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RESPONSES OF GRASSLAND INVERTEBRATES TO MANAGEMENT BY CUTTING

V. CHANGES IN HEMIPTERA FOLLOWING CESSATION OF MANAGEMENT

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SUMMARY

(1) From 1973 to 1975 the effects of cutting on the invertebrates of *Arrhenatherum*-dominated grassland were studied. Four treatments (cutting in May (M), July (J), both May and July (B) and no cutting (control, C) were applied annually.

(2) The reversion of the plots was studied from 1976 to 1978 by taking three standard vacuum net samples at fortnightly intervals in August. Adult Hemiptera (Heteroptera and Auchenorhyncha) were identified and counted.

(3) The hot, dry summer of 1976 had effects which were assessed on the C plots. In general, species of damp grasslands declined in abundance whereas those of dry, and of short, swards increased. Some phenological effects may have been detected.

(4) The 1976 fauna of Heteroptera was least similar to that of any other year but the Auchenorhyncha fauna in 1976 was similar to those of 1975 and 1977, with 1973 the least similar year.

(5) Heteroptera increased progressively in abundance from 1976 to 1978 on the previously-managed plots. No differences between treatments were recorded in the abundance of individual species, or for N and S (total number of individuals and species, respectively), but the rates of increase from 1975 to 1978 were significantly different, with the treatments tending to segregate as the two pairs J + B and M + C.

(6) The rates of increase in Auchenorhyncha N and S were similarly grouped, but the rate of increase in diversity (D) was greater on every treatment than on the controls. In 1978 mean D was significantly greater on the J and B treatments than on C.

(7) Auchenorhyncha species displayed various responses to cessation of management, with some differences between treatments persisting through 1976 and 1977, though not into 1978.

(8) Mean rates of increase were positive for most species, even on the C plots. On the J and B plots increases were generally significantly greater than on the M, and especially on the C, treatments.

(9) The relevance of the results to grassland management for nature conservation is discussed. The importance of rotational management and of the rejuvenating effect of cessation of management are emphasized.

INTRODUCTION

At least part of the invertebrate fauna of intensively-managed grassland is impoverished, as measured by the abundance of individuals, representation of species, and species diversity, compared with the fauna of otherwise similar, but less intensively-managed, land. Cessation of heavy, almost continuous, grazing by sheep allowed many species of a chalk grassland fauna to increase in numbers and diversity (Morris 1971a). Management by

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cutting adversely affected species of Heteroptera (Morris 1979a) and Auchenorhyncha (Morris 1981a) on oolitic limestone grassland, although a few species responded positively to cutting (Morris 1981b). However, the effects were strongly influenced by the timing and frequency of management. Species diversity of both Heteroptera and Auchenorhyncha was also reduced, at least on some occasions (Morris & Lakhani 1979). Although there is less information, burning of carboniferous limestone grassland had some effects similar to those caused by cutting (Morris 1975). The general principle that grassland Auchenorhyncha are greatly influenced by the vertical structure of the vegetation they inhabit, first detailed by Andrzejewska (1965), has since been confirmed for a wide range of different grassland types (reviewed by Waloff 1980, Morris 1981a).

Most lowland grasslands in Britain are plagioclimaxes which need to be managed if they are not to succeed to a different type of vegetation, usually some kind of scrub (Duffey *et al.* 1974). As management, at least when it is intensive, tends to impoverish the invertebrate fauna yet is necessary for maintenance of grassland, considerable interest attaches to the dynamics of change in managed grasslands. Of particular interest to wildlife conservationists is the rate at which faunas change in response to cessation of frequent, continuous or catastrophic management, such as burning or mowing.

The principle of rotational management has been recommended as a method to conserve the characteristic faunas and floras of grasslands of different structural type in nature reserves (Morris 1971b). However, there is little information available on suitable or optimal timing of cycles of rotational management, nor on the rate of recovery of a tall grass fauna in grassland which has been intensively and continuously managed. In this paper, the reversion of a calcareous grassland previously cut annually in a field experiment is examined with reference to the hemipterous fauna (Heteroptera and Auchenorhyncha).

SITE, MATERIAL AND METHODS

A field experiment to compare the effects of cutting treatments was established on oolitic limestone grassland dominated by *Arrhenatherum elatius* at Castor Hanglands NNR, Cambridgeshire (formerly Soke of Peterborough) (Morris & Lakhani 1979; Morris 1979a).

Four treatments—M (cutting in May), J (cutting in July), B (cutting in both May and July) and C (control)—were applied each year from 1973 to 1975. The D-Vac insect vacuum net was used to sample the fauna at 2–4 week intervals from October 1972 to December 1975. Similar samples were taken after experimental management ceased, from 1976 to 1978, but only during the month of August. Three samples were taken each year at about fortnightly intervals. Adult leafhoppers are at their most numerous on calcareous grasslands at this time of year (Morris 1981a). Comparisons of the Hemiptera recorded from the untreated plots were made using the August samples taken in the 6 years 1973–1978. The three samples taken in each year were pooled to give a single set of data for each year, and used for most analyses and comparisons. Nomenclature of Heteroptera follows Southwood & Leston (1959) and that of Auchenorhyncha Le Quesne & Payne (1981).

The methods of statistical analysis included those used by Morris & Lakhani (1979). The Hemiptera taken in the different years were also compared by Mountford's index of similarity (Morris 1969) and the classificatory method of Mountford (1962). The response of Hemiptera with time was examined by calculating the slopes of the linear change in population parameters from 1975 to 1978 for each plot, and subjecting them to a formal analysis of variance. Differences between each pair of treatment means were then examined for significance by *t*-tests.

HETEROPTERA

Composition of the fauna

From 1973 to 1975, thirty-three species of Heteroptera were recorded in the August samples alone (all plots), compared with thirty-nine species taken in all the samples during the 3-year period (Morris 1979a); thus, 85% of the species in the known fauna were represented in the August samples. Twenty-eight species were taken in the August samples from 1976 to 1978, with a total of thirty-six in the whole period of 6 years. Eight species were taken in August 1973–75 but not in 1976–78, and three in 1976–78 but not in 1973–75. These eleven species were represented by a total of only sixteen individuals, <1% of all the Heteroptera taken in the 6-year period.

Faunal changes, 1973–78

The numbers of individuals of Heteroptera (*N*) on the plots cut in July (J) and in both May and July (B), which were very low from 1973 to 1975, rose markedly and continually from 1976 to 1978 (Fig. 1). In 1976 the abundance of Heteroptera on the plots cut in May (M) and untreated plots (C) was lower than in previous years and remained low on the C areas in 1977. Numbers were much higher in 1978 than in the previous 2 years on all plots. Throughout the period 1976–78 there were no significant differences between values of *N* on the plots managed differently from 1973 to 1975, although during the period of management they varied significantly. Total *N* (all treatments) averaged about 250 for the August samples in 1973–75, fell markedly in 1976, rose only slightly to 183 in 1977 but increased to 554 in 1978 (Table 1).

The mean number of species (*S*) on the grassland receiving the J and B treatments was low in 1976, but on the M and C plots values of *S* were much lower than in 1975 and no significant differences between the treatments were observed (Fig. 1). Values of *S* increased on every treatment from 1976 to 1978 but on the C plots did not reach the levels recorded from 1973 to 1975. The total number of species recorded averaged 21·7 over the 6 years (1973–1978), but the value for 1976, thirteen, was clearly lower than the mean of $23 \cdot 4 \pm 1 \cdot 8$ for the other 5 years (Table 1). The mean number of individuals recorded per species averaged $9 \cdot 9 \pm 1 \cdot 8$ from 1973 to 1977, but was greater in 1978 at 26·4.

Mean species diversity (*D*, the Brillouin index) was low on the J and B treatments and significantly higher on the M and C treatments from 1973 to 1975 (Fig. 1). In 1976 only the values on the B and C plots were significantly different. *D* increased generally on the managed plots from 1976 to 1978 but did not reach the high values recorded on the C plots from 1973 to 1975. In 1976, *N*, *S* and *D* were all lower on the C plots than in previous years (Fig. 1).

Comparisons of Mountford's index of similarity for the August fauna, on the control plots only, in each year showed the 1976 fauna to be least similar to the fauna of any other year (Fig. 2). If directional or random changes in the composition of the fauna had occurred from year to year, it might be expected that the 1976 fauna would be most similar to that of 1975 or 1977. This is not the case: the index of similarity between the faunas of the 1976 and 1977 samples is only 0·3 and that between 1975 and 1976 particularly low at 0·07. The two most similar years are 1975 and 1978, with 1974 closely related to both of them.

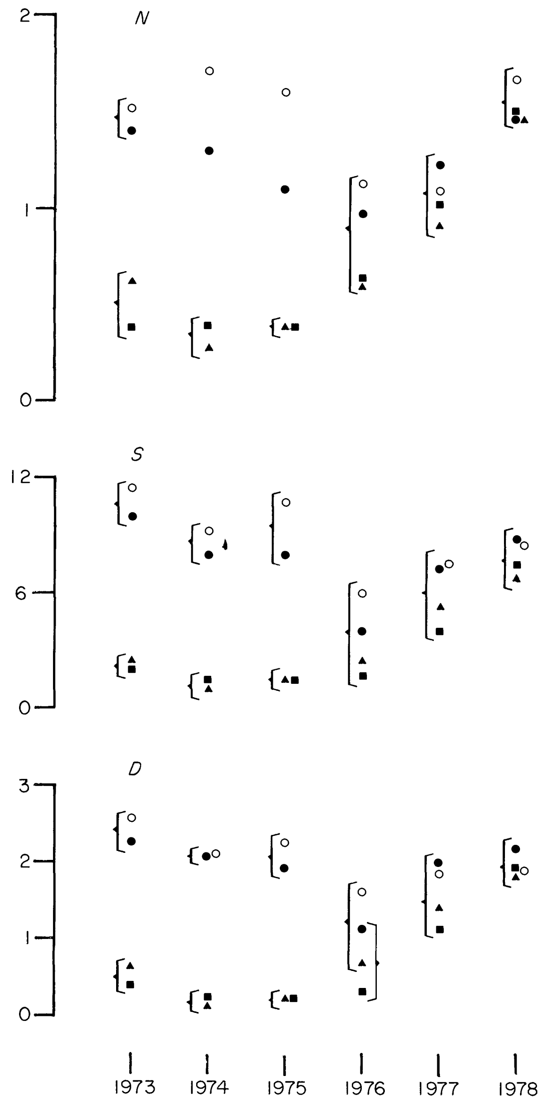

FIG. 1. Heteroptera. Mean numbers of individuals (*N*, as log $(n + 1)$, species (*S*) and diversity (*D*) per treatment/plot. Sums of three August samples/year. Values not significantly different are bracketed. ●, cut in May; ▲, cut in July; ■, cut in both May and July; ○, control (uncut).

TABLE 1. Numbers of species (*S*) and individuals (*N*) of Heteroptera and Auchenorhyncha on all plots in August samples 1973–1978

		1973	1974	1975	1976	1977	1978	Mean ± S.E.
Heteroptera	*S*	25	22	25	13	24	21	21·67 ± 1·86
	N	261	278	227	129	183	554	272
	N/S	10·4	12·6	9·1	9·9	7·6	26·4	
Auchenorhyncha	*S*	46	44	44	38	44	50	44·33 ± 1·58
	N	9926	8090	5381	4147	7066	16266	8479
	N/S	216	184	122	109	161	325	

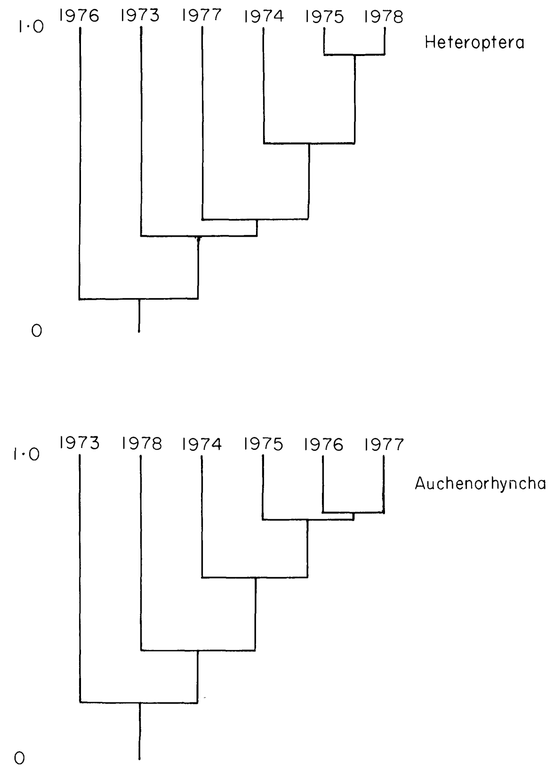

FIG. 2. Heteroptera and Auchenorhyncha. Similarity of faunas in each year (sum of three August samples): Mountford's index.

Responses of individual species

The abundance of different species, or groups of species such as Nabidae, did not differ significantly between treatments in any of the years 1976–1978. However, there were differences between years in the abundance of some species, and composition of the fauna and abundance of different species on the control plots varied considerably during the period 1973–78. Abundance of Nabidae on the control plots was low in 1976 compared with previous years and declined further in 1977, but numbers on the managed plots rose from 1976 to 1978, with a less obvious check in 1977 (Fig. 3a).

Of six nabid species recorded, five were common and showed very different changes over the period 1973–78 and particularly in the 3 years after cessation of management (Table 2). The small numbers of *Nabis flavomarginatus* recorded on the control plots did not vary obviously from year to year. Cutting in July and in both May and July reduced numbers (Morris 1979a) but in 1977 and 1978, *N. flavomarginatus* was as plentiful on these managed plots as on the controls. Cutting in July and both May and July also reduced numbers of four other species of Nabidae in each of the years 1973–1975 (Morris 1979a). Cutting in May significantly reduced numbers of *Stalia major* in 1975 and *Dolichonabis limbatus* in 1973. *S. major* increased in numbers on all the managed plots in 1976–78 but numbers were also particularly high on the control plots in 1978. *D. limbatus* was very scarce on the control plots as well as the managed ones in 1976 and 1977 but common on all plots in 1978. *Nabis ferus* and, to a less obvious extent, *N. rugosus*, were

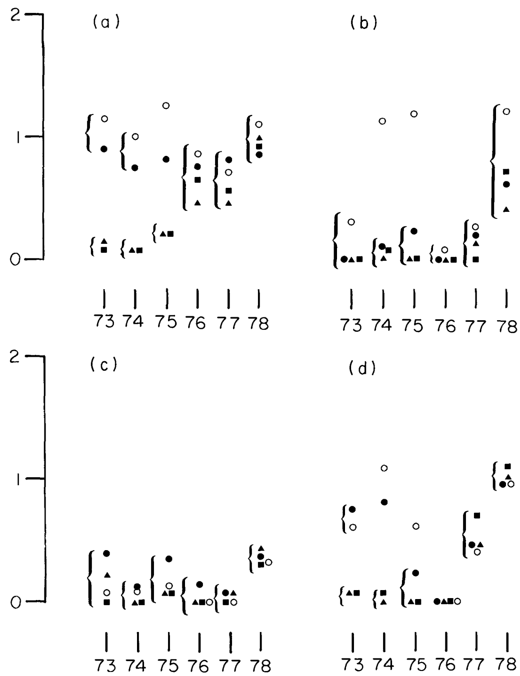

FIG. 3. Heteroptera: (a) Nabidae (all species); (b) *Tytthus pygmaeus*; (c) *Notostira elongata*; (d) *Megaloceraea recticornis*. Mean numbers per treatment/plot as log $(n + 1)$. Symbols and brackets as Fig. 1.

TABLE 2. Total numbers of adult Nabidae taken per treatment, August 1973–1978. M, cut in May; J, cut in July; B, cut in both May and July; treatments applied 1973–1975 inclusive; C, control

		1973	1974	1975	1976	1977	1978
Nabis flavomarginatus	M	0	2	2	3	11	3
	J	0	0	0	0	2	7
	B	0	0	0	0	6	3
	C	2	6	4	3	4	6
	All	2	8	6	6	23	19
Nabis ferus	M	8	5	6	14	2	1
	J	0	0	0	10	1	0
	B	0	1	0	11	0	0
	C	5	4	8	14	0	1
	All	13	10	14	49	3	2
Nabis rugosus	M	8	2	2	5	0	1
	J	0	1	1	3	0	1
	B	0	0	1	1	1	1
	C	12	3	11	4	2	0
	All	20	6	15	13	3	3
Stalia major	M	5	1	1	3	7	12
	J	2	0	1	1	4	8
	B	0	0	0	2	5	7
	C	12	7	7	11	7	27
	All	19	8	9	17	23	54
Dolichonabis limbatus	M	8	9	7	0	3	13
	J	0	0	0	0	3	21
	B	1	0	1	1	1	19
	C	25	19	27	2	2	15
	All	34	28	35	3	9	68

frequent on all plots in 1976 but infrequent on all, including the control plots, in 1977 and 1978. Southwood & Leston (1959) describe *N. ferus* as occurring in 'fairly dry conditions' and as being the predominant nabid of temporary habitats. In contrast, *D. limbatus* (the 'Marsh damsel bug') is 'especially common in damp meadows'.

Peritrechus geniculatus was not an abundant species at Castor Hanglands but nine individuals were taken on six different plots, mostly the C ones but on every treatment except B, in 1976. Only one individual was taken in each of the years 1975 and 1977 and none in August samples in other years. It is a species of 'dry, light sandy soils' (Southwood & Leston 1959).

Tytthus pygmaeus and *Notostira elongata* were scarce on all plots in 1976 and, less markedly so, in 1977, but numbers were higher in 1978 (Fig. 3b, c). Numbers of *T. pygmaeus* on the control plots fluctuated during the period 1973–1975, being low in 1973. Although in 1978 numbers were highest on the untreated plots, there were no significant differences between treatments and *T. pygmaeus* was evidently recovering from the effects of cutting, which were severe (Morris 1979a). Larvae of the species 'occur in swampy places' (Southwood & Leston 1959). *Notostira elongata*, which was relatively little affected by cutting (Morris 1979a), is often the most abundant stenodemine mirid of recently-disturbed grasslands. In 1978, numbers were higher on the control plots than in any other year (Fig. 3c).

No *Megaloceraea recticornis* were recorded in 1976, though numbers were high on the control plots from 1973 to 1975, and on all plots in 1978. Numbers were low in 1977 and there were no significant differences between treatments (Fig. 3d). There is evidence that competition occurs between *N. elongata* and *M. recticornis* (Gibson 1980) and this might be intensified in a stressful year such as 1976.

The lygaeid *Acompus rufipes* and the mirid *Phytocoris varipes* changed in abundance in different ways from 1973 to 1978. *A. rufipes* appeared to survive the first year of management reasonably well and to persist on the control plots until 1976 (Table 3), but none were taken in 1977 or 1978. *P. varipes* was significantly affected by each cutting treatment (Morris 1979a) but was taken on the M and J plots in 1977 and 1978 and on the former alone in 1976 (Table 3).

Heteroptera generally responded positively to cessation of management. However, species of particularly dry habitats, or damp ones, appeared to be affected by the abnormally hot and dry year of 1976. For instance, *Nabis ferus* was abundant, *Dolichonabis limbatus* scarce, in that year. The effects on abundance of Heteroptera resulting from cessation of management and from the weather in 1976 are discussed later. However, because the faunas were sampled only in August, some of the apparent changes

TABLE 3. Total numbers of adult *Acompus rufipes* and *Phytocoris varipes* taken per treatment, August, 1973–1978. Symbols as in Table 2

		1973	1974	1975	1976	1977	1978
Acompus rufipes	M	11	1	3	1	0	0
	J	2	1	1	0	0	0
	B	4	0	0	0	0	0
	C	16	7	8	0	0	0
	All	33	9	12	1	0	0
Phytocoris varipes	M	0	0	0	1	1	5
	J	0	0	0	0	1	2
	B	0	0	0	0	0	0
	C	3	3	4	1	4	1
	All	3	3	4	2	6	8

observed in 1976 could have resulted from acceleration of life-histories in response to above-average temperatures. In 1973–1975, adult *Tytthus pygmaeus* occurred from the second week of July to the beginning or middle of September. It is unlikely that phenology in 1976 was so accelerated that adults, at the 1974–1975 levels of abundance, had mostly died before the first sample was taken on 2 August. On the other hand, *Megaloceraea recticornis* is normally adult from the beginning of July to the end of August, and none was found to survive into September in 1973–1975. Peak abundance was in mid-July (early August in 1974 only). It is probable that any *M. recticornis* which survived in 1976 had become adult and died before sampling started on 2 August.

Rates of change

The mean linear rate of change in the number of individuals (N), species representation (S) and species diversity (D, Brillouin) recorded on the control plots from 1974 to 1978 did not differ significantly from zero (Table 4). Rates of change on the J and B plots were all significantly greater than zero ($P < 0{\cdot}01$, Table 4). The rate of change in the number of individuals (N) was the only quantity to differ significantly from zero on the plots cut in May.

Pairwise contrasts between rates of change showed that only the J and B treatments did not differ significantly for at least one of the parameters N, S and D. The only significantly different contrast between the M and C treatments was in N. Generally, the comparison of rates of change showed the pairs of treatments M + C and J + B to be the most similar to each other.

TABLE 4. Recovery of faunas, 1975–1978; mean slopes for each treatment (linear regression on time in years, N as log $(n + 1)$), with significance of individual treatments and of contrasts between treatments (***, $P < 0{\cdot}001$; **, $0{\cdot}001 < P < 0{\cdot}01$; *, $0{\cdot}01 < P < 0{\cdot}05$). S, number of species; N, number of individuals as log $(n + 1)$; D, diversity index (Brillouin); M, cut in May; J, cut in July; B, cut in both May and July (treatments applied 1973–1975); C, control

		N	*S*	*D*
Heteroptera				
Slope of linear regression equation	M	0·129*	0·55	0·154
	J	0·356***	1·85**	0·55**
	B	0·375**	2·025**	0·589**
	C	0·016	−0·525	−0·090
Contrast	M–J	—**		—*
	M–B	—**		—**
	M–C	*		
	J–B			
	J–C	***	**	***
	B–C	***	**	***
Auchenorhyncha				
Slope of linear regression equation	M	0·119*	2·925*	0·191*
	J	0·304***	5·15**	0·322**
	B	0·291**	5·75**	0·341**
	C	0·091*	1·9*	−0·014
Contrast	M–J	—**	—*	
	M–B	—**	—*	
	M–C			*
	J–B			
	J–C	**	**	**
	B–C	**	*	**

AUCHENORHYNCHA

Composition of the fauna

During the intensive sampling period from 1973 to 1975, sixty-nine species of leafhopper were recorded. Morris (1979b) listed seventy-one species but *Empoasca pteridis* (Dahlb.) should be *E. decipiens* Paoli, and *Youngiada pandellei* (Leth.) is synonymous with *Y. aurovittata* (Dougl.). Generic reassignations and synonyms of other species can be traced in Le Quesne & Payne (1981), but Booij (1981, 1982) has recently shown that the Castor Hanglands population of *Muellerianella*, though anomalous, is referable to *M. extrusa* Scott, a good species which he has raised from synonymy with *M. fairmairei* (Perris).

Fifty-four species were taken in the August samples alone from 1973 to 1975, 78% of the total for the 3 years. Fifty-five species were taken in the August samples from 1976 to 1978 and eight of these had not been recorded at all from 1973 to 1975. These eight species occurred as sixty-four individuals, <0·3% of the total number taken (Table 1). Twelve species were recorded in August 1973–75 but not August 1976–78, and five species taken in August 1976–78 were present at other times of the year in 1973–75.

Faunal changes, 1973–1978

Except in 1973, when there was a significant difference between the M and C treatments, the numbers of individuals of Auchenorhyncha (*N*) segregated into the two pairs of treatments (J + B) and (M + C) in each of the years 1973–1976 (Fig. 4). Mean *N* fell on every treatment during this period, except from 1973 to 1974. Numbers rose

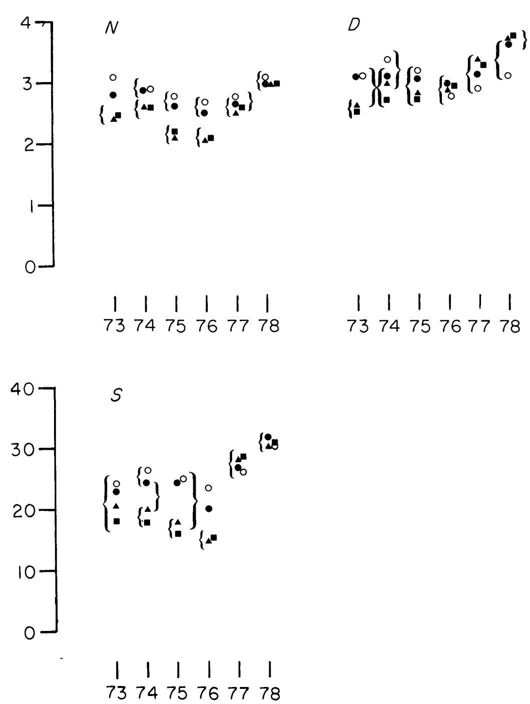

FIG. 4. Auchenorhyncha. Symbols and brackets as Fig. 1.

from 1976 to 1978 on all treatments and in 1977 there was still a significant difference between numbers on the J and C treatments. Only in 1978 were there no statistical differences between the numbers recorded on each treatment. Total *N* (all treatments) fell sharply from 1973 to 1975, largely because, in contrast to the Heteroptera (Fig. 1), numbers fell on the untreated plots as well as the managed ones (Fig. 4). The further decrease in 1976 appeared to continue a consistent decline on all treatments. Total *N* was particularly high in 1978 (Table 1).

Although throughout the period 1973–75 the mean number of species (*S*) was always lowest on the J and B plots, the treatments did not segregate consistently into the two significantly different pairs (J + B) and (M + C) (Fig. 4). In 1976 the treatments showed their clearest differences, with only the pair J and B not significantly different. In this year, mean *S* on each treatment, and total *S* for the whole set of samples, both reached their lowest values (Fig. 4, Table 1). In 1977 and 1978, mean *S* was high on all plots, with no significant differences between treatments. There was less variation in total *S* over the 6 years compared with the similar figures for the Heteroptera, though in both groups the lowest numbers were recorded in 1976 (Table 1).

Although mean species diversity (*D*, Brillouin) was low on the J and B treatments each year from 1973 to 1975, differences from the untreated control plots were not always significant (Fig. 4). In 1975 there were no significant differences between treatments. In contrast to the period 1973 to 1975, mean diversity was lowest on the unmanaged control treatments from 1976 to 1978 and in the last year diversity was significantly lower than on the J and B treatments (Fig. 4). The mean values of *D* on the three managed grasslands M, J and B were particularly high in 1978 and exceeded the values on the control treatment (all years) (Fig. 4).

A dendrogram of the similarity of the August faunas on the control plots only, using Mountford's index, showed several differences compared with the corresponding dendrogram for Heteroptera (Fig. 2). The 1973 Auchenorhyncha fauna was least similar to the others and the 1975, 1976 and 1977 faunas were closely related. The sequence of years 1974–1977 in the dendrogram suggests that relatively small changes in the faunal composition occurred during this period but that a major change took place in 1977–78. Possible reasons for this, and for the dissimilarity of the 1973 fauna with those of other years, are considered in the Discussion.

Responses of individual species

Auchenorhyncha exhibited a much greater variety of patterns of occurrence in the period 1976 to 1978 than did Heteroptera. Several species showed no differences between treatments during this period, but increased in numbers on all plots. Some, such as *Neophilaenus lineatus* (Fig. 5a) and *Conosanus obsoletus* (Fig. 5d), showed little decline in 1976 compared with previous years. In *N. lineatus* there was little change in 1977 but an increase in 1978, whereas *C. obsoletus* increased in 1977 and even more so in 1978. Both *Aphrodes albifrons* (Fig. 5b) and *A. flavostriatus* (Fig. 5c) were present in reduced numbers in 1976 but increased thereafter, *A. albifrons* progressively from 1977 to 1978 and *A. flavostriatus* mainly in the latter year. Other species which had at no time showed differences between treatments but were present in higher numbers at some time during the period 1976 to 1978 included: *Philaenus spumarius* (a small increase in 1978 only), *Aphrodes bicinctus* (a small, progressive increase from 1977 to 1978), *Arthaldeus striifrons* (an increase on all treatments in 1976 except M, followed by increases on all plots in 1977 and 1978), *Paluda flaveola* (absent on all plots in 1976 except one individual

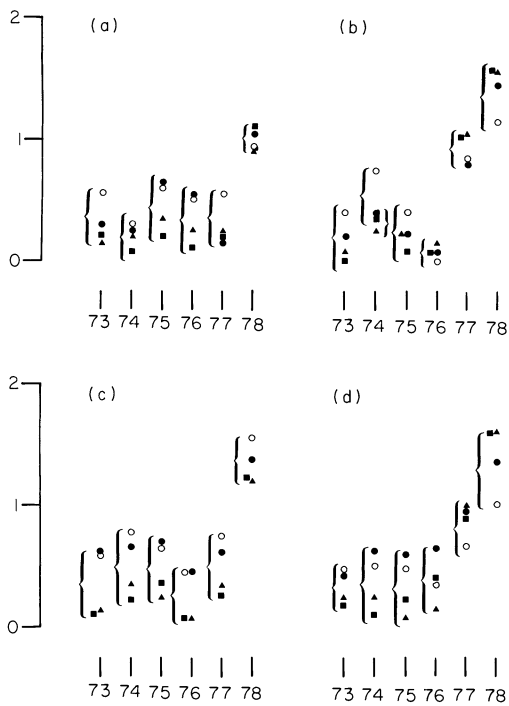

FIG. 5. Auchenorhyncha: (a) *Neophilaenus lineatus*; (b) *Aphrodes albifrons*; (c) *Aphrodes flavostriatus*; (d) *Conosanus obsoletus*. Mean numbers per treatment/plot as log $(n + 1)$. Symbols and brackets as Fig. 1.

on J, followed by a progressive increase 1977 to 1978) and *Elymana sulphurella* (little change in recorded abundance on the M and C plots, 1976 to 1978, but numbers on the J and B treatments showing progressive increases from 1975 to 1976 and subsequently). Other species which showed similar changes to those described above exhibited other features in their responses which are discussed below, as are the characteristics of some of the rates of change in numbers.

A smaller number of species showed a clear reduction in numbers in 1976, but with a much slower, or less obvious, recovery in subsequent years. In *Agallia consobrina* (Fig. 6c) numbers were zero on the 'treated' plots in 1976 and greatly reduced on the controls. A few individuals were recorded on all treatments in 1977 but not until 1978 were numbers at about the same level as those in the C plots in 1973–1975. On the control plots, *Dikraneura variata* continued a rapid fall in numbers from 1973 to 1975 into 1976 and 1977 (Fig. 6a). Numbers were greater on these plots in 1978 but did not reach the levels of 1973–75. On the previously-managed plots there were few changes in abundance from 1975 to 1977 (though numbers fell to zero on the M treatment in 1976) but there was an increase in 1978. The multivoltine *Zyginidia scutellaris* was affected rather inconsistently by cutting (Morris 1979b) and numbers were high on all treatments from 1973 to 1975 (Fig. 6b). They fell, again on all treatments, in 1976 with little change in 1977 but a greater increase in 1978. *Stenocranus minutus* was generally less abundant in 1976 than in previous years but the increase in numbers on the control plots was much less than on the managed ones (Fig. 6d). Two other species had patterns of occurrence similar to those shown in Fig. 6. *Cicadula persimilis* declined in abundance progressively on the control

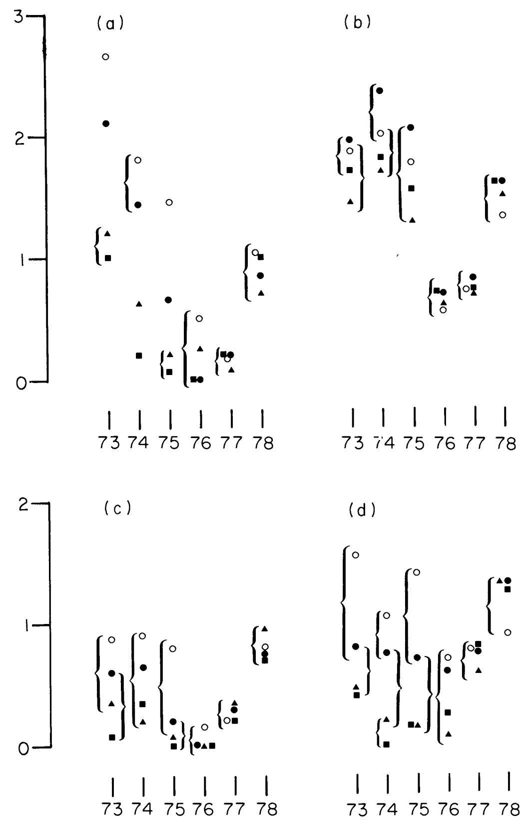

FIG. 6. Auchenorhyncha: (a) *Dikraneura variata*; (b) *Zyginidia scutellaris*; (c) *Agallia consobrina*; (d) *Stenocranus minutus*. Mean numbers per treatment/plot as log $(n + 1)$. Symbols and brackets as Fig. 1.

plots in 1976 and 1977, with an increase in 1978, whereas on the 'treated' plots numbers rose more rapidly in 1977 and 1978. On both the M and C plots numbers of *Arboridia parvula* were reduced from 1975 to 1976, but rose consistently during the following 2 years. On the J and B plots *A. parvula* was absent, or nearly so, in 1974, 1975 and 1976 but increased in numbers thereafter.

Three species declined markedly in 1976 compared with previous years and showed no indication of subsequent recovery. *Macrosteles laevis* was not recorded from the control plots from 1973 to 1978, but was taken on each of the managed treatments from 1973 to 1976, though the effects of the different cutting treatments were not entirely clear in 1973 or 1974 (Fig. 7a). The absence of *M. laevis* from all plots (one individual recorded in 1977) from 1976 onwards was predictable from the study of Andrzejewska (1962) and more recent work. *Macrosteles sexnotatus* was not recorded in 1977 or 1978, on any of the plots, and was in very low numbers in 1976. Although there were no significant effects of cutting in 1973 to 1975, most individuals were taken on the managed plots (Morris 1981b). A different pattern was shown by *Eupteryx vittata* (Fig. 7b). Present in small numbers, the species declined on all treatments from 1973 to 1975, and was not taken at all from 1976 to 1978.

Two species which had responded positively to cutting, *Neophilaenus campestris* and *Adarrus ocellaris* (Morris 1981b), did not decline in numbers like *Macrosteles laevis*. Both

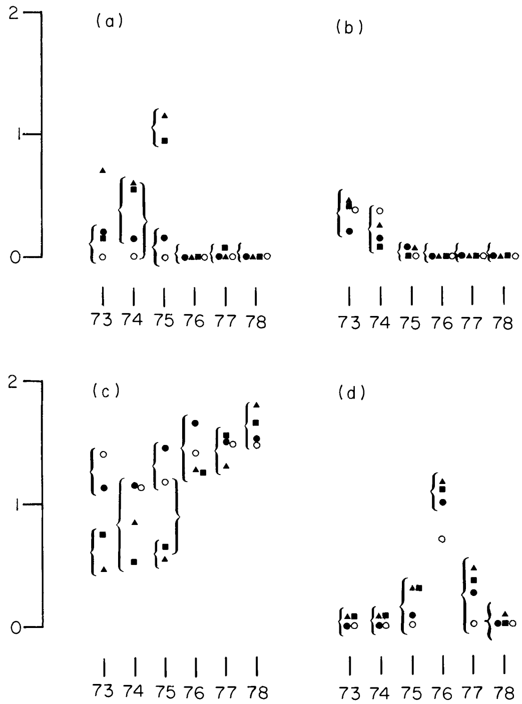

FIG. 7. Auchenorhyncha: (a) *Macrosteles laevis*; (b) *Eupteryx vittata*; (c) *Paluda adumbrata*; (d) *Psammotettix confinis*. Mean numbers per treatment/plot as log $(n + 1)$. Symbols and brackets as Fig. 1.

species persisted in small numbers on most treatments from 1976 to 1978 and on the control plots numbers were greater in 1978 than in any other year.

Increases in abundance in 1976 or 1977 were noted in a few species. *Paluda adumbrata* was more numberous on all treatments in 1976 compared with previous years and numbers were maintained at about the same level in subsequent years (Fig. 7c). Few *Psammotettix confinis* were recorded, mostly on the J and B plots, from 1973 to 1975. In 1976 numbers were much higher on all plots and significantly more were taken on the plots managed from 1973 to 1975 than on the untreated ones. Abundance declined progressively in 1977 and 1978 (Fig. 7d). *Psammotettix cephalotes* was not recorded at all until 1977, when a few were taken on the previously-managed plots. Smaller numbers were taken in 1978. Although confusion between the females of *P. confinis* and *P. cephalotes* is possible, the males are readily distinguishable. *Arocephalus punctum* was not recorded from 1973 to 1975 but a few were taken in each year 1976 to 1978. *P. adumbrata* and *A. punctum* are associated with dry grasslands (Le Quesne 1969).

In several species, differences between treatments observed in 1973–1975 persisted after cessation of management. In *Streptanus aemulans, Mocydia crocea* and *Javesella pellucida* there were significant differences only in 1976. In the first two species abundance was greater on the M and C treatments than on the J and B ones, whilst significantly more *J. pellucida* occurred on the untreated plots than on the J and B ones. Six other species showed significant differences between treatments in both 1976 and 1977, but in no case were there any differences in 1978.

Recilia coronifera occurred in low numbers, on one treatment only (M), in 1973 and increased thereafter, particularly on the M and C treatments, until 1977 (Fig. 8a). Only in

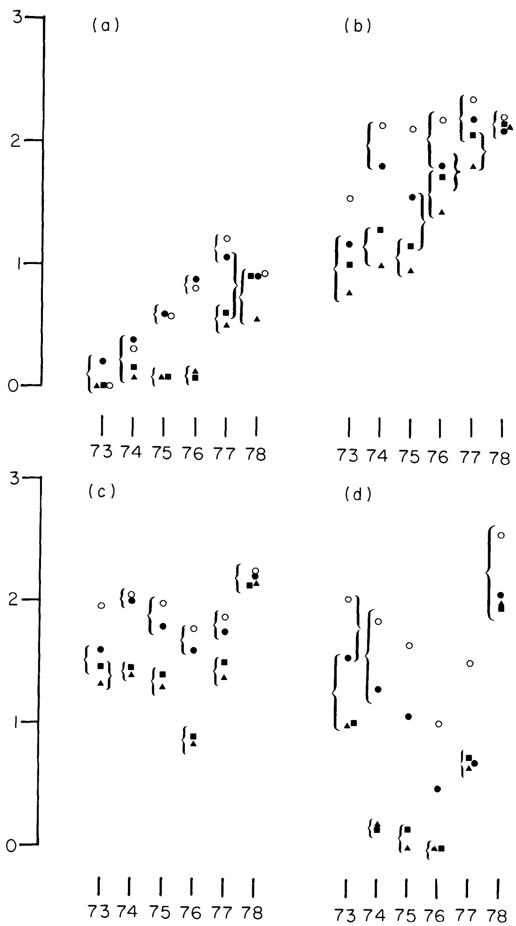

FIG. 8. Auchenorhyncha: (a) *Recilia coronifera*; (b) *Adarrus multinotatus*; (c) *Arthaldeus pascuellus*; (d) *Muellerianella extrusa*. Mean numbers per treatment/plot as log (n + 1). Symbols and brackets as Fig. 1.

1978 did numbers decline on these treatments. Abundance increased on the J and B plots from 1976 to 1978. A rather similar pattern was shown by *Mocydiopsis attenuata*, but numbers were lower and no significant differences between treatments were observed in 1973–1975, such differences only appearing in 1976 and 1977 after cessation of management. In 1976 significantly more *M. attenuata* occurred on the C plots than on the J and B ones and in 1977 numbers were significantly greater on the M plots compared with the B ones.

Adarrus multinotatus increased in abundance on all treatments in 1976 compared to 1975 (Fig. 8b). Some differences, mainly between the C and the J + B plots, persisted in 1976 and 1977, but numbers increased on these previously-managed plots throughout the post-management period. In contrast, numbers of *Arthaldeus pascuellus* were lower on all treatments in 1976 than in 1975 (Fig. 8c), with the decline on the J + B treatments more pronounced than that on the M + C ones. Abundance increased on all plots in 1977, with the increase greater on the J + B plots, and in 1978 numbers were particularly high on all treatments.

Muellerianella extrusa declined in numbers generally in 1976 but there were significant differences between all treatments except J and B (Fig. 8d). Although numbers on the previously-managed plots were higher in 1977, they were still significantly lower than on the C plots. Numbers were very high on all plots in 1978. *Hyledelphax elegantulus* was significantly more abundant on the C treatment than on the J and B ones in 1976, and on the C treatment than all the others in 1977.

Phenology

Most of the species of Auchenorhyncha recorded in August belonged to the 'high summer' or 'non-seasonal' faunas (Morris 1981a). Such species are either long-lived as adults, persisting into late September or October, or else overwinter in the adult stage. Neither group is likely to have been affected phenologically by the hot, dry summer of 1976, except that species which mature very late, such as *Mocydia crocea*, may have been recorded in larger numbers in 1976 because more were adult in August 1978 compared with other years. Any such effect was not very marked. In *Stenocranus minutus*, another species which matures late in normal years, any phenological effect was obscured by other factors and numbers fell substantially on the untreated plots compared with 1975. Numbers rose on all treatments in 1977 and again in 1978, although the increase was least on the untreated plots.

Rates of change

On all the plots which were treated from 1973 to 1975 the mean linear rate of change in the number of individuals (N), number of species (S) and diversity (D, Brillouin index) from 1975 to 1978 differed significantly between treatments (Table 4). None of the rates of change on the J plots differed significantly from those on the B plots, but rates of change on the M plots averaged about half those on the J or B plots and there were significant differences between the M–J and M–B contrasts for N and S, though not for D. The mean rate of change for Auchenorhyncha on the untreated plots, unlike that for Heteroptera, differed significantly from zero for N and S, though not for D. The rate of increase in diversity was significantly greater on all the managed treatments (M, J and B) than on the untreated plots (Table 4). For the other two parameters, N and S, the treatments divided into the pairs M + C and J + B, with no significant differences between the members of each pair, but significant differences between all other combinations.

In seventeen species there were significant differences between treatments in the rates of change of numbers from 1975 to 1978 (Table 5). *Macrosteles laevis* declined on all the plots managed from 1973 to 1975, and the declines were significant on the J and B treatments. The contrasts between all combinations of members of the two pairs of treatments M + C and J + B were significant, highly so in the J–C and B–C contrasts. All other rates of change on the J and B plots were positive, except those of *Adarrus ocellaris*. Twelve species increased in numbers significantly on the J treatment and nine on the B treatment. *Mocydia crocea* declined on both the M and C treatments, significantly so on the latter. Two other species, *Dikraneura variata* and *Stenocranus minutus*, declined on the untreated plots, though not significantly.

The rates of change of four species on the M treatment and three on the control were significant and positive. *Aphrodes albifrons* and *Muellerianella extrusa* increased significantly on both treatments and also on the two others, J and B. The mean rates of increase of *M. extrusa* on the J and B treatments were the highest recorded for any species.

TABLE 5. Recovery of Auchenorhyncha species 1975–1978; mean slopes for each treatment (linear regression of numbers as log (n + 1) on time in years), with significance of individual treatments and of contrasts between treatments. Symbols as Table 4

	Mean slope and significance				Contrast					
	M	J	B	C	M–J	M–B	M–C	J–B	J–C	B–C
Neophilaenus lineatus	0·0044	0·0080	0·0140	0·0056*						
Agallia consobrina	0·0101	0·0147**	0·0114	0·0002						
Aphrodes albifrons	0·0218*	0·0243*	0·0270**	0·0157*						*
Adarrus multinotatus	0·0101*	0·0219**	0·0189**	0·0028	—**	—*			**	*
Adarrus ocellaris	0·0057	–0·0056	–0·0050	0·0052					*	
Arthaldeus pascuellus	0·0067	0·0154*	0·0142**	0·0043					*	*
Conosanus obsoletus	0·0129	0·0274*	0·0231*	0·0116						
Streptanus aemulans	0·0137*	0·0281**	0·0261*	0·0081	—*				*	*
Paluda adumbrata	0·0015	0·0203*	0·0177	0·0062	—*					
Paluda flaveola	0·0053	0·0165*	0·0132	0·0095						
Elymana sulphurella	0·0032	0·0179**	0·0154**	0·0042	—**	—**			**	**
Mocydia crocea	–0·0051	0·0085	0·0092	–0·0111*					*	*
Macrosteles laevis	–0·0023	–0·0173*	–0·141**	0	*	*			—**	—***
Dikraneura variata	0·0038	0·0068	0·0153	–0·0078						
Stenocranus minutus	0·0101	0·0201	0·0191	–0·0070						
Muellerianella extrusa	0·0161*	0·0333*	0·0308**	0·0160*		—*				*
Javesella pellucida	0·0066	0·0197**	0·0147*	0·0050					*	

The contrasts between treatments grouped themselves into the pairs M + C and J + B. None of the M–C or J–B contrasts were significant. Six species had significant contrasts between M and either J or B or both, and ten species similarly significant contrasts between C and either J or B or both. Of the sixty-eight combinations of species and treatments, the mean rates of change were positive in fifty-nine and negative in only nine (Table 5).

DISCUSSION

Management ceased on the Castor Hanglands experiment after the 1975 application of treatments. 1976 was the year in which the first phases of recovery from management would have been expected. However, in Britain the summer of 1976 was the hottest and driest for over 200 years and clearly had important effects on the Hemiptera fauna. These effects can be assessed, at least in part, by examination of changes occurring solely on the untreated control plots (C). But because sampling from 1976 to 1978 was restricted to three occasions in August, instead of being throughout the year, trampling and disturbance of the control plots was much less in 1976 than previously, and these effects were confounded with those of the 1976 summer. Nevertheless, some effects of the drought are apparent, particularly in the relative abundance of species characteristic of dry and moist grasslands. A few events, such as the decline of *Megaloceraea recticornis* (Fig. 3d) are attributable to acceleration in life-history, but for most species the spread of three sampling dates throughout August ensured that the changes observed were ones of abundance. The declines in *Tytthus pygmaeus* (Fig. 3b), *Dolichonabis limbatus* (Table 2), *Stenocranus minutus* (Fig. 6d) and *Muellerianella extrusa* (Fig. 8d) are examples of the effects of a dry year on species normally associated with damp grasslands. There is evidence that some species declined more severely on the recently-managed plots J and B than on the control (and M) plots, for example *Arthaldeus pascuellus* (Fig. 8). Presumably the taller unmanaged grasslands gave greater protection, perhaps higher humidity, than the recently-cut swards which grew little in the hot, dry summer of 1976.

In contrast, species associated with dry conditions increased in numbers in 1976. The enhanced abundance of *Nabis ferus* on the control plots was not as marked as the decline of *Dolichonabis limbatus* (Table 2), but *Recilia coronifera* (Fig. 8a), *Adarrus multinotatus* (Fig. 8b), *Psammotettix confinis* (Fig. 7d) and *Paluda adumbrata* (Fig. 7c) were all more abundant on the untreated grassland in 1976 than in 1975. *P. adumbrata* is associated with dry grasslands and both *R. coronifera* and *P. confinis* with short ones (LeQuesne 1969). The occurrence of the last two species on the tall, unmanaged control plots at Castor Hanglands and their more usual association with short grasslands may indicate the importance of high insolation in their biology. Although *Arocephalus punctum* was recorded in only small numbers, its persistence in 1976 and the following 2 years, and absence from 1973 to 1975, is in agreement with its status as a species of dry situations (LeQuesne 1969).

The heteropterus fauna, or associations of species, in 1976 was least similar to that of any other year, but the Auchenorhyncha fauna in 1976 was similar to those of 1977 and 1975 (Fig. 2). Weather and climate appeared to affect the Heteroptera as a whole more severely than they influenced Auchenorhyncha. However, in both groups 1976 was the year in which fewest species were added to the collective total (Table 6). Also, more species were recorded in 1975 and not in 1976 than for any other pair of consecutive years (Table 6). These figures are those for all treatments and it might have been expected that the year following cessation of management would have been one of maximum change. Several of the species taken in 1975 but not in 1976 are members of the 'mid-summer fauna' (Morris 1981a), e.g. *Macustus grisescens, Dicranotropis hamata* and *Criomorphus albomarginatus*. They would not have been expected to occur in August samples in a hot year in which life-histories were accelerated. Both the reduction in species added to the cumulative total in 1976, and the absence of others in that year compared with 1975, may be at least in part attributed to the effects of the unusual summer. In both Heteroptera and Auchenorhyncha mean values of N, S and D were lowest for the untreated plots in 1976 (Figs 1 and 4); an exception was Heteroptera N, lowest in 1977. In Auchenorhyncha the reduction in N and S in 1976 was relatively slight, with a much larger fall in D, whereas in Heteroptera the reverse was the case.

One clear and expected change during 1976–1978 on the plots managed from 1973 to 1975 was the progressive increase in N, S and D for both Heteroptera and Auchenorhyncha (Figs 1 and 4). In every case the mean rate of increase (from 1975 to 1978) was much greater on the J and B plots than on the M ones and the differences between the rates of increase on the J + B plots compared with the M were significant for

TABLE 6. Changes in the species representation 1973–1978, experimental site (all plots). S, number of species recorded

	1973	1974	1975	1976	1977	1978
Heteroptera						
Cumulative S	25	29	33	33	35	36
New spp. added	–	4	4	0	2	1
Spp. absent but recorded previous year	–	7	2	12	1	6
Auchenorhyncha						
Cumulative S	46	51	54	56	60	67
New spp. added	–	5	3	2	4	7
Spp. absent but recorded previous year	–	7	4	11	2	3

N and *D* (Heteroptera) and *N* and *S* (Auchenorhyncha) (Table 4). No J–B contrast was significant, although in every case the mean rate of increase was slightly higher on the B than on the J plots. However, in twelve out of sixteen leafhopper species showing significant effects of the former treatments in their mean rates of increase, the positive rates of increase were greater on the J plots than on the B ones (Table 5). No differences between J and B treatments for any of these species were significant.

No significant differences in the numbers of individual species occurring on the managed plots were recorded for Heteroptera after 1975. However, significant differences occurred in 1976 and 1977, though not in 1978, in several species of Auchenorhyncha, mostly as the persistence of differences established in preceding years (Fig. 8). This may indicate that species of Auchenorhyncha respond less quickly than Heteroptera to cessation of management, but is more likely to be a result of the smaller numbers and greater variances recorded for the Heteroptera.

Although in both Heteroptera and Auchenorhyncha mean diversity on the untreated control plots was always lower in the period 1976–1978 than from 1973 to 1975, only in the Auchenorhyncha was there a clear difference between the relative values on these plots and the managed ones during the period of management and that which followed its cessation (Fig. 4). Nine values of *D* on the managed plots 1973–1975 were equal to or less than those on the control plots, whereas the same nine values 1976–1978 were greater than those on the untreated grassland, with some differences significant in 1978. As species richness (*S*) was significantly greater on the C plots than on the others in 1976, and as there were only small differences in 1977 and 1978, the difference between the managed and untreated plots lies in the evenness (equitability) of the species constituting the fauna; mean *N* was greater on the untreated plots than on the others throughout the 1973–1978 period. The most frequent species are a much higher proportion of the fauna on the control plots in 1978 than they are on the managed ones (Table 7).

Although a few species of Auchenorhyncha responded positively to management (Morris 1981b), most declined in numbers, with consequent reduction in *N*, *S* and *D* (Morris 1981a; Morris & Lakhani 1979). In Heteroptera there were even fewer positive responses than negative ones (Morris 1979). The results of cessation of management clearly show that species are favoured on previously-managed grassland but also that *S* and *D*, though not *N*, are increased on such grassland compared with the untreated control plots. The greater equitability on the previously-managed plots may be seen as a consequence of rejuvenation of the grasslands. The establishment of dominance by a few species in the fauna appears to take longer than the achievement of high species richness and diversity. Mean diversity in 1978 on all the previously-managed plots was much higher than that on the control plots throughout the period 1973–1978. The rate at which

TABLE 7. Numbers and percentage occurrence of the four most abundant Auchenorhyncha spp. on each treatment, 1978

	Treatment, 1973–75							
	M		J		B		C	
	No.	%	No.	%	No.	%	No.	%
Adarrus multinotatus	626	15·7	580	15·1	623	16·2	781	16·8
Arthaldeus pascuellus	663	16·6	563	14·9	553	14·4	683	14·7
Paluda adumbrata	165	4·1	283	7·5	293	7·6	133	2·9
Muellerianella extrusa	702	17·6	515	13·9	432	11·2	1662	35·7
Total (four spp.)	2156	54·0	1941	51·5	1901	49·4	3259	69·6

diversity increased was significantly higher on all the previously-managed plots than on the controls (Table 4). These facts suggest that rejuvenation after cutting is an important feature in the management of grassland faunas.

However, the fauna of the control plots also changed from 1975 to 1978. In the Heteroptera, the mean rate of increase in *N* was weakly positive and not significant and the rates of change in *S* and *D* were negative (also non-significantly). But in the Auchenorhyncha positive and significant rates of increase were recorded for *N* and *S* and only the rate of change in *D* was, very weakly, negative (Table 4). A significant rate of increase in *S* must mean the establishment, or at least the occurrence, of more species at the end of the 1975–1978 period than at the beginning. Thirteen out of seventeen in which there were significant mean rates of increase in numbers on at least one treatment in 1975–1978 had positive rates of increase on the control plots (Table 5). In three species these were significant.

The increase in *N* and *S* on the control plots from 1975 to 1978 may be the result of recovery of the fauna from the 1976 drought, but the relatively small declines in the values of both parameters from 1975 to 1976, and their particularly high values in 1978 compared with earlier years, suggest the operation of other factors. The main difference in the treatment received by the control plots in 1976–1978 compared with 1973–1975 was the absence, except during August, of trampling and disturbance caused by taking frequent vacuum net samples. The experimental plots were surrounded by untreated grassland from 1973 to 1978, a source of colonizing species if one was required. Although there is no direct evidence for an effect of trampling on Hemiptera on the control plots, even moderate trampling of grassland has a severe effect on many invertebrates (Duffey 1975).

Earlier work on grassland faunas has shown that continuous or intensive annual management has generally adverse effects on Hemiptera and other invertebrate animals. However, some species are characteristic of very short, intensively-managed, swards. These include the butterflies *Maculinea arion* (Thomas 1980) and *Lysandra bellargus* (Thomas 1983), and others of conservation importance, as well as *Macrosteles laevis* (Andrzejewska 1962 and other authors). Because grasslands must be managed to persist, and because of the very different requirements of both individual species and of faunas, rotational management of grassland nature reserves has been advocated (Morris 1973a, b, 1975, 1981b). The work reported here further supports rotational treatment as an appropriate system of management for such reserves. In particular, the rejuvenating effect of ceasing annual management has been demonstrated. Although the 1976 drought may have slowed the rate of recovery of previously-managed grassland, the results show that effects may be manifested at least 3 years after management ceased. The significantly higher diversity on the J and B plots compared with the controls was apparent only in 1978 (Fig. 4).

Unfortunately, nature conservation continues to be dominated by concepts of grassland management derived from agriculture and other inappropriate sources. Some nature reserves are still managed annually, by grazing, either because of mistaken adherence to an agricultural or historical principle, or because less frequent management is difficult where grazing stock has to be cared for. The timing and frequency of cutting are not constrained as is grazing by the need to manage grazing animals. Grasslands may be mown at appropriate times and, as shown here, allowed to rejuvenate or recover from management over a period of years. Rotational management, incorporating such periods of recovery, and including intensive, continual, treatment of some areas with special interests such as certain butterflies or other thermophilous species, is an optimal system of management for many grassland nature reserves. Light grazing, whether continuous or intermittent, is unlikely to establish or maintain the range of conditions necessary for conservation of the entire fauna. On the one hand defoliation, trampling and disturbance are likely to decrease species richness and diversity of Hemiptera and other animals, while on the other, light management will be insufficient to create the short turf conditions required by thermophilous species.

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REFERENCES

Andrzejewska, L. (1962). *Macrosteles laevis* Rib. as an unsettlement index of natural meadow associations of Homoptera. *Bulletin de l'Academie polonaise des Sciences, Classe II, Serie de Sciences biologiques*, **10**, 221–226.

Andrzejewska, L. (1965). Stratification and its dynamics in meadow communities of Auchenorhyncha (Homoptera). *Ekologia Polska, Seria A*, **13**, 685–715.

Booij, C. J. H. (1981). Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae), taxonomy, morphology and distribution. *Netherlands Journal of Zoology*, **31**, 572–95.

Booij, C. J. H. (1982). Biosystematics of the *Muellerianella* complex (Homoptera, Delphacidae): host-plants, habitats and phenology. *Ecological Entomology*, **7**, 9–18.

Duffey, E. (1975). The effects of human trampling on the fauna of grassland litter. *Biological Conservation*, **7**, 255–74.

Duffey, E., Morris, M. G., Sheail, J., Ward, L. K., Wells, D. A. & Wells, T. C. E. (1974). *Grassland Ecology and Wildlife Management*, Chapman and Hall, London.

Gibson, C. W. D. (1980). Niche use patterns among some Stenodemini (Heteroptera: Miridae) of limestone grassland, and an investigation of the possibility of interspecific competition between *Notostira elongata* Geoffroy and *Megaloceraea recticornis* Geoffroy. *Oecologia (Berlin)*, **47**, 352–64.

LeQuesne, W. J. (1969). Hemiptera: Cicadomorpha (Deltocephalinae). *Handbooks for the Identification of British Insects*, **II**, 65–148.

LeQuesne, W. J. & Payne, K. R. (1981). Cicadellidae (Typhlocybinae) with a check list of the British Auchenorhyncha (Hemiptera, Homoptera). *Handbooks for the Identification of British Insects*, **II.2(c)**, 1–95.

Morris, M. G. (1969). Associations of aquatic Heteroptera at Woodwalton Fen, Huntingdonshire, and their use in characterising artificial aquatic biotopes. *Journal of Applied Ecology*, **6**, 359–73.

Morris, M. G. (1971a). Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. IV. Abundance and diversity of Homoptera–Auchenorhyncha. *Journal of Applied Ecology*, **8**, 37–52.

Morris, M. G. (1971b). The management of grassland for the conservation of invertebrate animals. *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. by E. Duffey & A. S. Watt), pp. 527–552. 11th Symposium of the British Ecological Society.

Morris, M. G. (1973a). The effects of seasonal grazing on the Heteroptera and Auchenorhyncha (Hemiptera) of chalk grassland. *Journal of Applied Ecology*, **10**, 761–780.

Morris, M. G. (1973b). Chalk grassland management and the invertebrate fauna. *Chalk Grassland: Studies on its Conservation and Management in South-east England* (Ed. by A. C. Jermy & P. A. Stott), pp. 27–34. Kent Trust for Nature Conservation, Maidstone.

Morris, M. G. (1975). Preliminary observations on the effects of burning on the Hemiptera (Heteroptera and Auchenorhyncha) of limestone grassland. *Biological Conservation*, **7**, 312–319.

Morris, M. G. (1979a). Responses of grassland invertebrates to management by cutting. II. Heteroptera. *Journal of Applied Ecology*, **16**, 417–432.

Morris, M. G. (1979b). The effects of cutting on grassland—a preliminary report. *Scientific Proceedings of the Royal Dublin Society, Series A*, **6**, 285–295.

Morris, M. G. (1981a). Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorhyncha. *Journal of Applied Ecology*, **18**, 107–123.

Morris, M. G. (1981b). Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorhyncha. *Journal of Applied Ecology*, **18**, 763–71.

Morris, M. G. & Lakhani, K. H. (1979). Responses of grassland invertebrates to management by cutting. I. Species diversity of Hemiptera. *Journal of Applied Ecology*, **16**, 77–98.

Mountford, M. D. (1962). An index of similarity and its application to classificatory problems. *Progress in Soil Zoology* (Ed. by P. W. Murphy), pp. 43–50, Butterworth, London.

Southwood, T. R. E. & Leston, D. (1959). *Land and Water Bugs of the British Isles*. Warne, London.

Thomas, J. A. (1980). The extinction of the Large Blue and the conservation of the Black Hairstreak butterflies (a contrast of failure and success). *Institute of Terrestrial Ecology Annual Report*, 1979, pp. 19–23.

Thomas, J. A. (1983). The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lyceanidae) in Britain. *Journal of Applied Ecology*, **20**, 59–83.

Waloff, N. (1980). Studies on grassland leafhoppers (Auchenorhyncha, Homoptera) and their natural enemies. *Advances in Ecological Research*, **11**, 81–215.

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