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**Title: Epigeal s**pider assemblage responses to vegetation structure under contrasting grazing management in upland calcareous grasslands

**Running Title:** Spider responses to vegetation structure

**Key words:** Spiders; Grazing; Calcareous grassland; Vegetation Structure; Cattle; Sheep; Conservation; GLMM; Rarefaction

**Authors:** Ashley Lyons a, Paul A Ashton b, Ian Powell c, Anne Oxbrough d

a Department of Biology, Biosciences Building, Edge Hill University,St Helens Road,Ormskirk, Lancashire, L39 4QP, United Kingdom. lyonsa@edgehill.ac.uk (corresponding author)

b Department of Biology, Biosciences Building, Edge Hill University, St Helens Road,Ormskirk, Lancashire, L39 4QP, United Kingdom. ashtonp@edgehill.ac.uk

c Department of Biology, Biosciences Building, Edge Hill University, St Helens Road,Ormskirk, Lancashire, L39 4QP,United Kingdom. powelli@edgehill.ac.uk

d Department of Biology, Biosciences Building, Edge Hill University, St Helens Road,Ormskirk, Lancashire, L39 4QP, United Kingdom.oxbrouga@edgehill.ac.uk

Abstract

1. Calcareous grassland is one of the most species rich and diverse habitats within Europe, but has faced decline due to agricultural intensification and abandonment. In recent years conservation organisations have altered grazing practices in an attempt to maintain floristic components. However, there has been little consideration of the effects of changes in grazing practices on invertebrates. This study determines the impacts of commonly used grazing practices in upland calcareous grasslands on spiders in relation to vegetation structural complexity.
2. Typical grazing management regimes were examined in three regions of upland calcareous grassland in Britain. Spiders were sampled from April – August 2014 and vegetation structural complexity was recorded in 2 m x 2 m quadrats paired with pitfall traps sequentially throughout the sample period.
3. There were three distinct spider assemblages among the grazing regimes; ungrazed, heavy sheep grazed and one shared between cattle and light sheep (which had a comparable grazing intensity). The distinct spider assemblages among grazing regimes can be attributed to the interaction of grazing and habitat structure.
4. Increased vegetation structural complexity in ungrazed regimes resulted in an assemblage dominated by ‘sheet web weavers’ (dominated by Linyphiidae). In contrast, reduced vegetation structural complexity and homogeneity in heavy sheep grazing resulted in an assemblage dominated by ‘other hunters’ (including *Oedothorax* and *Erigone* genera).
5. Grazing regime alters vegetation structural complexity and is important in supporting distinct spider assemblages. This research indicates that low intensity conservation grazing regimes, in addition to no grazing, should be promoted across upland calcareous grassland landscapes to maintain heterogeneity.

Introduction

Calcareous grassland is among the most species rich and diverse habitats in Europe, supporting a range of specialised flora and fauna (WallisDeVries et al. 2002; Poschlod & WallisDeVries 2002). Due to wide scale loss and degradation following mid-20th century agricultural intensification, it is currently the focus of conservation efforts and is protected in international legislation (e.g. EU Habitats Directive) (Willems, 2001; Fischer and Stocklin 1997; Poschlod et al. 2005; Roesch et al. 2013; Wallis De Vries et al. 2002). However, despite the great diversity of both flora and fauna, conservation management, which is typically performed through grazing with livestock, generally aims to maintain particular plant communities through prevention of succession and domination by one or few species (Willems 2001; WallisDeVries et al. 2002). Further, monitoring of conservation management treatments mostly refers only to vegetation (Poschlod & WallisDeVries 2002). This single taxon approach to conservation management and monitoring fails to recognise the importance of invertebrates, or the impact that contrasting management has on them, in these internationally important habitats.

Selection of grazing regime has implications for invertebrate communities through its effects on plant community composition and vegetation structural complexity (Lyons et al. 2017; Dennis et al. 2015; Dennis et al. 2001; Morris 2000; Vickery et al. 2001; Krauss et al. 2003; Woodcock et al. 2005). Both livestock type and intensity of grazing influence plant species composition and structural complexity (Lyons et al. 2017; Dennis et al. 2015). Differences in dietary choice, disposition of dung and effects of trampling can impact habitat structure and niche availability (Rook et al. 2004; Grant et al. 1985; Betteridge et al. 1999; Maelfait & De Keer 1990; Woodcock et al. 2009; Denno 1980). For instance, sheep display greater selectivity of forbs than cattle, which are more inclined to graze tall fibrous components, resulting in increased cover of grasses at comparable moderate stocking densities (Lyons et al. 2017; Reyneri *et al.* 1994; Grant et al., 1985). The decline in vegetation structural complexity associated with high stocking densities results in the loss of spiders which are dependent upon aerial structures and plant litter e.g. large web weavers (Deng et al. 2013; Dennis et al. 2001; Gibson et al. 1992). In contrast, some spiders require the less structurally complex, more open swards created by higher intensity grazing e.g. *Erigone spp* (Bell et al. 2001; Gibson et al. 1992). Further, spider abundance and species richness increases with reduced stocking density due to greater vegetation structural complexity and reduced disturbance (Dennis et al. 2015; Woodcock et al. 2009; Horváth et al. 2009).

Spiders are among the most abundant animals in terrestrial ecosystems and occupy an important role in terrestrial food webs as both predators and prey (Turnbull, 1973; Uetz, 1991). They are sensitive to changes in plant structural complexity which render them useful indicators of habitat change (Dennis et al. 2001, 2015; Prieto-Benitez & Méndez, 2011; Duffey, 1962; Uetz, 1991; Marc et al, 1991). Their habitat requirements in grasslands differ among species with some such as *Ceratinella brevipes* (Westring, 1851) and *Allomengea scopigera* (Grube, 1859) favoured by more structurally complex vegetation with deep litter layers (McFerren et al. 1994; DeKeer et al. 1989). Whilst less structurally complex vegetation favours pioneer species characteristic of disturbed land such as those from *Erigone* and *Oedothorax* genera (Noel and Finch, 2010; Downie et al. 2000; McFerren et al. 1994; Malfait and DeKeer, 1990). Differences in spider species associations with vegetation structure are also linked to spider hunting strategies (Uetz, 1991; Alderweireldt, 1994; Bell, et al. 2001). Ground hunting species such as those from the *Pardosa* genus require a heterogeneous sward of open patches to search for prey and taller vegetation for refuge (Malfait & DeKeer, 1990), whereas orb web weaving spiders select structurally complex vegetation that provides increased web anchorage points (Diehl et al. 2013; Langellotto & Denno, 2004; McNett & Rypstra, 2000). Differences in foraging strategy, activity and substrate utilisation amongst species make grouping spiders into guilds an appropriate way to examine environmental impacts on them (Corcuera et al. 2015; Schweiger et al. 2005).

Not unlike calcareous grasslands elsewhere in Europe, upland calcareous areas within Britain experienced decline due to intensive grazing, typically with sheep (Dennis et al. 2008; Fuller and Gough 1999). Indeed, increased grazing pressure between the 1960s and 1990s coincided with the 37% loss of upland calcareous grassland in England between 1960 and 2013 (Ridding *et al.* 2015). Over the last 15 years, in an attempt to conserve the characteristic vegetation of this habitat, changes in management have occurred based on the perceived benefit to the plant community. This has typically involved a shift from grazing with high numbers of sheep to lower stocking densities of cattle, though occasionally some areas are managed with lower stocking densities of sheep or no grazing. In contrast to calcareous grassland elsewhere in Europe and lowland Britain, though the plant community in upland calcareous areas left without grazing becomes dominated by grasses such as *Sesleria caerulea* (Lyons et al. 2017), loss of habitat due to scrub encroachment is rare, even in areas left without grazing for 20 years (personal observation). Further, upland calcareous grasslands in Britain are often large and well connected in comparison to those found in other parts of Europe. This is demonstrated by the estimated 33, 419 ha of calcareous grassland in Britain being spread over 62 sites, in contrast to Germany’s comparable extent (estimated at 31, 079 ha) spread over 924 sites (Calaciura and Spinelli, 2008). The greater size of individual sites in Britain renders the impacts of fragmentation and isolation, which are major threats to biodiversity in calcareous grasslands in Germany and other parts of Europe, much lower and further highlights the international importance of the unique nature of upland calcareous grasslands in Britain.

Research has shown a decline in invertebrate species richness in response to increased grazing intensity in a lowland limestone grassland (Gibson et al. 1992), and research in other upland grasslands types has shown an increase in invertebrate abundance in response to reduced grazing intensity (Dennis at al. 2001). However, research which tests the impacts of low intensity conservation grazing regimes on invertebrates in these internationally important upland calcareous grasslands is scarce, and to the best of the author’s knowledge only one previous study addressing this exists thus far. Lyons et al. (2017) examined impacts of low intensity cattle grazing, low intensity sheep grazing and areas without grazing on aspects of plant and carabid beetle diversity, finding plant species composition differed among grazing regimes whilst carabid beetle species composition was similar between cattle and sheep grazed regimes but distinct in ungrazed regimes.

This study aims to further address the knowledge gap, being the first to determine the impact of high intensity sheep, low intensity sheep, low intensity cattle and ungrazed regimes on spider assemblages in upland calcareous grasslands of conservation importance. Further, this study explores how structural complexity, and its interaction with grazing, drives differences in spider assemblages. These findings are discussed in the context of upland calcareous grassland conservation and the role that grazing prescriptions can play in maintaining and enhancing a diverse spider fauna.

The study addresses the following hypotheses:

1. Since grazing directly alters the amount of biomass within the sward it is expected that vegetation structural complexity will increase with decreasing grazing intensity.

Supplementary to this, it is expected that owing to equal stocking densities, vegetation structural complexity will not differ between low intensity sheep grazing and cattle grazing regimes.

1. It is expected that as Lyons et al. (2017) found with carabid beetles, spider communities will differ among grazing regimes due to the influence of increasing vegetation structural complexity with decreasing grazing intensity. As with carabid beetles, it is expected that the spider community under low intensity sheep and cattle grazing will be comparable.
2. It is expected that the proportion of specialised foraging guilds of spider species will differ in each grazing treatment, reflecting changes in vegetation structural complexity highlighted in Hypothesis One.

Methods

Study Sites

Four grazing regimes were selected for study within the most extensive upland limestone areas in the UK. These were: ungrazed, low intensity cattle grazed, low intensity sheep grazed and high intensity sheep grazed (the latter hereafter referred to as cattle, light sheep and heavy sheep respectively). These represent the most commonly used and replicable grazing regimes across the regions of this study.

Each grazing regime was replicated across three geographically distinct regions separated by 17 – 47 km in Northern England (54°29′18.55″N, 002°32′33.00″W) (54°11′43.30″N, 002°21′00.13″W) (54°08′50.69″N, 002°06′32.54″W) (Supporting Information S1). In each region four extensive areas of limestone grassland (size 12 ha – 526 ha, median 42.5 ha) were selected, within which three sampling locations were established. These were separated by a minimum of 72 m (median 269 m) to ensure statistical independence of samples (Digweed et al. 1995), and a minimum of 50 m from the edge of the grazing regime and away from disturbance e.g. footpaths, water troughs etc. Further, spatial independence of samples was confirmed with Moran's I test based on nearest neighbour distances for all 36 locations for spider abundance, showing there was no significant spatial autocorrelation (Moran’s I ± SD: --0.07 ± 2.60, p = 0.99) (Bivand et al., 2014).

Across all sampling locations the current grazing regime had been in place for at least ten years prior to investigation. Cattle and light sheep grazed regimes were considered lightly grazed for the conservation of upland calcareous grassland with stocking densities of less than 0.24 Livestock Units per Hectare per Year (LU/ha/y-1), whereas heavy sheep grazed regimes had a stocking ratio of more than 0.36 LU/ha/y-1 (Backshall et al. 2001) calculated as: Annual Equivalent Stocking Density = ((N\*GLU/H)\*(M/12)

Where: N = Number of individuals, GLU = Grazing Livestock Unit (taken from Nix, 2004), H = Hectares and M = Number of months grazed.

Elevation ranged from 288 – 396 m, median 335 m. Soil across the sites was generally base rich with some deposits of glacial till and peat. All areas were characterised by a mix of calcareous grassland, upland heath and limestone pavement, and were surrounded by a mix of extensively and intensively grazed open grassland. Typical areas of calcareous grassland were selected for study using detailed habitat maps and aerial photographs. Within each location surveys of vegetation and epigeal spiders were conducted between May – August 2014.

Epigeal Spider Sampling

Within each sampling location a line of six pitfall traps, spaced 2 m apart, were established to capture spiders. Traps consisted of a plastic cup approximately 7 cm in diameter and 9 cm deep and were covered with a square plastic lid suspended 1 cm from the ground by pegs to prevent rain water and debris from entering. These were filled with 1 cm depth of antifreeze to act as a killing and preserving agent. To prevent traps being trampled or interfered with by livestock, in grazed areas each trap was protected by a secured cage made from 2.5 cm x 2.5 cm gauge mesh. These cages do not affect the trapping rates of ground-dwelling invertebrates (Oxbrough et al., 2012). Traps were set between 01/05/2014 and 22/08/2014 and were changed every 21 days, giving a maximum total of 105 trap days. Samples from five of the traps within each location were pooled for analysis. The total number of trap days for each location is displayed in Supporting Information S2.

Pitfall traps are a widely used sampling method to catch active ground dwelling invertebrates in grasslands and heathlands (Gardner et al. 1997; Haysom et al. 2004; Lyons et al. 2017). This method estimates relative invertebrate activity rather than an absolute measure of density, reflecting species abundance and movement rates (Greenslade, 1964; Mazia et al. 2006). Consequently, they are less likely to capture sedentary species or those occupying higher levels of vegetation. Nevertheless, their high catch rate, ease of setting up and objectivity render their use appropriate in large scale studies with multiple sites (e.g. Oxbrough *et al.* 2012; Taboada *et al.* 2010; Niemela *et al.* 1993).

All adult spiders were identified to species level using Roberts (1993) and nomenclature follows the World Spider Catalogue (2017). Information on conservation status was gathered from Dawson et al. (2008). Since it was not possible to reliably identify most juvenile species these were excluded from the study. Spider reference specimens are housed at the Edge Hill University Department of Biology arthropod collection.

Spider Hunting Guilds

Following identification of spiders to species, they were divided into five separate guilds based on hunting strategy as suggested by Cardoso et al. (2011): sheet web weavers, ground hunters, space web weavers, other hunters and ambush hunters. However, whilst Cardoso et al.’s (2011) classification includes all Tetragnathidae in the orb web guild, in this study the single species captured from this genus was *Pachygnatha deegri* (Sundevall, 1830) which does not spin orb webs as an adult but occupies the ground layer (Roberts 1993; Harvey et al. 2002) and since only adult specimens were identified it is included in the ground hunter guild in this study. The list of spider species and associated guilds is included in Supporting Information S3.

Vegetation Structural Complexity Measurements

Within 1m from pitfall traps, two 2 m x 2 m quadrats, spaced 2 m from each other were set up at approximately three week intervals from 6th May 2014 to 1st August 2014, giving a total of 10 quadrats per sampling location. Within each quadrat the vertical distribution of vegetation was recorded as the number of ‘contacts’ in each 5 cm height interval of a pin 5 mm in diameter passed vertically through the vegetation at 10 points (separated by 15 cm), a method adapted from Wiens (1974), Woodcock et al. (2007) and Azpiroz & Blake (2016). The type of vegetation in contact with the pin was also recorded as graminoids, thatch (dead vegetation), moss and herbs. Data from all 10 pins per quadrat were summed to give a single unit of structural complexity. The median of this unit of structural complexity was then calculated for all ten quadrats at each sampling location to account for seasonal variation, giving a single unit of structural complexity per sampling location for the entire sampling period. Within each quadrat per cent cover of all vascular plants and bryophytes was estimated to the nearest five per cent. Per cent cover data collected at each sampling location for the duration of the sampling period was averaged, giving a single measurement of vegetation cover from the 10 quadrats recorded at each location.

Data Analysis

To account for differences in trapping effort due to trap loss all samples were standardised by trap day by calculating the abundance of each species at each location and dividing it by the number of actual trap days at that location and then multiplying it by the maximum number of trap days across all locations (105) a standard method in studies using pitfall trapping (Bergeron et al. 2013; Blanchet et al. 2012: Pinzon et al. 2013). The number of trap days for each location is displayed in Supporting Information S2.

All statistical analyses were carried out with R statistical software version 3.3.2. (R Core team 2016) with the exception of rarefaction curves which were calculated using EstimateS version 9.1.0 (Colwell 2013).

Differences in spider species richness were examined with raw species data (not standardised by trap day) using sample based rarefaction scaled by the number of individuals. This technique accounts for differences in sampling effort by standardising species richness for the number of individuals within a sample. Rarefaction estimates the number of species expected in a random sub-sample extracted from a larger sample (Magurran 1988, 2004).

Differences in spider abundance (as measured by the accumulated catches at each location) among grazing regimes were examined with Generalised Linear Mixed Models (GLMMs) performed with Poisson errors using the glmer function of the lme4 package (Bates et al. 2015). The interaction of grazing regime and vegetation structural complexity was modelled as a fixed factor with region modelled as a random factor. The model was tested for over dispersion of Poisson errors and was found to be overdispersed (dispersion = 24.12). To combat overdispersion the model was recalculated using negative binomial errors (Thomas 2017). The model was tested for significance using the Anova function of the Car package (Fox & Weisberg 2011) and post hoc Tukey pairwise comparisons were used to test for differences among grazing regimes, correcting p values for multiple comparisons with the Holm method using the glht function of the multcomp package (Hothorn et al. 2008).

The impacts of grazing and vegetation structural complexity on the comparative proportion of each hunting guild were examined with GLMMs, this time computed with Binomial errors to account for the use of proportion data (Crawley 2012). The interaction of grazing regime and vegetation structural complexity was modelled as a fixed factor with region modelled as a random factor. GLMMs were computed for sheet web weavers and ground hunters. Ambush hunters, space web weavers and other hunters were not included as the data sets for each of these were too small or contained too many zero observations and instead main trends were discussed in the text. To correct for overdispersion, observation level random effects were included in the overall model (Harrison 2014) (dispersion: sheet web weavers = 10.03; ground hunters = 20.18) and the significance of models were tested as above. Bonferonni correction was applied to the confidence intervals to account for the multiple testing of the abundance data (e.g. split into five guilds). However, as the number of species was not divided equally among the five guilds the confidence intervals at which statistical significance was determined using the Bonferonni correction were not set equally (e.g. 0.05/5) but rather as the proportion that each guild comprised of the data set (required confidence intervals to infer significance: sheet web weavers < 0.025; ground hunters < 0.019) following Neuwald and Green (1994).

To determine if vegetation structural complexity or plant species richness was different among grazing regimes GLMMs were again performed with grazing modelled as a fixed factor and region modelled as a random factor, this time using Poisson errors in the final model as overdispersion was not detected (vegetation structural complexity dispersion = 1.19; plant species richness dispersion = 1.69). Variability of vegetation structural complexity was assessed using the Brown-Forsythe test for equality of variances, as a measure to determine structural heterogeneity within each grazing regime. Significance was tested using Kruskal-Wallis applied to the function using the lawstat package. Brown-Forsythe’s test for equality of variances determines absolute deviation of scores from group medians and can be used on non-normally distributed data (Brown & Forsythe, 1974; Sheskin, 2011). To compare the proportion of vegetation structural complexity that was accounted for by thatch among grazing regimes a GLMM was performed with Binomial errors with grazing regime modelled as a fixed factor and site modelled as a random factor. The model was tested for over dispersion of Binomial errors and was found to be overdispersed (dispersion = 10.15). To correct for overdispersion observation level random effects were included in the overall model (Harrison 2014). Proportional Bonferonni correction was applied as above, requiring a confidence interval of < 0.026 to infer significance. Thatch was examined in isolation as it constituted a large portion of the vegetation structural complexity in some regimes and is known to be important in providing refuge for some spider species (Rypstra et al. 1999).

Spider species composition was examined through Redundancy Analysis (RDA) computed on Hellinger transformed spider species data using the RDA function in the vegan package (Oksanen et al. 2016). Grazing, vegetation structural complexity and the interaction of grazing and vegetation structural complexity were included as the main terms in the model with region included as a random factor. A permutation test, with 9999 permutations, was used to test final significance of the model.

Indicator Species Analysis (Dufrene & Legendre 1997) was computed to identify species that were strongly associated (both common and frequent) with each grazing regime using the indval function of the labdsv package (Roberts, 2015). Significance of indicator values was assessed using a Monte Carlo randomisation procedure with 4999 iterations.

Results

A total of 16,056 individual spiders were collected, of which 4162 (25.91% of overall abundance) were juveniles and 157 (0.98% of total abundance) were damaged specimens. Neither of these groups could be identified and were therefore omitted from the data set. A total of 11,737 individuals from 101 species were included in the analyses. A full list of species is given in the Supporting Information S3. Overall, six species individually comprised more than 5% of the total spider abundance, together totalling nearly 60% of the total catch: *Pardosa pullata* (Clerk, 1757) (20.5%), *P. degeeri* (10.25%), *Silometopus elegans* (O. P.-Cambridge, 1873) (9.5%), *Pocadicnemis pumila* (Blackwall, 1841) (7.13%), *Palliduphantes ericaeus* (Blackwall, 1853) (7.04%) and *Tiso vagans* (Blackwall, 1834) (5.5%).

Assessment of conservation status according to Dawson et al. (2008) revealed two endangered species: *Jacksonella falconeri* (Jackson, 1908) (50 individuals) and *Porrhomma egeria* Simon, 1884 (1 individual), and eight vulnerable species; *Agyneta subtilis* (O.P.-Cambridge, 1863) (265 individuals); *Walckenareia dysderoides* (Wider, 1834) (13 individuals); *Walckenaeria inscisa* (O.P. Cambridge, 1871) (10 individuals); *Allomengea scopigera* (Grube, 1859) (7 individuals); *Trichopternoides thorelli* (Westring, 1861) (4 individuals); *Maro minutus* O.P.-Cambridge, 1906 (1 individual); *Walckenaeria monoceros* (Wider, 1834) (1 individual); *Walckenaeria obtusa* Blackwall, 1834 (2 individuals).

Vegetation structure and diversity among grazing regimes

Vegetation structural complexity was significantly different among grazing regimes (*X*2 (3, *N* = 36) = 203.15, p < 0.001) and was driven by greater structural complexity in ungrazed compared to cattle, light sheep and heavy sheep regimes and significantly lower structural complexity of heavy sheep compared to cattle, light sheep and ungrazed (Fig. 1a). Vegetation structural complexity was significantly variable in cattle, light sheep and ungrazed regimes (H N = 36 = 165.55, p < 0.001; H N = 36 = 221.28, p < 0.001; H N = 36 = 27.16, p < 0.001) but not so in heavy sheep (HN = 36 = 10.83, p > 0.21), indicating vegetation structural complexity was homogeneous in the latter and heterogeneous in the former.

The proportion of vegetation structural complexity comprised of thatch was also significantly different among grazing regimes (*X*2 (3, *N* = 36) = 112.18, p < 0.001) with a greater proportion of thatch in ungrazed compared to all other grazing regimes and a significantly lower proportion of thatch in heavy sheep grazing compared to all other regimes (Fig. 1b). Plant species richness was significantly different among grazing regimes (*X*2 (3, *N* = 36) = 22.49, p < 0.001) and was driven by greater species richness in cattle compared to light sheep and ungrazed regimes and greater richness in heavy sheep compared to ungrazed regimes (Fig. 1c).

Spider species diversity among grazing regimes

Rarefaction curves showed that spider species richness did not differ among grazing regimes (Fig. 2), as indicated by almost complete overlap of confidence intervals. Total spider abundance was significantly different among grazing regimes (*X*2 (3, *N* = 36) = 17.41, p < 0.01) though post hoc testing could not determine which grazing regimes were driving this difference, likely due to the conservative nature of these tests (and correction for multiple comparisons). However, examination of data suggests overall model significance may reflect the greater abundance in cattle and light sheep regimes compared to those of heavy sheep and ungrazed regimes (Fig. 3). There was no significant relationship between spider abundance and vegetation structure (*X*2 (1, *N* = 36) = 0.05 p > 0.05) or with interaction between grazing and vegetation structure (*X*2 (3, *N* = 36) = 6.01, p > 0.05).

Spider Guilds

The most abundant guild was the sheet web weavers (6129 individuals, 49.39%) which were mostly from the Linyphiidae family, then ground hunters (4866 individuals, 39.19%) comprised largely of Lycosidae and Tetragnathidae (which were exclusively *P. degeeri*) but also Gnaphosidae and Liocranidae, other hunters (1258 individuals, 10.13%) comprised largely of *Erigone spp* and *Oedothorax spp* which are separated from other species in the Linyphiidae family due to their versatile hunting strategies, ambush hunters (97 individuals, 0.78%) exclusively from the Thomisidae family and space web weavers (63 individuals, 0.51%) which were all *Robertus lividus* (Blackwall, 1836).

Examining the proportion that each guild contributed to the overall assemblage within each regime showed that the proportion of sheet web weavers was significantly different among grazing regimes (*X*2 (3, *N* = 36) = 15.94, p < 0.025, Bonferroni corrected p values) and was driven by a lower proportion in heavy sheep compared to ungrazed, cattle and light sheep (ungrazed - z = 3.37, p < 0.01; cattle - z = 3.53, p < 0.001; light sheep – z = 3.36, p < 0.01) (Fig. 4). Vegetation structure did not significantly influence the proportion of sheet web weavers among grazing regimes (*X*2 (1, *N* = 36) = 2.97, p > 0.025), though the interaction of grazing and vegetation structure did (*X*2 (1, *N* = 36) = 28.98, p < 0.025). Ground hunter proportion was significantly different among grazing regimes (*X*2 (3, *N* = 36) = 30.16, p < 0.014), though post hoc testing could not find a significant difference among grazing regimes. Examination of data suggests overall model significance may reflect the much lower proportion of ground hunters in heavy sheep regimes compared to the other regimes (Fig. 4). Further, ground hunter proportion was not significantly impacted by vegetation structure or the interaction between grazing and vegetation structure (*X*2 (3, *N* = 36) = 0.99, p > 0.014, *X*2 (1, *N* = 36) = 2.72, p > 0.014).

Spider Assemblages

Spider assemblage differed significantly among grazing regimes (F3, 25 = 7.40, p = 0.001, variation explained = 33.02%), by vegetation structure (F1, 25 = 3.02, p = 0.02, variation explained = 4.51%) and by the interaction of vegetation structure and grazing (F3, 25 = 1.7, p = 0.04, variation explained = 8.12%). The RDA plot (Fig. 5) shows ungrazed and heavy sheep regimes are separated along RDA1. In contrast, cattle and light sheep regimes are not separated from each other and occupy an intermediate position on this axis. Both ungrazed and heavy sheep regimes display a similar spread across RDA2 whereas light sheep and cattle form much tighter clusters.

Indicator species analysis revealed 10 species associated with ungrazed, 10 with heavy sheep, three with cattle and three with light sheep (Table 1). Of the 10 species associated with ungrazed regimes all were from the sheet web weaver guild and either had a habitat preference for leaf litter or humid conditions (Table 1). Six of the 10 species associated with heavy sheep grazing belong to the *Oedothorax* or *Erigone* genera, both of which occupy the ‘other’ hunting guild category and are associated with short vegetation in highly disturbed habitats (Table 1). Further the shade intolerant ambush hunter, *Xysticus cristatus* (Clerck, 1757), was also associated with heavy sheep grazing. The three species associated with light sheep grazing (*Bathyphantes gracilis* (Blackwall, 1841), *Dicymbium tibiale* (Blackwall, 1836) and *T. vagans*) were all from the sheet web weaver guild and have a preference for vegetation close to the ground (Table 1). There were three species associated with cattle grazing, one of which was the only ground hunter associated with any of the grazing regimes and is associated with patchy grassland habitats whilst the remaining two were from the sheet web guild.

Discussion

This study found that the spider fauna of upland calcareous grasslands is influenced by both grazing type and vegetation structural complexity, and that the impacts of vegetation structure are not consistent among the regimes. The distinct spider assemblages in ungrazed and heavy sheep grazed regimes reflects the interaction of grazing and structural complexity and is in concordance with experimental studies from a lowland calcareous grassland and upland *Nardus stricta* grasslands which examined the impacts of vegetation height on spiders (Gibson et al. 1992; Dennis et al. 2001). The overlap in assemblage between light sheep and cattle grazed regimes in the current study is reflective of the comparative structural complexity in these regimes, suggesting the differences in assemblage are influenced more by grazing intensity than the type of grazing animal used. Lyons et al. (2017) found the same relationship with carabid beetles and grazing intensity in upland calcareous grasslands, suggesting that the relationship found here holds for more than one invertebrate taxa. The contrasting assemblages among grazing regimes in the present study can be accounted for by the response of spider species to vegetation structure. Six of the ten species associated with ungrazed regimes in this study (Table 1) are acknowledged as having habitat preferences for plant litter (Harvey at al. 2002). The greater amount of plant litter (in this case thatch) in ungrazed regimes provides increased refuges for spiders (Rypstra et al. 1999). Structural differences in vegetation influences microhabitat conditions such as humidity, which in turn influences the distribution of some spider species (Bell et al. 2001; Almquist, 1973). For example, greater structural complexity from ungrazed vegetation provides a more stable and humid microclimate than grazed vegetation by protecting from extreme climatic conditions (van Klink et al. 2015; Pétillon et al. 2010; DeKeer et al. 1989). The combination of high structural complexity and a well-developed layer of thatch may be particularly important for maintaining a stable microclimate in free draining upland calcareous grasslands, especially where temperatures can range from below freezing up to 27 °C in the summer months. In the present study, six of the ten species that had strong associations with ungrazed regimes have preferences for damp/humid conditions (Table 1). In addition, all the indicator species of the ungrazed regime are sheet web weavers, which capture prey on small webs laid over or amongst vegetation. This suggests that the lack of disturbance by livestock in ungrazed areas shapes assemblages by providing a structurally stable habitat and microclimate.

By comparison, the reduced structural complexity and reduced proportion of thatch of the heavy sheep grazed regime provides conditions for species associated with short vegetation and good dispersal abilities which are well known from disturbed habitats e.g. *Erigone atra* Blackwall, 1833*, Oedothorax fuscus* (Blackwall, 1834)*, T. vagans* (Duffey, 2005; McFerren et al. 1994). Spider assemblages in heavy sheep grazing have been referred to as pioneer (Duffey 1993), consisting of species that are active aeronauts, able to disperse freely and exploit open ground where competition is low. The reduced potential web anchorage points due to low structural complexity favour the versatile foraging strategies of *Erigone* and *Oedothorax* species (Alderweireldt, 1994). Six of the ten species associated with this regime belong to either of these genera, all of which are in the ‘other’ hunting guild. This guild constitutes the greatest proportion of all guilds in heavy sheep grazing and is proportionally greater than in all other regimes. It is comprised of species with varied and often versatile hunting strategies which may help survival in highly disturbed habitats e.g. *Erigone* species may vary their mode of foraging between actively catching prey and capturing prey in a small web which is not reliant on tall vegetation but is usually constructed very close to the surface of the ground (Maelfait & De Keer, 1990; Alderweireldt, 1994). The association of the shade intolerant ambush hunter *X. cristatus* which can adopt a hunting position on the ground surface, thus not relying on complex vegetation, also reflects the influence of reduced vegetation structural complexity and low levels of thatch present in this regime (Harvey et al. 2002).

The reduced structural complexity in heavy sheep grazing also accounts for the reduced proportion of ground hunters compared with other grazing regimes. Ground hunters, such as those in the genus *Pardosa*, require increased structural complexity as they utilise different aspects of the vegetation in different life stages (Vlijn & Kessler-Geschiere, 1967). *Pardosa* species use open patches to search for prey or copulation partners by sight, females utilise sites exposed to sunlight to warm their cocoons and juveniles seek refuge in taller vegetation to overwinter (Bristowe, 1958; DeKeer et al, 1989; Malfait & DeKeer, 1990). The present study suggests intermediate structural complexity promotes increased spider abundance, as evidenced by the greater abundance in cattle grazing than heavy sheep grazing. Here, the interaction of grazing and vegetation structural complexity may be important as demonstrated by the association of *Pardosa pullata* (Clerck, 1757), which was found in much greater abundance in cattle grazing (30% of total spiders in this regime) than heavy sheep grazing (6% of total spiders in this regime). The greater disturbance in heavy sheep regimes as a result of increased grazing pressure resulted in structural homogeneity. This is in contrast with the heterogeneous structure of cattle grazed regimes which result from reduced grazing pressure. Under this reduced grazing pressure structural complexity increases as stock are able to avoid unpalatable vegetation (e.g. around dung, less favoured plants etc.) which creates more niches (Grant et al. 1985; Maelfait & De Keer, 1990; Woodcock et al. 2009). Indeed, Maelfait & De Keer (1990) found that juvenile *Pardosa palustris* (Linnaeus, 1758) utilised taller vegetation growing around cattle dung as overwinter refuge. The disturbance activity at reduced grazing levels creates heterogeneity, and thus more niches, in the vegetation structure through vertical niche differentiation (Denno, 1980). In comparison, few niches are available in heavy sheep regimes as a result of reduced and more homogenous vegetation structural complexity.

In the present study grazing regime affected heterogeneity of vegetation structural complexity. Vegetation structure was heterogeneous in ungrazed, cattle and light sheep regimes whilst structure in heavy sheep regimes was homogeneous. Though vegetation structure was heterogeneous in cattle, light sheep and ungrazed regimes, the latter was distinct in having greater overall structural complexity. This is reflected in differences in spider abundance among these regimes which is greater in cattle and light sheep compared with ungrazed (Fig. 3). This is contrary to previous experimental studies on spider abundance in relation to stocking densities similar to those in this study, which found spider abundance increased with decreasing stocking densities 12 – 18 months after changes in grazing regime (Dennis et al. 2015; Mysterud at al. 2010). Further, whilst assemblages differed amongst grazing regimes this was driven by changes in composition and abundance rather than spider species richness, where similar numbers of spider species were supported amongst the grazing regimes in upland calcareous grassland. This contrasts with the observation of greater species richness with reduced stocking density reported by Dennis et al. (2015) and Mysterud et al. (2010) in other grassland habitats, though the former conceded that the period of equilibrium following changes in grazing practices needed further investigation. In the present study, grazing had been in place for a minimum of 10 years prior to sampling. The contrasting results of spider abundance and richness in the present study compared to those of Dennis et al. (2015) and Mysterud et al. (2010), where grazing was in place for only three years and one year prior to investigation respectively, may reflect adequate time for equilibrium to be reached in upland calcareous grasslands. Indeed, the finding on spider species richness among grazing regimes in the present study is in concordance with the result of Lyons et al. (2017) for carabid beetle species richness among grazing regimes in upland calcareous grasslands.

Conservation significance and management recommendations

In this study vegetation structural complexity did not increase with greater plant species richness but instead responded to grazing intensity, as observed in ungrazed regimes. Further, spider species richness did not differ among grazing regimes but spider assemblage, guild proportion and presence of rare species did, likely due to differences in vegetation structural complexity and disturbance. Therefore, it is recommended that management decisions include the consideration of maintaining varied structural complexity to support a diverse epigeal spider community across the landscape.

The intermediate structural complexity of light sheep and cattle grazing produces a distinct assemblage and greater abundance than high intensity sheep grazing and no grazing. The latter possibly being driven by the success of *P. pullata*. Further, ungrazed regimes provide a unique habitat, with high structural complexity and increased thatch layer, which produces a distinct spider assemblage consisting of species that require a specific microclimate as indicated by the association of species with habitat preferences for high humidity. Given the scarcity of ungrazed grasslands and the length of time taken to produce its structural complexity, coupled with the presence of the endangered *P. egeria* and *J. falconeri* and the vulnerable *A. subtilis*, *W. dysderoides*, *W. inscisa* and *W. obtusa*, the continuation of this regime is recommended.

The distinct assemblage in heavy sheep grazing reflected a community of commonly found disturbance tolerant pioneer species, with little in common with the diverse assemblages that could be supported by lighter grazing regimes. Though *J. falconeri,* *A. subtilis* and *W. dysderoides* were recorded in heavy sheep grazing they were not exclusive to this treatment and as this grazing regime is common across the landscape the cessation of heavy sheep grazing on internationally important calcareous grassland is recommended. Spider assemblages were comparable between light sheep and cattle grazing, and both support *J. falconeri,* *A. subtilis*, *W. dysderoides*, and *W. inscisa.* However, since a few vulnerable spiders were only found with cattle (*A. scopigera*, *M. minutus* and *T. thorelli*) or light sheep (*W. monoceros*) there is a strong argument for the continuation of both grazing types across the landscape.

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**Table 1:** Spider species associated with grazing regime. Indicator Species Analysis produces an Indicator Value between 0 – 1, with values closest to 1 signifying a perfect indictor (always present in a particular treatment and exclusive to that treatment). P values signify significance of Indicator Values for each species based on Monte Carlo randomisation procedure with 4999 iterations. Hunting guilds were gathered from Cardoso et al. (2011) and habitat preferences gathered from Harvey et al. (2002). All species were categorised as of least concern in Britain by Dawson et al. (2008). GH = ground hunter; SW = sheet web weaver; O = other hunter, SP = space web weaver; AM = ambush hunter. p < 0.05 = \*; p < 0.01 = \*\*; p < 0.001 = \*\*\*

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Family | Guild | Habitat Preferences | Indicator Value |
| Ungrazed |  |  |  |  |
| *Monocephalus fuscipes* | Linyphiidae | SW | Litter in woodland but also in grassland | 0.62\*\*\* |
| *Robertus lividus* | Theridiidae | SP | Leaf litter | 0.60\*\* |
| *Palliduphantes pallidus* | Linyphiidae | SW | Litter and under stones | 0.56\*\* |
| *Pocadicnemis pumila* | Linyphiidae | SW | Grassland, moorland, blanket bog (damp conditions) | 0.53\*\*\* |
| *Saaristoa abnormis* | Linyphiidae | SW | Leaf litter | 0.51\*\* |
| *Palliduphantes ericaeus* | Linyphiidae | SW | Amongst plant stems, litter, require humid conditions | 0.50\*\* |
| *Bathyphantes parvulus* | Linyphiidae | SW | Grasslands, also marshes and fens | 0.46\* |
| *Walckenaeria acuminata* | Linyphiidae | SW | Damper substrates, any habitat in the ground zone | 0.44\* |
| *Micrargus apertus* | Linyphiidae | SW | Litter | 0.33\* |
| *Centromerus dilutus* | Linyphiidae | SW | Detritus  | 0.32\* |
| Cattle |  |  |  |  |
| *Gongylidiellum vivum* | Linyphiidae | SW | Grassland, damp situations | 0.44\* |
| *Pardosa pullata* | Lycosidae | GH | Grassland with tussocks | 0.44\* |
| *Silometopus elegans* | Linyphiidae | SW | Grass, wet or marshy places | 0.38\* |
| Light Sheep |  |  |  |  |
| *Hahnia nava* | Hahniidae | SW | Moss and other low vegetation and amongst stones | 0.63\*\*\* |
| *Agyneta cauta* | Linyphiidae | SW | Litter, detritus, occasionally moss on damp sites | 0.46\* |
| *Peponocranium ludicrum* | Linyphiidae | SW | Unimproved grassland, close to the ground. | 0.44\* |
| Heavy Sheep |  |  |  |  |
| *Erigone atra* | Linyphiidae | O |  Low vegetation – ubiquitous | 0.77\*\*\* |
| *Bathyphantes gracilis* | Linyphiidae | SW | Grasslands – ubiquitous | 0.69\*\*\* |
| *Oedothorax retusus* | Linyphiidae | O | Grassland and agricultural fields | 0.65\*\* |
| *Dicymbium tibiale* | Linyphiidae | SW | Under stones | 0.63\*\* |
| *Oedothorax gibbosus* | Linyphiidae | O | Moist/disturbed habitats  | 0.56\*\* |
| *Oedothorax fuscus* | Linyphiidae | O | Short grassland | 0.55\*\* |
| *Xysticus cristatus* | Thomisidae | AM | Disturbed grasslands, shade intolerant | 0.47\* |
| *Erigone dentipalpis* | Linyphiidae | O | Low vegetation – ubiquitous | 0.45\* |
| *Tiso vagans* | Linyphiidae | SW | Grassland - aeronaut | 0.43\* |
| *Oedothorax agrestis* | Linyphiidae | O | Saturated habitats | 0.33\* |

**Figure 1** (a) vegetation structural complexity among grazing regimes, (b) thatch cover among grazing regimes, (c) plant species richness among grazing regimes. U= ungrazed, C = cattle, LS = light sheep, HS = heavy sheep.

**Figure 2** Sample based rarefaction curves scaled by the number of individuals, indicating spider species richness. U = ungrazed, LS = light sheep grazed, HS = Heavy sheep grazed and C = cattle grazed. Bars indicate 95% confidence intervals.

**Figure 3** Spider abundance among grazing regimes. The letters indicate significance of post hoc Tukey test, where letters are different this indicates significant difference at p < 0.05. U = ungrazed, C = cattle, LS = light sheep, HS = heavy sheep.

**Figure 4** Relative proportion of each guild in each grazing regime. The letters indicate significance of post hoc Tukey, where letters are different this indicates significant difference (p < 0.05).

**Figure 5** RDA ordination of spider community assemblages by grazing and vegetation structure, and their interaction, constrained by geographical location. The percent of variation explained by each RDA axes after removing the contribution of site is: RDA1 is 31.84% and by RDA2 is 10.81%. Circles = ungrazed; triangles = cattle; squares = light sheep; diamonds = heavy sheep.