Available online at www.sciencedirect.com

ScienceDirect

Agriculture, Ecosystems and Environment 124 (2008) 219–228

Agriculture Ecosystems & Environment

www.elsevier.com/locate/agee

Impacts of sheep grazing a complex vegetation mosaic: Relating behaviour to vegetation change

S.P. Oom [a,1], A.M. Sibbald [a,*], A.J. Hester [a], D.R. Miller [a], C.J. Legg [b]

[a] *Macaulay Institute, Craigiebuckler, Aberdeen AB15 8QH, UK*
[b] *University of Edinburgh, School of Earth, Environmental & Geographical Sciences, The King's Buildings, Mayfield Road, Edinburgh EH9 3JU, UK*

Received 3 May 2007; received in revised form 11 September 2007; accepted 25 September 2007
Available online 3 December 2007

Abstract

The impact of grazing animals on vegetation is usually considered as a single process, despite the knowledge that behaviours such as defoliation and trampling are likely to have different effects. A 3-year study was carried out to assess the different impacts of sheep on a natural dwarf-shrub and grass mosaic, by relating animal behaviour to vegetation change, using a spatially explicit design. Sheep grazed at average stocking rates of 2, 3 or 4 animals ha^{-1} in six 1 ha plots. Spatial patterns of defoliation were obtained from field measurements of grazing damage, other aspects of behaviour from direct observation and vegetation change from aerial photographs.

Over the 3 years, there was a net change of 907 m^2 (1.5% of the total study area) from 'shrub' (heather *Calluna vulgaris* and blaeberry *Vaccinium myrtillus*) to 'mixed' (grass and blaeberry) vegetation and degraded heather, but no overall net change in grass cover. Over the whole study area there were significant linear relationships between heather defoliation rate and the percentage change in shrub and mixed vegetation at defoliation sites, where relatively small, local changes in the vegetation were seen. However, differences between individual plots showed no relationship with sheep stocking rate. Larger, spatially aggregated changes were also seen, but these were not associated with grazing; they tended to be concentrated in areas used by the sheep for resting. Grass and mixed vegetation cover increased by 351 m^2 at these sites, equivalent to 27% of the total area initially identified as resting sites. Since the impacts of the sheep differed in both intensity and spatial pattern for the processes of defoliation and resting, we suggest that the effects of these component behaviours should be considered separately when attempting to predict vegetation change in complex environments.

Keywords: Defoliation; Grazing; Sheep; Social behaviour; Vegetation change; Vegetation patches

1. Introduction

Despite the existence of a strict definition of grazing as 'the partial removal of herbage by a herbivore' (Spedding, 1971), the term is generally used to cover the whole complex of processes associated with foraging (i.e. defoliation, trampling, lying, defaecation, etc) (e.g. Adler et al., 2001). Indeed, the impact of herbivores on vegetation is usually considered simply as the outcome of all these processes, implicitly assuming a linear spatial correlation between them. In agricultural grazing systems, which utilize plant species highly tolerant of grazing and where spatial heterogeneity is often kept low (Heady and Child, 1994), this may be the case. However in natural vegetation mosaics, spatial heterogeneity is generally high and grazing-tolerant species may be intermixed with grazing-intolerant species. In these systems, where wild or domestic herbivores are generally free-grazing, the spatial interactions between the various processes associated with the presence of grazing animals are more complex.

Three main physical processes are responsible for the impact of large herbivores on vegetation, namely

---

[*] Corresponding author. Tel.: +44 1224 498200; fax: +44 1224 311556.
E-mail addresses: sander@oomvanlieshout.net (S.P. Oom), angela.sibbald@macaulay.ac.uk (A.M. Sibbald).

[1] Present address: DHV B.V., P.O. Box 1132, 3800 BC Amersfoort, The Netherlands.

0167-8809/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.agee.2007.09.014

defoliation, trampling and lying, and these processes all have an important spatial component. While the spatial pattern of the vegetation itself has a major effect on animal distribution (Bailey et al., 1996) and hence the pattern of defoliation and associated trampling, the location of watering points (e.g. Weber et al., 1998) and shelter sites (Hunter, 1962; Taylor et al., 1987) are also important, as will be predator avoidance activities, particularly in the case of wild herbivores. The final outcome of the foraging process, however, depends on the relative vulnerability of different plant species to defoliation and trampling damage. The vulnerability of woody species, such as the dwarf-shrub heather (*Calluna vulgaris*), to both activities (Grant et al., 1978, 1981; Palmer and Hester, 2000), together with the lower attractiveness of heather than grass to sheep and other large herbivores (Clarke et al., 1995a; Hester et al., 1999; Palmer et al., 2003), makes the heather-grass mosaic an interesting system to study. From all previous work, we would clearly predict greater impacts of both grazing and trampling activities on heather than grass. Comparing trampling with grazing impacts: for the more vulnerable species (heather) we would predict more severe impacts of trampling than grazing if grazing removed less than about 40% of current year's shoots (Gimingham, 1972; Grant et al., 1978, 1981; Palmer and Hester, 2000), due to physical breakage of the woody stems and difficulty of regrowth from stem bases of these woody plants when mature. Otherwise we would predict similar effects of both activities, if heavy grazing repeatedly removed most green material, making regrowth difficult.

Heather is also an actively conserved, internationally important vegetation type with a range of biodiversity and conservation designations (Thompson et al., 1995; Jackson and McLeod, 2002; European Commission, 2006). Its abundance and condition have declined dramatically across its range in the last 50+ years, with one of the main causal factors being 'overgrazing' (Tudor and Mackey, 1995; Hester et al., 1996; Webb et al., 2000; Mackey et al., 2001). Other land use changes have also led to more localised losses, including cultivation for forestry or agriculture (Tudor and Mackey, 1995; Hester et al., 1996; Bartolomé et al., 2005), and reductions or prohibition of fires (Bartolomé et al., 2005). The strong need for grazing management advice is widely recognised (Pakeman et al., 2003), but management regimes or grant-aid incentives often just consider stocking rate (e.g. Scottish Office, 1997; Pakeman et al., 2003; Scottish Executive, 2004), which may fail to achieve the desired targets with heterogeneous resources, when spatial differences in behaviour by the animals result in strong, differential effects on the vegetation.

In this paper, we report on a 3-year study of the impact of sheep grazing a natural heather-grass mosaic at different stocking rates, in which field measurements of heather defoliation and sheep behaviour were related to changes in the vegetation, measured by remote sensing. The aim of the study was to investigate the mechanisms through which the presence of sheep affects heterogeneous resources such as this, by linking spatially explicit information about defoliation rates and behaviour with details of vegetation change at different animal densities.

2. Materials and methods

2.1. Experimental site and design

The experiment was carried out at the Macaulay Institute's Glensaugh Research Station in the north-east of Scotland (latitude 56°54′N), between June 1998 and November 2001. The experimental site was at an altitude of 200–250 m and consisted of six 1 ha plots, fenced within a NNW-facing area of *Calluna*-dominated moorland (see Fig. 1 and Oom, 2003). Three grazing treatments of 4, 3 and 2, 1-year-old female Scottish Blackface sheep ha^{-1} were stratified (top and bottom block) and randomly allocated to plots 1 and 5, plots 2 and 6, and plots 3 and 4, respectively (Fig. 1), between March and November each year. The treatments were applied by putting groups of six animals in each of the plots for different numbers of days in a 3-week rotational schedule, thus creating the desired

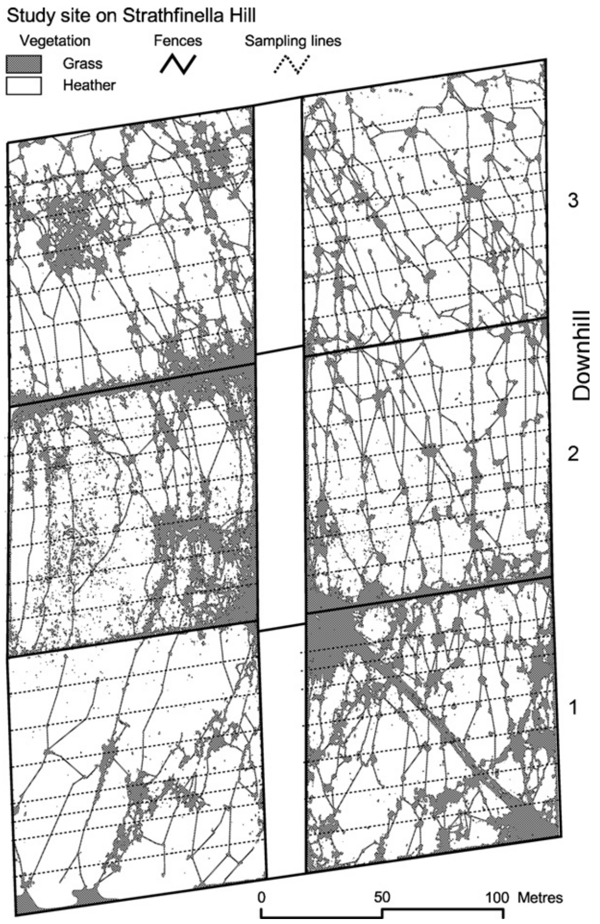

Fig. 1. Map based on the vegetation classification made at the end of the experiment (2001), showing areas of grass (grey) and heather (white).

average stocking rates while keeping animal densities the same. The site was left ungrazed for 1 year prior to this study, while an earlier experiment on the site involved grazing for 8 weeks per year (from 1991) with sheep and red deer combinations (roughly equivalent to the lower grazing levels used in this study) (Hester and Baillie, 1998; Hester et al., 1999).

Heather defoliation was measured in October and April each year, at the beginning and end of the grazing season. During the third year of the study, observations of sheep behaviour were carried out over an intensive 11-day period in June, while a group of six sheep grazed in each of the plots. Vegetation change was measured from aerial photographs, taken at the beginning (October 1998) and end (October 2001) of the experiment.

2.2. Defoliation measurements

Heather defoliation was recorded using seven, regularly spaced, 100 m sampling lines in each of the plots, with transects laid out at each grass-heather boundary crossed by the sampling lines (Oom et al., 2002; Oom, 2003). The transects were placed perpendicular to the grass-heather boundaries and heather defoliation was measured at fixed distances (0, 0.25 and 0.5 m) from the boundaries, following the method described by Hester and Baillie (1998) and recording 0, <50%, 50–100% and >100% removal of the current season's growth. For the purposes of this paper, the three heather defoliation measurements were averaged across all seasons and years, providing a single estimate of edge-heather defoliation for each of the grass patches sampled. The heather defoliation values were angular transformed (Snedecor and Cochran, 1989) to normalise the data for analysis.

2.3. Behaviour measurements

Each sheep was given a unique fleece marking, so that individuals could be identified from a distance. The plots were observed with binoculars or telescope from a position facing the hillside, at a distance of approximately 500 m. Each day, 25 scan samples (Martin and Bateson, 1986) were taken between 0730 and 2130 h. During each scan, the spatial locations of all 36 sheep were marked on vegetation maps of the plots (Fig. 1) and their individual activities (grazing, lying, standing, walking, or drinking) recorded. Sheep locations were subsequently digitized using ArcView (ESRI, USA; Version 3.2).

Two behaviour categories were used in the analyses for this paper. These categories were (1) foraging: which included grazing and walking and (2) resting: which included only lying. Standing was not included in the analyses, since it could be a component of either foraging or resting behaviour and was only observed 3% of the time, nor was drinking, which was rarely observed (<1%).

2.4. Measurements of vegetation change

2.4.1. Aerial photography

In order to detect changes in the vegetation over the whole study area, vegetation maps were created from aerial photographs taken at the start and end of the 3-year period. To minimize differences in the appearance of the vegetation, caused by season and light conditions, photographs were taken at the same time of year and at midday on days that were characterized by high altitude cloud, leading to high contrast but neither direct sunlight nor associated shadows. The photographs were digitally scanned at a resolution of 3600 dots per inch, producing digital images of approximately 7300 × 7300 pixels which were then re-sampled to a ground resolution of 0.05 m for analysis. The photographs were ortho-rectified with reference to a set of fixed ground points, in order to adjust for the position of the aeroplane and the slope of the hillside. Ortho-rectification was carried out using OrthoMAX (Vision International, USA; Version 8.3), a module available in Erdas Imagine (ERDAS Inc., USA; Version 8.3). Details of these procedures and their associated sources of error are described in full elsewhere (Oom, 2003).

2.4.2. Image classification

The images were classified using the unsupervised classification algorithm in Erdas Imagine. With this iterative method, individual pixels are allocated to clusters based on their spectral characteristics, initially on the basis of arbitrary cluster means and thereafter on the basis of cluster means recalculated after each iteration. Pixels are reallocated to clusters in this way until a pre-set proportion (in this case 0.95) of pixels remain in their assigned cluster from one iteration to the next. This fully automated method avoids errors associated with the traditional manual classification of images (Green and Hartley, 2000). The process was constrained to distinguish between 15 different classes (i.e. clusters), which were then grouped into four summary classes, defined as 'grass', 'mixed', 'degraded heather' and 'shrub', based on a visual interpretation of the ortho-images and on observations in the field.

Field observations showed that vegetation classified as grass was dominated by *Agrostis capillaris* L., *Agrostis canina* L., *Deschampsia flexuosa* L. Trin. and *Festuca ovina* (Rodwell, 1992; NVC = U4 '*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland'). Mixed vegetation was derived from a single class coinciding with a mixture of vegetation types (predominantly grass and blaeberry (*Vaccinium myrtillus* L.)) bordering the grass class. Degraded heather was also derived from a single class and associated strongly with heather (*Calluna vulgaris* (L) Hull) plants in the degenerate phase (Watt, 1947) with low cover and a high wood:green biomass ratio, and generally occurred at the edge of the shrub class. The summary shrub class was formed from 10 of the remaining original classes, all dominated by the shrubs *Calluna vulgaris* and, in lower quantities, *Vaccinium myrtillus* L. (Rodwell, 1991, NVC = H12 '*Calluna vulgaris-Vaccinium myrtillus* heath'). Full details of the classification process are described elsewhere (Oom, 2003). The resulting vegetation map obtained from the images obtained at the end of the experiment (2001) is shown in Fig. 1.

2.4.3. Calculation of vegetation change

Changes in the total area of each vegetation class in each plot were calculated by summing the data for each of the 0.05 m × 0.05 m cells and pair wise comparison of data from the two sets of aerial photographs. A spatial analysis of the changes was also carried out by using a grid overlay, with a 2 m resolution, and comparing the percentage cover for each vegetation class within the individual cells. Finally, an analysis was carried out using individual grass patches as the sampling unit. This enabled vegetation change to be linked with sheep behaviour, since sheep tend to focus their activities on grass patches (Hester and Baillie, 1998; Sibbald and Hooper, 2003). To facilitate this analysis, individually identified grass patches were compared at the beginning and the end of the experiment. For each patch, changes in cover were calculated for all the vegetation classes, by estimating the amount of each vegetation class present within a clearly defined area (the 'union patch') which encompassed the two areas identified as the patch in the two sets of photographs. A union patch would normally be equivalent to the largest representation of the patch, i.e. the patch as mapped in 1998, if its size had decreased during the experiment, or the patch as mapped in 2001, if it had increased. Union patches were sometimes larger than either of the actual patches, due to a slight, non-systematic misalignment of patches in the two maps. When such misalignment occurred, union patches could include some of the shrub or degenerate heather vegetation close by. However, the use of union patches as a basis for the analysis minimised the chance that 'false' vegetation changes would be recorded due to misalignment.

2.5. Statistical analysis

Relationships between heather defoliation rate and vegetation change, quantified as percentage change in cover, were investigated by linear regression analysis for each vegetation class. Relationships between change in cover and initial cover (both expressed as m^2) for the four vegetation classes and between change in cover and sheep stocking rate, were also investigated by linear regression analysis, using plot mean values. In each case, change in cover was the response variable. Changes in grass cover at resting sites and across each plot as a whole (also expressed as m^2) were compared using Residual Maximum Likelihood (REML) analysis in Genstat (Genstat, 2002) with resting site v whole plot designation as a fixed effect and plot as a random effect.

3. Results

3.1. Changes in vegetation cover

The percentage cover for the different vegetation classes varied considerably between plots at the start of the experiment, with the ratio of shrub to grass ranging from 30:1 in one plot to 4:1 in another (see Table 1). Over the mosaic as a whole, there was very little change in grass cover during the experiment, although there were changes to and from grass within the plots, which ranged from −171 m^2 in one plot to +212 m^2 in another. There was a net change of 151 m^2 per plot from shrub to mixed vegetation and, to a lesser extent, to degraded heather (Table 1), although these changes also varied considerably between plots (SE 161.2 m^2). Between-plot differences in vegetation change were not related to differences in initial vegetation cover or to sheep stocking rates, except in the case of mixed vegetation, where there was a greater increase in mixed vegetation for plots with higher initial heather cover ($P < 0.05$) (Table 1). In all other cases, therefore, it appears that specific activities or locational choices within plots were driving local vegetation change. This is examined below.

3.2. Changes in spatial pattern of vegetation

Comparison of the vegetation maps based on the 2 m grid (Fig. 2) showed that the magnitude of the changes for each of the vegetation classes varied spatially within, as well as between, plots. Within plots, small changes in the vegetation, where < 10% by area of the vegetation in the 2 m grid cells had changed, were spread fairly evenly across the mosaic.

Table 1
Areas covered by each vegetation class (grass, mixed, degraded heather and shrub) at the beginning of the experiment (1998), and change in cover for each class between 1998 and 2001

Plot	Stock rate (sheep ha^{-1})	1998 cover (m^2)				Change in cover (m^2)			
		Grass	Mixed	Degraded heather	Shrub	Grass	Mixed	Degraded heather	Shrub
1	4	1850	430	277	7444	−85	−2	−123	210
2	3	898	144	170	8788	−92	142	44	−93
3	2	765	165	97	8974	−171	86	117	−32
4	2	312	262	53	9372	−19	−65	7	78
5	4	1316	353	471	7861	212	612	88	−912
6	3	1411	496	123	7970	119	−63	102	−157
Total		6552	1850	1191	50,409	−38	709	235	−907

Larger changes, particularly changes from shrub to mixed vegetation, were concentrated in only a few areas (Fig. 2b and d).

3.3. Effects of heather defoliation

Correlation between vegetation change and heather defoliation was possible through the patch-based photographic analysis. Across all plots, there were significant linear relationships between heather defoliation rate and the percentage decrease in shrub vegetation ($R^2 = 5.2\%$, $P < 0.004$) or increase in mixed vegetation ($R^2 = 8.9\%$, $P < 0.001$) associated with the adjacent grass patches ($n = 137$). However, relationships between defoliation rate and percentage changes in grass and degraded heather were not significant (Fig. 3).

3.4. Effects of sheep resting behaviour

The map of all the recorded sheep locations (Fig. 4) shows that the pattern of resting behaviour was highly aggregated, with resting locations often coinciding with the larger vegetation changes shown up by the grid analysis (see Fig. 2). Since the behavioural observations showed that sheep spent an average of 26% of their time resting, individual grass patches were classified as 'resting sites' when the percentage of observations in which sheep were seen resting there exceeded 30%. On this basis, grass patches identified as resting sites made up 20% of the total grass area at the start of the experiment and 24% at the end, corresponding to a 16% increase in the size of those patches, while there was a net decrease in grass cover overall (Table 2). The difference between the mean change in grass cover at resting sites (+35.2 m^2) and over whole plots (-18.8 m^2) was significant at $P = 0.078$, even though resting sites made up less than 25% of the area. In the grid analysis, 41% of the cells in which changes to grass were detected were associated with resting sites. The combined increase in grass and mixed vegetation cover at resting sites of 351 m^2 (Table 2), was equivalent to an increase of 27% by area of the grass patches originally classified as resting sites at the start of the experiment.

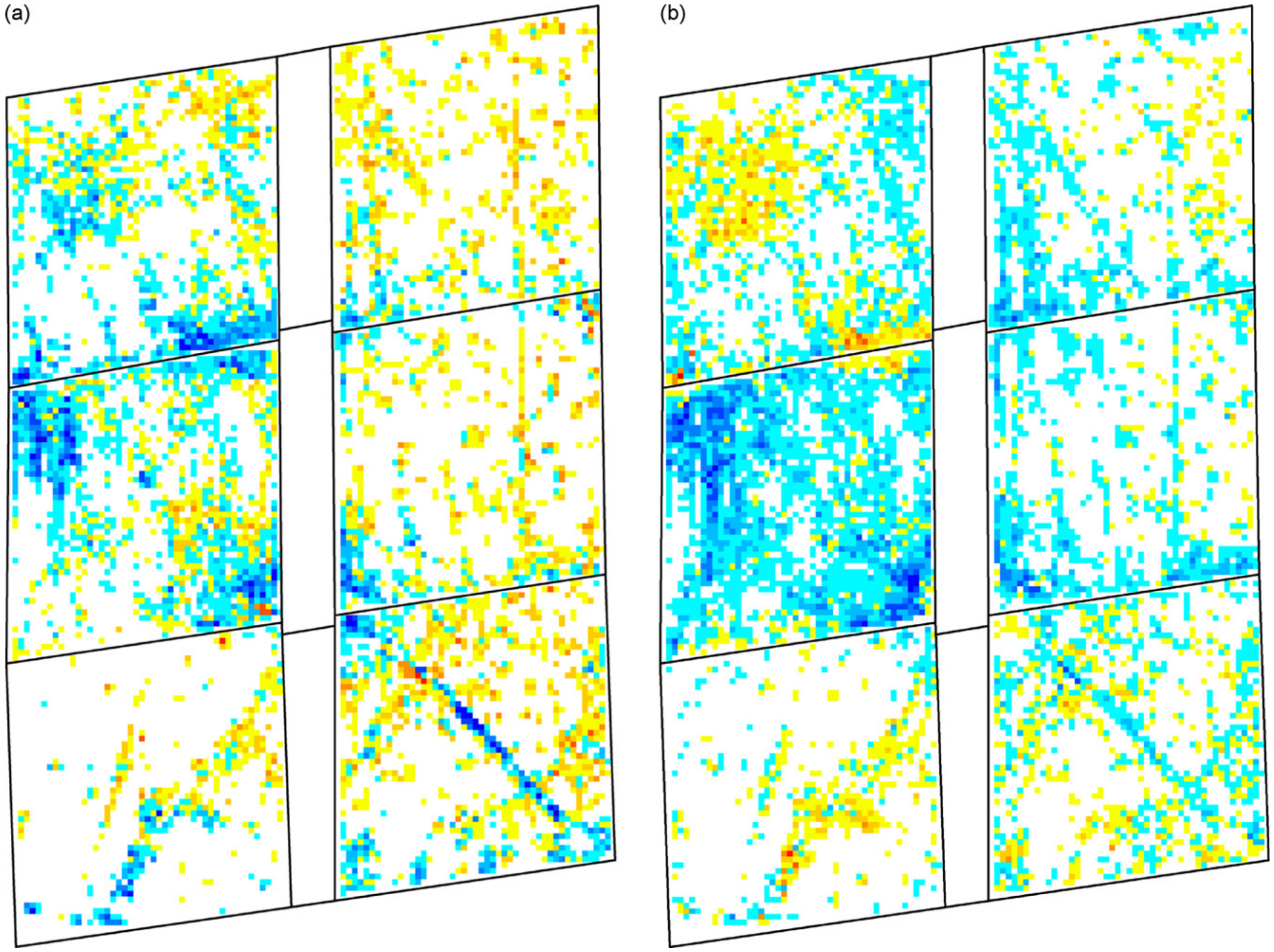

Fig. 2. Map showing the percentage change in cover for each vegetation class within 2 m grid cells between the start (1998) and end (2001) of the experiment for (a) grass (b) mixed (c) degraded heather and (d) shrub, with amount of change indicated by a colour gradient from dark red (strong decrease) through yellow and light blue to dark blue (strong increase).

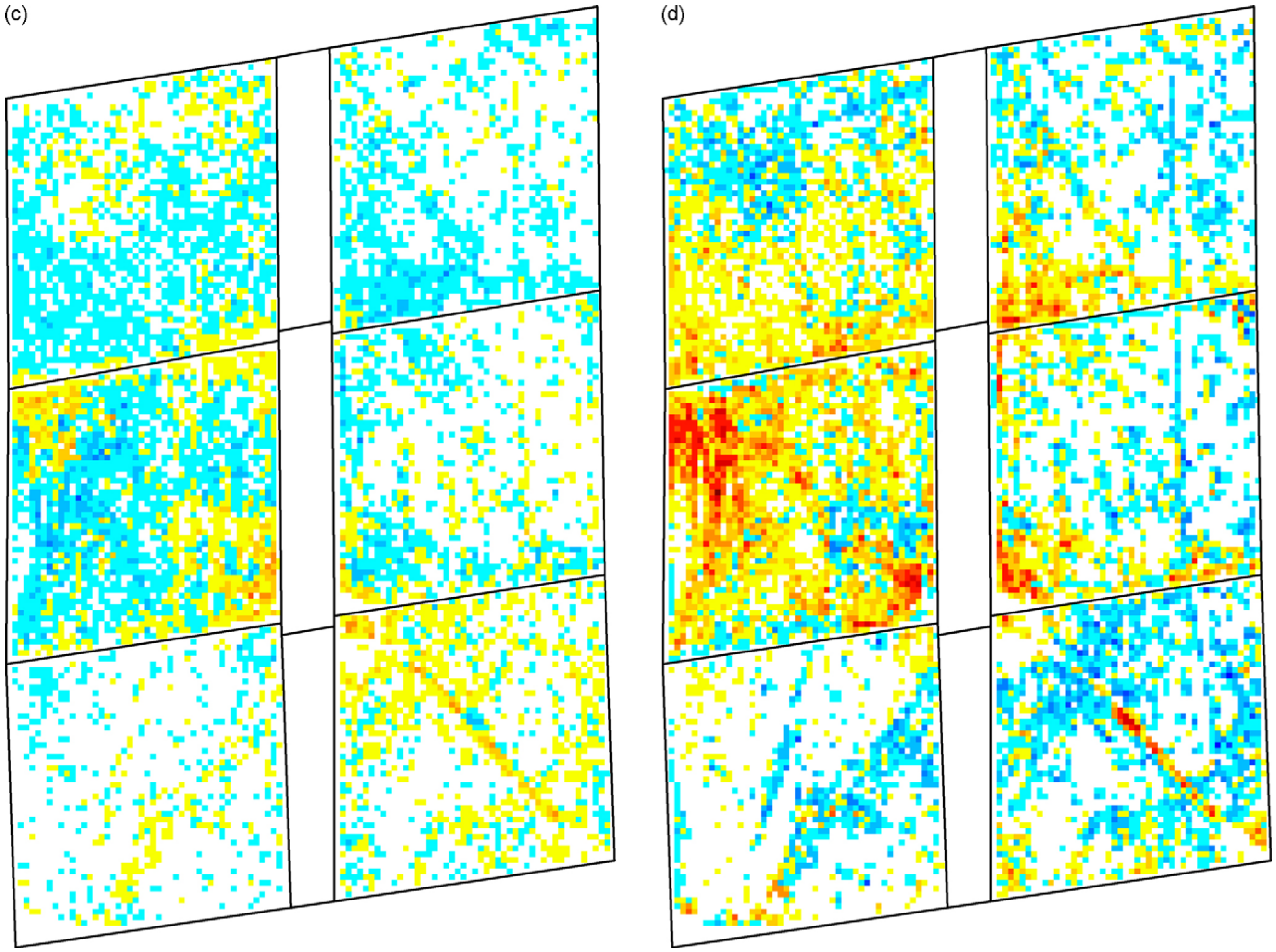

Fig. 2. (*Continued*).

4. Discussion

The results presented in this paper provide insights into the mechanisms of herbivore impacts on vegetation, by linking spatial information about vegetation change with measurements of defoliation rate and animal behaviour. The use of detailed vegetation maps, made possible by remote sensing techniques, allowed an examination of the relationships between vegetation change and herbivore activity at different scales. The remote sensing procedures were based on two sets of images taken at the beginning and the end of the experiment, 1998 and 2001, respectively. No replicate images were available within years, thus preventing a rigorous error analysis. However, due to the very high resolution of the images and the large spectral contrast between grass and heather, it was considered to be unlikely for systematic errors to occur in the remote sensing procedures, which in turn could have effected the vegetation change analysis.

At the largest scale, over the whole 6 ha, the results indicate that the presence of sheep led to changes in some areas from vegetation dominated by dwarf shrubs to vegetation dominated by a mixture of grasses and blaeberry, while grass cover changed very little. At the intermediate (1 ha plot) scale, the results show large variations between plots which were clearly not related to sheep stocking rate, but could have been influenced by spatial differences in behaviour and/or differences in initial vegetation cover. At the smallest scale, the spatially explicit grid-based analysis showed that vegetation change was spatially heterogeneous

Table 2
Net changes in the area covered by grass and mixed vegetation at resting sites and over the whole plot, using data for grass patches that existed in both 1998 and 2001

Plot	Grass (m^2)		Mixed vegetation (m^2)	
	Resting sites	Whole plot	Resting sites	Whole plot
1	32	−68	−24	−115
2	20	−82	24	152
3	7	−146	19	169
4	6	−14	1	−50
5	132	163	126	576
6	14	34	−6	66
Total	211	−113	140	798

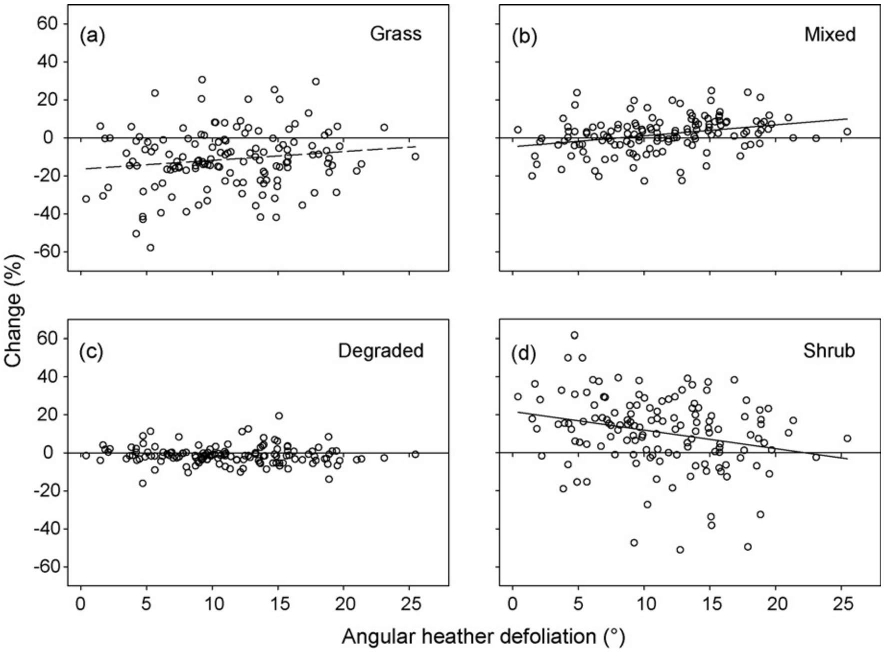

Fig. 3. Scatter plots and corresponding regression lines (dashed if $P > 0.05$) showing the percentage change in cover of (a) grass ($R^2 = 1.1\%$, $P = 0.115$) (b) mixed ($R^2 = 8.9\%$, $P < 0.001$) (c) degraded heather and (d) shrub ($R^2 = 5.2\%$, $P < 0.01$) classes within patches ($n = 137$) between 1998 and 2001, plotted against mean angular heather defoliation within the first 0.5 m of two transects drawn uphill and downhill from the grass-heather boundary.

within plots, with large changes concentrated in small areas and small changes spread relatively evenly across the plots. The patch-based analysis, linking vegetation change with direct observations of sheep behaviour, offers some explanation for these differences. It appears that, while heather defoliation accounts for the smaller, disaggregated changes, the concentration of resting behaviour in some areas close to the fences could explain the larger, spatially aggregated changes in vegetation.

The increase in mixed vegetation at the expense of shrub is consistent with previous work on the impact of herbivores on heather-grass mosaics (Thompson et al., 1995; Hester et al., 1996; Hester and Baillie, 1998; Palmer and Hester, 2000). Grazing by sheep and red deer has been identified as a major factor causing shifts from heather moorland to unimproved grassland (Thompson et al., 1995; Hester et al., 1996), and it has been suggested that heavy defoliation of heather plants, beyond a threshold of 40% or less of the current season's shoots, will inevitably lead to a reduction in heather cover (Grant et al., 1978; Palmer and Hester, 2000). Other research has also shown that the impact of grazing varies according to the spatial pattern of the vegetation (Grant et al., 1978; Clarke et al., 1995b, Hester and Baillie, 1998; Palmer et al., 2003). However, notably only one of these studies (Hester and Baillie, 1998, but without photographic vegetation change data) attempted to separate spatially the effects of grazing versus trampling, which have been clearly shown in this experiment to be locationally different. This has important implications for herbivore management in woody vegetation mosaics, as well as the location of water troughs and other management activities which influence patterns of animal movement.

Since the experiment was carried out using a natural mosaic, there were inevitably differences in the spatial pattern of the vegetation in the various plots (see Fig. 1) and vegetation pattern can clearly affect animal movements and behaviour (Clarke et al., 1995a, Hester et al., 1999; Dumont et al., 2002). Clarke et al. (1995a) and Dumont et al. (2002), for example, both showed that increased fragmentation of preferred vegetation reduced the amount of time spent feeding on it. Previous experiments have also shown that heather defoliation is generally negatively correlated with distance from grass patches (Clarke et al., 1995b; Hester and Baillie, 1998; Oom and Hester, 1999; Palmer et al., 2003). Therefore in the experiment reported here, we propose that the variable patch distribution and sizes are likely to have directly affected the patterns of heather utilization across the plots. Indeed, these effects seem to have been so important as to completely mask any overall effects of stocking density, which has strong implications for management regimes that use stocking density as a means of prescribing grazing on these vegetation types (Scottish Office, 1997; Gordon et al., 2004; Scottish Executive, 2004). As stated earlier, the sheep stocking densities applied in this experiment could not be used to explain the between-plot differences in vegetation change. In contrast, spatially aggregated patterns of behaviour (i.e. resting) clearly played an important role and these would have been driven, in part, by the initial spatial patterns of vegetation in the different plots. In addition to spatial pattern, it is also worth noting

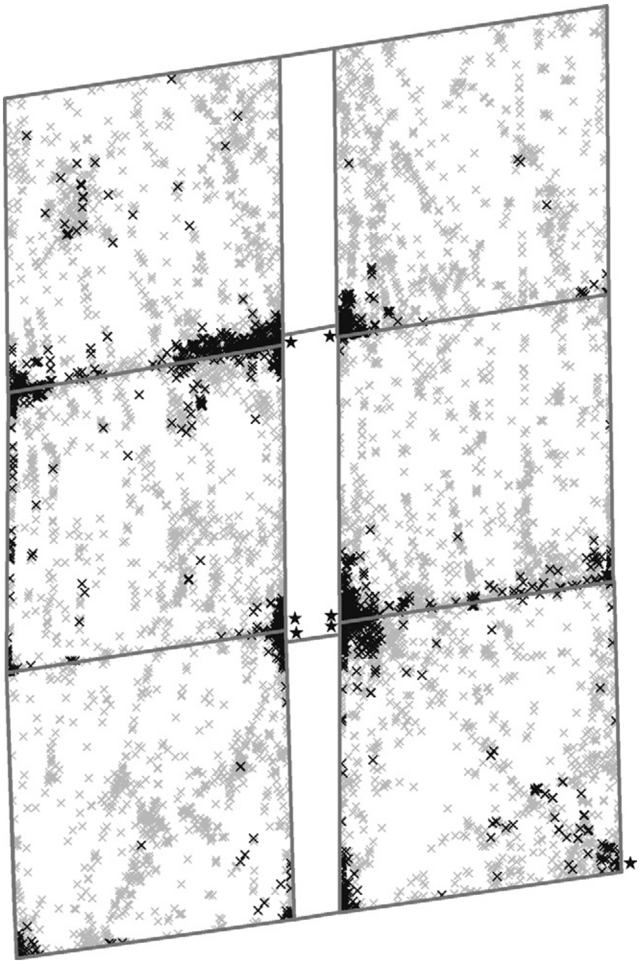

Fig. 4. Map showing all individual locations recorded for resting sheep (black cross) and grazing or walking sheep (grey cross) during the 11-day observation period in 2001, with stars indicating entrances to the plots.

here that the initial condition of the vegetation may also have influenced vegetation change, but to a lesser extent. For example, although Plots 1 and 5 shared the same stocking rate, Plot 5 was initially characterised by highly fragmented heather cover of generally poor quality, while Plot 1 contained more vigorous and less fragmented heather. It is known that old heather can withstand grazing less well than young heather (Grant et al., 1981; Palmer and Hester, 2000) and, in this experiment, Plot 5 showed the biggest decrease in shrub vegetation, while Plot 1 showed the only significant increase.

An earlier analysis of the heather defoliation data, using a spatial interaction model (Oom et al., 2002), suggested that the rate of heather defoliation at any location was influenced by the attractiveness of the nearest grass patch, attractiveness being defined as a function of patch area and distance of the patch from the defoliation site. However, heather defoliation and resting behaviour had spatial patterns of impact that were distinctly different from one another. Heather defoliation led to a disaggregated pattern of vegetation change across the plots, with the main change being from shrub to mixed vegetation, rather than grass. In contrast, the large impact on vegetation which appeared to result from resting behaviour showed a highly aggregated pattern of change, again with shrub changing to mixed vegetation but also, significantly, changing to grass. In management terms, this suggests that complete loss of heather may be more strongly associated with resting areas than grazing areas.

It is well known that Scottish Blackface sheep establish relatively small night-time resting areas (Hunter, 1962; Hester et al., 1999), leading to concentrated trampling, soil compaction and defecation (Hunter, 1962; Taylor et al., 1987) and the pattern of resting behaviour in this study is consistent with this. Studies of sheep in hilly areas have shown that they tend to rest high up overnight and move into lower areas during the day (Lynch et al., 1992). Although observations could only be made during daylight hours in this experiment, it is unlikely that the sheep would have chosen different resting areas at night, due to the relatively small size of the plots and the lack of topographical variation within them. Comparison with results of an earlier experiment with sheep and red deer on the same site (Hester et al., 1999) showed some interesting differences which we believe also indicate the importance of vegetation pattern in defining patterns and distribution of herbivore behaviour. Firstly, there were very few large grass patches in the plots during the study of Hester et al. (1999), and sheep tended to spread out over the smaller patches to rest on their own. During the years between the two experiments, several large grass patches developed as a result of trampling/lying damage inflicted on the heather in areas that the red deer had used for resting (Hester et al., 1999); the ground initially became bare and was then colonised by grass. In the experiment reported here, the sheep tended to congregate on these large grass patches, as would be predicted from previous work (Clarke et al., 1995a; Hester and Baillie, 1998; Hester et al., 1999). Secondly, it is possible that the sheep in this experiment were less willing to spread out across the smaller patches and/or more willing to stay together because they had stronger social bonds between them. The sheep in this experiment had been kept in their small groups and prevented from mixing with other sheep for 6–8 weeks before the observations were made. In contrast, those in the earlier experiment were picked from a large flock at random and formed into groups only when they were introduced to the plots (Hester et al., 1999). It has been shown that, within domestic sheep breeds, familiarity increases the strength of social bonds between animals (Boissy and Dumont, 2002; Winfield et al., 1981) and particular associations between individuals can be detected in small groups of peers established for a period of just a few weeks (Sibbald et al., 2005). These differences have important implications for choice of animal groups and study sites for animal experiments and highlight the importance of taking such factors into account in inter-study comparisons and wider extrapolation of results.

In conclusion, from the different impacts of defoliation and resting behaviour shown here, it is clear that herbivore foraging should not be considered as a single process when studying the impact of herbivores on vegetation. Instead, the various components of foraging behaviour should be considered separately. A better understanding of the effects of the different behavioural processes, and their spatial characteristics, is crucial for predicting and managing herbivore impacts in heterogeneous environments.

Acknowledgements

We thank Russell Hooper and Roslyn Anderson for their assistance with the animal observations and Bill Ekin for his excellent photography. Alan Duncan, Glenn Iason and Han Olff made helpful comments on earlier drafts. Sander Oom thanks the Macaulay Development Trust for the funding of his work. Angela Sibbald, Alison Hester and David Miller were funded by the Scottish Executive Environment and Rural Affairs Department.

References

Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465–479.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., Sims, P.L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. J. Range Manage. 49, 386–400.

Bartolomé, J., Plaixats, J., Fanlo, R., Boada, M., 2005. Conservation of isolated Atlantic heathlands in the Mediterranean region: effects of land-use changes in the Montseny biosphere reserve (Spain). Biolog. Conserv. 122, 81–88.

Boissy, A., Dumont, B., 2002. Interactions between social and feeding motivations on the grazing behaviour of herbivores: sheep more easily split into subgroups with familiar peers. Appl. Anim. Behav. Sci. 79, 233–245.

Clarke, J.L., Welch, D., Gordon, I.J., 1995a. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. J. Appl. Ecol. 32, 166–176.

Clarke, J.L., Welch, D., Gordon, I.J., 1995b. The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. II. The impact on heather. J. Appl. Ecol. 32, 177–186.

Dumont, B., Carrère, P., D'Hour, P., 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Anim. Res. 51, 367–381.

European Commission, 2006. Communication from the commission. In: Halting the Loss of Biodiversity by 2010 and Beyond: Sustaining Ecosystem Services for Human Well-being, European Commission, Brussels.

Genstat, 2002. Genstat, 6th Edition, Copyright 2002. Lawes Agricultural Trust, Rothhamsted.

Gimingham, C.H., 1972. Ecology of Heathlands. Chapman and Hall, London.

Gordon, I.J., Hester, A.J., Festa-Bianchet, M., 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. J. Appl. Ecol. 41, 1021–1031.

Grant, S.A., Barthram, G.T., Lamb, W.I., Milne, J.A., 1978. Effects of season and level of grazing on the utilization of heather by sheep. 1. Responses of the sward. J. Brit. Grassland Soc. 33, 289–300.

Grant, S.A., Hamilton, W.J., Souter, C., 1981. The responses of heather dominated vegetation in north-east Scotland to grazing by red deer. J. Ecol. 69, 189–204.

Green, D.R., Hartley, S., 2000. Integrating photointerpretation and GIS for vegetation mapping: some issues of error. In: Alexander, R.W., Millington, A.C. (Eds.), Vegetation Mapping: from Patch to Planet. John Wiley & Sons Ltd., pp. 103–134.

Heady, H.F., Child, R.D., 1994. Rangeland Ecology and Management. Westview Press.

Hester, A.J., Baillie, G.J., 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. J. Appl. Ecol. 35, 772–784.

Hester, A.J., Gordon, I.J., Baillie, G.J., Tappin, E., 1999. Foraging behaviour of sheep and red deer within natural heather/grass mosaics. J. Appl. Ecol. 36, 133–146.

Hester, A.J., Miller, D.R., Towers, W., 1996. Landscape scale vegetation change in the Cairngorms, Scotland, 1946–1988: implications for land management. Biolog. Conserv. 77, 41–51.

Hunter, R.F., 1962. Home range behaviour in hill sheep. In: Crisp, D.J. (Ed.), Proceedings of the Third Symposium British Ecological Society: Grazing in Terrestrial and Marine Environments. Blackwell Scientific Publications, pp. 155–171.

Jackson, D.L., McLeod, C.R. (Eds.), 2002. Handbook on the UK status of EC Habitats Directive interest features: provisional data on the UK distribution and extent of Annex I habitats and the UK distribution and population size of Annex II species, Revised 2002. JNCC Report 312, 1–180.

Lynch, J.J., Hinch, G.N., Adams, D.B., 1992. Grazing behaviour in sheep. In: The Behaviour of Sheep, CAB International, Wallingford, pp. 9–47.

Mackey, E.C., Shaw, P., Holbrook, J., Shewry, M.C., Saunders, J., Hall, J., Ellis, N.E., 2001. Natural Heritage Trends, Scotland 2001. Scottish Natural Heritage, Battleby, Perth.

Martin, P., Bateson, P.P.G., 1986. Measuring Behaviour: an Introductory Guide. Cambridge University Press.

Oom, S.P., 2003. Pattern and process in the fragmentation of heather moorland. Unpublished Phd thesis, University of Edinburgh.

Oom, S.P., Hester, A.J., 1999. Heather utilization along paths by red deer and sheep in a natural heather/grass mosaic. Bot. J. Scotland 51, 23–28.

Oom, S.P., Hester, A.J., Elston, D.A., Legg, C.J., 2002. Spatial interaction models: from human geography to plant-herbivore interactions. Oikos 98, 65–74.

Pakeman, R.J., Hume, P.D., Torvill, L., Fisher, J.M., 2003. Rehabilitation of degraded dry heather [*Calluna vulgaris* (L.) Hull] moorland by controlled sheep grazing. Biolog. Conserv. 114, 389–400.

Palmer, S., Hester, A.J., 2000. Predicting spatial variation in heather utilization by sheep and red deer within heather/grass mosaics. J. Appl. Ecol. 37, 616–631.

Palmer, S.C.P., Hester, A.J., Elston, D.A., Gordon, I.J., Hartley, S.E., 2003. The perils of having tasty neighbours: grazing impacts of large herbivores at vegetation boundaries. Ecology 84, 2877–2890.

Rodwell, J.S., 1991. Mires and heaths. British Plant Communities, 2. Cambridge University Press.

Rodwell, J.S., 1992. Grasslands and montane communities. British Plant Communities, 3. Cambridge University Press.

Scottish Executive, 2004. The Rural Stewardship Scheme 2005. Web-only publication: http://www.scotland.gov.uk/Publications/2004/04/19163/35139.

The Scottish Office, 1997. Countryside Premium Scheme. In: Scottish office Agriculture, Environment and Fisheries Department, The Stationery office, Edinburgh.

Sibbald, A.M., Hooper, R.J., 2003. Trade-offs between social behaviour and foraging by sheep in heterogeneous pastures. Behav. Proc. 61, 1–12.

Sibbald, A.M., Elston, D.A., Smith, D.J.F., Erhard, H.W., 2005. A method for assessing the relative sociability of individuals within groups: an example with grazing sheep. Appl. Anim. Behav. Sci. 91, 57–73.

Snedecor, G.W., Cochran, W.G., 1989. Statistical Methods. Iowa State University Press, Ames.

Spedding, C.R.W., 1971. Grassland Ecology. Clarendon Press, Oxford.

Taylor, J.A., Robinson, G.G., Hedges, D.A., Whalley, R.D.B., 1987. Camping and feces distribution by merino sheep. Appl. Anim. Behav. Sci. 17, 273–288.

Thompson, D.B.A., Hester, A.J., Usher, M.B., 1995. Heaths and Moorlands: Cultural Landscapes. HMSO, Edinburgh.

Tudor, G., Mackey, E.C., 1995. Upland land cover change in post-war Scotland. In: Thompson, D.B.A., Hester, A.J., Usher, M.B. (Eds.), Heaths and Moorlands: Cultural Landscapes. HMSO, Edinburgh, pp. 28–42.

Watt, S.A., 1947. Pattern and process in the plant community. J. Ecol. 35, 1–22.

Weber, G.E., Jeltsch, F., Van Rooyen, N., Milton, S.J., 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. J. Appl. Ecol. 35, 687–699.

Webb, N.R., Rose, R.J., Clarke, R.T., Traynor, C.H., 2000. Heathland changes in Dorset, England, between 1987 and 1996. Biolog. Conserv. 93, 117–125.

Winfield, C.G., Syme, G.J., Pearson, A.J., 1981. Effect of familiarity with each other and breed on the spatial behaviour of sheep in an open field. Appl. Anim. Ethol. 7, 67–75.