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Spatial interaction models: from human geography to plant-herhivore interactions

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The spatial pattern of defoliation by mammalian herbivores across vegetation mosaics bas been frequently discussed, but rarely spatially quantified. Here we considered the role of plant-herbivore interactions in determining the spatial distribution of shrub defoliation by a large mammalian herbivore across a grass-shrub mosaic.

We investigated the spatial pattern of heather defoliation by sheep in heather-grass mosaics. Heather-grass mosaics are two-phased vegetation mosaics, in which a spatially localized plant community (grass) fulfils nutritional needs, whilst a spatially extensive plant community (heather) meets energy requirements but is nutritionally marginal.

We used a spatial analysis method, originating from human geography, to show that heather defoliation was not spread across the mosaic homogeneously, but that the spatial pattern was determined by geometric characteristics of the mosaic, grazing intensity, and the contrast between preferred and less preferred communities.

The spatial analysis method proved to be a powerful tool to describe the spatial pattern of shrub defoliation. Applications of the method are explored and the implications of the spatial distribution of shrub defoliation are discussed.

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This paper considers the spatial distribution of shrub defoliation by a large mammalian herbivore across a grass-shrub mosaic. A grass-shrub mosaic is an example of a two-phased vegetation mosaic, in which a spatially localized (preferred) plant community fulfils nutritional needs, whilst a spatially extensive (less preferred) plant community meets energy requirements but is nutritionally marginal (McNaughton and Banyikwa 1995). The less preferred plant community plays a crucial role in the stability of plant-herbivore systems, as the herbivores can switch to the less preferred plant community when the preferred plant community is unavailable (Wallis de Vries 1991, Illius and O'Connor 2000). Management of these two-phased mosaics requires different strategies for different range management objectives. Sustainable animal production requires a balance between preferred and less preferred plant communities that is favourable to the herbivore (Archer 1996), whilst nature conservation is aimed at maintaining or increasing important flora and fauna. Limited understanding of the complexity of these ecosystems can lead to inappropriate management strategies (Bailey et al. 1998).

Spatial heterogeneity plays an important role in ecological processes (Kotliar and Wiens 1990, Kolasa and Pickett 1991). The study of plant-herbivore interactions in two-phased vegetation mosaics requires a spatial approach (Noy-Meir 1981, McNaughton 1984, Senft et

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al. 1987, Coughenour 1991, Archer 1996, Bailey et al. 1996). Although the spatial distribution of defoliation is influenced by both abiotic and biotic factors (Bailey et al. 1996), here we considered only the biotic factors: forage biomass, digestibility and nutritional content. Based on these biotic factors, Senft et al. (1987) predicted spatial patterns of defoliation at community, landscape and regional scale. Focusing on the community scale, herbivores are predicted to select for the highest quality plant community, resulting in overmatching (Staddon 1983) as the proportion of the plant community in the diet exceeds the proportion of that plant community in the vegetation mosaic.

The prediction of overmatching at the community scale has implications for the spatial distribution of defoliation of preferred and less preferred plant communities at this scale. As herbivores focus their grazing on the preferred community, their use of the mosaic will be concentrated on those areas of the mosaic where the preferred community is abundant. Further, the defoliation of the less preferred community will be strongly influenced by the pattern of use of the mosaic. Thus the spatial pattern of defoliation of the less preferred community is expected to be strongly correlated with the distribution of the preferred community.

Spatial heterogeneity in defoliation patterns has been discussed and modelled in several two-phased vegetation mosaics (Ring et al. 1985, Archer 1994, Wallis de Vries 1996, Morellet and Guibert 1999, Bokdam and Gleichman 2000, Weber et al. 2000), but the spatial pattern of defoliation has, as far as we can ascertain, only been quantified for heather moorland (Clarke et al. 1995a, Hester and Baillie 1998).

A series of experiments in the North-East of Scotland has investigated the spatial plant-herbivore interactions within heather moorland, an internationally important natural resource for recreation and wildlife conservation (Gimingham 1972, Thompson et al. 1995). This heather moorland consisted of grass (mainly *Agrostis capillaris* L. and *Festuca ovina* L.) dominated patches in a heather (*Calluna vulgaris* (L.) Hull) dominated matrix. Grass patches were either artificially created in the heather matrix (Clarke et al. 1995a) or part of a natural heather-grass mosaic (Hester and Baillie 1998). The proportion of grass in the vegetation mosaics varied between 15% and 20%. For both experimental sites, Cuartas et al. (2000) found that sheep (*Ovis aries*) and red deer (*Cervus elaphus* L.) showed overmatching of grass consumption, as the proportion of grass in the diet was at least a factor of two higher than the proportion of grass in the vegetation mosaic.

Clarke et al. (1995a) found that heather defoliation by sheep is higher near the edge grass patches than further away. This is confirmed for natural grass patches (Hester and Baillie 1998) and for paths (Oom and Hester 1999). Clarke et al. (1995a) also found that heather defoliation at the edge of grass patches increases with grass patch size. This effect is confirmed for red deer, but not for sheep, foraging in natural heather-grass mosaics (Hester and Baillie 1998).

To investigate the correlation between the spatial pattern of defoliation and vegetation pattern, we employed a spatial analysis method originating from human geography. Many questions in human geography involve interactions between spatial distributions of resources and consumers. In order to study and predict spatial patterns of consumer behaviour as a function of resource patterns, a range of spatial interaction models (SIM) has been developed (see for review: Sen and Smith 1995, Fotheringham et al. 2000). Geographers realized that many individual spatial behaviour decisions by consumers can lead to an aggregated pattern of movement. This aggregation effect has also been suggested for foraging decisions by herbivores (Staddon 1983). SIMs attempt to describe these aggregate patterns.

SIMs have been successfully used to predict road network usage, to predict optimal locations for supermarkets and petrol stations in relation to urban areas and to predict the felling probability of a patch of forest depending on the distance to wood mills. The first equations used in SIMs resembled Newton's law of gravity, and were thus named gravity models. In parallel with the law of gravity, SIMs predict the attraction at a given location based on the distance between the current location and the resource, and the attractiveness of a resource (where attractiveness is the product of the resource magnitude and the attractiveness per unit resource). The basic SIM contains a distance-decay function which predicts that the attraction of a resource will decrease with distance. For many spatial choice processes a quadratic distance-decay function has been applied, leading to the basic SIM:

$$\text{attraction} = \frac{\text{attractiveness of resource}}{\text{distance}^2} \tag{1}$$

Using the quadratic distance-decay function assumes the resource of attraction to be a point source. Fig. 1 illustrates the relationship between the predicted attraction and the distance and the attractiveness of the resource. The attraction is then used as a predictor for a response variable. For instance, the probability that people from a suburb will be customers of a particular supermarket can be used to estimate the number of potential customers in supermarkets around a city. A regression analysis determines the relationship between the response variable and the attraction.

SIMs are powerful tools for describing the aggregate pattern resulting from many individual behaviour decisions. At the same time the models are poor in revealing the underlying mechanisms as individual decisions are obscured by the aggregation (Fotheringham et al. 2000). But in the quest to understand spatial foraging behaviour, the regression of defoliation on the SIM can be used to reveal the spatial pattern of vegetation defoliation by herbivores.

Theory

As the defoliation of a less preferred plant community is strongly correlated with the distribution of the preferred community, we used grass as the attraction resource to predict the attraction to sheep at a given location. We assumed a positive correlation between attraction and habitat use and hence defoliation of the less preferred community. We used grass patch area to represent the magnitude of the attraction resource. The resource attractiveness was considered to be constant and was thus ignored in the model. Within the heather-grass mosaics, the grass patches are connected by paths to form a network within a heather matrix. Because habitat use by sheep is strongly confined to this network (Hester et al. 1999), distances were determined as shortest path-distance to the nearest grass patches.

As reviewed in the previous section, heather defoliation generally declines away from the grass-heather edge. But what is the heather defoliation at a given location on the grass-heather edge? To answer this question we investigated the correlation between the attraction at a given location on the network (at the edge of a patch or a path) and the heather defoliation in a 0.50 m wide zone bordering this location (heather edge zone). Entering the basic SIM gave the following regression equation, in which a and b are the regression slope and intercept respectively:

$$\text{heather defoliation} = a + b \times \frac{\text{grass patch area}}{\text{distance}} \quad (2)$$

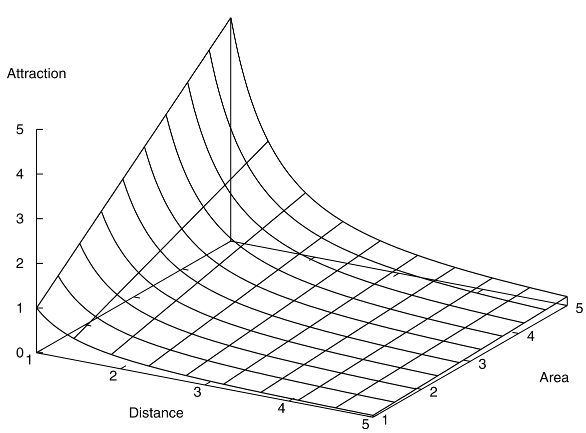

Fig. 1. Surface plot of the attraction (as predicted by the SIM) against the distance to and the attractiveness of a resource (based on eq. 1).

Although it has been shown that herbivores use a mental map of grass patches (Edwards et al. 1996, Roguet et al. 1998, Dumont et al. 2000), it is unknown how they perceive clusters of patches surrounding a given location. We therefore assumed that sheep consider grass patches within a certain radius from their current location, and calculated a cumulative attraction value for several grass patches. This led to a second SIM and a second regression equation (n is the number of patches in the cluster):

$$\text{heather defoliation} = a + b \times \sum_{i \to n}^{n} \frac{\text{grass patch area}_i}{\text{distance}_i^2} \quad (3)$$

The performance of this regression depended on the ability of herbivores to estimate patch area and distance accurately. However, in accordance with both Weber's law (Carlson 1990, Bateson and Kacelnik 1998) and the 'psychophysical law' (Stevens 1957, 1975), animals and humans tend to mentally underestimate a stimulus when the stimulus is strong and the underestimation increases with increasing strength of the stimulus. This leads to a logarithmic relationship between the perceived and the objective strength of a stimulus, In this third SIM we assumed sheep underestimate larger values of both area and distance, leading to the third regression equation:

$$\text{heather defoliation} = a + b \times \sum_{i \to n}^{n} \frac{\log(\text{grass patch area}_i)}{(\log(\text{distance}_i))^2} \quad (4)$$

Although the individual foraging decisions will be influenced by grass patch area and distance, the level of the aggregated heather defoliation will depend on the number of sheep present per unit grass area. We therefore introduced a measure of grazing intensity, leading to the final regression equation which predicted the spatial pattern of heather defoliation at the edge zone in heather-grass mosaics:

$$\text{heather defoliation} = a + b \times \frac{\text{sheep number}}{\text{total grass area}} \times \sum_{i \to n}^{n} \frac{\log(\text{grass patch area}_i)}{(\log(\text{distance}_i))^2} \quad (5)$$

In parallel with theory and observation we expected heather defoliation at the heather edge zone to be higher at the edge of large grass patches than at the edge of small grass patches and heather defoliation, along grass paths, to be higher near grass patches as compared to further away. This would predict a positive correlation between heather defoliation and the attraction predicted by the SIM.

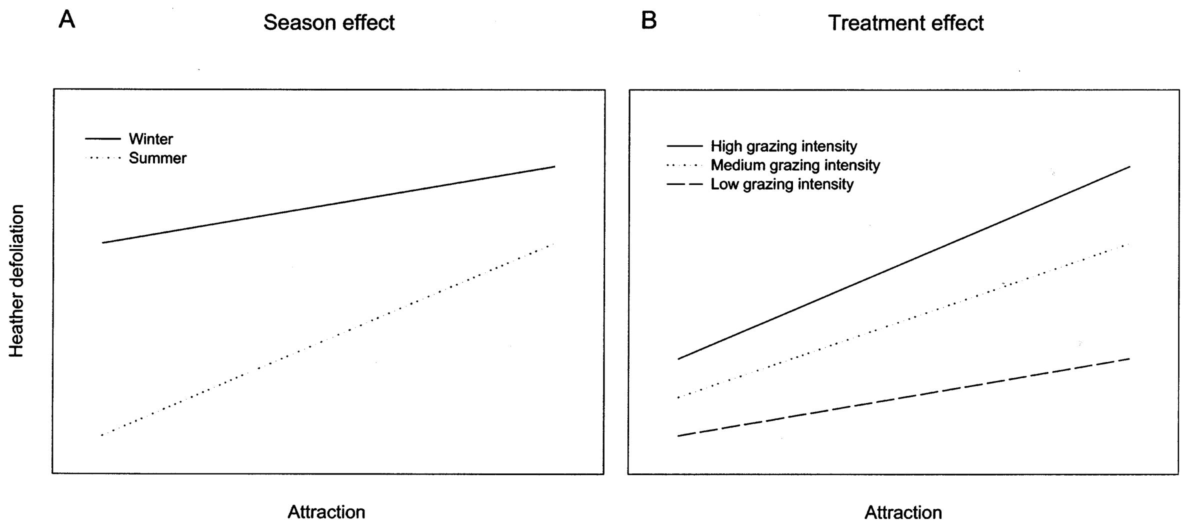

Fig. 2. Hypothetical effects of season and grazing intensity on the relationship between heather defoliation and the attraction (as predicted by the SIM).

As for the effect of season and the grazing intensity, we would expect differences in the slope and intercept of the regression of heather defoliation and the attraction. Grass quantity and quality drop significantly during the winter (Armstrong and Milne 1995), leading to a decrease in contrast between grass and heather. As the relative attraction of grass decreases, the sheep are expected to be less biased by the grass patch area in that season, leading to a decrease in the slope. The increased heather defoliation in the winter would lead to an increase in the intercept (Fig. 2A). When increasing grazing intensity within a season, we would also expect an increase in heather defoliation leading to an increase in the intercept, but we would also expect sheep to remain biased towards the grass, leading to a stronger increase at high attraction values, i.e. near large grass patches, and thus an increase in the slope (Fig. 2B). As larger grass patches become exhausted with higher grazing intensity, sheep are forced on the less attractive areas of the mosaic, leading to an increase in the intercept and thus a decrease in the slope (not shown).

This section describes the parsimonious process of accepting more complexity in subsequent models only when the fit between model and data is improved. Several distance-decay functions were tested, but none performed better than the quadratic distance decay function used in this model. In the following sections we only present the methods and results for the final model.

Methods

Heather defoliation was observed during a three-year experiment (1998–2001) of sheep grazing natural heather-grass mosaics. The experimental site, at the Macaulay Institute's Glensaugh Research Station, consisted of six one-hectare plots, containing natural heather-grass mosaics (described in: Hester and Baillie 1998). The plots were located on a north north-west facing slope with a slope angle of 17°. Three grazing intensity treatments, 2, 3 and 4 sheep per hectare, were applied year round on plots 1 and 5, 2 and 6, and 3 and 4 respectively (Fig. 3). In spring and autumn heather defoliation away from grass-heather boundaries was measured along transects laid out in the field using measuring tapes. To determine transect locations, seven 100 m lines were laid out across each plot along the slope (Fig. 3). A transect was then allocated to each grass-heather boundary, either at a path or a grass patch, crossed by a line. Transects were drawn from the edge of the grass into the heather perpendicular to the grass-heather edge. As the geometry of the paths and patches generally followed the contours, the majority of transects were up- and downhill. Transects going off the same path or grass patch, on any one line, were grouped together into a 'transect location'. This resulted in a total of 358 transect locations. Because of the different mosaics in each plot, the total number of transect locations per plot varied between 36 and 78. Heather defoliation was measured at fixed distances along each transect (0, 0.25, 0.50 m) according to the method described by Hester and Baillie (1998), providing an estimate of the percentage of current year's growth removed at each distance.

A vegetation map was created using colour aerial photographs, specially taken in October 1998 at the start of this experiment, which were digitally scanned from negatives. The resulting digital images were orthorectified, mosaiced and classified using Erdas Imagine (ERDAS 1997). The classification resulted in a vegetation map containing grass patches in a heather matrix. As much as possible, grass patches were defined by the classification process. Where the classification resulted in a conglomerate of individual patches (in approx. 10 cases), individual patches were manually defined according to assumed sheep perception of the mosaics, as derived from previous work on these plots (Hester and Baillie 1998, Hester et al. 1999). However, as the SIM model used in this study evaluates conglomerates of patches in the same way as clusters of individually-defined patches, any division of conglomerates did not affect the results of the SIM analysis. Despite the high resolution of the image (cell size 0.05×0.05 m), the lighting condition and spectral reflectance characteristics of the vegetation (generally low grass cover) prevented the classification of paths. Paths, indicated by an interruption of the heather canopy, were therefore surveyed in the field and manually digitized. The vegetation map and path elements were joined to get a map of a connected grass network in a heather matrix.

The starting point of each transect, at the grass-heather boundary of the path or grass patch, was manually digitized onto the grass network. For each of these transect positions, the distance to the edge of the

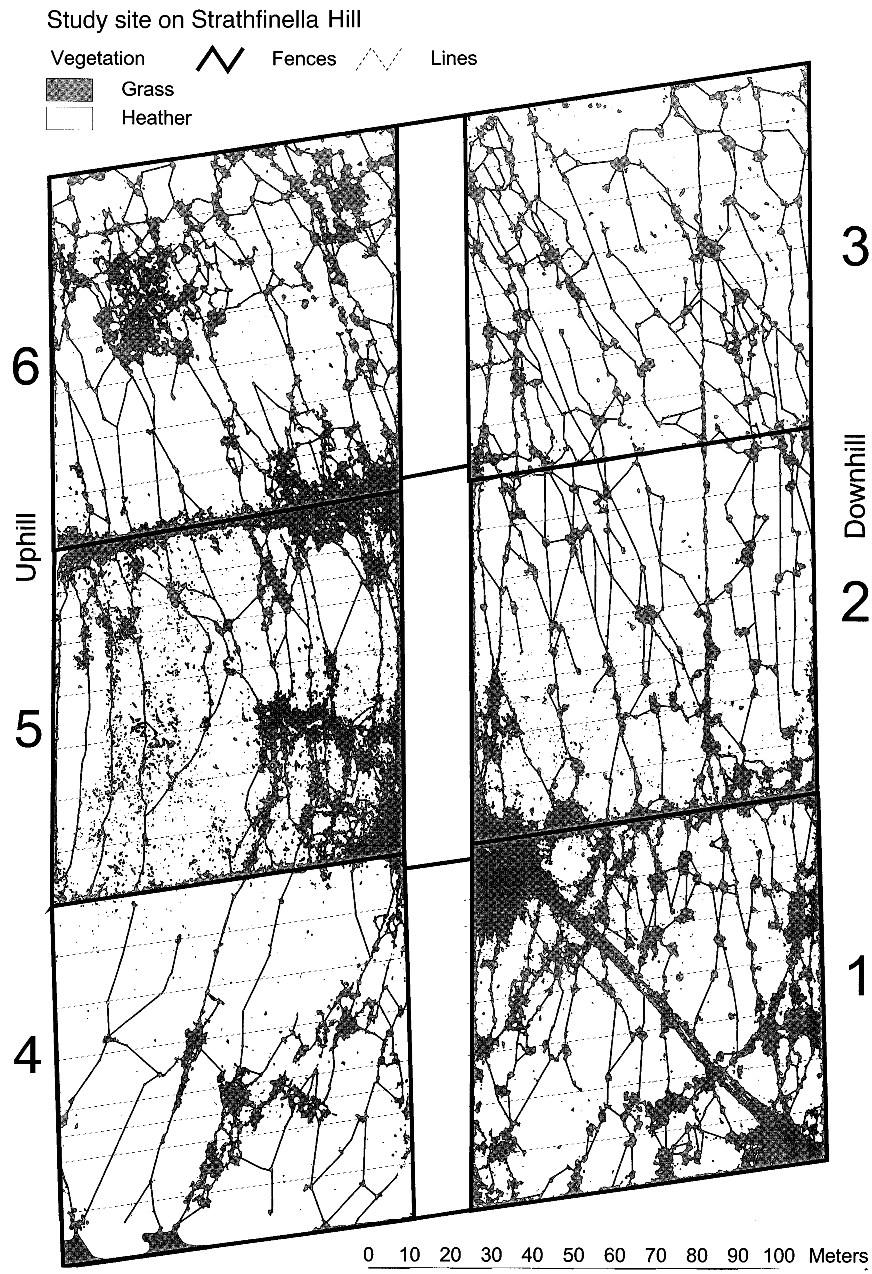

Fig. 3. Vegetation map of the experimental site at Macaulay Institute's Glensaugh Research Station. Dotted lines indicate the lines used to determine transect locations for the measurement of heather defoliation away from grass/heather edges. Numbers indicate the respective plots.

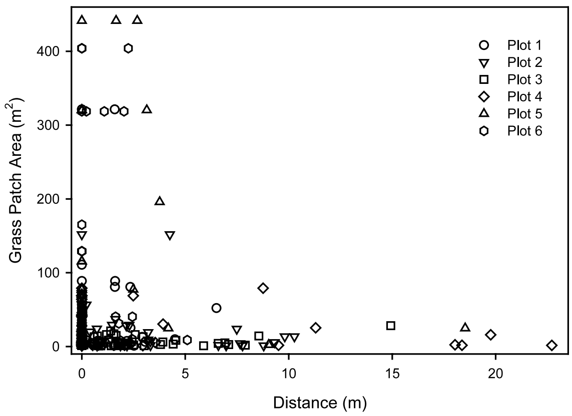

Fig. 4. Scatter plot of grass patch area against distance (for the nearest grass patch) for each transect location (labelled by plot).

nearest grass patch, measured along the grass path, and the associated patch area were determined using the 'cost-distance' function in Arclnfo (ESRI 1997). To accommodate the model, the distance was set to one metre for all distances less than one metre. In order to calculate the cumulative attraction of the cluster of neighbouring patches, we repeated the 'cost-distance' method for each successive larger patch connected with the transect position along the grass network. Because attraction declines rapidly with distance (i.e. distant patches contributing little to the cumulative attraction) we only considered patches within a 25 m radius from the location. All attraction values were summed to get a cumulative attraction for the transect location.

The severity of heather defoliation at the edge of grass patches and paths is known to be higher uphill than downhill (Hester and Baillie 1998, Oom and Hester 1999). But the data analysed here showed no significant difference in the spatial distribution of heather defoliation up- and downhill. Therefore, a single mean was calculated for the six observations at each transect location (i.e. combining the heather defoliation measurements at 0, 0.25 and 0.50 m away from the heather for both the uphill and downhill transects). Because about 90% of the observations had a heather defoliation of less than 25%, i.e. the data were negatively skewed, the percentage heather defoliation was angular transformed before averaging. The transformation resulted in residuals not significantly different from a normal distribution. Values presented in tables and figures are based on transformed data.

The purpose of this analysis was to determine the relationship between the heather defoliation and the attraction predicted by the SIM. A regression analysis was considered most suitable for this purpose, producing slope and variation in slope, while allowing for known effects of the grazing treatment and season. The experimental design was unbalanced, due to the varying number of transects per line. Because of the hierarchical design of transects within lines within plots, correlation in the data may have arisen due to effects of plot, line and transect. To take into account the hierarchical, unbalanced design, we used the Residual Maximum Likelihood (REML) method (Genstat 5 Committee of the Statistics Department-Rothamsted Experimental Station 1993, 1997). REML treats factors, giving rise to different slopes and intercepts, as fixed effects and handles the correlations via the variance components associated with the random effects.

We analysed the heather defoliation data using treatment, season and SIM as fixed effects and plot, line, and transect as the random effects. The regression analysis was based on the mean angular heather defoliation per transect location. For presentation purposes, the scatter plots are based on the average mean angular heather defoliation for ten classes (containing equal numbers of transect locations), calculated with REML, using the same random model as used for the regression analysis.

The output from REML gave a Wald statistic (Genstat 5 Committee of the Statistics Department-Rothamsted Experimental Station 1993, Elston 1998) for each fixed effect added to the model, which provided a significance estimate equivalent to the F-test in an ANOVA. To obtain an estimate of the variance explained by the fixed effects model, an Adjusted R^2 was calculated based on the stratum variance provided by REML. The stratum variances estimate the unexplained variances of means of the different levels for each random effect and are adjusted for the degrees of freedom in the fixed effects model. Because of the hierarchical nature of the random model, a separate Adjusted R^2 had to be calculated for each random effect (plot, line, transect). The stratum specific Adjusted R^2 were calculated using the following formula: $100\% \times (1 - SV_a/SV_n)$. Where SV_a and SV_n are the stratum variances for the alternative model (with fixed effects) and the null model (without fixed effects) respectively.

Results

Across all plots, values for distance ranged from 0 to 23 m, while the values for grass patch area ranged from 1 to 441 m^2. Fig. 4 shows that the values for patch area and distance were not equally represented across the six plots. The analysis for SIM was therefore strongly unbalanced at the plot level, i.e. confounded with the grazing intensity treatment.

There were significant effects for season and the SIM (Table 1), but no significant interactions between fixed effects (not shown). As the season effect was well balanced, with all transects having all seasons, the Wald statistic came out very high. On the other hand

Table 1. Significance of fixed effects of the REML model based on the Wald statistic as calculated using REML. P values have been calculated using the F-value, based on the Wald statistic divided by the numerator degrees of freedom.

Fixed effect	Wald statistic	Numerator df	Denomerator df	P
SIM	28.1	1	1571	<0.001
Treatment	4.6	2	3	NS
Season	296.8	1	1571	<0.001

the treatment effect (sheep per plot) was not well balanced, with only a third of the transects having any one treatment, leading to a non-significant Wald statistic.

The character of the significant effect of the SIM is revealed by Fig. 5. As expected, the relationship between heather defoliation and the attraction predicted by the SIM showed a positive correlation. When the data were analyzed according to season, the same relationship is found for both summer and winter (Fig. 6). The intercept for winter was significantly higher than that for summer, but the slopes were not significantly different (Table 2). The results for treatment and season × treatment interactions, although not significant, have been included for completeness (Table 2).

Much of the variance explained by the fixed model was explained in the plot stratum (42%), with less variance explained in the plot.line (12%) and plot. line. transect (7%) strata (Table 3). The low Adjusted R^2 for SIM, despite the high significance of the regression, was a result of the high variability of the heather defoliation about the regression line (see for example Fig. 7). This small-scale heterogeneity in foraging intensity could be caused by a high variability in the defoliation of individual plants. Hartley et al. (1995) showed that herbivores can use chemical cues to differentiate the quality of individual plants within a species. This was confirmed by visual observation on the experimental plots, which showed that individual heather plants may be heavily grazed whilst neighbouring plants are untouched.

Discussion

In this paper we have shown that a simple SIM based on distance from a grass patch and grass patch area could successfully predict heather defoliation in natural heather-grass mosaics. As foreseen by theory and observations, heather defoliation and the attraction predicted by the SIM were strongly positively correlated. This implies that the heather defoliation was not spread homogeneously across the heather-grass mosaic, but that high heather defoliation locally coincided with low defoliation elsewhere. Furthermore, the positive slope of the regression showed that heather defoliation was positively associated with grass patch area, i.e. heather defoliation decreased with distance away from grass patches and increased with grass patch area.

The SIM approach worked well for sheep foraging in heather-grass mosaics, as their habitat use is strongly confined to the grass network (Hester et al. 1999). When extending the approach to other herbivores, differences in foraging characteristics, such as diet selection and body size (i.e. the ability to walk through high vegetation), might influence the correlation between the SIM and heather defoliation. For example, the correlation might be weaker for red deer, as their use of the heather-grass mosaics is less influenced by the grass

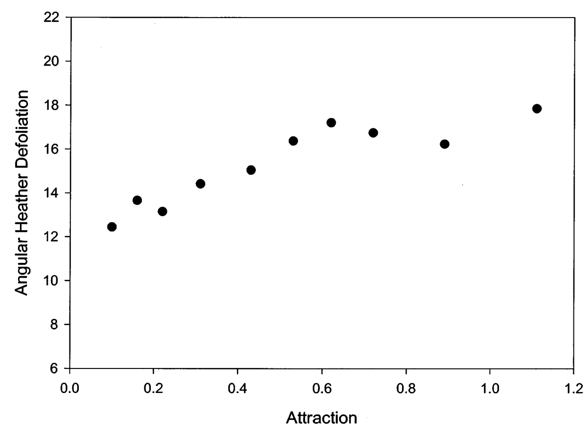

Fig. 5. Scatter plot of mean angular heather defoliation against attraction (as predicted by the SIM). Values are average mean angular heather defoliation for ten classes calculated using REML.

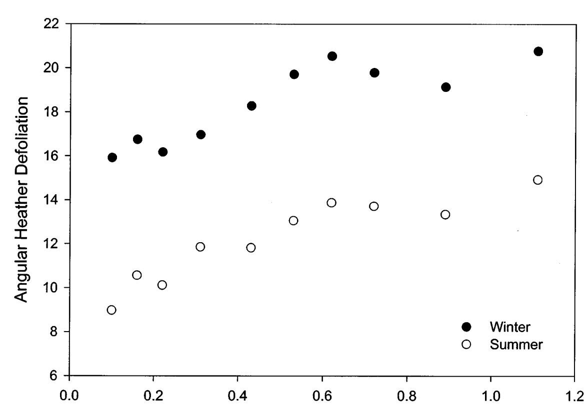

Fig. 6. Scatter plot of mean angular heather defoliation for season against the attraction (as predicted by the SIM). Values are average mean angular heather defoliation for ten classes calculated using REML.

Table 2. Slopes and intercepts for SIM and the interactions between SIM and treatment, and season, including mean standard error of differences (SED). All fixed effects contain the interactions between treatment and season; these have been averaged in the table to match the level at which the regression on SIM has been estimated.

Fixed effects	Slope		SED	Intercept		SED
SIM	5.0			12.8		
SIM.Treat						
Low	4.6			10.8		
Medium	3.8		2.4	13.3		2.5
High	6.9			14.0		
SIM.Season						
Winter	4.6		1.1	16.0		0.7
Summer	5.3			9.6		
SIM.Treat.Season						
	Winter	Summer		Winter	Summer	
Low	4.8	4.5	2.0[1]	14.2	7.4	1.2[1]
Medium	2.6	4.6	2.8[2]	16.7	10.0	2.6[2]
High	6.7	7.0		17.0	11.0	

[1] SED within plot(i.e. Season within Treatment); [2] SED between plots (i.e. all other comparisons); degrees of freedom for SIM and Season $\approx \infty$; degrees of freedom for Treatment = 3.

Table 3. Adjusted R^2 for fixed effects based on the approximate stratum variances as calculated using REML. Adjusted R^2 are calculated for each model compared with the null model (without fixed effects) for each random stratum (plot, plot.line and plot.line.transect).

Stratum	Adjusted R^2 (relative to null model) %			
	Treatment	Season	SIM	SIM × Treatment × Season
Plot	44	1	7	42
Plot.Line	0	0	12	12
Plot.Line.Transect	0	0	7	7
Units	0	18	0	18

network (Hester et al. 1999). On the other hand the strong decline of heather defoliation away from the grass-heather edge suggests that heather defoliation by deer is also strongly influenced by the pattern of grass (Clarke et al. 1995b, Hester et al. 1999).

When extending the approach to other grass-shrub mosaics, the correlation between shrub defoliation and attraction will depend on the contrast in preference between the preferred and less preferred plant community. A decrease in contrast is expected to lead to a decrease in the slope of the regression. The same effect would be expected when comparing two vegetation mosaics of different contrasts in preference. This effect was not shown in this study, despite the fact that the contrast between heather and grass communities decreases during the winter, with grass quality and quantity falling sharply and heather quantity and quality falling only slowly (Armstrong and Milne 1995). We can only speculate that the grass availability was low throughout the year, or that patch geometry had an overruling influence on sheep foraging behaviour.

The SIM can be applied in three ways in addition to the application described above. Firstly the model could be used to derive a spatially explicit sampling scheme for a grazing impact study. The model from Equation 3 (i.e. without considering grazing intensity) could be used to calculated attraction values for a given vegetation map. Based on this map, a sampling

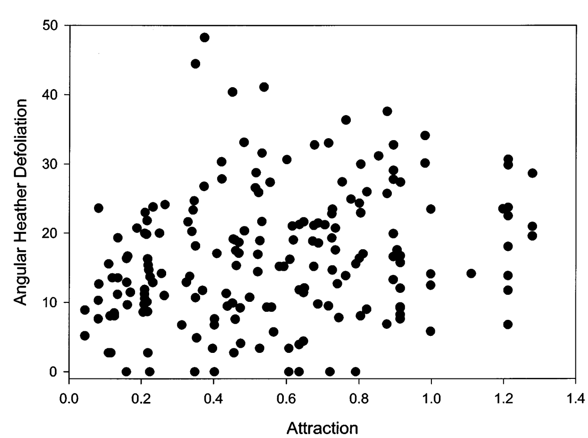

Fig. 7. Scatter plot of angular heather defoliation against attraction (as predicted by the SIM) for a subset of observations, to illustrate variation between transects. The scatter plot is based on mean angular heather defoliation per transect (up- and downhill), averaged across three years. Observations included are for winter defoliation in plots with the high grazing intensity treatment (i.e. one value for each transect in plots 1 and 5; n = 189).

scheme could be deployed to quantify the slope of the regression between heather defoliation and the attraction. The slope of the regression will differ with different plant communities, different herbivores and different grazing intensities. Secondly the SIM provides a tool to extrapolate heather defoliation measurements from part of a mosaic across the whole mosaic, using the regression between heather defoliation and the attraction. The result is an interpolation surface of predicted heather defoliation based on locations with known heather defoliation. Thirdly the predictions of the SIM can be used to test predictions of more mechanistic spatially explicit foraging models, such as SAVANNA (Coughenour 1993), EASE (Moen et al. 1997) and the model developed by Turner et al. (1993). None of these models consider grass-heather mosaics, but do consider other grass-shrub combinations. The interpretation of these model outputs has focussed on the animal performance as a result of the interaction between foraging behaviour and the spatial distribution of the resources. However, these models do produce spatially explicit output which could be tested against the predictions of the SIM. Again, the strength of the SIM is in predicting the pattern of defoliation, such that the testing of model predictions should be through correlation.

The results of this study have two major implications for the management of grass-shrub mosaics. Firstly, the management of the balance between preferred (grass) and less preferred plant communities (shrub) strongly depends on the characteristics of the vegetation pattern. In highly fragmented mosaics, in which grass and shrub are intimately mixed, a large proportion of the less preferred community cover will be affected by herbivores, whilst in lightly fragmented mosaics large areas of the less preferred community will be little affected. This supports the more detailed discussions in Hester and Baillie (1998) and Clarke et al. (1995a). Secondly, as the spatial distribution of herbivore foraging is dictated by the spatial pattern of resources, it is expected that the spatial pattern of defoliation can be influenced by changing the spatial characteristics of the vegetation. For example, creating a grazing lawn dominated by a preferred species in one location, might relieve grazing intensity elsewhere in the mosaic.

We have shown that a simple SIM could be used to describe the spatial pattern of heather defoliation in heather-grass mosaics. The method should be applied to other grass-shrub mosaics and to other habitat use indicators (e.g. dung distribution, trampling). The method could thus serve as a simple but powerful tool to describe the spatial patterns of habitat use. Insights generated by the description of spatial patterns should then be used to develop more mechanistic hypotheses, which can then be tested in experimental studies. Only with increased mechanistic understanding of spatial plant-herbivore interactions, could SIMs ultimately be dismissed as being too descriptive.

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