dung. Fresh pellet groups (defined as 10 or more unweathered pellets lying close together) were classified as sheep, red deer, roe deer, or unidentified (Welch et al. 1990) and the number within each circular plot was counted. Unidentified pellets usually comprised less than 10% of the total. Pellet groups at the edge of a plot were counted only if more than half the pellets fell inside the plot. Where dung was weathered or the amount present was insufficient to class as a pellet group, it was given the arbitrary value of half a pellet group, to distinguish areas with a small amount of dung from those where none was found. Pellet group counts for sheep, red deer, and total ungulate (including roe deer and unidentified) from control and reduced-sheep areas at each site were compared using Mann-Whitney U-tests, since the data

rarely conformed to a normal distribution. The repeatability of pellet group counts between years was compared by calculating in-traclass correlation coefficients (r_t) for the reduced-sheep and control data (Snedecor and Cochran 1967). Numbers of roe deer and unidentified pellet groups were too few to analyze separately.

The droppings of mountain hare and rabbit do not usually occur in discrete groups, but tend to be scattered. It was time-consuming to count them, so numbers of droppings were estimated on an ordinal scale where: 1–10 pellets=1, 11–25=2, 26–50=3, 51–100=4, >100=5. Differences between scores on the reduced-sheep and control areas at each site were examined using Mann-Whitney U-tests. Droppings of red grouse were recorded as present or absent and the frequency on reduced-sheep and control areas compared using chi-square tests.

Vole Signs

The activity of voles was assessed from signs (Hayne and Thompson 1965, Lidicker 1973, Tapper 1979, Village and Myhill 1990), in the same plots where vegetation and dung were measured. Vole runs were searched for by gently parting the lower layers of vegetation and tracing out any runs that were found. A vole run was recorded as present if at least 1 m was found in a plot and less than 1 m was recorded as trace. Fresh droppings, grass, and rush clippings were also noted. Chi-square tests were used to compare the proportion of plots containing runs, droppings, and clippings between the reduced-sheep and control areas. Since droppings and clippings were only found at 5 sites, the relationship between vole signs and vegetation structure was investigated using only the data on vole runs. The difference in the frequency of vole runs between the reduced-sheep and control areas at each site, was plotted against the difference in mean vegetation height.

To examine the relationship between vole runs and vegetation height in more detail, plots from all sites were grouped into vegetation height classes (2 cm intervals); the frequency of plots containing vole runs in each height interval (y) was plotted against the mid-points of the height intervals (x) and a linear regression calculated. To examine whether vole runs were associated with particular sward components, vole run frequency, the mean height of each layer, and the percentage of plots containing tussocks were calculated, by vegetation type and grazing regime, and examined by Principal Components Analysis. The frequency of vole runs was then compared with the resulting principal component scores in a multiple regression. Simple linear regressions of the frequency of vole runs against individual principal component scores were also calculated.

Results

Floristic Composition

There were a number of significant differences in the Domin cover scores of individual plant species between the reduced-sheep and control areas (Table 3). Dwarf shrubs showed few differences, although *Calluna vulgaris* L. Hull had higher cover scores ($P < 0.05$) on the reduced-sheep areas at 3 sites. Differences in cover scores were found more frequently amongst the grasses; the cover of *Agrostis* L. spp., *Festuca* L. spp., and *Molinia caerulea* (L.) Moench. were usually greater on the control areas

($P < 0.05$), while the cover of *Carex* L. spp. and *Deschampsia flexuosa* (L.) Trin. tended to be higher on reduced-sheep areas ($P < 0.05$). No consistent pattern emerged for the cover of the main rush and herb species. For mosses, trends differed among species. Cover scores for *Sphagnum* L. spp., *Racomitrium lanuginosum* (Hedw.) Brid. and *Hypnum cupressiforme* Hedw. were most often higher on the control areas, while those of *Rhytidiadelphus* (Hedw.) Warnst spp. tended to be higher on the reduced-sheep areas ($P < 0.05$); however the opposite trends were also observed for most of these species on at least 1 site. Overall, there was no consistent difference ($P < 0.05$) in the number of species recorded on reduced-sheep and control areas (Table 4).

Sward Structure

Vegetation was usually taller ($P < 0.05$) on reduced-sheep areas, most notably at 4 sites in the western Highlands and 1 site in the northern Highlands (Table 5). At sites where sheep had been removed for over 5 years, differences were most pronounced in the dwarf shrub, grass, and moss layers (Fig. 2a-c). At 2 sites where sheep removal had occurred 1-3 years before the study

Fig. 2. Bar charts showing the extent of each sward component or layer at selected height intervals; the contrasts between the control and reduced-sheep areas in these 8 vegetation types were typical of those seen in the study overall (% figures are mean values for 'n' samples): a) grassland, Glen Branter; b) dry heather moor, Drumrunie; c) wet heather moor, Coire Circe; d) meadow-grass grassland, Coire Croe; e) rush pasture, Coire Croe; f) grassland, Glen Carron; g) dry heather moor, Glen Tanar; h) wet heather moor, Glen Carron. Key to layer shadings: tree/shrub - solid; rush - vertical dashes; dwarf shrub - diagonal hatching; grass - vertical dashes; moss - stippled; herbs - cross hatching; litter - horizontal dashes.

Table 4. Comparison of the number of plant species on control (C) and reduced-sheep (R) areas.

Bioclimatic zone	Site	n	Number of species		Chi-square value	P
			C	R		
West	Coire Croe	45	60	65	0.20	0.66
	Glasdrum	45	85	77	0.40	0.53
	Glen Branter	30	46	39	0.97	0.45
	Coire Circe	45	80	62	2.28	0.13
North	Inchnadamph	51	84	91	0.28	0.60
	Glen Carron	35	55	59	0.14	0.71
	Drumrunie	41	50	50	0.00	1.00
	Achnasheen	39	53	53	0.00	1.00
East	Glen Moy	45	57	55	0.04	0.85
	Glen Dye	43	62	65	0.07	0.79
	Glen Tanar	48	71	61	0.76	0.38

Table 5. Mean height of vegetation layers (cm) on control areas, with heights on reduced-sheep areas where significantly taller; values in brackets indicate where a layer was taller on the control area.

Bioclimatic zone	Site	Vegetation type	Layer						
			Bracken	Rush	Dwarf shrub	Grass	Moss	Herb	
------(cm)-----									
West	1. Coire Croe	Meadow-grass grassland		28	7	9/13**	2	3	
		<i>Nardus</i> grassland		12		14/17*	3	4/6*	
		Rush pasture		22		12	4/5**	4	
		<i>Vaccinium</i> heath		10/18*	7	11/14*	3	4/5***	
	2. Glasdrum	Bent-fescue grassland				8/14***	3/4*	5	
		Flushed grassland		28		11	3	5	
		Dry heather moor			7	9/13*	4	4	
		Rush pasture		27/55*		14	5	5	
	3. Glen Branter	Bracken	46			9	6	(6/4*)	
		Grassland				7/25***	2/7**	3/10***	
		Wet heather moor			10/18***	15/25***	4/8***		
		<i>Juncus squarrosus</i> heath		11	9/15**	17	5	6/13**	
	4. Coire Circe	Blanket bog			13/18**	18/25***	6		
		Dry grassland			12/30**	11/14*	3/4*	6	
		Dry heather moor			13/28**	11/14*	3/5*	5	
		Flushed grassland			22/40**	12/16*	3/6*		
		Wet heather moor			20/35***	12/17**	4/7***	6	
	North	1. Inchnadamph	Base-rich grassland				4/5**	1/2*	2/3**
			Bent-fescue grassland	46			9	4	4
Dry heather moor					15/24**	10	2	4/5*	
Wet heather moor				8	18/24*	16	3		
2. Glen Carron		Grassland			12	10	2	6	
		Blanket bog			17	22	2		
		Dry heather moor			19	22	2		
		Wet heather moor		7	17	20	2		
3. Drumrunie		Grassland	48/67***		11	14/27***	5/9***	7/13***	
		Blanket bog			8/15*	(22/19*)	5		
		Dry heather moor			22/31**	24	3/6**	9	
		Wet heather moor			18	18	2/5***	8/12*	
4. Achnasheen		Blanket bog			(17/14*)	22	2		
		Grassland			12	10	14	6	
		Dry heather moor			(19/6***)	(20/10***)	(2/1**)	8	
		Wet heather moor		7	(17/12***)	(20/17*)	(2/1*)		
East		1. Glen Moy	Dry grassland				11	1	
			Flushed grassland				11		
			Rush pasture		41/57**		14	5	3
	Pioneer dry heather moor				5	5	1		
	2. Glen Dye	Mature dry heather moor			26	7	3		
		Wet heather moor			(41/23*)	19	5		
		Pioneer dry heather moor			4	7			
		Mature dry heather moor			29	20	2		
		Bracken	60			11	1	6	
		Grassland				9	2	6	
		Rush Pasture		36		21	3	11	
		Pioneer dry heather moor			(8/4**)	8	1		
	3. Glen Tanar	Mature dry heather moor			27	14	3		
		Flushed grassland			26	22	2		
		Rush pasture		74		27	3		

*, **, *** Significant at the 0.05, 0.01 and 0.001 levels respectively (t-test).

began, differences were mostly confined to grass, herb, and rush layers (Fig. 2d-e). However at the 6 remaining sites there were few differences in the height of sward components (Fig. 2f-h). Analysis of patch size showed few consistent differences between reduced-sheep and control areas when all vegetation types were grouped together (Table 6, grazing term). However patches of heather moor tended to be larger and patches of grassland smaller on reduced-sheep areas at western and some northern sites, resulting in an interaction ($P < 0.05$) between vegetation type and grazing regime (Table 6, interaction term).

Herbivore Dung

There were usually fewer sheep pellet groups on reduced-sheep areas than on controls ($P < 0.05$), although sheep did sometimes

stray onto areas from which they had been removed (Fig. 3a). Nevertheless, sheep pellet group counts were largely repeatable between years (intraclass correlation for control $r_1 = 0.78$, $P < 0.01$; reduced-sheep $r_1 = 0.59$, $P < 0.01$). Red deer pellet groups were less numerous than those of sheep at most sites (Fig. 4b). More red deer pellets were found on control areas than on reduced-sheep areas at western sites, although the differences were not always significant. Red deer pellet counts were repeatable between years on reduced-sheep areas ($r_1 = 0.70$, $P < 0.01$), but more variable on control areas ($r_1 = 0.30$, $P > 0.05$). Total ungulate pellet group counts were repeatable between years on both control ($r_1 = 0.69$, $P < 0.01$) and reduced-sheep ($r_1 = 0.84$, $P < 0.001$) areas. Again, there were usually more pellet groups on the control areas, especially at western sites (Fig. 4c).

Mountain hare and rabbit droppings were present at 6 sites, but a consistent difference in pellet scores occurred only at the Glen Branter site, where there were more hare droppings on the reduced-sheep area than the control area in both years ($P < 0.05$). Red grouse droppings were present in small amounts at most sites, but there was a difference only at the Achnasheen site, where there were more droppings on the reduced-sheep area in both years ($P < 0.05$).

Vole Signs

Vole runs were found at all 11 sites and in most vegetation types. The proportion of plots containing vole runs at each site was similar in both years. Runs were more frequent in plots on reduced-sheep than on control areas at 4 sites in the western Highlands and at 1 site in the northern Highlands (Table 7). Including records of trace with presence scores did not change the results. Where they were present, fresh droppings and clippings showed the same difference between grazing regimes (Table 7). The difference in the frequency of vole runs between reduced-sheep and control areas was correlated with the difference in sward height at the same sites (Fig. 4). The regression equation relating vole run frequency (y) and sward height (x), $y = 53 \log_{10} x - 20$ ($n=20$; $r^2=0.84$), intercepted the x axis at 5 cm, indicating that runs were found only when the sward was taller than this.

Principal components analysis of layer height and tussock frequency (Table 8a) explained 87% of the variation in vole run fre-

Fig. 3. Mean number of pellet groups on all 11 sites in 1989 (left-hand bars) and 1990 (right-hand bars). *, **, ***, indicate the significance of differences between the control and reduced-sheep areas at the 0.05, 0.01 and 0.001 levels respectively.

Fig. 4. Difference in sward height versus the difference in the frequency of vole runs between the reduced-sheep and control areas at each site; positive values indicate that the sward was taller and vole runs were more frequent on the reduced-sheep versus the control area, negative values indicate a difference in the opposite direction.

quency in terms of 4 principal components. These were interpreted as: i) tall grass, moss, rush, and litter layers, with tussocks present, ii) tall dwarf shrub layer, with some moss but few rushes, iii) tussocks without litter and iv) tussocks with litter. Regressions of vole run frequency on the scores for these 4 principal components showed that only the scores for the first 2 principal components had significant explanatory value (Table 8b); the first principal component was the best single explanatory variable (Table 8c).

Discussion

In previous studies where sheep have been removed from rangeland in upland Britain, initial rapid increases in the height of vegetation have usually been followed in successive years by gradual increases in the cover of dominant species, particularly dwarf shrubs such as *Calluna vulgaris*, with a decline in the cover of most grasses and herbs (Jones 1967, Ball 1974, Rawes 1981, Marrs et al. 1988). In the present study, sheep removal appears to have resulted in similar vegetation changes at 5 of the sites. Although the differences in species cover and composition found in the present study are less marked than in some earlier work, this could be partly due to differences in methods. For example, we stratified sampling within vegetation types, to avoid confusing differences due to small variations in edaphic conditions with grazing-induced differences. Thus, what previous authors recorded as changes in species composition, could have been recorded by us as apparent changes in the extent of different vegetation types. In particular, the overall tendency for patches of heather moor to be larger and grassland to be smaller on reduced-sheep compared to control areas suggests that, where soils are relatively freely drained, a reduction in grazing pressure leads to the expansion of dwarf shrub-dominated vegetation at the expense of grassland, until patches eventually coalesce to form a continuous sward. Presumably when grazing pressure is increased this process is reversed, as in habitat fragmentation (Wiens 1989).

The removal of sheep apparently had little effect on either the composition or structure of the vegetation at 6 sites, even where

Table 6. Analysis of variance for vegetation patch size (using two-class SAS General Linear Model procedure).

Site	Summary of differences on reduced-sheep relative to control areas.	Significance levels					
		Patch width			Patch length		
		Vegetation type	Grazing treatment	Interaction	Vegetation type	Grazing treatment	Interaction
West							
Coire Croe	<i>Vaccinium</i> heath patches larger, grassland patches smaller.	0.046	<0.001	0.002	0.008	NS	0.170
Glasdrum	Dry heather moor patches larger, grassland patches smaller.	<0.001	NS	NS	<0.001	NS	NS
Glen Branter	Patches of grassland and <i>Juncus squarrosus</i> heath smaller.	0.001	NS	NS	<0.001	NS	NS
Coire Circe	Wet heather moor patches larger, grassland patches smaller.	<0.001	NS	<0.001	<0.001	0.025	NS
North							
Inchnadamph	Dry heather moor patches larger, grassland patches smaller.	0.02	NS	0.008	NS	NS	NS
Glen Carron	Wet heather moor patches larger, grassland patches smaller.	<0.001	NS	0.012	<0.001	NS	NS
Drumrunie	Wet heather moor patches larger, grassland patches smaller.	<0.001	NS	0.007	<0.001	NS	NS
Achnasheen	Wet heather moor patches larger, grassland patches smaller.	<0.001	NS	NS	<0.001	NS	0.005
East							
Glen Moy	Patches of pioneer and mature heather moor and grassland larger.	<0.001	NS	NS	<0.001	0.004	NS
Glen Dye	Patches of all vegetation types larger.	<0.001	NS	NS	<0.001	0.015	NS
Glen Tanar	No consistent differences.	<0.001	NS	NS	<0.001	NS	NS

sheep had been absent for many years. At these 6 sites, red deer pellets on the reduced-sheep areas were at least as numerous as on the respective control areas, resulting in little difference in the total amount of ungulate dung between grazing regimes. Although direct counts of red deer were not made, the standing crop of dung gives a good indication of feeding dispersion for red deer on open rangeland (Charles et al. 1977, Mitchell et al. 1983, Welch et al. 1990). Obviously the dung counts made during this two-year study may not always represent longer term patterns of

site use particularly well, for example at Coire Circe where a recent break in a fence had allowed some animals into the reduced-sheep area for a short period before the start of the study. Also, potential differences in the rate of decomposition precluded any quantitative comparison of dung data between the different sites. Nonetheless, this was unlikely to invalidate comparisons between control and reduced-sheep areas within sites. Hence we suggest that the removal of sheep at these 6 sites has been followed by increased use of the rangeland by red deer, which has

Table 7. Differences in the frequency of vole signs between control (C) and reduced-sheep (R) areas from chi-square tests.

Site	<i>n</i>		Summer 1989			<i>n</i>		Summer 1990		
	C	R	Runs	Droppings	Clippings	C	R	Runs	Droppings	Clippings
West										
Coire Croe	45	45	**	—	—	36	33	*	***	—
Glasdrum	45	45	**	—	—	33	36	**	*	—
Glen Branter	33	30	**	—	—	35	30	***	NS	—
Coire Circe	45	50	*	—	—	28	30	*	NS	—
North										
Inchnadamph	51	51	NS	—	—	44	43	NS	—	—
Glen Carron	43	41	NS	—	—	35	36	NS	—	—
Drumrunie	42	41	**	—	—	34	34	*	*	*
Achnasheen	43	39	(**)	—	—	35	38	NS	—	—
East										
Glen Moy	45	45	NS	—	—	40	40	(*)	—	—
Glen Dye						43	44	NS	—	—
Glen Tanar	48	48	NS	—	—	31	31	NS	—	—

*, **, *** Significant at the 0.05, 0.01 and 0.001 levels respectively; more signs were found on the reduced-sheep areas in all case, except where indicated by brackets. — indicates signs were absent or too infrequent to test.

Table 8. Analysis of the relationship between vole runs and sward structure, grouping the data (from 1989) by site and grazing regime. (a) Principal components analysis of mean layer height and tussock frequency. (b) Results of a multiple regression of vole run frequency on the principal component scores of the first 4 axes. (c) Results of linear regressions of vole run frequency on the component scores for axes 1 and 2.

(a) Variables	Eigenvectors			
	Prin 1	Prin 2	Prin 3	Prin 4
Dwarf shrub layer height	-0.05	0.75	0.19	-0.07
Grass layer height	0.62	0.10	0.23	-0.21
Moss layer height	0.51	0.37	-0.37	-0.26
Litter layer height	0.35	-0.12	-0.61	0.52
Rush layer height	0.35	-0.52	0.24	-0.39
Proportion of plots of tussocks	0.32	0.05	0.57	0.67
Eigenvalues	1.84	1.33	1.06	0.93
Percentage of variation explained	31	22	18	16

(b) Variable	Degrees of freedom	Parameter estimate	Standard error	Ho Parameter=0	
				T	P
Intercept	1	45.8	2.52	18.2	<0.001
Prin 1	1	15.4	1.89	8.2	<0.001
Prin 2	1	6.3	2.20	2.9	0.005
Prin 3	1	0.7	2.46	0.3	0.776
Prin 4	1	1.3	2.63	0.5	0.609

F = 19.1 $r^2 = 50\%$

(c) Variable	F value	Significance	r^2 (%)
Prin 1	63.2	<0.001	44
Prin 2	4.6	0.035	5

suppressed any significant changes in vegetation composition or structure. The continued practice of rotational heather burning at most of these sites is also likely to have helped maintain the composition and structure of heather-dominated vegetation (Gimingham 1972).

There are similar findings in previous work. The floristic composition of species-rich grassland on the Isle of Rhum changed very little following the removal of sheep and cattle, due to increased red deer grazing (Ball 1974). In north-east Scotland few differences were detected in heather moorland grazed by an equal biomass of sheep or red deer (Welch 1984a, Welch 1984b), or after red deer replaced sheep (Grant et al. 1981).

Voles

The results suggest that vole activity increased following the removal of sheep grazing, at the 5 sites where vegetation height increased. The effect appears to have been more pronounced the taller the resulting sward. A number of studies have shown the importance of vegetation cover to microtine populations (Taitt et al. 1981, Taitt and Krebs 1983, Kotler et al. 1988). In the present study, it appeared that the amount of cover above a height of 5 cm had a large influence on vole activity. Tall grass and moss layers presumably provide good cover, along with food in the case of grass. Tussocks and tall rushes are probably important because they provide good sites for tunneling and nest building. The dwarf shrub layer may be less important because it provides adequate cover but is of little food value.

Implications for Other Herbivores

The overall lack of differences in dropping of hares, rabbits, and red grouse between reduced-sheep and control areas suggests

that removal of sheep had little effect on these species, probably because red deer grazing and heather burning prevented the vegetation from changing at most of the sites where signs of these species were found. However the changes in vegetation seen at the other study sites following the removal of sheep are likely to be important to wild herbivores (Miller et al. 1970, Hewson 1976, Savory 1986, Watson et al. 1987).

Conclusions

In accordance with previous work, we conclude that reduced sheep grazing can quickly result in taller vegetation, which may be followed by a slower shift from grassy vegetation to dwarf shrubs and trees on unburned rangeland. Such changes in vegetation structure and composition will affect other wild herbivores; in particular the abundance of voles is likely to increase as the height of grassy vegetation increases above 5 cm. However, removing sheep from rangeland in the Scottish Highlands is likely to have little effect on vegetation in areas where there are appreciable numbers of red deer or where heather burning is continued.

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