# Differential indirect effects of excluding livestock and rabbits from chalk heath on the associated leafhopper (Hemiptera: Auchenorrhyncha) fauna

# David Fisher Barham and Alan J.A. Stewart<sup>\*</sup>

Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton, UK; \*Author for correspondence (e-mail: a.j.a.stewart@sussex.ac.uk; phone: +44-1273-877476; fax: +44-1273-678433)

Received 15 April 2005; accepted in revised form 1 June 2005

Key words: Auchenorrhyncha, Calcareous grassland, Chalk heath, Grassland, Grazing, Leafhoppers

# Abstract

Preliminary results are presented of sampling the leafhopper assemblages on a field experiment designed to examine the differential effects of rabbits and livestock (mainly sheep) on the vegetation of chalk heath in southern England. Experimental plots that excluded livestock either allowed entry by rabbits or excluded them. Results were compared with those from plots grazed by both livestock and rabbits. After 7 years, exclusion of grazing herbivores had resulted in predictable increases in vegetation height, but no major changes were detected in the species composition of the vegetation. As expected, ungrazed plots had higher species richness and greater abundances of several individual leafhopper species. However, plots grazing plots. It is suggested that rabbit grazing may have subtle effects on grassland invertebrate assemblages that are not necessarily predictable from an examination of the species composition of the vegetation. Chalk heath vegetation contains an unusual mixture of calcicole and calcifuge plant species, but the leafhopper assemblage included a restricted number of calcareous grassland specialist species and only one species strongly associated with acidic grasslands; most leafhoppers recorded were generalist grassland species.

# Introduction

Lowland calcareous grasslands contain some of the most diverse plant and invertebrate communities in Britain and frequently support a number of rare species (Ratcliffe 1977; Keymer and Leach 1990; McLean 1990; Rodwell 1992). The botanical diversity of this habitat is a result of the dry, baserich and nutrient-poor soil conditions in combination with grazing. The resultant plant community is composed mainly of slow-growing stress-tolerant species; fast-growing, nutrientdemanding and competitive species are prevented from achieving dominance because of their inability to cope with the poor soils and the action of grazing herbivores. Calcareous grasslands are essentially plagioclimax communities that would normally revert to scrub and then woodland if action was not taken to restrict the growth of woody shrubs and trees. Management of such sites for conservation is therefore aimed at arresting or reversing the natural process of succession, usually involving some sort of grazing, although there is much debate and uncertainty about precisely what grazing regime is most appropriate in different circumstances.

In Britain, large amounts of this habitat type have been lost, often to arable cultivation, with surviving patches of habitat becoming progressively smaller and more isolated. Remnant sites have also suffered from habitat deterioration as a result of insufficient grazing or agricultural intensification (e.g. fertilizer or herbicide application) that is designed to improve the quality of the pasture for grazing livestock. In this way, over 80% of the calcareous grassland habitat in Britain has been lost or substantially degraded from a conservation perspective over the last 50 years (Keymer and Leach 1990). Blackwood and Tubbs (1970) reported that less than 4% of the chalk soils of the South Downs in south-east England still supported grassland.

Most vertebrate herbivores graze selectively between the different plant species available to them (Ausden and Treweek 1995). Grazing preferences and patterns vary between different herbivores, both wild and domesticated, and also between different breeds and ages of livestock animal and at different times of year (Olff and Ritchie 1998). Careful judgement is required to decide on the right combination of grazing animals and an appropriate intensity and timing of grazing to meet particular conservation objectives, given the nature of the site. Exclusive use of one type of herbivore for conservation grazing can produce overgrazing of favoured plant species and will allow species that are avoided to spread. Use of a mixture of herbivores is sometimes regarded as the solution, as the different grazing preferences can complement each other (Ausden and Treweek 1995). Considerable fine-tuning of livestock grazing impacts can be achieved by varying the grazing intensity (density of animals), type of livestock used (species and breed), duration, frequency and seasonality of grazing (Morris 1990).

Grazing by domestic livestock is implemented against a background of uncontrolled grazing by wild herbivores, the most significant of which in the UK are rabbits (*Oryctolagus cuniculus*). Since the middle of the eighteenth century, they have had a profound effect on many lowland grassland sites in Britain. The rapid spread of scrub onto many grassland sites following dramatic declines in rabbit numbers due to the spread of myxomatosis in the 1950s was testament to their role in arresting succession (Thomas 1960). Rabbits are more selective grazers than most livestock and produce a much shorter sward (Oates 1995). Differences in the balance in grazing pressure between livestock and rabbits can produce remarkably divergent types and structures of vegetation. However, very few studies have examined this in detail.

It has long been known that grazing, and its artificial substitute, mechanical cutting, have profound effects on the structure and composition of grassland invertebrate communities (Duffey et al. 1974; Morris 1990, 2000). Leafhoppers, planthoppers, froghoppers and related groups (collectively known as the Auchenorrhyncha, but hereafter referred to as 'leafhoppers') are often abundant in grasslands and have characteristic assemblages that exhibit rapid responses to management and habitat change (Biedermann et al. 2005). They are therefore an appropriate group for studying the effects of grazing on grassland invertebrate communities.

We report on the preliminary results of sampling leafhopper assemblages on a field experiment that had originally been designed to examine the differential effects of livestock and rabbit grazing on grassland vegetation. The experiment was set up on an area of chalk heath, an unusual and diverse plant community comprising a mixture of calcicole and calcifuge plant species. This vegetation type generally occurs where a thin layer of acid soil overlies calcareous bedrock, allowing obligate calcicole and calcifuge plants to coexist by rooting at different depths (Tansley and Adamson 1926; Grubb et al. 1969). The leafhopper assemblages associated with acidic and calcareous grasslands are strongly divergent, although there is some overlap in species composition (Morris 1971, 1990; Waloff 1973). Against this background, one might predict the leafhopper fauna of chalk heath to contain species drawn from these two assemblage types.

Our study had two principal objectives. Firstly, we wanted to test whether the impact on the leafhopper fauna of rabbit grazing was different to that of rabbits and livestock in combination or the complete exclusion of grazing. Secondly, given that many grassland leafhopper species are stenophagous and have rather precise habitat associations (Nickel 2003), we wanted to test the hypothesis that the leafhopper fauna of chalk heath would comprise a mixture of species associated with calcareous grasslands and acidic grassland heaths.

### Methods

# Study site

The study was done at Lullington Heath National Nature Reserve in south-east England (National Grid Reference TQ 543017). The site comprises one of the largest remaining areas of chalk heath in Britain, with soils derived from loessic material overlying chalk (Tansley and Adamson 1926; Grubb et al. 1969). The experimental plots are located on an area of species-rich chalk heath containing typical chalk grassland forbs and grasses intermixed with Calluna vulgaris, Erica cinerea and other calcifuge species. Patches of scrub (mostly Ulex europaeus and Crataegus monogyna) that harbour substantial rabbit warrens are located within 50 m of the plots. The area is grazed all year by a flock of approximately 20 sheep (Hebridean breed) and in winter by three ponies (Exmoor and New Forest breeds) (Denyer 2005) over an area of approximately 15 ha. Densities of rabbits have not been quantified but are evidently high. The experimental site is on ground that gently slopes in a south-westerly direction at an altitude of approximately 100 m.

#### Experimental design

Sampling of leafhoppers was done on experimental plots that had been set up in 1997, and maintained continuously since, to investigate the differential effects of rabbit and livestock grazing on the chalk heath vegetation. Grazing exclosures  $(4 \text{ m} \times 4 \text{ m} \text{ in area, with } 1 \text{ m high fencing})$  had been constructed either with 15 cm mesh netting to exclude sheep and other large livestock but to allow access by rabbits, or of 2.5 cm netting to exclude both livestock and rabbits. Companion unfenced plots had been established as controls. Thus, there were three grazing treatments: (i) ungrazed by livestock or rabbits, (ii) grazed by rabbits but not by livestock, and (iii) unrestricted grazing by rabbits and livestock. The three treatments were replicated in four spatially-separated blocks, giving a total of 12 plots. Within each block, the three plots were arranged in a northsouth line and positioned 6 m apart, with treatments assigned randomly to the three possible positions within the block (Figure 1).



*Figure 1.* Layout of experimental plots at Lullington Heath NNR. Three treatments arranged in four blocks: unshaded, ungrazed; pale-shaded, rabbit-grazed; dark-shaded, mixed grazing. Plots are  $4 \times 4$  m in area, spaced 6 m apart.

## Insect and vegetation sampling

Insect samples were taken on four occasions in 2004 at approximately 4-week intervals (30th June, 26th July, 18th August and 16th September), chosen to span the typical seasonal phenology of most grassland leafhopper species. Suction samples were obtained using an apparatus modelled on the Vortis suction sampler (Arnold 1994; Stewart 2002) with an inlet nozzle diameter of 18 cm. Each sample comprised 10-second sucks from 10 arbitrarily chosen points within a plot and thus represented an area of 0.25 m<sup>2</sup>. One such sample was taken from each plot on the first sample date and two samples per plot were taken on all three subsequent sampling occasions. Samples were placed in plastic bags in the field and were later stored in a laboratory freezer, prior to sorting and identification of all adult leafhoppers. Many individuals in the genus Aphrodes were intermediate between A. makarovi and A. bicinctus in terms of diagnostic characters (Ossiannilsson 1981); in view of the current uncertainty about the taxonomic status of this species group, we assigned these individuals to A. bicinctus (sensu lato). Leafhopper nomenclature follows Holzinger et al. (1997).

The percentage cover of all vascular plant species was estimated by eye (to an accuracy of 5%) in all the experimental plots in August 2004. The mean height of the vegetation within each plot was estimated using a 'sward stick' (Stewart et al. 2001) placed at 10 arbitrarily chosen points.

#### Data analysis

Data on the numbers of each leafhopper species sampled were combined across replicate plots and sampling dates to give year totals for each plot. Data for individual species (only those occurring more commonly) were analysed using one-way Analysis of Variance with fixed treatment effects (three levels: ungrazed, rabbit grazed and mixed grazing) and the four blocks treated as replicates. Where necessary, data were log transformed (log n + 1) to meet the assumption of normal distribution and equality of variances.

Detrended correspondence analysis (DCA) was used to examine patterns in the vegetation data. We used a constrained ordination, canonical correspondence analysis (CCA in CANOCO; ter Braak and Smilauer 2002), to relate leafhopper assemblage composition to grazing type (using the presence or absence of livestock and rabbits as nominal variables) and mean vegetation height as a surrogate of vegetation structure. The Morisita– Horn index of similarity (Magurran 2004) was used to quantify how similar the vegetation and the leafhopper assemblages were between treatments.

#### Results

# *Composition and structure of the vegetation in relation to grazing treatments*

A total of 42 species of forbs, nine species of grasses and two species of sedge were recorded from across the experimental plots. Plant species richness varied between 27 and 35 on individual plots, but showed no effect of experimental treatment  $(F_{2,9} = 0.26; p = 0.78)$ . Shannon diversity and evenness varied slightly between plots (H' = 2.22-2.98; E = 0.66-0.84), but neither showed any significant response to treatment (H':  $F_{2,9} = 0.15$ ,  $p = 0.86; E: F_{2,9} = 0.49, p = 0.63$ ). Both calcicole and calcifuge species were present, but the former predominated. The grasses were dominated by Festuca ovina, with frequent Helictotrichon pratense and occasional Briza media and Bromus erectus. Carex flacca was widespread. All plots had a diverse mixture of calcareous forbs, including Sanguisorba minor, Filipendula vulgaris, Thymus pulegioides and Leontodon hispidus. The most

important calcifuge species were *E. cinerea* and *C. vulgaris*, both of which were spatially patchy but reached 40 and 15% cover respectively on certain plots. When tested individually, none of the above species showed any significant treatment effects.

An initial exploration of the vegetation data using DCA showed partial differentiation between the ungrazed plots compared to the other plots, but no discrimination between rabbit grazed and mixed grazing plots. Direct comparison of species cover values using the Morisita–Horn index showed that the different treatments had little effect on the composition of the vegetation. Greatest similarity occurred between rabbit grazed and mixed grazing plots ( $C_{\rm MH} = 0.95$ ), but separate comparisons of ungrazed plots with rabbit grazed plots and with mixed grazing plots also showed considerable similarity ( $C_{\rm MH} = 0.88$  and 0.89 respectively).

The mean height of the vegetation varied significantly between treatments ( $F_{2,9} = 5.21$ ; p = 0.031) declining from tallest in ungrazed plots, through rabbit grazed plots, to shortest in mixed grazing plots ( $20.3 \pm 3.9$  cm,  $11.7 \pm 2.0$  cm and  $5.4 \pm 0.4$  cm respectively). However, regression analysis showed that there was no relationship between species richness and mean vegetation height within plots ( $F_{1,10} = 0.48$ ; p = 0.51;  $r^2 = 0.05$ ).

## Composition of the leafhopper fauna

Twenty-four species of leafhopper were sampled from the 12 experimental plots. With one exception (*Ribautiana tenerrima*, recorded as a singleton), all of the species were associated with grasses and low-growing herbs, rather than shrubs and trees, and therefore probably sustained breeding populations within the experimental plots (although eight species were represented in the samples by less than four individuals).

In terms of habitat associations, seven of the recorded species are normally associated with calcareous grasslands, one species is associated with acid grassland and the remaining 16 species have more general affinities with a range of grassland types including both calcareous and acid ones (Table 1). The only species strongly associated with acid grasslands, *Sardius argus*, was also the most numerous (21.7% of all individuals across the experimental site). Approximately half

	U	R	М	$F_{(2,9)}$	р	Habitat
Neophilaenus exclamationis	19	40	35	0.70	0.521	Calc.
Neophilaenus lineatus	5	10	3	_		Gen.
Megophthalmus scabripennis	6	21	6	3.62	0.070	Gen.
Evacanthus interruptus	1	0	1	_		Gen.
Eupelix cuspidata	1	8	4	-		Gen.
Anoscopus albifrons	10	0	0	_		Gen.
Aphrodes bicinctus (sensu lato)	14	15	5	1.60	0.255	Gen.
Doratura stylata	1	0	2	-		Gen.
Recilia coronifera	0	0	1	_		Gen.
Turrutus socialis	69	54	22	6.86	0.015	Calc.
Psammotettix confinis	3	5	18	4.62	0.042	Gen.
Rhytistylus proceps	45	8	1	13.28	0.002	Calc.
Sardius argus	65	107	34	4.05	0.056	Acid
Euscelis incisus	1	0	0	-		Gen.
Mocydiopsis attenuata	2	0	1	—		Calc.
Eupteryx notata	83	69	17	2.64	0.125	Calc.
Eupteryx stachydearum	0	1	0	—		Gen.
Zyginidia scutellaris	65	17	2	14.13	0.002	Gen.
Ribautiana tenerrima	0	0	1	—		Gen.
Arboridia parvula	15	4	0	—		Calc.
Kelisia guttula	4	4	0	—		Calc.
Hyledelphax elegantulus	12	3	0	—		Gen.
Javesella pellucida	1	0	1	—		Gen.
Kosswigianella exigua	2	2	4	—		Gen.
Total individuals ( <i>n</i> )	424	368	158			
Total species richness (S)	21	16	18			
Mean <i>n</i> per plot	106.0	92.0	39.5	12.73	0.002	
Mean S per plot	14.0	12.8	7.8	2.42	0.144	
Shannon diversity $(H')$	2.12	2.02	1.96	0.71	0.519	
Shannon evenness (E)	0.80	0.80	0.84	0.56	0.592	

Table 1. Total leafhopper individuals sampled, across all dates, for three treatments (four replicates each): U = ungrazed; R = rabbit-grazed only; M = mixed rabbit and livestock grazing.

*F*-values and significance levels (*p* values less than 0.05 in bold) refer to results from one-way ANOVA tests of treatment effects after log (n + 1) transformation (dashes indicate test not performed due to small sample size). Habitat refers to normal habitat preference of each species between calcareous grassland (Calc.), acid grassland (Acid) or generalist (Gen.).

(51.8%) of the individuals were calcareous grassland species, the remainder (26.5%) being habitat generalists.

# *Grazing treatment effects on individual leafhopper species*

Individual leafhopper species responded very differently to the three grazing treatments (Figure 2). Of the nine species that occurred in sufficient numbers (>25) to allow analysis, four showed statistically significant treatment effects (Table 1). One of these, *Psammotettix confinis*, was most numerous on the mixed grazing plots, but the rest reached greatest abundance on one of the grazing exclusion plots. The six most numerous species across the experimental area showed different responses to grazing treatment (Figure 3). The most abundant species overall, S. argus, had highest numbers on the rabbit grazed plots, although the overall treatment effect did not reach formal significance. Turrutus socialis, Rhytistylus proceps and Zyginidia scutellaris all showed significant treatment effects and significant differences between the treatment extremes (ungrazed vs. mixed grazing) based on post-hoc tests. In these species, the rabbit grazing treatment was always intermediate between the other two, although not always statistically distinct from them. Eupteryx notata was the second most numerous species and exhibited a similar, but non-significant, trend. Three of the less common species, Anoscopus albifrons, Arboridia parvula and Hyledelphax



*Figure 2.* Leafhopper rank abundance plots for (a) ungrazed, (b) rabbit grazed, and (c) mixed grazing treatments. Species are ranked according to their log(n + 1) abundance in ungrazed plots as follows: 1, *Eupteryx notata*; 2, *Turrutus socialis*; 3, *Sardius argus*; 4, *Zyginidia scutellaris*; 5, *Rhytistylus proceps*; 6, *Neophilaenus exclamationis*; 7, *Arboridia parvula*; 8, *Aphrodes bicinctus*; 9, *Hyledelphax elegantulus*; 10, *Anoscopus albifrons*; 11, *Megophthalmus scabripennis*; 12, *Neophilaenus lineatus*; 13, *Kelisia guttula*; 14, *Psammotettix confinis*; 15, *Mocydiopsis attenuata*; 16, *Kosswigianella exigua*; 17, *Evacanthus interruptus*; 18, *Eupelix cuspidata*; 19, *Doratura stylata*; 20, *Euscelis incisus*; 21, *Javesella pellucida*; 22, *Recilia coronifera*; 23, *Eupteryx stachydearum*; 24, *Ribautiana tenerrima*.



*Figure 3.* The effect of grazing treatment on the abundance (mean  $\pm$  SE) of the six commonest (total individuals > 50) leafhopper species, arranged in order of total abundance. Experimental treatments: white bars, ungrazed plots; hatched bars, rabbit grazed plots; dark bars, mixed grazing plots. Species labels: Sa, *Sardius argus*; En, *Eupteryx notata*; Ts, *Turrutus socialis*; Ne, *Neophilaenus exclamationis*; Zs, *Zyginidia scutellaris*; Rp, *Rhytistylus proceps*. Within species that show a significant treatment effect (from one-way ANOVA, Table 1), treatments not sharing common letters differ significantly (p < 0.05, *post-hoc* Tukey tests).

*elegantulus*, had highest numbers on the ungrazed plots and were completely absent from the mixed grazing plots, although numbers were too low to test the formal significance of this difference. *Neophilaenus exclamationis*, the fourth most abundant species, was somewhat exceptional in having lowest numbers on the ungrazed plots, although the overall treatment effect was not significant. Likewise, *Neophilaenus lineatus* and *Megophthalmus scabripennis* were both more numerous on the rabbit grazed plots, but numbers were too small to be statistically significant.

# Grazing treatment effects on the leafhopper assemblage

Grazing treatment had a profound effect on the total abundance of leafhoppers across the experiment, numbers being substantially lower on the mixed grazing plots compared to those with either type of grazing exclusion. However, there was no significant treatment effect on species richness, Shannon diversity or evenness (Table 1), although there was a significant positive relationship between vegetation height and leafhopper species richness ( $F_{1,10} = 6.06$ , p < 0.05;  $r^2 = 0.38$ ).

A constrained ordination (CCA) of the leafhopper data produced a clear separation of the assemblages on the 12 experimental plots into three distinct groupings that corresponded with the grazing treatments (Figure 4a). The first two axes explained 42.6 and 10.0% respectively of the variance in the species data alone and 74.4 and 17.4% respectively of the variance in the species– environment interaction. Axis 1 was strongly negatively correlated with vegetation height, the treatment groupings being widely spaced along the



*Figure 4.* Biplots for (a) experimental plots and (b) species of the first two canonical axes of a CCA ordination of leafhoppers and environmental variables. (a) Closed squares, ungrazed plots; closed triangles, rabbit-grazed plots; open squares, mixed grazing plots. (b) The nominal variables rabbits and livestock are plotted as their centroids. The strength of the continuous variable vegetation height and its relationship to the species in the ordination plot is depicted by the length and orientation of the arrow. Total inertia: 0.389; eigenvalue for first axis: 0.166; eigenvalue for second axis: 0.039. Model tested with an unrestricted Monte Carlo permutation test (499 permutations); significance of first canonical axis = 0.002; significance of second canonical axis = 0.002. Species abbreviations: *Ano alb, Anoscopus albifrons; Aph bic, Aphrodes bicinctus; Arb par, Arboridia parvula; Eup cus, Eupelix cuspidata; Eup not, Eupteryx notata; Hyl ele, Hyledelphax elegantulus; Kel gut, Kelisia guttula; Kos exi, Kosswigianella exigua; Meg sca, Megophthalmus scabripennis; Neo exc, Neophilaenus exclamationis; Neo lin, Neophilaenus lineatus; Psa con, Psammotettix confinis; Rhy pro, Rhytistylus proceps; Sar arg, Sardius argus; Tur soc, Turrutus socialis; Zyg scu, Zyginidia scutellaris.* 

axis in the sequence: ungrazed, rabbit grazed, mixed grazing plots. Axis 2 differentiated between the rabbit grazed plots and the others, demonstrating that rabbits had produced an effect on the leafhopper fauna that was distinct from that driven by vegetation height. Inspection of the ordination biplot for species (Figure 4b), shows that species known to be associated with short dry grasslands, such as P. confinis and Kosswigianella exigua, were strongly associated with the presence of livestock. Other species normally associated with taller swards, such as A. albifrons, H. elegantulus and A. parvula were strongly associated with grazing exclusion. Amongst the six most abundant species, T. socialis and E. notata occupied nearly identical positions on the ordination diagram, indicating very similar responses to grazing treatment (see also Figure 3), whilst Z. scutellaris and N. exclamationis responded in opposite directions to vegetation height (positively and negatively respectively). There was substantial overlap in species composition of the assemblages between the treatments, but lowest similarity was shown between the ungrazed plots and the others  $(C_{\rm MH} = 0.67$  for both rabbit-grazed and mixed grazing plots compared to ungrazed plots); greatest assemblage similarity was shown between the rabbit grazed and the mixed grazing plots  $(C_{\rm MH} = 0.79).$ 

# Discussion

Our prediction that the leafhoppers found on chalk heath would comprise a mixture of species drawn from calcareous and acidic grassland assemblages was only partly supported. In fact, the leafhopper assemblage recorded from this particular chalk heath site represents an unequal and idiosyncratic mixture of the two species pools. Only one species, S. argus, could be described as strongly associated with acidic grassland or heathland habitats, although this was the most numerous species across the experimental site. Seven of the species recorded have strong affinities with calcareous grasslands, at least in this region of southern England. However, this list is a relatively small subset of the local species pool for this habitat. Species that were notably absent, but frequent at other calcareous grassland sites in the vicinity, included P. cephalotes, Mocydia crocea

and Paluda adumbrata. Most of the species present could be described as generalists associated with a wide range of different grassland types. However, even in this category there are some surprising absences, for example Arthaldeus pascuellus, Deltocephalus pulicaris, Stenocranus minutus and Macrosteles spp. In all these cases, potential host plant species were present in the vegetation, but some other aspect of the conditions was evidently unsuitable for them. The leafhopper fauna of this example of chalk heath was therefore poorer than expected and biased towards calcareous grassland species. The site is located in an area dominated by calcareous grasslands and is possibly too far from the nearest acidic grassland to recruit many species from this latter habitat type.

No treatment effects were detected on the species composition of the vegetation in the experimental plots. This may have been because the data were collected using a somewhat subjective method (percentage cover estimation by eye) at a comparatively coarse scale. However, the results accord with a more detailed analysis of vegetation composition, based on the central square metre of each plot (Denyer 2005). Thus, whilst the plant species composition was broadly similar across plots, the main difference between treatments was in the physical structure of the vegetation, as measured by its height. Any response in the leafhopper assemblages to the treatments therefore appears to be more the result of differences in the structure of the vegetation than to any major differences in the balance between plant species.

The effects of grazing exclusion on the leafhopper assemblage were largely predictable from the results of previous studies (Morris 1971; Morris and Plant 1983; Brown et al. 1992; Kruess and Tscharntke 2002), which showed that total abundances and species diversity of leafhoppers tend to be higher in ungrazed compared to grazed grassland. Grassland leafhopper assemblages are vertically stratified (Andrzejewska 1965), allowing a greater number of species to coexist in tall compared to short vegetation. Taller vegetation has more structural heterogeneity and hence more microhabitats for feeding and oviposition than short vegetation (Denno 1994). Our data were collected 7 years after the experimental exclosures were erected, so any effects of grazing cessation would have had plenty of time to develop. Ungrazed plots in this study had slightly more species than either rabbit grazed or mixed grazing plots, but the treatment effect was not significant. However, highest levels of species turnover (as measured by the Morisita–Horn index of similarity) were shown between the ungrazed and the other treatments.

As expected, several species had much higher abundances in the plots from which grazers had been excluded. Thus, higher numbers of T. socialis, Z. scutellaris and R. proceps in the ungrazed plots were consistent with previous evidence that these species are more abundant in taller uncut vegetation (Morris 1973, 1981a). Similarly, the fact that N. exclamationis had higher densities on the grazed compared to the ungrazed plots is supported by previous evidence that this species responds positively to mechanical cutting (Morris 1981b). P. confinis had largest numbers on the mixed grazing plots and is also known to be associated with short swards (Morris 1981b). E. notata feeds entirely on low growing dicots rather than grasses (Stewart 1988); potential host plants that were present in the experimental plots included Leontodon hispidus, Prunella vulgaris and Thymus pulegioides. All of these plant species would have grown taller, and therefore provided more resources for E. notata, in the ungrazed plots.

The most interesting result of the study was that when rabbits were the only grazers, this resulted in a different leafhopper assemblage to that produced when rabbit grazing was accompanied by livestock grazing. Although mean vegetation height in the rabbit grazed plots was intermediate between that in the other two treatments, the composition of the leafhopper assemblage was not. A number of species reached their highest densities in the rabbit grazed plots, including the most abundant species, S. argus. The CCA ordination plot shows that rabbit grazed plots were intermediate between the ungrazed and the mixed grazing plots on the first axis, but were clearly displaced from them on the second axis. This suggests that allowing rabbits to remain after livestock grazing had been removed deflected the development of the leafhopper assemblage away from the course that it would otherwise have taken in response to grazing cessation. The mechanism behind this is not immediately apparent, but a number of possibilities exist. Firstly, being far more selective grazers than livestock, rabbits may have had direct effects on the availability of host plants for particular

leafhopper species. Similarly, rabbit grazing may have induced subtle changes in the palatability of plant species as hosts for leafhoppers. Finally, rabbit-induced changes to the structure of the vegetation could have altered the suitability of the microclimatic conditions for individual leafhopper species. One would need to know much more about how the feeding preferences of the rabbits interact with the host plants of the leafhopper species to distinguish between these possibilities. Information about the host plants of many of the leafhopper species is incomplete (Waloff and Solomon 1973; Cook 1996; Nickel 2003) and host plant preferences are likely to vary according to the local availability and growing conditions of potential hosts.

Rabbit grazing has two disadvantages on sites that are managed for conservation. Firstly, rabbit numbers are not easy to control and are subject to wide fluctuations over time. Secondly, because they rarely graze further than 100 m away from their burrows (Cowan et al. 1989), grazing effects tend to be highly localised. At low to medium densities, their selective feeding and avoidance of rank vegetation can produce a mosaic of closecropped turf in between patches of taller vegetation, which may provide structural heterogeneity that is beneficial to certain invertebrates such as butterflies (Oates 1995) and Orthoptera (Cherrill and Brown 1992). However, if numbers build up, high rabbit grazing pressure produces a uniform short sward that is of limited value to most invertebrates (Kirby 1992) and may reduce the diversity of plants.

Grazing is widely used for managing important and sensitive lowland grassland sites. However, the impact of background levels of grazing by wild herbivores is rarely considered, even though they may exert a strong influence that is additional to, or runs counter to, that of managed livestock. The preliminary results reported here suggest that rabbit grazing has an effect on the leafhopper assemblage that is distinct from that of livestock. Furthermore, such an effect could not have been predicted solely from an examination of the species composition of the vegetation. Managers of species-rich grasslands should consider how to harness the grazing potential of rabbits in a way that is complementary to livestock grazing and that best conserves the invertebrate as well as the botanical interest of the site.

## Acknowledgements

We are grateful to Malcolm Emery and Tim Beech (English Nature) for access to the site, constructing the exclosures and for providing background information. The experiment was originally designed by Dr Libby John. Jo Denyer provided useful advice and information on her study of the vegetation.

#### References

- Andrzejewska L. 1965. Stratification and its dynamics in meadow communities of Auchenorrhycnha (Homoptera). Ekol. Pol. Ser. A 13: 685–715.
- Arnold A.J. 1994. Insect suction sampling without nets, bags or filters. Crop Protect. 13: 73–76.
- Ausden M. and Treweek J. 1995. Grasslands. In: Sutherland W.J. and Hill D.A. (eds), Managing Habitats for Conservation. Cambridge University Press, Cambridge.
- Biedermann R., Achtziger R., Nickel H. and Stewart A.J.A. 2005. Conservation of grassland leafhoppers: a brief review. J. Insect Conserv. (in press).
- Blackwood J. and Tubbs C.R. 1970. A quantitative survey of chalk grassland in England. Biol. Conserv. 3: 1–5.
- Brown V.K., Gibson C.W.D. and Kathirithamby J. 1992. Community organisation in leaf hoppers. Oikos 65: 97–106.
- Cherrill A.J. and Brown V.K. 1992. Ontogenetic changes in the micro-habitat preferences of *Decticus verrucivorus* (Orthoptera: Tettigoniidae) at the edge of its range. Ecography 15: 37–44.
- Cook A.A. 1996. The host plants of calcareous grassland Auchenorrhyncha (Hemiptera). Entomol. Monthly Mag. 132: 151–175.
- Cowan D.P., Hardy A.R., Vaughan J.P. and Christie W.G. 1989. Rabbit ranging behaviour and its implications for the management of rabbit populations. In: Putman R.J. (ed.), Mammals as Pests. Chapman & Hall, London, pp. 178– 185.
- Denno R.F. 1994. Influence of habitat structure on the abundance and diversity of planthoppers. In: Denno R.F. and Perfect T.J. (eds), Planthoppers their Ecology and Management. Chapman & Hall, London, pp. 140–160.
- Denyer J. 2005. Interactions between rabbits, plants and soil and their consequences for chalk grassland and chalk heath vegetation communities. D. Phil. thesis. University of Sussex.
- Duffey E., Morris M.G., Sheail J., Ward L.K., Wells D.A. and Wells T.C.E. 1974. Grassland Ecology and Wildlife Management. Chapman & Hall, London.
- Grubb P.J., Green H.E. and Merrifield R.C.J. 1969. The ecology of chalk heath: it's relevance to the calcicole-calcifuge and soil acidification problems. J. Ecol. 57: 175–212.
- Holzinger W.E., Fröhlich W., Günthart H., Lauterer P., Nickel H., Orosz A., Shedl W. and Remane R. 1997. Vorläufiges Verzeichnis der Zikaden Mitteleuropas (Insecta: Auchenorrhyncha). Beiträge zur Zikadenkunde 1: 43–62.

- Keymer R.J. and Leach S.J. 1990. Calcareous grassland a limited resource in Britain. In: Hillier S.H., Walton D.W.H. and Wells D.A. (eds), *Calcareous* Grasslands – Ecology and Management. Bluntisham Books, Huntingdon, pp. 11–17.
- Kirby P. 1992. Habitat Management for Invertebrates: A Practical Handbook. JNCC/RSPB.
- Kruess A. and Tscharntke T. 2002. Contracting responses of plant and insect diversity to variation in grazing intensity. Biol. Conserv. 106: 293–302.
- Magurran and A.E. 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.
- McLean I.F.G. 1990. The fauna of calcareous grasslands. In: Hillier S.H., Walton D.W.H. and Wells D.A. (eds), *Calcareous* Grasslands – Ecology and Management. Bluntisham Books, Huntingdon, pp. 41–46.
- Morris M.G. 1971. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. IV. Abundance and diversity of Homoptera-Auchenorhyncha. J. Appl. Ecol. 8: 37–52.
- Morris M.G. 1973. The effects of seasonal grazing on the Heteroptera and Auchenorrhyncha (Hemiptera) of chalk grassland. J. Appl. Ecol. 10: 761–780.
- Morris M.G. 1981a. Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorhyncha. J. Appl. Ecol. 18: 107–123.
- Morris M.G. 1981b. Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorhyncha. J. Appl. Ecol. 18: 763–771.
- Morris M.G. 1990. The effects of management on the invertebrate community of calcareous grassland. In: Hillier S.H., Walton D.W.H. and Wells D.A. (eds), *Calcareous* Grasslands
  Ecology and Management. Bluntisham Books, Huntingdon, pp. 128–133.
- Morris M.G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biol. Conserv. 95: 129–142.
- Morris M.G. and Plant. 1983. Responses of grassland invertebrates to management by cutting. V. Changes in Hemiptera following cessation of management. J. Appl. Ecol. 20: 157–177.
- Nickel H. 2003. The Leafhoppers and Planthoppers of Germany (*Hemiptera*, *Auchenorrhyncha*): Patterns and Strategies in a Highly Diverse Group of Phytophagous Insects. Pensoft, Sofia/Moscow.
- Oates M.R. 1995. Butterfly conservation within the management of grassland habitats. In: Pullin A.S. (ed.), Ecology and Conservation of Butterflies. Chapman & Hall, London, pp. 98–112.
- Olff H. and Ritchie M.E. 1998 Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13: 261–265.
- Ossiannilsson F. 1981. The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark. Part 2. The Families Cicadidae, Cercopidae, Membracidae and Cicadellidae (excl. Deltocephalinae). Fauna Entomologica Scandinavica 7(2). Scandinavian Science Press, Klampenborg.
- Ratcliffe D.A. (ed.) 1977. A Nature Conservation Review. Cambridge University Press, Cambridge.
- Rodwell J.S. 1992. British Plant Communities, Vol. 3. Grasslands and Montane Communities. Cambridge University Press, Cambridge.
- Stewart A.J.A. 1988. Patterns of host plant utilisation by leafhoppers in the genus *Eupteryx* (Hemiptera: Cicadellidae) in Britain. J. Natural History 22: 357–379.

Stewart A.J.A. 2002. Techniques for sampling Auchenorrhyncha in grasslands. Denisia 4: 491–512.

- Stewart K.E.J., Bourn N.A.D. and Thomas J.A. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. J. Appl. Ecol. 38: 1148–1154.
- Tansley A.G and Adamson R.S. 1926. Studies of the vegetation of the English Chalk: IV. A preliminary survey of the Chalk Grasslands of the Sussex Downs. J. Ecol. 14: 1–32.
- ter Braak C.J.F. and Smilauer P. 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA.500.
- Thomas A.S. 1960. Changes in vegetation since the advent of myxomatosis. J. Ecol. 48: 287–306.
- Waloff N and Solomon M.G. 1973. Leafhoppers (Auchenorrhyncha: Homoptera) of acidic grassland. J. Appl. Ecol. 10: 189–212.