The use of GPS to study the associations between cattle activity and vegetation within the Limestone Pavements of the North Yorkshire Dales National Park

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Summary

1. Extensively managed upland agricultural landscapes have been in decline over the past decades. Agricultural intensification and increased stocking densities of sheep, driven by government policy and agricultural subsidy, have led to a loss of mixed farming systems. These management practices have led to a decline in species and habitat structural diversity. Recent agricultural policy has become more sympathetic to conservation objectives, and agri-environment schemes are reducing stocking densities and reintroducing mixed farming systems.
2. Limestone grasslands are an important habitat for which maintenance by grazing is essential to maintain botanical diversity. However, both over- and under- grazing are resulting in the deterioration of many such sites. The creation of sward heterogeneity through grazing has been theorised to increase plant diversity, while cattle have been theorised to be the best grazers for plant diversity due to their relative lack of selectivity.
3. In the present study, the movements and behaviour of native breed cattle on two limestone pastures within the North Yorkshire Dales National Park (Sulber and High Brae) were investigated using GPS collars. In particular, the intensity of spatial usage by the cattle was investigated using various methods to estimate the home ranges of the cows and their utilization distribution (UD).
4. Home range analysis of the movements of the cattle was undertaken using three different techniques: Minimum Convex Polygons (MCP), Kernel analysis and LoCoH. Neither MCP nor Kernel analysis accurately reflected the actual movement of the cattle. Both techniques included large areas of the fields within their estimates of the cattle’s home ranges that were rarely used by the animals. LoCoH proved a much better technique for estimating the utilization of the fields by the cattle.

5. Compositional analysis of habitat use by the cattle was undertaken to investigate whether the cattle were making any preferences with regard to the habitat that was available to them. When the habitat composition within the 100% home ranges (using any of the techniques) of the cattle were compared with the area available to them, it was found that habitats were used at a level that reflected their availability *i.e.* the cattle were not making any preferences. However, the 90% utilization distribution estimated by LoCoH was significantly smaller than the 100% area and the compositional analysis of this area showed that the cattle, while grazing on most habitats in proportion to their availability, were significantly avoiding the calcareous grasslands.
6. Over the past 5 years, vegetation surveys have been undertaken to compare fields within the Limestone Country Project with varying level of grazing. However, the results from these surveys have been largely inconclusive. These past surveys were generally made by taking random quadrats within the fields. The present study suggested that, as there are areas within the studies fields that had high concentrations of cattle activity and large areas that were mainly unused by the cows, that this random sampling approach may not be appropriate. Instead, vegetation surveys were undertaken in relation to the intensity of cattle activity. to determine whether the cattle were having any effects on the vegetation. This approach involved directing the vegetation sampling to compare areas of different cattle usage. This animal-orientated vegetation sampling gave significantly different results to those obtained from randomly selecting quadrats. Another major finding of the current vegetation survey was that existing phase I NVC maps upon which the compositional analysis was based were inaccurate when compared to the survey data.

7. Numerous associations between individual species and the level of cattle activity were detected, most of which were positive and consistent with prevalent theories of plant-trait mediated associations with grazing. Species richness and Shannon diversity index were positively associated with cattle activity in Sulber but not in High Brae. Environmental factors such as nutrient flow could be masking grazing impacts on diversity in the latter field. Sward heterogeneity did not vary significantly with cattle activity, suggesting this was not the avenue through which grazing was affecting plant diversity. Taller swards were associated with lower cattle activity, but again did not fit patterns of diversity. However, sward thinning and the interactions with underlying environmental heterogeneity may be driving the effects of grazing on the vegetation. The incidence of bare earth was also positively related to cattle activity, suggesting disturbance effects of grazing on community dynamics. The results suggest that the current grazing regime is having positive conservation impacts.
8. The overall results of this study suggest that the use of GPS tracking of grazing animals can play an important role in determining the effects that the animals are having on biodiversity of an area. Furthermore, by using the utilization distributions of the animals it is possible to direct the vegetation sampling to compare those areas that are actually used by the animals with those that they avoid. For managing an area effectively for its biodiversity, it is possible to manipulate the movements of the cattle through both preventative (*e.g.* electric fences) and incentive (*e.g.* water trough location) methods.

Introduction

Background

Extensively managed agricultural habitats have declined dramatically during the last six decades in Europe (Pacha and Petit, 2008). Past government agricultural policies have led to intensification of agricultural practice and overgrazing (Mowle & Bell in Usher & Thompson, 1988). Over the last 40 years, the numbers of native cattle grazing limestone pastures has decreased as they have been replaced by large numbers of sheep (Eastwood and Tallowin, 2007; Newton 2004). This has led to a loss of species and habitat structural diversity. Sheep select the most palatable grasses and herbs to graze, which results in a short, tightly grazed sward with areas of rank grass (Eastwood and Tallowin, 2007). Traditional hardy cattle, on the other hand, are thought to be unselective. Within the limestone pavements, cattle have the additional benefit to conservation objectives as they avoid the actual pavements as they graze. The reduction in diversity of the characteristic plants has also led to declines in other species that are associated with those plant groups such as the Northern Brown argus butterfly. Overgrazing and abandonment both pose a threat to the host plant of this species (Ellis, 2003).

Recent agricultural policy is becoming more sympathetic to conservation. Natural England is working with farmers to implement changes to Common Agricultural Policy and agri-environment schemes are being established to support the multiple uses of grasslands. In their handbook on grazing for wildlife conservation, Natural England (2005) highlights the importance of reducing stocking levels and introducing mixed grazing with cattle. There are two main contrasting trends threatening high nature conservation grasslands in Europe; intensification and abandonment (Eastwood and Tallowin, 2007). The floristic communities of these areas have been shaped by human influence and disturbance through farming and consequently, the greatest threat to grassland diversity can be from the cessation of grazing (Hessle *et al*. 2007; Luoto *et al*. 2003). Therefore, simply removing all livestock is not an appropriate solution to restore these degraded habitats.

Upland calcareous grassland and limestone pavements

Limestone pavements are an internationally rare feature of ecological importance, characterised by protrusions of limestone rock from the ground surface. Hydrological processes of erosion and solution of the rock have resulted in the formation of raised areas of rock known as clints, containing fissures, shallow channels and solution hollows and supporting a diversity of distinctive flora. Between clints, the pavements are characterised by areas of calcareous grassland (Ward & Evans, 1976). Much attention has focussed on the loss of the distinctive clint habitats due to rock extraction (Ratcllife, 1974), and all pavements now have statutory protection from further physical damage thanks to the introduction of Limestone Pavement Orders (DEFRA, 2007). However, the calcareous grassland associated with limestone pavements has not received such attention, and upland calcareous grasslands are nationally facing significant problems, which seems to be strongly linked to grazing (Williams, 2006).

The importance of grazing in conservation policy

English Nature (now Natural England; 2005) state that livestock grazing is “essential” for the management of many wildlife habitats, in particular grassland, by controlling more competitive plant species and suppressing the onset of succession to scrub. They also propose that cattle are the most beneficial livestock for floristic diversity, as their method of ingestion (by pulling vegetation with their tongue) is not conducive to selecting flower heads or consuming vegetation close to the ground in the same way that sheep and horses are capable of doing.

The responses of vegetation to grazing

Numerous studies support the widely held view that grazing can have a range of potentially useful impacts on plant communities (Briske, 1996; Bullock *et al.* 2001) and that these changes in plant communities in response to grazing are likely to be a result of changes to the competitive balance. Whereas without grazing, species investing in high resource utilisation for vertical growth and few resistance mechanisms will be most successful, grazing should move the competitive balance more in favour of the resistant species which are less competitive in a non-grazed environment (Bullock, 1996). It is, however, unlikely that the intensity of grazing is the sole factor affecting vegetation (Noy-Meir *et al*. 1989; Maschinski & Whitham 1989). Under high grazing intensities, even resistant species may be grazed detrimentally due to depletion of more easily consumed species. At low grazing densities the competitive balance still does not entirely favour grazing resistance but may instead favour intermediate species; highlighting the importance of competitive interactions (Noy-Meir et al., 1989).

The feeding habits of cattle and sheep and their potential effects on plant communities

Few available studies directly compare the feeding habits of sheep and cattle. In contrast to sheep, cattle were not able to increase the proportion of different species of plant compared with those available (Grant *et al.,* 1985). Cattle also showed much less variation in their diet both between and within animals, suggesting a lower ability (or preference) to select vegetation. However, cattle did increase the proportions of some species in their diet relative to their abundance due to the cattle having preferential areas in which to graze (Grant *et al.,* 1985; Bokdam and Gleichman, 2000). These findings would appear to support the proposition that cattle should be useful conservation tools, as their grazing of the upper sward should, in theory, benefit lower-growing plants. In addition, their lack of selectivity may protect more nutritious plant elements such as flower-heads from overexploitation.

Grazing in relation to plant conservation

In practice, grazing has been shown to have the potential to increase and maintain the species richness of plant communities if managed appropriately (Bullock *et al.,* 2001). It was found that there were significant changes in cover associated increasing grazing intensity. These changes occurred among the dominant species where there was a shift away from the vigorous agricultural grasses. This was coupled with an increase in the abundance of herb species. Species also responded differently to the timing of grazing. It was found that spring grazing had an overall positive effect on species richness, but no effect for winter grazing and a negative effect for heavier summer grazing (Briske, 1996). Another important consideration is that grazing animals may affect the characteristics of a habitat throughthe impacts, for example, of defecation and trampling (Semmartin & Oesterheld, 2001). Provided there is no supplementary feeding, grazing animals do not generally alter the net nutrient balance of their enclosure (Milchunas & Lauenroth, 1993), although they have been observed to redistribute nutrients (Bokdam & Gleichman, 2000).

Cattle movements

It is generally accepted that cattle are less selective than sheep and are therefore often the species of choice when it comes to conservation. The actual movements of cattle however, and therefore the areas with which they come into contact, has been less studied. Physical features of an area will direct cattle along preferential paths (Ganskopp et al 2000) and hence, while the cattle have free choice within an area, they can be effectively steered into particular areas by the topography of their range. Within an area there may be areas that have high and low cattle activity which, in turn, will affect their effect on the habitat and floral communities. Coupled with this is the herding effect. Cattle are much more closely linked in herds (Putfarken *et al.* 2007) than perhaps other grazing species such as sheep and horses. This will again affect the actual intensity of grazing in an area.

Assessing habitat preference of animals

The preferential use of habitat by cattle is likely to be a major determinant of their impacts on vegetation. Cattle have been observed to vary in their habitat use within fields, seeking out areas of preferred vegetation within small (Van Den Bos & Bakker 1990) and large (Jewell *et al.* 2005) fields. Many habitat-use studies have been made with a variety of wild and domestic animals, using quite different methods of analysis to detect preference (Garshelis, 2000). The most common methods centre on the long established concept of “use-availability”. A habitat within which an animal spends a large proportion of its time relative to the area of the habitat is regarded as being relatively preferred while those that are utilised proportionally less than their area are regarded as being relatively avoided.

Johnson (1980) identifies different orders of habitat selection.

i. The first order is the selection of a physical or geographical range.
ii. The second order is the selection of a home range of an individual or group within which most of their time is spent.
iii. The third order is the selection of habitat components from within a home range.
iv. The fourth is the selection of food items from within a particular feeding site.

While the first order is not generally available to farmed animals, the other three are of paramount importance when looking at the implications of grazing on biodiversity. It is essential that we know where the animals spend most of their time, whether they select particular habitats within those preferred areas and if they are feeding on particular species within the preferred habitats. The fourth order of selection is beyond the scope of the present study but it is the second and third orders that will be directly investigated: the first through home range analysis and the second through resource selection analysis.

Home range analysis

The home range of an animal can be estimated via a number of different techniques (Kernohan *et al*. 2001). The oldest, and still widely used method, is that of minimum convex polygon (MCP). This method simply assigns a home range to an animal based on the extent of all locations of that animal; there is no assessment of any preferential areas within that home range. Other techniques focus on “utilisation distributions” (UD) in which there are contours drawn around different intensities of usage. The most commonly used of these UD methods is the kernel method and it is generally accepted that the fixed kernel method gives the most consistent results that best reflect an animal’s use of an area (Seaman & Powell, 1996).

However, these methods have been developed to analyse the movements of radiotracked animals. Radio fixes are usually few and far between, techniques for the analysis of such data have been developed that take into account the sparse returns, error in position etc. that are inherent in the techniques. The analytical techniques such as home range analysis that form the backbone to radiotracking studies (Kenward 2001) and how animals interact with their environment may however, be flawed when it comes to high resolution data (both spatially and temporally) as it is with GPS archival units. First, the 95% home range analysis can extends beyond any physical boundaries thereby extending the influence of the cattle beyond the real limits of the environment. Second, we know where these cattle are with a relatively high precision, therefore, where the home ranges extend beyond the actual tracks made by the animals by more than ~6m, it is again providing an erroneous estimate of the area that the cattle are using. The third point is that the behaviour of an animal may occur in discrete areas. The kernel analyses do not accommodate this and will again includes areas that are not used by the animal.

More recently, it has been suggested that a “local nearest-neighbour convex-hull” (LoCoH) method provides a better estimate of spatial use, particularly where there are hard boundaries to an animal’s range e.g. due to habitat features such as a lake edge or man-made structures such as fences (Getz & Wilmers 2004). This LoCoH method can be regarded as an integration of both the MCP and non-parametric kernel methods. LoCoH essentially builds a series of small MCPs around subsets of the locations and then combines these ‘mini MCPs’ (the so-called ‘local hulls’) to produce a UD (Getz and Wilmers, 2004; Getz et al. 2007). However, it should be noted that this analytical procedure is still in its infancy and has yet to be fully compared with more established methods.

Resource selection

Resource selection (RS) studies are usually concerned with habitat selection by animals (Erickson *et al*. 2001) and, as with home range estimation, there are numerous techniques to analyse these. RS studies can be divided into one of four designs (I, II, III or IV) depending on whether the analysis of availability and utilisation of a resource were made at the animal or population level (Erickson et al 2001; Thomas and Taylor, 1990). In design I studies, animal location data are pooled from several individuals (utilisation) and the availability is also set at the population level *e.g.* the entire study area. Design II studies have the availability at the population level but the utilisation at the animal level *i.e.* the locations of an individual animal are analysed separately with respect to the whole study area. In design III studies, the utilisation is again at the animal level but so to is the resource availability *i.e.* availability is derived from the home range of the animal. The final group of studies, design IV, have the utilisation derived separately for each individual location of an animal. Design I studies are generally no longer used as there is a chance of pseudoreplication occurring. For the other designs, the most robust method is that of compositional analysis (Aebischer *et al.* 1993) in which ratios are calculated for use and availability between each pair of habitats, and then the pairwise differences between the logs of these ratios are calculated to give a measure of relative preference between each habitat. The number of habitats over which each habitat is relatively preferred can then be used to rank them in order of preference. Importantly, this further reduces sensitivity to inclusion/exclusion of elements (Aebischer *et al.,* 1993; Garshelis, 2000). In a study such as this, it is important to know whether plants and communities in particular are being sought out disproportionately to their abundance. Regardless of whether there is real preference, elements that are used disproportionately more will probably undergo the largest grazing impacts.

Aims & Objectives

There is clearly a need for information on the interactions between grazing cattle and limestone grasslands. A vital first step in this process must be the identification of plant species and communities that are associated with cattle activity. This study therefore aims to:

1. Determine the movements of the cattle within the limestone pavements.
2. Determine whether the cattle exhibit any habitat preferences.
3. Detect any relationships between plant communities and the level of cattle activity.
4. To ground truth the current National Vegetation Classification Maps.

Methodology

Overview

The study site consisted of two pasture fields (High Brae and Sulber) over limestone bedrock with interspersed areas of limestone pavement in Ingleborough National Nature Reserve in the North Yorkshire Dales National Park. Sulber has an area of approximately 120 ha and is located on a plateau with mostly gentle relief. High Brae is located adjacent to Sulber and at a lower elevation, with an area of approximately 80 ha. High Brae is located over a series of shelves and steep slopes. Sulber is grazed by low stocking densities of sheep, while both fields are also grazed by separate herds of around 20 heifers, most of which are of the hardy Blue-Grey breed. For each field, a National Vegetation Classification map prepared four years ago was also available. The main stages of the study are outlined below before being discussed in detail:

- The movements of some of the cattle were tracked using collars equipped with Global Positioning System (GPS) devices. Compositional analysis of habitat use by the cattle was performed by analysing their use of each of the mapped NVC communities.
- Vegetation surveys were performed using quadrats and the cattle tracking data was used to assign a level of cattle activity level to the location of each of these quadrats. Analysis of quadrat data took place in relation to cattle activity levels, to detect associations between different aspects of the vegetation data and the level of cattle activity.
- The existing NVC maps upon which the compositional analysis was based were tested for accuracy using the quadrat data from the vegetation surveys.

Recording cattle locations using GPS collars

Two different types of collars were deployed on the cattle; one produced by BlueSky Telemetry Ltd. (LR400; Fig.1a) and two produced by Lotek Wireless Inc (GPS2200; Fig.1b). While these different collars have important differences in their operation (details of which will not be explored here), they both work in essentially the same way in that they both record the position of the animal at set time intervals and record these positions in memory along with associated information such as movement, external temperature and position accuracy.

Collar deployment

A cow was randomly selected from the herd, held in a temporary crush and the collar placed around the neck. The collar itself was closed and secured either using poppers and Velcro (BlueSky Telemetry) or using cable ties (Lotek Wireless Inc) (Figure 2).

Each collar was programmed to record position at set time intervals. This was varied so that the optimum sampling protocol could be determined. Initially it was set to one every minute but this was decreased to every 5 min during the day and 30 min during night. For the Lotek collars, the sampling regime was set at one sample every 10 min for 2 days followed by one sample every 30 min for 2 days and this cycle was repeated. Using this recording regime meant that the length of monitoring period could be extended while retaining the high time resolution.

We monitored the spatial position of animals from December 2004 to February 2007. It was not possible, however, to monitor animals over the entire year as the cattle were generally not put out onto the fields until mid summer and were taken off early January/February. This was due to the harsh conditions of the site over the winter and the need to separate the cattle and sheep grazing periods at the beginning of the season (sheep being put onto the fields first). However, there was a certain degree of flexibility within this pattern in the different years such that we monitored cattle activity in all months except March, April and June.

At the end of a GPS collar deployment, the data were downloaded to a computer and converted to a format that could be manipulated by GIS analysis software (ArcMap 9.2 or ArcView 3.1, ESRI Inc.).

Cattle tracking data

Using the positional information collected from the animals, the home range of each individual was estimated. For each deployment, three different estimates of home range were calculated:

- MCPs were calculated using Hawth's Tools for ArcGIS 9.2
- Fixed kernel analysis was used to calculate the percentile areas used by the cattle again using Hawth's Tools for ArcGIS 9.2. For the calculations, a fixed value of h_{ref} of 0.35 was used. Seaman et al (1999) recommend that fixed kernel smoothing through LSCV. However, Erickson et al. (2001) note that there are drawbacks to this technique especially with large numbers of locations when the kernels become concentrated in very small areas. Preliminary results found that this occurred with the present data set and hence the fixed value method was used instead.
- *k*-LoCoH, where all kernels were constructed from *k*-1 nearest neighbours of root points, was calculated using the NNCH suite of scripts for R (Getz *et al*. 2007). From preliminary investigations, it was found that using a value of k = 10 was the most appropriate.

While the k-LoCoH method appeared to be the best for describing the movements of the cattle (see later), the computing power needed to generate the home ranges was too great to do more than the basic home ranges for each deployment (each home range took between 5-7 h for a 2 GHz computer to analyse). As such, most of the analyses had to be undertaken using the more traditional kernel analysis.

As the home ranges estimated by the MCP and kernel analyses passed beyond the wall boundaries, the home ranges were clipped (ArcTools v9.2) to encompass only those areas that were available to the cows.

Location data from each individual animal was also subdivided into broad behaviour categories based on the speed at which the animal was moving between locations (Puttfarken et al. 2007). An animal was deemed to have been resting at a particular point if the calculated speed between two consecutive points was <0.02 m s-1. If the calculated speed was between 0.02 – 0.33 m s -1 then the cow was thought to have been grazing. All other points were classed as being walking.

Several attempts were made to validate the behaviour analysis by taking visual observations of the cattle. On four separate days in Dec 2007 and Feb 2008, the behaviour of all the cows in Sulber was monitored at 20 min intervals. The monitored cattle included two with GPS collars. However, the behavioural data were never taken at a time when the collars were successfully recording data and so the procedure used to split the animal’s time into behaviours could not be fully corroborated.

Along with the behavioural data that was recorded, the position of each cow within the field was determined using triangulation. This meant that it was possible to get some estimate of the cohesiveness of the herd and the area over which the herd spread at any time. These data were use to judge the area that the herd was using (and hence the herd impact) as opposed to the data that is gained from the GPS collars where only the movements of that individual is known.

Compositional Analysis

Habitat use relative to habitat availability was investigated using compositional analysis (Aebischer et al 1993; Browne & Aebischer 2003). This technique converts proportional data (as is the case of the habitat availability vs. habitat use) to log ratios that can be statistically analysed by MANOVA. For each animal, a number of comparisons were made to investigate RS selection in the form Designs II, III and IV type studies. Habitat composition was derived for each area using ArcMap and these data were used to compare with the overall habitat availability (see Table 1). Design II approach was undertaken by comparing the habitat composition of the different home range estimates (usage) against the overall habitat composition of the relevant fields (availability). A design III study was undertaken by comparing the habitat found at each location derived from the GPS collars (usage) with the overall habitat of the fields (availability). Finally, design IV study was undertaken by comparing the individual locations (usage) against the various estimates of home range (availability).

Table1. Habitat classification of the Sulber and High Brae with measurements of the area of each habitat type, the vegetation groups that were combined to assign those habitat types, the proportion of each habitat and the proportion of locations that were found in those habitats (see also Figs.3 and 4)

Field	**Habitat Type**	**Vegetation groups**	**Area (ha)**	**%of total area**	**% of total counts**
High Brae	Acid grassland	U4a/U4e/U5a/U5e	9.77	13.0%	20.6%
	Basic flush	M38/U4e/S23	0.68	0.9%	3.8%
	Calcareous grassland	CG9b/OV39b/OV40/U4a/U4e	45.41	60.5%	61.4%
	Limestone Pavement	LP/CG9b	18.43	24.5%	14.2%
	Neutral grassland	MG6a	0.82	1.1%	0.0%
Total			**75.11**	**100%**	**100.0%**
Sulber	Acid grassland	U4a/U4e/U5a	6.49	5.4%	16.3%
	Basic flush	M10b/M25a	3.14	2.6%	3.4%
	Bog	M3/M15a/M17c/M25a/CG9b	3.85	3.2%	3.8%
	Calcareous grassland	CG9b/OV39b/U4e/U5a	80.62	67.4%	65.4%
	Limestone Pavement	LP/CG9b/M10b/M15a	16.85	14.1%	6.1%

	Wet Heath/Acid grassland	M15a/M25a/U5a/U5e	8.74	7.3%	5.0%
Total			**119.69**	**100%**	**100.0%**

Vegetation surveys

Collection of quadrat data

Surveys were carried out between 2nd and 24th July 2007 using 4m^2 quadrats. Nomenclature follows Stace (1997). Quadrats were located using a hand held GPS (Garmin Etrex). ***Percentage cover values*** of each vascular plant species along with moss, bare ground and bare rock were estimated to the nearest 5% within each quadrat. Where values were below 5%, the following scale was used: 1= one or few individuals, 2= several individuals, 3= many individuals.

Sward height was also measured at four points within each quadrat (30cm from each corner at an angle of 45°). This was simply a measurement of the maximum height at which a tape measure was touched by any foliage when extended vertically to the ground. ***Quadrat sward height*** was then calculated for each quadrat, being the mean of these four height measurements. The coefficient of variation of the four sward height measurements was also calculated to give each quadrat an index referred to as ***quadrat sward heterogeneity***. ***Shannon biodiversity indices*** (*H'*) were calculated for each quadrat using:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

Where p_i is the proportional abundance of the *i*th species (Magurran, 1998) and S is the number of species.

Quadrat coverage

Quadrat sampling locations were arranged across each field at regular 200 m intervals in Sulber and 100 m intervals in High Brae (fig. 5). This density was doubled in areas of high CA in order to ensure that there were sufficient coverage of these areas given that initial results suggested that the areas that the cattle mainly used were much smaller than the overall area of the field (fig. 5) The higher density of quadrats in High Brae compared with Sulber was necessary to give an adequate number of quadrats in that field.

Within Sulber, three exclosures were also included as part of the vegetation sampling. These were protected against cattle grazing from 2003, but were open to sheep and small mammals. Three quadrats were placed randomly in each of these.

Data manipulation and analyses

The level of cattle activity was assigned to each quadrats for subdividing the quadrat data. This was with the hope of finding associations with intermediate levels of cattle activity that might not be detected by a simple High-Low analysis. Areas within 25% of the mean CA were regarded as *Intermediate.* Areas with values above 125% of the mean were labelled *High* and areas below 75% of the mean *Low.* The choice of zonal definitions was limited by the distribution of *CA* figures across the quadrats. These zonal definitions struck the best possible balance between gaining a reasonable sample size in each zone and having meaningful differences in *CA* between the zones. The number of quadrats within High Brae's Intermediate zone was unavoidably small. In Sulber the exclosures were labelled *Zero* cattle activity (there were no such areas within High Brae).

Where any significant differences between percentage cover, mean sward height and quadrat heterogeneity were found between the different activity levels, Tukey's LSD post hoc pairwise comparisons was used to determine which activity levels were different. If the residuals were not normally distributed, then Kruskall-Wallis Test was used for the pairwise comparisons.

Redundancy Analyses and Ordinations

CANOCO (v. 4.52) was used to create ordinations of association with environmental variables for each species. Prior to ordination, DCA was performed for each field using detrending by segments and default settings, showing the lengths of the first gradient for each field to be short enough for RDA analysis. RDA was then performed using default settings, except under "Scaling/Linear Methods" divide by SD and Focus on inter-species correlations were selected, with centring by species only. RDA was performed using percentage cover values for each quadrat as the species data.

The species data was used in three separate RDAs for each field with the environmental data set to:

1) CA for each quadrat
2) Quadrat sward height for each quadrat
3) Quadrat sward heterogeneity for each quadrat

An ordination was plotted when $p<0.05$.

Ground truthing current NVC maps

Each quadrat was assigned NVC communities and "ground-truthing" of the existing maps was performed to test their consistency with the present survey.

Tablefit (version 1.0; Hill 1996) was set to assign NVC communities to each individual quadrat. Percentage cover figures for each separate quadrat were inputted and classifications were performed using "top few species, descending abundance, no quant.". This was assumed to equate most accurately with the methods during the previous NVC mapping, which did not record quadrat data and which presumably used obvious visual boundaries of cover such as would be provided by the top few species. Setting Tablefit to assign communities using the top few species also avoids differences in classification between the present and previous surveys arising due to seasonal or annual variations in minor community components. All communities in the uppermost goodness-of-fit bracket assigned by Tablefit, provided they were “fair” or better, were recorded for a quadrat. For example, where there was one “good” fit and two “fair” fits, one good fit was recorded. Where there were four “fair” fits, all four were recorded. Goodness-of-fit brackets are discussed further by Hill (1996).

The NVC communities assigned to each individual quadrat were compared at the community level with those predicted to be at that location by the existing maps. If a one of the communities assigned to the quadrat by Tablefit matched a community predicted by the map for that location, this was regarded as a match. For example, a site mapped as [Limestone Pavement/CG9] compared with a quadrat which was assigned [U4, U5, CG9] was regarded as a match. Where communities did not match but were from the same grouping, e.g. calcicolous grasslands (Rodwell 1992), this was recorded as “related”. For example, [Limestone Pavement/CG9] compared to [U4, US, CG1O] would be recorded as “related”.

The ground-truthing was performed to give an indication for this study, reserve managers and future researchers of the reliability of the existing maps in relation to present vegetation, and whether there is any need for revisions to these maps.

The information collated for each quadrat and used during the analyses were:

- *CA*
- 2-zone cattle activity zone
- % cover values
- Quadrat sward height
- Quadrat sward heterogeneity
- Predicted community from NVC map
- NVC community assigned using % cover data

Statistical analyses were carried out using SPSS (v14, SPSS Inc) or R. Non-parametric tests were only used when attempts at the transformation of non-normal data had failed. Means are given as ± 1 SE. Any statistical analyses undertaken were deemed significant at $p<0.05$.

Results

Fourteen deployments of the GPS collars were made between December 2004 and Feb 2008; 11 of which produced useable data. A total of 255 days of data were recorded which consisted of 121,612 positions (Fig. 6). Each position also had date, time, height, temperature, pitch and roll, numbers of satellites and an assessment of the accuracy of the fix associated with it.

One of the collars fell off the animal and remained recording its position for over 5 days. From this, it was therefore possible to get some estimate on the accuracy of the fix using these data. While in its fallen position, the collar made 3,194 fixes. The distribution of the nothing and easting around the mean position was used to get an idea of the accuracy and precision of the collars. It was assumed that the centre of the distribution reflected the true position of the collar and that the scatter of fixes around that mean position reflected the variation associated with each fix when the collars are on the cows. While these assumptions may have been invalid, it does provide some measure of the accuracy of the data. For each fix, a distance east and a distance north from the mean position was calculated. The average distance from the mean position was 0.4 ± 0.05 m east and 0.7 ± 0.1 m north. From the distribution of data around the mean, 97% of all fixes were within 6 m of the mean position.

Cattle behaviour

Displaying all of the GPS data points for each cow file (Figure 6) highlighted trends in the movements of the cattle from each of the GPS collars. Each collar was on different cattle and at different times of year but it is clear that each cow favoured similar areas. Clusters of points are shown around the edges of the field and following the public footpaths across the site. On High Brae, there is a cluster of points shown around the gate, at the northern end of the field near the road. On both High Brea and Sulber the areas shown to be limestone pavement on the OS map have most sparse distribution of points recorded.

Figure 7 shows the July 2005 and May 2005 cattle data files displayed as both actual points and as the home ranges derived from the three techniques used namely MCP, kernel analysis and k-LoCoH densities. This illustrates the difficulties in estimating home ranges. It is clear that only the k-LoCoH estimate truly reflects the animal's movements. Both of the other estimates give areas that overestimate the ranges of the cows. The overall home range area used by the animals (estimated from the various techniques) can be seen in figure 9. There was a significant difference between the techniques (ANOVA, $p = 0.011$) with k-LoCoH providing the smallest estimate.

Kernel analysis is, through its density function, able to provide some indication of the areas that are most often used by the animals. However, fig. 9 shows that it is only when the analysing the 50% isopleths will a provided a picture of where the herd spent most of their time. The high density areas (red) are where the herd would have spent the majority of their time. On Sulber these are concentrated around the northern side of the field, with no high density areas over the limestone pavement on the site. On High Brae, the cattle occupy the lower terrace the majority of the time, with the upper limestone terraces occupied least. The areas of high density are focused around the road gate at the north and footpath entrance to the south with another area of high density centred around one of the water troughs on the site.

Habitat usage

The overall area available to the cows is shown in figure 10 where it is compared with the proportion of locations that occur in those habitats. Compositional analysis of these data showed that there was no significant difference between the habitats that were available to the cows and their usage of those habitat; the cows would, it seem, be foraging randomly. However, it can be seen that the proportion of habitat usage changes through the year (Fig. 11). However, there were too few data sets from each month to test this.

The data from the collars were split into the different behaviours according to the average speed between fixes. While it was not possible to validate the method, the pattern of behaviours (Fig.12) are comparable with other studies that have observed cattle directly with (during the summer months at least) two peaks in grazing associated with the morning and evening. This would tend to support the use of speed to differentiate behaviours.

From the observations that were made on the herds, the average radius of the herd was 70m (Fig. 13). This was used to produce a buffer when estimating the home range when using k-LoCoH. The 90% isopleth was significantly smaller than one containing all the data points but still produced a home range that closely reflected the movement of the cattle (Fig.14). When this area was used to compute the compositional analysis, there was a significant difference between the area available to the cows and the area that they used ($\lambda = 0.0494$, $p = 0.008$).This difference was due to the cattle significantly underutilising the calcareous grassland.

Factors affecting home range estimation

The concentration of the cattle movements into specific area is clearly seen in figure 15 for grazing animals. This is also true for resting animals but the areas are discrete. The home ranges used by resting and grazing animals were significantly different with the resting animals using a smaller overall area than those that were grazing (Fig 17; ANOVA $p < 0.001$) in both Sulber and High Brae. The extent of the 95% home ranges of the individual animals varied considerably across the season (Fig.18). The 95% home ranges varied between 22.1 ha in Dec 2004 to 120.8 ha in July 2006. The 50% home range, are, by definition smaller than the 95% ranges (mean = 5.9 ± 1.4 ha) but there was also less variation between the different months (Fig.18). The most restricted range of the cows occurred in July when the cow spent 50% of her time in a very restricted area of only 1.12 ha.

Vegetation Surveys

Quadrat coverage

A total of 95 quadrats were analysed (51 in Sulber and 44 in High Brae). Table 2 summarises the numbers of quadrats falling within each of the zones of cattle activity. Despite the increase in quadrat density within the areas of high cattle activity, an equal number of quadrats in the 'Above Average' and 'Below Average' cattle activity zones was not achieved in either field nor were they equally distributed between the Zero, Low, Intermediate and High categories.

Table 2 The number of quadrats falling within each of the zones analysed.

Field	**Zone**	**No. quadrats**	**Zone**	**No. quadrats**
Sulber	Below average	30	Zero	9
	Above average	21	Low	19
			Intermediate	10
			High	13
	Total	**51**		**51**
High Brae	Below average	27	Zero	0
	Above average	17	Low	26
			Intermediate	6
			High	12
	Total	**44**		**44**
Total number of quadrats =		**95**		**95**

Two zone analysis

In Sulber, there were ten plant species associated with cattle activity (seven species with significantly more % cover with Above Average and three with Below Average) (Table 3). In High Brae, there were eleven species showing an association with cattle activity; 9 with greater % cover with Above Average activity and 2 with greater coverage with Below Average activity. In High Brae, there was also significantly (P=0.001) more bare earth associated with high cattle activity.

Table 3 Species for which a significant (p<0.05) difference in % cover between Above Average and Below Average cattle activity zones was detected in Sulber using the grid only *and* stratified *quadrat data. + indicates association with Above Average, - indicates association with Below Average. ANOVA (GLM) was used where residuals were normally distributed. Otherwise, differences were tested with the Kruskal-Wallis Test.*

Field	*Species*	*Association with activity zone*
Sulber	*Agrostis capillaris*	+
	Anthroxanthum odoratum	+
	Bromus erectus	+
	Cerastium fontanum	+
	Cirsium vulgare	+
	Cynosurus cristatus	+
	Sesleria albicans	-
	Tnfolium repens	+
	Viola hirta	-
High Brae	Bare	+
	Bellis perennis	+
	Carex panicea	+
	Cirsium palustre	+
	Cynosurus cristatus	+
	Leontodon hispidus	+
	Ranunculus acris	+
	Ranunculus bulbosa	+
	Rumex acetosa	+
	Sanguisorba minoj	+
	Vaccinium myrtillus	-
	Viola riviniana	-

Multi-zone analysis

The multi-zone analysis reveals thirteen significant associations with cattle activity zone in Sulber and fourteen in High Brae (Table 4). In both fields, the number of associations detected by multi-zone analysis is higher than by the two-zone analysis.

Table 4. Species for which a significant (p<0.05) difference in cover across multiple cattle activity zones was detected. Letters signify significant zonal differences in % cover for each species derived by pairwise comparisons.

Sulber	**P**[*]	**Zero**	**Low**	**Int**	**High**
Agrostis capillaris	<0.001	B	B	A	A
Anthroxanthum odoratum	<0.001	B	B	A	A
Bare	0.037	B	AB	AB	A
Bromus erectus	0.007	C	BC	A	AB
Cerastium fontanum	0.028	AB	B	AB	A
Cirsium vulgare	0.028	AB	B	AB	A
Cynosurus cristatus	0.028	AB	B	AB	A
Gentianella cempestris	0.002	A	B	AB	B
Luzul sp.	0.008	AB	B	B	A
Ranunculus repens	0.028	AB	B	AB	A
Seslena albicans	<0.001	A	A	AB	B
Tnfolium repens	<0.001	B	B	B	A
Viola hirta	0.003	A	B	B	B
High Brae					
Bare	0.000		B	B	A
Bellis perennis	0.023		B	A	A
Carex panicea	0.010		B	BA	A
Cirsium palustre	0.015		B	BA	A
Coryllus avellana	0.042		B	A	AB
Cynosurus cristatus	0.009		B	AB	A
Dactylis glomerata	0.042		B	A	AB
Galium saxatile/sterneri	0.047		B	AB	A
Helianthemum nummularium	0.039		B	A	A
Leontodon hispidus	0.014		B	A	A
Ranunculus acris	0.002		B	B	A
Rumex acetosa	0.003		B	AB	A
Sanguisorba minor,	0.001		B	A	B
Viola riviniana	0.020		A	A	A

[*] Kruskal-Wallis Test

In Sulber (Table 4), *Agrostis capillaris* and *Anthroxanthum odoratum* exhibit an association with Intermediate/High activity compared to Zero/Low. Bare earth is significantly associated with High activity only compared to Zero activity, *Sesleria albicans* is more abundant in Zero/Low activity areas compared to High activity, *Trifolium repens* is more associated with High activity than with all three other activity levels and *Viola hirta* is significantly associated with Zero activity relative to all three other levels. The other species exhibit more complex associations. *Luzula spp., Cynosurus cristatus, Cirsium vulgare* and *Ranunculus repens,* although more associated with High activity than with Low or Intermediate activity do not differ significantly between Zero and High activity.

Gentianella campestris is more associated with Zero activity than with Low and High, but not Intermediate. *Bromus erectus* is most associated with Intermediate activity, with higher abundance in Intermediate areas than in Zero and Low activity areas, and higher abundance in High activity areas than in Zero activity areas.

In High Brae (Table 4) *Bellis perennis, Helianthemum nummularium* and *Leontodon hispidus* are more associated with Intermediate/High activity than with Low activity. *Carex panicea, Cirsium palustre, Cynosurus cristatus, Galium saxatile/sterneri.* and *Rumox acetosa* are more associated with High than with Low activity. Bare ground and *Ranunculus acris* are associated with High activity relative to Low/Intermediate activity. *Coryllus avellana* and *Dactylis glomerata* are more associated with Intermediate than Low activity, and *Sanguisorba minor* is more associated with Intermediate than both High and Low activity. Despite a significant relationship being detected using all three zones, no significant pairwise differences between activity zones for *Viola riviniana.*

There are differences between the relationships detected by the two-zone and multi-zonal analyses. For both fields, more relationships are shown by multi-zone analysis, although some relationships are only detected by two-zone stratified analysis. Bare ground, *Gentianella campestris* and *Luzula spp.* show significant relationships under only the multi-zone analysis in Sulber. In High Brae, relationships for *Campanula rotundifolia* and *Vaccinium myrtillus* are only detected by the two-zone analysis while relationships for *Coryllus avellana, Dactylis glomerata* and *Helianthemum nummularium* are only shown by the multi-zone analysis.

CANOCO ordinations of individual species associations with cattle activity and sward properties

Figure 19a and 19b shows the ordinations from the significant CANOCO RDA analyses of species associations with CA. In Sulber, there are some clear groupings of species in relation to cattle activity (Figure 19a). The species that exhibited significant associations with grazing, such as *Cynosurus cristatus, Cerastium fontanum, Trifollum repens* are closely grouped. *Trifolium repens* and *Agrostis capillaris* are the most strongly associated with cattle activity. Bare earth also shows a positive relationship, which could be important and was not detected by the other analyses. There are two main groups of species not associated with cattle activity. *Sesleria albicans* is the most negatively correlated, and is accompanied by *Thymus polytrichus, Linum cat harticum, Viola riviniana, Campanula rotundifolia, Carex flacca* and *Euphrasia agg.*. These appear to represent limestone grassland communities. Another grouping is only slightly negatively related to cattle activity, being composed of calcifugous species such as *Erica tetralix, Empetrum nigrum, Vaccinium spp.* and *Calluna vulgaris. Viola hirta* is also negatively related to cattle activity but is not closely associated with any other species, although it falls closer to the calcicolous than acidic species.

In High Brae, there are less clear groupings of species in relation to cattle activity (Figure 19b). However, again the significant relationships can be detected, with bare earth showing the strongest association and *Lolium perenne*, *Cynosurus cristatus*, *Ranunculus acris* and other mesotrophic species falling nearby. *Viola riviniana* and *Carex panicea* are the least associated with grazing, followed by *Vaccinium myrtillus* and *Sesleria albicans*.

Sward associations with cattle activity

There was a significant difference in the mean sward height of the different activity zones in Sulber (ANOVA, p=0.025) and in High Brae (ANOVA, p=0.020). In Sulber, sward height was significantly lower in the High activity zone than in the Low (Figure 20b) while in High Brae there was a significantly higher mean sward height in the Low/Intermediate activity zones than in the High activity zone (Figure 20b). There was no significant differences between the activity zone and quadrat sward heterogeneity in either Sulber or High Brae (Figure ??d).

Botanical diversity associations with cattle activity

In Sulber, significant relationships were detected between cattle activity zone and species richness (ANOVA, p<0.038).and Shannon index (ANOVA, p<0.001) (Figures 20a and 20c). Shannon index was significantly higher in High activity areas than in Low and Zero, and higher in Intermediate than Zero (Figure 20c). Species richness was significantly higher in High than Low activity areas, but notably did not differ significantly between Zero and High activity areas (Figure 20a). There were no significant relationships between species richness or Shannon Index and the cattle activity zones in High Brae. Mean quadrat species richness in High Brae was 18.9 ± 1.1, which was significantly higher than that of Sulber at 16.1 ± 0.7 (ANOVA, p=0.018, r^2=6.86%). Total species richness was 79 and 75 in High Brae and Sulber respectively.

Quadrat-by-quadrat ground-truthing of NVC maps

The number of comparisons was fewer than the total number of quadrats analysed as not all quadrats were assigned a fair or better match with a community, and that some fell outside the areas covered by the existing NVC maps. In Sulber, of the 32 comparisons made, 6 were matched at the community level, 9 were related (*i.e.* from the same grouping of communities; Rodwell 1992), and 18 were mismatches (Table 5). This means that, within Sulber, only 18.75% of the areas were classified correctly in the previous survey. In High Brae, there was a slightly better agreement between the original NVC survey and the present study where there were 9 matches, 11 were related and 9 were mismatches. This is a match rate of only 31%. In both fields the areas mapped as calcicolous grasslands appear to contain the most deviation. The mapped mesotrophic grassland communities are mostly confirmed by the present survey.

Table 5. Quadrat-by-quadrat comparisons of NVC map unit and NVC communities assigned to each quadrat by TABLEFIT. In the case of the exclosures, quadrats were pooled to give one comparison per exclosure. Where the mapped community matches one assigned to the quadrat, "match" is recorded. Where the community is from the same family as a community assigned to the quadrat, i.e. initial letters e.g. "CG" or "U", "related" is recorded. Where there is no match, "unrelated" is recorded. "no fair matches" indicates no fair community matches were returned by TABLEFIT for a quadrat; "-" denotes the subsequent lack of a comparison. All letter/number codes refer to NVC classifications (Rodwell 1992) except "LP", which denotes limestone pavement.

Quadrat number	***Community classification predicted by existing map for each quadrat***	***Community classifications from present survey data for each guadrat***	***Comparison***
Sulber			
1	CG9	CG2, CGI	Related
2	CG9	U4, UI	Unrelated
3	CG9	No fair matches	-
4	CG9	M10	Unrelated
5	CG9	No fair matches	-
6	CG9	CG3, CG5	Related
7	CG9	CG8, CG2	Related
8	CG9	H14,H12,HI0,H13	Unrelated
9	CG9	U1	Unrelated
10	CG9	CG9	Match
11	CG9	CG2, CG9	Match
12	CG9	U4	Unrelated
13	CG9	U4, U1	Unrelated
14	CG9	U4,U1	Unrelated
15	C09	No fair matches	-
16	CG9	No fair matches	-
17	CG9	U1, CG3	Related
18	CG9	U4, U1	Unrelated

19	CG9	CG3	Related
20	CG9	U1	Unrelated
21	CG9	CG3, CG5	Related
22	CG9	U4	Unrelated
23	CG9	No fair matches	-
24	CG9	No fair matches	-
25	COY	No fair matches	-
26	CG9	No fair matches	-
27	CG9	U4, U1	Unrelated
28	CG9	CG8	Related
29	CG9	H14, H13, H1	Unrelated
30	CG9	H14 H1	Unrelated
31	LP/CG9	No fair matches	-
32	LP/CG9	CG2, CG8, CGI	Related
33	LP/CG9	U4	Unrelated
34	LP/CG9	U1	Unrelated
35	LP/MI0	U1, H14	Unrelated
36	M10/M25	U4, U1	Unrelated
37	MI5	H14,U2,H10,U2,H13	Unrelated
38	M15/M17	H14,U2,H12,H10	Unrelated
39	U4	U4	Match
40	U4	U1, U4	Match
41	U4	U4, U1	Match
42	U4	U4	Match
43	U5	U4, U1	Related
High Brae			
44	CGI0/U4	No fair matches	-
45	CG9	U4, U1	Unrelated
46	CG9	No fair matches	-
47	COY	U1	Unrelated
48	CG9	CG3	Related
49	CG9	U4, U1	Unrelated
50	CG9	U4, U1	Unrelated
51	CG9	U1	Unrelated
52	CG9	U4	Unrelated
53	CG9	No fair matches	-
54	CG9	U1	Unrelated
55	CG9/U4	U4, U1	Match
56	CG9/U4	U4, CG10	Match
57	CG9/U4	CG8	Related
58	CG9/U4	CG3	Related
59	CG9IU4	No fair matches	-
60	CG9/U4	U4	Match
61	CG9/U4	U5, U1, U4, CGI2, CGI0	Related
62	CG9/U5	CG3, U1	Related
63	LP/CG9	No fair matches	-
64	LP/CG9	No fair matches	-
65	LP/CG9	CG1O	Related
66	LP/CG9	No fair matches	-
67	LP/CG9	U4, U1	Unrelated
68	LP/CG9	CG10, U1	Related
69	M10/U4	U4	Match
70	OV39/CG9	No fair matches	-
71	OV39/CG9	CG10	Related
72	OV39/CG9	No fair matches	-
73	OV39/OV40/CG9	CG2, CGI	Related
74	OV39/OV40/CG9	No fair matches	-
75	OV39/OV40/CG9	U4, U1	Unrelated
76	U4	U4, U1	Match
77	U4	U4	Match
78	U4	U4, U1	Match
79	U4	No fair matches	-

80	U4	U4, U1	Match
81	U4	U4	Match
82	U5	U4	Related
83	U5	U2, U4	Related

Discussion

Cattle movements

One of the main aims of the present study was to determine the movements of the cows grazing on two fields within the area covered by the Limestone Country Project and to investigate the link between these movements and the underlying botanical diversity.

Cattle and other species are increasingly being used as tools to aid conservation. However, there is little scientific evidence that this strategy actually affects the biodiversity of an area in the way that land managers would like. Within the Limestone Project, an attempt was made to determine the effects of the cattle by comparing the botanical diversity within fields that had had different level of grazing and different grazing species. Random sampling within the fields was used to monitor this diversity and then fields were compared and related to cattle/sheep activity (Smith et al 2007). While this would appear to be a sensible way of addressing the issue, there may be problems if the grazers are not affecting the sward in a uniform manner. If animals within the field have preferential areas for different activities then this will affect the impact of the cattle on the different areas.

The cattle in the present study had very definite areas that they preferred over other areas. The traditional methods for analysing the movements and area covered by an animal, did not find any differences between the areas that the cattle covered and the area available i.e. they were not making any preferences. However, these traditional areas were obviously flawed as they contained large areas where the animals were hardly ever present. A more recently developed method for analysing habitat use, gave very different results, the first being that the total area used by the cattle was significantly less than that available to them. This in itself is important as it means that there are areas without any cattle activity. If any of the plant sampling occurs in these areas (and they must do if randomly located) then there will be a mix of results with some coming from areas of cattle activity while others are derived from areas that have little or no link with the cattle. Any cattle related changes will be lost by this pooling effect. Furthermore, it was found that one specific habitat type (calcareous grasslands) was being used at a lower rate than would be expected from the extent of this community. Whether these areas are being avoided or whether the other areas are being preferred is difficult to judge. The fact that the other areas are used at the same level as their extent suggests that there is no preference for these but that, instead, the cattle are actively avoiding the mainly *Sesleria* dominated calcareous grasslands.

Botanical diversity

The positive relationship between botanical diversity and cattle activity in Sulber is consistent with many studies linking grazing with the maintenance of botanical diversity. However, it also represents a step forward from simple grazing cessation/restoration studies (e.g. Hill et al. 1992, Pykala 2003) and stocking rate trials (Vesk & Westoby 2001) by showing that diversity can vary in association with within-field habitat use. This is in contrast with unpublished research simply comparing grazed and ungrazed fields that did not detect grazing-mediated differences in botanical diversity.

It seems noteworthy that the species richness/grazing associations are lower than for the Shannon index, suggesting that evenness is playing a major role in these Shannon index values. The slightly more complex relationship between species richness and cattle activity is also explicable in the light of this evidence. Since one of the exclosures is located within a High activity zone and another in an Intermediate activity zone, their species pools may be replenished by seed from surrounding populations, the seed production of which is a product of different community dynamics. The exclosures may also have not yet finished paying off their pre-exclosure “species debt” (Hill *et al.* 1992). Shannon Index values may thus be maintained at a low level in opposition to relatively high species richness by the high level of dominance due to reduced upper sward off take.

This observation of low evenness in the exclosures is also consistent with observed differences between cattle and sheep grazing (Grant et al. 1985). Whereas cattle tend to graze from the upper sward, thus theoretically reducing the cover of whatever species are dominant and benefiting sub-canopy species, sheep are able to concentrate their grazing below the canopy. The fact that sheep have access to the exclosures may be operating to some extent to reduce Shannon Index values if they are selectively grazing subordinate species relative to the cattle.

Increased evenness is probably a major factor contributing to the species richness of more highly grazed areas, as reduced dominance is likely to increase light penetration, moisture and nutrient availability. This in turn may allow the exploitation of suppressed niches existing at small scales. For example, where soil properties and drainage vary at small scales, diversity that might arise from this environmental heterogeneity could be suppressed to some extent by a highly dominant canopy species. Reduced dominance and increased diversity have been linked in disturbance studies, for example by Armesto & Pickeft (1985) and grazing studies (e.g. Bokdam & Gleichman 2000).

The lack of a relationship between cattle activity and species richness or Shannon index in High Brae is curious in the light of the correlations in Sulber and those reported in the literature. However, the observations at High Brae are not necessarily anomalous or contradictory to prevalent theories of grazing benefits for plant diversity. The findings from High Brae could be explained in terms of the intermediate disturbance hypothesis (Armesto & Pickett 1985). This states that botanical diversity peaks where disturbance is high enough to prevent resource monopolisation by a few effective competitors and provide niches for opportunists, while low enough not to exceed the tolerance of large numbers of species. In Sulber, which has the lowest cattle density of the two fields, high activity may really correspond to a theoretical “intermediate”, while in High Brae this theoretical “intermediate” may not have been properly sampled. This could be tested by further stratification in both fields, concentrating on the most intensely grazed areas of Sulber and intermediate areas of High Brae. Objective measurements of grazing intensity that can be compared between fields and studies would be helpful. Another possible explanation for the lack of a relationship between diversity and cattle activity in High Brae is that cattle were present, on High Brae during the study period. If these cattle were exhibiting a different pattern of grazing to previous grazing seasons, this could have altered patterns of diversity.

Although one mechanism through which this disturbance is theoretically expected to operate is the creation of sward heterogeneity (Rook & Tallowin 2003), this was not supported here. However, bare ground cover was positively associated with cattle activity in high Brae, providing niches for opportunistic species, and sward height was negatively associated with cattle activity in both fields. This suggests that resource monopolisation is indeed being reduced by grazing with increased light and space available for early-successional species. These issues are discussed in the next section.

Sward properties

Grazing is often regarded as without exception leading to increases in sward heterogeneity, thus increasing grassland species richness through the creation of more niches in terms of light, moisture and nutrient availability (e.g. Rook et al. 2004). However, two findings have emerged from this study that appear to contradict this simple and popular theory. Firstly, in High Brae no relationship was found between grazing and species richness or Shannon Index; secondly, although grazing and species richness/Shannon Index were linked in Sulber, this relationship does not appear to operate via sward heterogeneity, as this was not correlated with grazing.

Cattle are regarded as being relatively unselective grazers at the feeding station level (Grant et al. 1985), and this means that at small scales they should not be expected to increase sward heterogeneity (Adler *et al.* 2001). There is also evidence that where variation between vegetation manifests itself in large, discrete communities, it is more efficient for grazers to focus their selection on these rather than searching for small patches of favoured vegetation. This could add to large-scale heterogeneity by maintaining discrete areas of high and low grazing pressure (Adler *et al.* 2001, Jewell et al2005, Van Den Bos & Bakker 1990). This would simultaneously create a negative feedback effect by reducing grazing pressure whenever grazing begins to increase the amount of necessary searching-effort by increasing small-scale heterogeneity (Marion et al 2005).

Selection does appear to be operating at the community level in High Brae, and is not evenly distributed in Sulber (although factors other than community selection must be regarded as dominant in this field). This presents the possibility that grazing is creating larger scale heterogeneity that has been missed by the present study. The significant differences in quadrat sward height between cattle activity zones can be regarded as a form of larger-scale heterogeneity. Despite the fact that within High Brae, no relationship was found between botanical diversity and level of cattle activity, the possibility, also remains that species richness is maintained at the scale of the whole field by grazing. It is likely that without grazing, many of the species that would normally be associated with cattle activity would be lost and the field's net species richness would decrease (Hill et al. 1992, Pykala 2003).

The mechanisms by which changes to the sward influence species richness also need to be addressed in the light of the fact that higher diversity in grazed areas in Sulber was not accompanied by matching patterns of sward heterogeneity. There are known to be many drivers of botanical diversity at a variety of scales (Lundholm & Larson 2003, Pausus & Austin 2001). Despite this, much of the literature relating plant diversity to grazing seems to omit this fact, as if the creation of sward heterogeneity is the only mechanism by which grazing can alter species richness, omitting the possibility of grazing/environment interactions (e.g. Armesto & Pickett 1985, Rook & Tallowin 2003, Rook *et al.* 2004). It is possible, as mentioned earlier, that a reduction of sward height could on its own increase species richness by increasing light and water availability for less competitive species, assuming there is a larger pool of such species. Here it is proposed that dominance by tall species or by a dense canopy could also interact with the environment to create a phenomenon of “niche-suppression”. Underlying niches created by small-scale variations in such features as soil, aspect and moisture levels might not exploited by their specialist species due to resource monopolisation by dominants. Sward shortening or thinning through grazing, even if uniform and not adding to structural heterogeneity, could release these niches and allow them to be occupied. This is a simple development from prevalent theories, but is subtly different, as the effects of grazing would depend’ in part on the level of underlying heterogeneity.

Within Sulber very small-scale variations in soil have been observed at a scale as small as 30-50cm, with calcareous rendzinas above thinly covered limestone and more acidic soils over old grikes and hollows which have been filled with free-draining silt (Smith et al. 2004). These have been linked with the distribution of acid-and limestone-indicator species, for example with *Potentil!a erecta* being associated with acidic patches and *Thymus po!ytrichus* with calcareous patches. On the other hand, High Brae is not regarded as containing such noteworthy microtopographical heterogeneity. This may mean that in Sulber, grazing has a significant “niche release” effect whereas in High Brae it does not. Although mean species richness was higher in High Brae, seemingly in opposition to this theory, this is likely to be the result of the less stressful environment of High Brae (being lower lying rather than on a plateau) rather than being reflective of underlying environmental heterogeneity.

Sward density rather than height may be the driving factor in niche release as sward height did not vary in the same manner as species richness. If the top layer of the sward, from which cattle mostly graze (Grant et al. 1985) is reduced in density then light penetration and niche release could occur without actual reductions in sward height. Further studies measuring sward density might be appropriate to test this theory.

The scale of environmental variation can also interact with the scale of grazer selectivity to determine whether grazing increases or decreases sward heterogeneity. Where grazer selectivity operates at a larger scale than existing sward variation, it has been theorised that sward heterogeneity may decrease (Adler et al. 2001). It may be the case that in both fields natural heterogeneity does indeed exist at finer scales than those at which cattle selectivity operates. The measurement of heterogeneity at a variety of scales in both fields will be necessary to clarify the situation.

Complicating factors influencing vegetation distribution

Numerous factors that can influence the distribution of individual species and species richness have not been included in this study. Consequently, it is perhaps not surprising that there were no detectable relationship between species richness and grazing in High Brae. In addition, there was no relationship for most individual species, and for those where values were obtained the majority of variation was not explained by grazing. Before discussion of those species that did show associations, it is important to consider the variety of factors that were beyond the scope of the present study.

Studies in southern Swedish pastures have shown a clear link between past land use and patterns of diversity (Cousins & Erisksson 2001, Cousins & Eriksson 2002, Gustavsson et al. 2007). Cousins & Eriksson (2001) investigated the distribution of 52 rare grassland species in relation to land-use history and a variety of environmental factors and found that out of any factor analysed, land-use continuity over 300 years was associated with the largest number of species (seventeen). Cousins & Eriksson (2002) also analysed pastural species richness in relation to past land-use and found areas already being grazed in the 17th and 18th Centuries were the most species rich. Gustavsson *et al.* (2007) performed similar analyses and found that species richness and Shannon Index values were most significantly correlated with $_{18}$th Century land use, and with land use continuity, but not with current or 1961 land use. They also found that where grazing had been abandoned or switched to cutting, species richness fell to the same level regardless of time since abandonment, implying rapid payoff of “species debts”. These studies together suggest that accumulation of grazing-adapted species can take place over hundreds of years, and yet species loss occurs rapidly. If land-use history varies over different parts of Sulber and High Brae this could have heavily influenced the results. The lack of species-richness correlations in High Brae could, for example, be partially accounted for by discontinuity in the lower parts of the field (where grazing is now concentrated) if these were ever used for hay production. Another likely past land-use is the extraction of limestone, which may have created new areas of grassland where pavement once existed and which have yet to gain their full complement of species.

As already touched upon earlier, edaphic variation can also alter species distributions and species richness. Species richness is generally reduced by high fertility as this favours more limited assemblages of competitors that are able to exploit nutrients through rapid growth rates (Pausus & Austin 2001). Low fertility can also cause low species richness, but such low fertility is almost never found in nature (Proulx & Mazumder 1998). Different NVC communities are associated with different soil complexes in the two fields, which implies a relationship between soils and individual species distributions (Smith *et al.* 2004) and suggests that diversity will be varying according to differences in soil fertility. As already mentioned, soil variation also occurs at sub-community scales, notably within Sulber (Smith et al. 2004). Soil fertility can also affect the impact grazing has upon species richness. At higher fertility levels, grazing generally has a more positive effect upon species richness than at lower fertility levels, as the control of resource-exploiters becomes more important (Proulx & Mazumder 1998).

Soil fertility therefore presents two avenues of influencing the species richness recorded in this study: fertility may be lower in High Brae than in Sulber, reducing the beneficial effects of grazing and contributing to High Brae's higher mean species richness. This seems unlikely due to the prevalence of mesotrophic grassland. On the other hand, fertility may be higher in the grazed areas of High Brae relative to the ungrazed areas, thus reducing species richness in these areas and masking the beneficial effects of grazing. This effect seems to be likely, as more fertile soils are associated with the most grazed (i.e. mesotrophic) communities in the compositional analysis (Smith et al. 2004). The most grazed areas of High Brae are also lower in the field and likely to be receiving leached nutrients, whereas the uppermost and more sloping areas are likely to be shedding nutrients. It might be the case that, were it not for grazing, species richness in these areas would be naturally lower than in the less grazed areas, and that grazing is increasing diversity from a lower starting point thus giving the appearance of having no effect. In Sulber, there is less variation in topography and less potential for nutrient flow between parts of the field, which may mean that the beneficial effects of grazing on species richness are not masked.

Other grazers are also likely to be exerting a considerable influence on vegetation patterns. Sulber is presently grazed by low densities of sheep, while rabbit droppings and burrows were regularly observed in both fields. Grazing behaviour differs between species, so the effects of these other grazers may manifest themselves in different ways to those of the cattle. Sheep are much more selective grazers at the feeding station level than cattle (Grant et al. 1985), and their activity is therefore likely to have a negative effect on the abundance of subordinate plants on a small scale relative to the effects of cattle, exerting a relative homogenising effect on species distributions. Because heterogenising and homogenising effects are relative, by increasing the homogeneity of species distributions relative to the scale of selectivity shown by cattle, the presence of sheep in Sulber could theoretically increase the detectable contribution of cattle towards heterogeneity in species distributions (Adler et al. 2001).

As increased selectivity has been linked to smaller grazer sizes (Rook et al. 2004), it is likely that rabbits exert small-scale species-specific pressures that also tend to homogenise the vegetation. Rabbits have also been observed to concentrate their grazing on *Nardus stricta* and *Calluna vu!garis,* both of which are regarded as generally unpalatable to livestock (Fenton 1940). Behaviour such as this, acting in opposition to the preferences of cattle, may have blurred plant-trait mediated responses to cattle grazing by mitigating the advantages of any resistance strategies which are specific to cattle.

Other environmental variables are also likely to have played a role in determining species distributions and levels of diversity. Aspect can affect species distributions by influencing levels of sunlight and exposure to the elements, as well as larger-scale topography (Pausus & Austin 2001). Mean temperatures in Sulber are likely to be lower than High Brae due to its higher elevation, for example, with stronger winds causing desiccation pressure. Slope can’ also affect soil depth and moisture availability and has been linked with shallower soils in the study area (Smith et al. 2004). The distribution of these variables at different scales is likely to play a large role in explaining the variation observed here. The level of intersection of different niches at the scale of the quadrat is also likely to have influenced patterns of species richness (Lundholm & Larson 2003, Pausus & Austin 2001), masking or exaggerating detected correlations. Without proper analysis of these variables it is important not to underestimate their complex potential influence on the results.

Animal directed sampling

The sensitivity of the multi-zone analysis was limited in High Brae by the small number of Intermediate quadrats, but this was unavoidable without further directed sampling. Multi-zone analysis added to the usefulness of the study by revealing a many associations and trends e.g. that the biodiversity index of areas increased with increasing cattle activity High Brae *Sanguisorba minor* was shown to be associated with Intermediate activity areas, a relationship missed by two-zone analysis. Multi-zone analysis was also highly illuminating in revealing the critical levels of cattle activity across which some associations take place: for example, some species are divided between Low and Intermediate/High, others between Low/Intermediate and High.

By moving beyond random sampling and two-zone analysis this study has shown that results can vary depending on the surveying technique and analysis methods used. Such method-effects could be the reason for failure to detect differences in vegetation between grazed and ungrazed fields in nearby. Here, random sampling underrepresented the areas favoured by cattle. Random sampling from within a grazed field might in effect be sampling an ungrazed field because most of the samples would be within ungrazed areas. This would undermine any comparisons with other fields. Future studies should approach data collection and analysis in as flexible a way as possible to ensure maximum detection and accuracy, as when grazer activity is not evenly distributed random sampling will always under represent some areas. It is possible that with more directed surveying and zonation, yet more subtle relationships could be detected.

Habitat use

In Sulber, the fact that some pairs of communities that are little used separately but highly used when combined suggests cattle may be selecting combinations of vegetation that provide complementary nutrition as a more efficient strategy than moving between disparate communities to obtain necessary nutrients (Marion et al 2005). Beyond this, it is hard to draw many conclusions. The fact that U4 *Festuca ovina- Agrostis capillaris- Galium* *saxatile* grassland communities appear consistently well used and CG9b grassland is generally only moderately or little used fits with individual species correlations (*Sesleria albicans* is negatively correlated with cattle activity and *Agrostis capillaris* is positively correlated). This observation also fits with expected levels of productivity of these communities, U4 grassland being of relatively productive and CG9 being grassland being of relatively low productivity (Rodwell 1992). This suggests cattle may be selecting areas of more rapid growth, although soil fertility can also increase palatability and nutrient content (Backshall 2001). Since the most used communities are also those over relatively fertile soil (Smith et al 2004) it seems likely that soil properties may also be playing a role by influencing species composition and the properties of individual plants. It is important to note in any case that compositional analysis of habitat use did not detect significant discrimination between communities in Sulber.

In High Brae, it is easier to draw conclusions. The two most used communities are dominated by M38 spring vegetation, suggesting perhaps the availability of drinking water is playing a role in determining cattle movements. Water has been identified water as a dominant factor in determining cattle movements in arid pasture (Ganskopp 2001), and there is no reason to doubt that water plays a direct role in the study area, especially during hot weather (see Smith et al 2007). Water may also allow greater vegetation growth during the summer, increasing the grazing value of these communities. *Nardus stricta* grassland also appears well used. This is in contrast with a lack of association between grazing and *Nardus stricta* on a species level, and cattle are not known to select it except in the winter (Rodwell 1992). This suggests that these communities may have arisen as a result of an unrelated concentration of cattle activity thanks to their resilience to this activity.

The rankings of habitat use are certainly not simple, and probably reflect the interplay between many factors that influence habitat use besides the seeking out of favoured forage. Topography can be important; for example, sheep have been observed to avoid particularly steep areas, avoid grazing facing downhill and walk perpendicular to slopes (Hester *et al.* 1999). Topography could also influence exposure to the elements: no studies could be found to confirm this, but it seems logical that warmth and shelter should form a part of grazer decision-making to attain a balance between energy intake and expenditure. Underlying soils, drainage, aspect and exposure can also influence the productivity and palatability of vegetation, which could be expected to influence habitat use (Backshall 2001). Likewise, grazing itself can be self-reinforcing by stimulating the growth of more palatable and digestible plant matter and reducing the amount of litter (VanDen Bos & Bakker 1990). This means that grazing could be following patterns laid down by other grazers. It must also be remembered that past management practices are likely to have influenced the present distribution of communities much more than the present regime. For example, some of the areas of *Nardus* grassland could have been encouraged by overgrazing by sheep which avoid *Nardus* to its advantage (Rodwell 1992).

The specific animals tagged are also important. Even within breeds, animal size, weight, age, reproductive status and even disease status can be important. For example, larger animals are less selective, gestating animals may seek out particular nutrients and parasitised animals may seek out plants containing mildly toxic tannins (Rook *et al.* 2004). Behaviour can also vary during short timescales, for example with cattle selecting clover at night and grasses in the morning (Rutter *et al.* 2004). On the other hand, the use of rest areas may be coincident with but not directly related to the vegetation community, for example rest areas could be coincident with communities favouring sheltered conditions.

Another factor that could have affected the accuracy of the zonations used to divide areas of cattle activity is social behaviour. During the course of the survey the cattle were observed to move in groups and were never seen alone. Sheep have been observed to fail to use preferred food when this food is beyond a certain distance from any other individuals (Dumont & Boisy, 2000) and it is likely that, cattle effectively make group decisions about grazing based on similar social pressures. This means that for each point location obtained from the cattle tracking data, there may have been a surrounding area also occupied by cattle, thus blurring the boundaries between the cattle activity zones used here. To make any adjustments to the zonation methods used here, quantification of this effect would be necessary.

NVC ground-truthing

The low rate of matches between this survey and the existing NVC maps suggests that the existing maps do not represent the whole range of variation that this survey has detected. There are three possible explanations for the mismatches. The original survey may have missed small patches of different habitat that have been sampled here, the communities assigned here by Tablefit are erroneous, or the vegetation has changed since the original maps were made.

The fact that no sub-community matches were made suggests that the assignment of sub-community types to large units of land may be misleading. As an aggregate, an area could be regarded as belonging to a sub-community, but could in fact be a mosaic of other vegetation types. The mismatches at the community level and beyond are even more suggestive of a potential masking of variation by the existing maps. The apparent occurrence of mesotrophic grasslands within areas mapped as calcicolous could be particularly important as these communities are quite different in their species composition and soil properties. It seems unlikely that such mismatches could occur due to differences in survey or classification techniques, and this must cast doubt on the value of any attempts at compositional analysis of habitat use, since the community units upon which these were based may be inaccurate. It could also explain the lack of a significant difference in habitat use across the communities in Sulber, which had the highest mismatch rate. It is recommended that the findings of this study be tested by the placement of further random quadrats. If necessary, the resolution of the maps should be increased or additional labels assigned to map units to represent the level of deviation from the titular communities to avoid overconfidence in the maps' accuracy. Given that the fields are under a relatively new management regime, it may also be worthwhile periodically re-testing the NVC maps further into the future to test for ongoing changes in community boundaries.

Conclusions

This study has shown that the uneven distribution of cattle activity within the surveyed fields is associated with differences in species distributions even though the grazing regime is relatively recent and that, at least in one of the fields, higher cattle activity can be linked to increased botanical diversity. The individual associations of species could mostly, but not entirely, be explained in relation to their life-strategies and resistance mechanisms to grazing. The study therefore adds to a variety of research suggesting that grazing can benefit species richness and can fairly predictably influence species distributions.

In conservation terms, the importance of this study lies in its discrimination between areas of cattle activity within the fields. This analysis suggests that simple stocking rate prescriptions will not give consistent effects across a field, and also that the critical intensity of grazing pressure at which species distributions are affected varies between species. This means that species-specific conservation objectives for any such grazed site will need to be considered, for example, whether grazing is likely to affects SSSI indicator species. Detailed models to predict likely cattle movements would be necessary to do this. Patterns of diversity were not explained by cattle activity in High Brae. However, this does not discount its beneficial effects in this field. There is much potential for the masking of grazing effects on diversity by environmental factors, such as through the concentration of grazing in more fertile areas. The measurement scale was also relatively small, and could have missed larger-scale effects on botanical diversity.

Quadrat sward height was apparently only affected by grazing in Sulber, while there was no detected effect of cattle activity upon quadrat sward heterogeneity. This is particularly important, as it means the effects upon quadrat species richness/ Shannon index in Sulber and on individual species in both fields must be operating through other mechanisms. One such mechanism could be “niche release”, whereby underlying environmental heterogeneity would influence the level of impact of sward thinning on species richness. The scale of measurement used could also have influenced the results. It is likely that, as cattle are relatively unselective grazers, they operate to increase sward heterogeneity at scales beyond that of the quadrat.

The compositional analysis of cattle habitat use did not offer a comprehensive view of the choices made by cattle at this site. To an extent this could be due to the analytical methods employed but other factors, not just the activity of the cattle, will be exerting an influence on plant communities such as shelter, topography, water and social behaviour. At the same time, it should be noted that the plant communities will be influencing cattle movements and that this might alter depending on the time of the year and physiological and reproductive status of the animals. The results from the ground-truthing of the NVC maps also suggest that the value of any habitat-use studies at the site will be limited until refinements are made to these maps.

In conclusion, this study has demonstrated the wealth of information that can be gathered using GPS collars to track cattle movements and how these data can be used to direct vegetation sampling when investigating the effects of grazing. The study has demonstrated the intricate links between cattle movements, vegetation communities, plant diversity, species distributions and sward properties. Many of the associations between cattle activity and vegetation were significant and most of these associations were positive, with encouraging implications for the conservation of limestone grasslands using hardy cattle. It warrants further studies, to investigate the use of cattle management techniques to direct the cows to particular areas (especially those that are under utilised by the cows).

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