

AUCHENORRHYNCHA OF A CALCAREOUS GRASSLAND

by

A.A.Cook M.Sc. (Durham)

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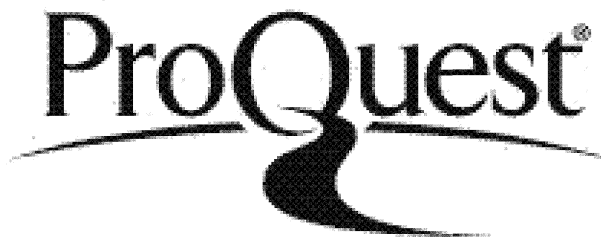
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To Anne, Jo, Izzy & Amy

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1. INTRODUCTION AND LITERATURE REVIEW

1.1 General Introduction

Auchenorrhyncha, especially the families Cicadellidae and Delphacidae, are an important constituent of the fauna of most grasslands (Whittaker, 1969; Waloff & Solomon, 1973; Morris, 1974; Whitcomb, Hicks, Lynn, Blocker & Kramer, 1987). More than 60 species have been recorded from a single site and the numbers of nymphs may exceed 1000 m⁻² (Waloff, 1980). Grassland Auchenorrhyncha feed mainly on the Gramineae, but also on a variety of dicotyledonous species, by sucking out the contents of mesophyll cells or the sap from the phloem or xylem. These insects were, until fairly recently, a neglected group (Waloff, *op. cit.*), but over the last 30 years a number of detailed studies have been made on grassland Auchenorrhyncha in Britain (Whittaker, 1969; Waloff & Solomon, 1973; Morris, 1971 - 1990; Waloff, 1979; Prestidge & McNeill, 1981, 1983; Prestidge, 1982a), continental Europe (Andrzejewska, 1965; Raatikainen & Vasarainen, 1976; Muller, 1978) and North America (Whitcomb, Kramer, Coan & Hicks, 1987; Whitcomb, Hicks & Lynn, 1987).

In Britain, the information available on the host plants of grassland Auchenorrhyncha and the factors determining host choice, comes mainly from studies on acid grassland at Silwood Park (Waloff & Solomon, 1973; McNeill & Southwood, 1978; Prestidge & McNeill, 1981, 1983; Prestidge, 1982a). These studies have shown that many grassland Auchenorrhyncha appear to be opportunistic, moving from one host species to another as plant nitrogen levels change (Crawley 1983). Work on the Auchenorrhyncha of calcareous grasslands, although extensive, has been largely concerned with the effects of management on the fauna (Morris, 1971a, 1973, 1981). This has shown that the diversity of Auchenorrhyncha is greater in tall, structurally diverse grassland than in shorter,

cut or grazed vegetation.

According to Crawley (1983, p. 175) : “ We know almost nothing about the preferences of grass feeding insects. This is partly due to a traditional reluctance on the part of entomologists to identify these plants, and also to the difficulty of collecting insects from individual grasses; ‘swept from low herbage’ is as close to botanical precision as labels on some entomological collections come”. Relatively little is known about the plant host relationships of grassland Auchenorrhyncha in Britain, despite the abundance of the group and its association with a dominant plant family.

The aims of this study were to describe the Auchenorrhyncha community of an area of calcareous grassland in the East Midlands and to obtain information on the grass hosts of the more abundant Delphacidae and Cicadellidae. As grasses usually grow naturally as an intimate mixture of species it is difficult to attribute mobile insects like Auchenorrhyncha to particular species. An attempt was made to overcome this problem by growing grasses from the site in pots and using these plants for field and greenhouse choice experiments. They were also used for greenhouse no-choice experiments in which Auchenorrhyncha were confined on plants in clip-cages. The field choice experiments included an investigation into the influence of total leaf nitrogen on host choice by grassland Auchenorrhyncha. Cicadellid nymphs formed an important part of the samples obtained in the field and these were identified and described.

1.2 Literature review

1.2.1 The grass hosts of grassland Auchenorrhyncha: data from field surveys and choice experiments

Information on the grass hosts of Auchenorrhyncha has been obtained from general surveys of grassland Auchenorrhyncha communities, from choice

experiments in both field and laboratory and from studies on the grasses used for oviposition in the field.

From his extensive survey of grassland Auchenorrhyncha in North Karelia, Finland, Kontkanen (1950) considered that the majority of species were polyphagous and that their distribution was determined mainly by moisture requirements, although no detailed account of the grass species present on his sites was given. Lack of specificity is implied by the conclusion of Andrzejewska (1965), from her work on Polish meadows, that "different species forming meadow communities of Auchenorrhyncha exhibit a tendency to occupy definite layers in the meadow community, regardless of the character of this habitat"(p. 699). Morris (1971a & b, 1973, 1981) has also emphasised the importance of grassland structure in determining the diversity of Auchenorrhyncha communities. Whittaker (1969, p 35) concluded from his survey of limestone grassland at Upper Seeds in Wytham Woods, Oxfordshire, that "it seems likely, but difficult to prove until more is known about the food plants of the Auchenorrhyncha, that both botanical and structural diversity are important if an area is to support a rich fauna of this group of insects".

One of the major studies on the plant hosts of grassland Auchenorrhyncha was that of Waloff & Solomon (1973), who worked on the acid grasslands at Silwood Park, Berkshire. Information on grass hosts was obtained from field work on the distribution of Auchenorrhyncha among the different plant communities, from their association with different grasses sown in experimental plots and from breeding experiments. Although they provide information on the most common host grasses for 28 species of Auchenorrhyncha, only a few showed consistent host plant specificity. Waloff & Solomon (*op. cit.*) considered that plant architecture was probably as important as plant species composition in determining distribution patterns.

Further work on Auchenorrhyncha / plant host relationships was carried out at

Silwood Park by Prestidge & McNeill (1981, 1983). Their research was based on sown plots of six grass species that were common in the area; *Agrostis capillaris* L., *Dactylis glomerata* L., *Festuca pratensis* Hudson, *Holcus lanatus* L., *Lolium perenne* L. and *Poa pratensis* L. The plots were 5 m x 3 m and replicated five times for each species, except for *A. capillaris* which was grown as a single 150 m² plot. Out of the 10 most abundant Auchenorrhyncha, species all occurred on all grasses with the exception of *Stenocranus minutus* (Fab.) which was virtually confined to *D. glomerata* (an association also found by May (1971) and Waloff & Solomon (*op. cit.*). Prestidge & McNeill (1981) quantified the degree of host specificity by calculating an index based on chi-squared for each of the 10 species. The index is calculated by first expressing the numbers of a species of leafhopper caught on each species of grass as a percentage of the total number caught. The deviation of these percentages from a uniform distribution is assessed as a chi-squared and this value is divided by the maximum possible chi-squared, which is obtained by assuming all the leafhoppers occurred on one grass host. (An example of the calculation is given on page 78). The index ranges from 1 (complete specialist) to 0 (complete generalist).

Prestidge & McNeill (*op. cit.*) found that apart from the high specificity of *S. minutus* for *D. glomerata* (specificity index = 0.96) only one other species showed a close association with a particular grass; this was *Adarrus ocellaris* (Fallen), which occurred on *Holcus mollis* (s.i. = 0.77). The other eight species, *Macrosteles leavis* (Ribaut), *Arthaldeus pascuellus* (Fallen), *Ribautodelphax angulosus* (Ribaut), *Psammotettix confinis* (Dahlbom), *Euscelis incisus* (Kirschbaum), *Zyginidia scutellaris* (Herrich-Schaeffer), *Javesella pellucida* (Fab.) and *Euscelis lineolatus* (Brulle), had indices below 3. Nevertheless, despite the relatively low indices given to *A. pascuellus* (s.i. = 0.2) and *M. leavis* (s.i. = .27), with this method of calculation, both showed a marked preference for certain grass species. *A. pascuellus* was associated primarily with *L. perenne* and *F. pratensis* and *M. laevis* with *H. lanatus* and *A. capillaris*.

Morris (1990a & b) described the colonisation of sown grassland plots in Royston, Hertfordshire, by Auchenorrhyncha. Plots of two grass mixtures were sown on chalk soil, one mixture containing the coarse-leaved grasses *Dactylis glomerata*, *Festuca arundinacea*(Schreber), *Lolium perenne* and *Phleum pratense* and the other containing the fine-leaved grasses *Agrostis capillaris*, *Cynosurus cristatus* L., *Festuca ovina* L., *F. rubra* L. and *Poa pratensis*. Although the study was not designed to give precise information on the feeding habits of the Auchenorrhyncha that colonised the plots the results give interesting indications of host preference. Species that were associated with the coarse grass plots included *Mocycdia crocea* (Herrich-Schaeffer), *Stenocranus minutus* and *Zyginidia scutellaris* and those that were associated with the fine grass plots included *Criomorphus albomarginatus* Curtis, *Dikraneura variata* Hardy, *Euscelis incisus*, *Paluda adumbrata* C. Sahlberg, *Rhytistylus proceps* Kirschbaum and *Turrutus socialis* (Flor). Species that showed variable responses were *Arthaldeus pascuellus*, *Macrosteles* spp. and *Javesella pellucida*.

Port (1981), during a study of roadside verges, found that *Paluda adumbrata* only occurred where *Festuca rubra* was present.

Den Bieman (1987) studied the host plant relationships of the genus *Ribautodelphax* (Delphacidae), a difficult genus taxonomically which consists of nine clearly defined species in western Europe plus a number of taxa of uncertain status. Field records of the host plants of the different species were obtained by catching the planthoppers with a pooter directly from known grass species in over 100 sites in western and southern Europe. Most of the *Ribautodelphax* species appeared to be monophagous in the field. Further information on plant hosts was obtained from laboratory choice experiments. These were carried out in a cage (90 cm x160 cm x100 cm) with walls of black plastic sheets and a top covering of fine gauze. Six plants of each of twelve grass species that field data indicated were

host plants were grown in pots and placed randomly in the cage in a bed of moist sand. Artificial light was provided by a 400 W sodium lamp. Planthoppers reared on their field host plants were released into the cage as 6 - 10 day adults, by placing two or three animals on each plant, and collected after 48 hours. From this work, and from no-choice experiments described in the next section, Den Bieman found that the eleven *Ribautodelphax* species and undescribed taxa he worked on showed a strong preference for their field host plant.

Laboratory (or outdoor insectary) choice tests have been reported by a few other authors for grassland Auchenorrhyncha in other countries (Drosopoulos, 1977; Sowaga & Pathak, 1970; Raatikainen, 1967) but this approach does not appear to have been used to obtain information of the plant hosts of grassland Auchenorrhyncha in Britain.

In North America, Whitcomb and colleagues, in a series of papers, have described the considerable body of information on cicadellid / plant host relationships they have accumulated from a wide range of grasslands. Much of their work has been based on field collections from native grasslands, despite the difficulty of finding host plant stands of sufficient purity for reliable information to be obtained. In addition collections were made from plots of grasses and forbs planted by other researchers, highway departments, etc. Whitcomb, Hicks, Lynn, Blocker and Kramer (1987) provide the following classification of cicadellid feeding strategies based on over 2000 collections from N. American grasslands:

Grass specialists. Species confined to one native genus or a set of closely related genera.

Grass generalists. Species that feed on a wide variety of grasses, but never dicotyledonous plants.

Forb specialists. Species confined to a single forb species or a number of closely related species.

Forb generalists. Species with a wide host range of forbs, often including plants in more than one family.

Habitat specialists. A few species with a complex life history involving oviposition and maturation on different host plants.

Supertramps. Species with a wide array of grass and forb hosts.

(The authors do not explain why grass specialists are confined to a single genus or closely related genera, while forb specialists are confined to a single species or closely related species.)

In all grassland types studied by Whitcomb, Hicks *et al.* (*op. cit.*), grass specialists made the greatest contribution to leafhopper diversity (species richness), comprising between 35% and 64% of all species collected. Whitcomb, Hicks, Lynn, Allred and Blocker (1987) quantified host plant range using a simple "coefficient of oligophagy", calculated as follows:

$$O_{ij} \text{ (coefficient of oligophagy)} = n_{ij} / n$$

where n_{ij} is the number of specimens of a particular cicadellid species found associated with a single plant taxon and n is the total number of that species collected. Whitcomb, Kramer, Coan & Hicks (1987) suggest that the majority of grassland cicadellids show considerable specificity, some being monophagous and many being confined to a particular grass genus or tribe.

1.2.2 Survival and reproduction of Auchenorrhyncha on potential grass hosts

A number of laboratory studies have been reported on the survival and reproduction of grass feeding delphacids and cicadellids on potential hosts, often to support data collected in the field. Den Bieman (1987) tested the ability of eleven species and taxa of uncertain status of *Ribautodelphax* to develop and reproduce on different grass species. Field and laboratory choice test data already referred to

indicated that the majority were monophagous. The planthoppers were confined with the test plants in cages and in nearly all cases the shortest nymphal development time and the highest reproductive rate were found to occur on the grasses with which they were associated in the field. Adult survival in many of the *Ribautodelphax* species was as good on at least one other species as on the field host, although this other host species was often a congener of the field host. No species was polyphagous in its responses, although the potential host range of many was wider than field results and choice experiments indicated. Den Bieman (*op. cit.*) suggests that, in the field, behavioural aspects dominate the physiological in the choice of host plants. What is especially interesting about this work is that a fairly large group of closely related planthoppers are practically monophagous on different grass hosts.

A high degree of host specificity has also been found in Dutch populations of the genus *Muellerianella* (Delphacidae) (Drosopoulos, 1977). *M. fairmairei* (Perris) is mainly associated with *Holcus lanatus*, although it appears to require *Juncus effusus* L. for winter oviposition, and *M. brevipennis* (Boheman) is monophagous on *Deschampsia cespitosa* (L.) Beauv. In laboratory tests adult survival and oviposition was highest for both species on their field host plants, but *M. fairmairei* was able to survive and reproduce on a much wider range of species than *M. brevipennis*. *M. fairmairei* reproduced on 9 out of 13 test grass species from the Aveneae and Triticeae including *H. mollis*. It failed to reproduce on *Oryza sativa* L. on which it is said to occur in Japan (Drosopoulos, *op. cit.*). The longevity and egg production of *M. brevipennis* on *Avena sativa* L. and *Hordeum vulgare* L. was similar to that of *M. fairmairei*, but it failed to reproduce on the congener of its field host plant, *Deschampsia flexuosa* (L.) Trin., as well as on all other test grasses.

The responses of grassland cicadellids to a range of grasses from three sub-families, the Pooideae, Panicoideae and Chloridoideae, in no-choice experiments were found by Whitcomb, Kramer *et al.* (1987) to be only partly in accordance with

their field observations. *Graminella oquaka* Crumb and *G. villica* Crumb, specialists on the panicoid species *Panicum virgatum* L. (switchgrass) and *Paspalum laeve* Michaux. respectively could only be reared on grasses from this subfamily. *G. oquaka* was reared on one other species besides its field host (*Brachiaria ramosa* Griseb.) but failed to survive on 15 other grasses from the three subfamilies while *G. villica* was reared on seven panicoid species including its field host, survived on one pooid grass and failed on the remaining pooid and panicoid test species (it was not tested on any chloridoid hosts). In contrast, *Polyamia apicata*, which appeared from field observations to be a strict specialist on the panicoid grass *Panicum lanuginosum* L., was reared from grasses belonging to all three subfamilies. In accordance with field observations, the widest spectrum of hosts suitable for rearing was found in the generalist species *Planicephalus flavicostatus*.

There have been a number of studies on the survival and oviposition of leafhoppers that are vectors of crop viruses in the USA. *Deltocephalus sonorus* (Ball), a vector of corn stunt virus, is a grass feeding species with a wide host range. When confined on 60 potential grass hosts it reproduced on 54 of them (Gustin & Stoner, 1968). Using nymphal survival as a measure of host suitability for the painted leafhopper *Endria inimica* (Say), a vector of striate mosaic disease in wheat, Coupe & Schultz (1968) found that nymphs survived to become adults on all five grasses tested, which came from a range of tribes and included *Triticum durum* Desf. *Dalbus maidus* (DeLong & Walcott), another vector of corn stunt virus, is a subtropical species with an apparently limited host range. In greenhouse tests using a wide variety of plants *D. maidus* fed on 33 species including some dicotyledons although adult survival was best on grasses. Oviposition was more or less restricted to grasses. Nymphal mortality, however, was high on most of the test species and only on *Zea mays* L did nymphs successfully develop into adults.

Waloff & Solomon (1973) included breeding experiments in their work on acid

grassland Auchenorrhyncha, although a limited number of grass species, and sometimes only the presumed field host, were used as experimental hosts. *Psammotettix confinis* Dahlbom was bred on *Agrostis capillaris*, its main host in acid grassland, and also *Festuca rubra* and *Holcus lanatus*. *Arthaldeus pascuellus*, *Streptanus sordidus* Zetterstedt and the delphacid *Struebingianella dalei* Scott were reared on *A. capillaris*. *Javesella pellucida* and *Dicranotropis hamata* Boheman were reared through 7 generations on *Holcus mollis*. *Balclutha punctata* Fab. was reared on *Deschampsia cespitosa*, *Doratura stylata* Boheman on *A. capillaris* and *Jargassus pseudocellaris* Flor. on *A. capillaris*, *F. rubra* and *H. mollis*. May (1971), also working at Silwood Park, reared *Stenocranus minutus* on *Dactylis glomerata*.

1.2.3 Factors affecting host selection in Auchenorrhyncha

Southwood (1973) has pointed out that relatively few orders of terrestrial insects have evolved to feed on flowering plants and has suggested that this is due to a number of evolutionary hurdles that phytophagous insects have had to overcome. These hurdles include the problem of attachment to plant surfaces, desiccation, defensive plant chemicals and the nutritional content of plant material. It is this last hurdle that has featured most prominently in work on the factors determining host choice in Auchenorrhyncha.

Plants contain on average 13.4% protein, yet synthetic insect diets must generally contain 25% protein to be successful (McNeill & Southwood, 1978). It seems likely that obtaining the right balance of amino acids and proteins in sufficient quantities is a major component of the nutritional hurdle (McNeill & Southwood, *op. cit.*). As far as grass feeding Auchenorrhyncha are concerned it has been found that their food is generally sufficient for adult and nymphal survival but may not be optimum for egg maturation (Hill 1982). Although many insects have restricted plant host ranges, it appears that once initial barriers to colonisation have been overcome, insects develop phenologies to synchronise with suitable levels of nitrogen in their

hosts. They may also move to different structures on the same plant or move between different hosts in response to the availability of nitrogen during a season (McNeill & Southwood, *op. cit.*).

Prestidge & McNeill (1983) concluded from their work on nitrogen in the ecology of grassland Auchenorrhyncha that a number of species are polyphagous in terms of grass hosts but specialists in terms of nitrogen requirements. They move from host to host during a season tracking optimum levels of nitrogen in the form of particular amides and amino acids. The nitrogen content of most grasses follows a characteristic seasonal pattern (Hill, *op. cit.*; McNeill & Southwood, *op. cit.*). In *Lolium perenne* there is a peak in spring (up to 6% dry weight) followed by a decline in the summer (down to 2% dry weight) and a second smaller peak in the autumn. Although this pattern is generally similar in different grasses there is variation in the timing and amplitude of the changes and in the mean annual levels of nitrogen. Prestidge & McNeill found that mean annual total nitrogen levels of grasses on plots at Silwood Park varied between 4.4% dry weight (*Poa pratensis*) and 2.8% dry weight (*Dactylis glomerata*).

Prestidge & McNeill (*op. cit.*) suggested, that, as grasses contain low concentrations of secondary chemicals (Harborne & Williams, 1976), nutritional characteristics may be of prime importance in determining host selection by grass feeding Auchenorrhyncha. In their work, based on sown plots of six different grasses they found that the numbers of some Auchenorrhyncha (*Zyginidia scutellaris*, *Javesella pellucida*, *Euscelis incisus* and *E. lineolatus* Brulle) were positively correlated with grass nitrogen levels during the ovipositional period. A second group (*Stenocranus minutus* and *Adarrus ocellaris*) were host specialists and showed no correlation with nitrogen levels. A third group (*Macrostelus leavis* Ribaut and *Psammotettix confinis*) was opportunistic and showed no correlation with nitrogen levels or association with particular plant hosts. The plots of grasses used in this experiment were treated with a basal fertiliser applied in the spring.

Work with different fertiliser treatments on grass plots by Prestidge (1982a), provided additional information on the responses of different species of Auchenorrhyncha to the nutrient status of their food plants. An area of acid grassland on Elm Slope at Silwood Park was divided into 25 m² plots (all with a natural mixture of plant species) which were treated with different levels and types of fertiliser. The effect of increasing levels of nitrogen was to increase the overall numbers of leafhoppers present. This was mainly due to an increase in the numbers of delphacids (*Javesella pellucida* and *Dicranotropis hamata*). The numbers of the opportunist *Macrostelus leavis* and the host specialist *Adarrus ocellaris* also increased. The univoltine cicadellids *Elymana sulphurella* (Zetterstedt), *Diplocolenus abdominalis* (Fabricius), *Mocydiopsis parvicauda* (Ribaut) and *Recilia coronifera* (Marshall) were more abundant on plots that were not treated with nitrogen fertiliser. Because of the dramatic increase in the numbers of a few species in response to fertiliser treatment the species diversity decreased on fertilised plots. The effect of the fertiliser (applied annually in the spring) was to increase the total leaf nitrogen (as measured in *Holcus mollis*, a common grass on the site), from 2.2 - 2.4% dry weight (control) to 3.5 - 3.8% dry weight (highest application rate of 1200 kg NH₄NO₃ per hectare). Equivalent values for stem soluble nitrogen were 0.3% (control) and 1.4% (highest application rate). The peak abundance of *Dicranotropis hamata* occurred on plots with leaf soluble nitrogen around 0.4 % dry weight, while for *Adarrus ocellaris* peak abundance occurred where values were around 0.3 % dry weight.

To explain the differences in the responses to nitrogen levels shown by the various species of Auchenorrhyncha, Prestidge (*op. cit.*) suggested that delphacids, many of which overwinter as nymphs, are likely to have their physiologies geared to perform optimally at high nitrogen levels as their life-history strategies ensure that the females are reproducing at the time of the spring flush in nitrogen. Many cicadellids, on the other hand, overwinter as eggs and reproduce during the summer when nitrogen levels are low. One of the cicadellids that showed a positive

response to nitrogen levels, *Euscelis incisus*, overwinters as a nymph but two others, *Macrosteles leavis* and *Adarrus ocellaris*, that also showed a positive response, overwinter as eggs.

The different responses of *Adarrus ocellaris* and *Macrosteles leavis* to nitrogen levels in a range of grasses (Prestidge & McNeill, 1983) and to nitrogen levels on a range of plots treated with different levels of fertiliser (Prestidge, 1982) may be significant. In the former case neither showed any response and in the latter both showed a positive response. *A. ocellaris* is strongly associated with *Holcus lanatus* and may well show a preference for *H. lanatus* plants with higher nitrogen levels. The same may be true for *M. leavis* which Prestidge & McNeill found to have a slight preference for *H. lanatus*.

In experiments involving fertilisers it is difficult to differentiate the effect of changes in the nutrient status of the plants from the effect of changes in the amount of plant material present and the consequent increase in the amount of living space available for insects. Prestidge & McNeill (1981) and Prestidge (1982a) measured the structural diversity or plant architecture (Lawton, 1978) of grassland as follows:

$$\text{Architecture index} = \text{Plant Biomass (Kg m}^{-2}\text{)} \times \text{Mean Pasture Height (cm)}$$

They found a good relationship between the density of Auchenorrhyncha and the architecture index on fertilised plots and considered that this was an equally good explanation for the correlation between the density of Auchenorrhyncha and fertiliser levels. They thought it likely that both plant architecture and nutrient levels were important in determining the abundance of Auchenorrhyncha. After the application of fertiliser to grass plots, plant nitrogen and the numbers of Auchenorrhyncha increased rapidly but as the plant nitrogen decreased so did the number of Auchenorrhyncha. After three weeks there was an increase in the plant architecture index, followed by another increase in the numbers of

Auchenorrhyncha (Prestidge & McNeill, *op. cit.*).

Little work appears to have been done on plant characteristics other than nutrient status that may affect host plant choice by grassland Auchenorrhyncha. Oviposition behaviour has been studied in detail for species associated with *Holcus* spp. in acid grassland by Thompson (1978). He looked at four species of cicadellid and one species of delphacid and found that they all differed in egg laying behaviour. The delphacid *Dicranotropis hamata* laid most of its eggs within the grass stems of *Holcus* spp. while the cicadellids (*Adarrus ocellaris*, *Diplocolenus abdominalis*, *Elymana sulphurella* and *Recilia coronifera*) laid most of their eggs in leaf or leaf sheath tissue, generally within the tissue between the upper and lower epidermis. There was variation among the cicadellids in their use of living and dead tissue for oviposition. *E. sulphurella* laid all its eggs within living tissue while *Adarrus ocellaris* and *R. coronifera* laid 50% and *D. abdominalis* laid 80% of their eggs within dead tissue. All the cicadellids laid at least 70% of their eggs in leaf sheaths with the exception of *E. sulphurella* which divided its eggs equally between leaf sheaths and leaf blades. There was also variation in the vertical distribution of the eggs of different species. Thomson concluded that utilisation of different parts of the plant for oviposition may be one of the important factors enabling the species to coexist.

Details of oviposition sites on host plants are given for *Muellerianella* spp. by Drosopoulos (1977), for *Javesella pellucida* by Raatikainen (1967) and for *Stenocranus minutus* by May (1971). Tay (1972) examined the distribution of eggs of *Cicadella viridis* in stems of *Juncus effusus* and found that it did not oviposit in stems with a diameter of less than 1.5 mm. Bakkendorf (1933) in the course of his work on Hymenopterous egg parasites, found that a number of cicadellids and delphacids used the stems of *Juncus* spp. for egg laying. Drosopoulos (*op. cit.*) has shown that the bivoltine delphacid *Muellerianella fairmairei* lays overwintering eggs in *Juncus* spp. but otherwise feeds and oviposits on *Holcus* spp. It is always

found in habitats where *Juncus* spp. and *Holcus* spp. grow together. Although leafhoppers are obviously exacting in their requirements for oviposition there is little evidence to show that this is an important factor in determining host choice.

The role of secondary chemicals in host selection by grass feeding

Auchenorrhyncha has been considered unimportant (Whitcomb, Lynn, Hicks *et al.*, 1973). The diversity and concentration of secondary chemicals in the Poaceae is relatively low (Prestidge & McNeill, 1983) although various flavonoids and hydroxamic acids have been isolated from a wide range of species (Harborne & Williams, 1976; Harborne, 1988; Argandona, Luza, Niemeyer & Corcuera, 1980).

Resistance of cereals (*Hordeum distichum* L, *Triticum aestivum* L, *T. durum* L and *Secale cereale* L) to the aphid *Metopolophium dirhodum* (Walker) has been shown by Argandona *et al.* (1980) to be related to the concentration of the hydroxamic acid 2,4-Dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA). They showed that DIMBOA was deleterious to aphids at concentrations found in resistant varieties of cereals. In a greenhouse experiment Argandona *et al.* (1981) found that the numbers of the aphid *Schizapsis graminum* (Rondani) on the leaves of *T. durum* was inversely related to hydroxamic acid content. The hydroxamic acid content of *Zea mays* has also been found to be correlated with resistance to *S. graminum* (Argandona *et al.*, 1983, 1985).

1.2.4 Host plant specificity in grassland Auchenorrhyncha

The information available on the host plant relationships of British grassland Auchenorrhyncha suggests that host plant specificity is not very common. This is in contrast to the situation in temperate woodlands where leafhopper communities contain a high proportion of monophagous species (Claridge & Wilson, 1976). Claridge *et al.* (*op.cit.*) suggest that the species diversity of woodland canopy leafhoppers is more closely linked to the species diversity of the plants than is the case in grassland habitats. They speculate that the reasons for the difference in

specificity in the two habitats may be the size and permanence of the host plants; trees being large and long lived while grasses are relatively small and ephemeral. Short flights made by Auchenorrhyncha in grassland will normally result in loss of contact with a particular host grass while in woodland contact with a host tree will be easily maintained. They suggest that selective pressure may favour specialisation of feeding and oviposition in tree-feeding leafhoppers, leading to the most efficient use of a narrow range of host plants, and a broader host range in grassland allowing leafhoppers to exploit different plants encountered during trivial movements.

Differences in the degree of specificity shown by Auchenorrhyncha in woodland and grassland habitats may be partly accounted for by the wider taxonomic range of trees (Aceraceae, Fagaceae, Salicaceae, Ulmaceae etc) than of grasses (Gramineae) (Bullock, pers. comm.).

Port (1978) suggested that Auchenorrhyncha in grassland are usually oligophagous not only because the structure of the habitat favours a broader host range but also because grasses lack deterrent chemicals. He considered that "Auchenorrhyncha in other habitats that are less species diverse (than grassland) will tend toward monophagy which may be enforced by the presence of specific allelochemicals in the host plant" (p. 107). In his studies on the feeding biology of the Auchenorrhyncha, Port (*op. cit.*) found that out of the 53 species tested, 48 fed on, and produced salivary sheaths in, *Avena sativa* L.

The results of work on leafhopper / plant host relationships in grassland from either side of the Atlantic have led to rather different conclusions, or, at least, points of emphasis. The importance of host specificity is stressed by N. American workers (Whitcomb, Hicks, Lynn, Blocker & Kramer,

1987) while British and continental European work has emphasised the importance of habitat structure and plant nitrogen in determining distribution and host choice within a group of predominantly generalist feeders (Waloff & Solomon, 1973; Prestidge & McNeill, 1981, 1983). Whitcomb, Kramer, Coan, & Hicks (1987) suggest that this difference is in large part due to the predominant grass sub-families in America and Europe. Most of the grasses in Europe belong to the sub-family Pooideae while in N. America two other sub-families, the Chloridoideae and Panicoideae are also common, especially in the southern states. Whitcomb, Kramer *et al.* (*op. cit.*), found there was extensive overlap in the guilds of leafhoppers present on pooid grasses compared with those present on chloridoid and panicoid grasses. They did, however, find some very specific associations between cicadellids and pooid grasses.

European work has also shown a number of grassland Auchenorrhyncha to be host specific (May, 1971; Drosopoulos, 1977; Booij, 1982; Prestidge & McNeill, 1981; Den Bieman, 1987). Booij (*op. cit.*) investigated the host preferences of *Muellerianella* spp. (*M. brevipennis*, *M. extrusa* and *M. fairmairei*) and found they were all monophagous in the field but would accept other hosts in the laboratory (cf. Drosopoulos *op. cit.*). It is ^{may be} significant that the majority of these host specific species / genera are delphacids (*Dicranotropis hamata*, *Muellerianella* spp., *Ribautodelphax* spp., and *Stenocranus minutus*). Denno & Roderick (1990) have pointed out that monophagy is widespread in grass feeding Delphacidae in contrast to grass feeding Cicadellidae in which examples of oligophagy are more common.

Some clarification is required on the definitions of the terms monophagous, oligophagous and polyphagous, which are given different meanings by different authors (Strong, Lawton & Southwood, 1984). Monophagy can refer to feeding on one species, one genus, a few closely related genera or a single tribe. Oligophagy generally means feeding on a restricted range of plants, but this restricted range

may not be very different from some definitions of monophagy. Again, one author's oligophagy may overlap with another's polyphagy. The following quotes from work on grassland Auchenorrhyncha illustrates the different usage of the terms: ...

"leafhoppers in general, unlike some other phytophagous insects, are not markedly mono- or oligophagous" (Morris, 1974, p 16); "... strong leafhopper - host plant associations are uncommon. The current study, however, presents an hypothesis to explain some of the reasons for oligophagy" (Prestidge & McNeill, 1983, p 336).

Whitcomb, Hicks, Lynn *et al.* (1987) whose classification of feeding strategies has already been referred to, use the term specialist to include monophagous and oligophagous species and generalist to describe polyphages. Denno & Roderick (1990) define monophagy as feeding on one or several closely related species, presumably meaning a single genus. This seems a satisfactory definition of monophagy. Oligophagy could then be defined as feeding on a set of closely related genera (a single tribe), and polyphagy as feeding on a broad assemblage of plants in different tribes, sub-families or families.

Crawley (1983) suggested the term 'specialist' to describe species that feed on a well defined group of plants, which could be a genus or even a family. The Cruciferae, for instance, is a well defined family of plants with a characteristic secondary chemistry, and insects feeding on this group can justifiably be called specialists. He used the term 'generalist' to describe broadly oligophagous or polyphagous species. These terms can be used to convey a reasonably precise meaning in a particular context and may be preferable to those that attempt to be more exact. An insect might also be considered a specialist if it feeds on a particular type of plant tissue in a range of hosts (Strong *et al.* 1984).

Added complications in defining feeding habits arise if an insect feeds on a variety of species throughout its geographical range, but is a specialist on a local scale, a

situation which may be fairly common (Fox & Morrow, 1981), or if it feeds on a variety of plants within its habitat but can only complete its life cycle if a particular species is present. Bakkendorf (1933) (cited by Claridge & Wilson, 1976) described how a number of species of cicadellids and delphacids use stems of *Juncus* spp. for oviposition. These plants survive longer than many of their food plants and provide relatively safe sites for overwintering eggs.

1.2.5 Summary of Plant Hosts

A summary of the information available on the host plants of the Auchenorrhyncha identified during this research is given in table 1.1.

TABLE 1.1 Summary of published data on the plant hosts of Auchenorrhyncha recorded at the Deeps. (Author code in parenthesis)

	Plant Hosts
Cicadellidae	
<i>Adarrus multinotatus</i>	<i>Brachypodium</i> spp. (8)
<i>Aphrodes albifrons</i>	<i>Brachypodium pinnatum</i> (1), <i>Holcus</i> spp, <i>Dactylis glomerata</i> (2)
<i>A. bicinctus</i>	<i>Carduus nutans</i> , <i>Knautia arvensis</i> (1)
<i>Arthaldeus pascuellus</i>	<i>Agrostis capillaris</i> (2), <i>Festuca pratensis</i> , <i>Lolium perenne</i> (3), Grasses, <i>Juncus</i> spp (4).
<i>Bactracomorpus irroratus</i>	<i>Helianthemum nummularium</i> (5)
<i>Dikaneura variata</i>	Fine grasses (6)
<i>Diplocolenus abdominalis</i>	<i>Holcus</i> spp (2)
<i>Doratura stylata</i>	<i>Agrostis capillaris</i> (2,3), <i>Festuca rubra</i> (2)
<i>Elymana sulphurella</i>	<i>Holcus lanatus</i> (2,3), <i>H. mollis</i> (2,4)
<i>Euscelis incisus</i>	<i>Festuca pratensis</i> , <i>Lolium perenne</i> (3), fine grasses (6)
<i>Graphocraerus ventralis</i>	<i>Poa pratensis</i> , <i>Anthoxanthum odoratum</i> (4)
<i>Macustus griseus</i>	<i>Holcus</i> spp. (2)
<i>Mocydia crocea</i>	<i>Brachypodium pinnatum</i> (1,5), <i>Bromus erectus</i> , <i>Dactylis glomerata</i> (5), <i>B. pinnatum</i> , <i>B. erectus</i> , <i>Lolium perenne</i> (9)
<i>Paluda adumbrata</i>	<i>Festuca rubra</i> (7), fine grasses (6)
<i>Psammotettix confinis</i>	<i>Agrostis capillaris</i> (2,3), <i>Festuca pratensis</i> (3)
<i>Rhytistylus proceps</i>	<i>Festuca rubra</i> (2,3), fine grasses (6)
<i>Streptanus sordidus</i>	<i>Agrostis capillaris</i> (2,3)
<i>Turrutus socialis</i>	Fine grasses (6)
<i>Zyginidia scutellaris</i>	<i>Brachypodium pinnatum</i> (1), <i>Holcus</i> spp (2), <i>Dactylis glomerata</i> (2,5), <i>Festuca rubra</i> (5), coarse grasses (6)
Delphacidae	
<i>Criomorpus albomarginatus</i>	<i>Holcus</i> spp. (2), fine grasses (6)
<i>Dicranotropis hamata</i>	<i>Holcus lanatus</i> (3)
<i>Hyledelphax elegantulus</i>	<i>Festuca rubra</i> (2), <i>Deschampsia flexuosa</i> (4)
<i>Javesella pellucida</i>	<i>Festuca pratensis</i> , <i>Dactylis glomerata</i> (2). Wide host range (10)
<i>Kelisia vittipennis</i>	Sedges (5)
<i>Stenocranus minutus</i>	<i>Brachypodium pinnatum</i> (1), <i>Dactylis glomerata</i> (1,2,3,4), coarse grasses (6)

Authors: (1) Whittaker 1969; (2) Waloff & Solomon 1973; (3) Prestidge & McNeill 1983; (4) Ossiannilsson 1978,1981,1983; (5) Le Quesne 1960,1969, 1981; (6) Morris 1990b; (7) Port 1981; (8)Shiemenz 1969; (9) Muller 1987; (10) Raatikainen (1967)

2. DESCRIPTION OF STUDY SITE AND PRELIMINARY SURVEY OF AUCHENORRHYNCHA

2.1 Introduction

Information is available on the Auchenorrhyncha communities of a range of temperate grassland habitats in Britain and Europe (Kontkanen, 1950; Andrzejewska, 1965; Whittaker, 1969; Morris 1971a & b, 1973, 1974, 1983, 1990, Waloff & Solomon, 1973; Hollier, 1987; Baharith, 1989). Among British grassland habitats the communities of calcareous grasslands have been the most widely sampled (Morris, 1971 - 1990; Whittaker, 1969), although detailed information is also available for a few acid and neutral grassland sites (Waloff & Solomon, 1973; Hollier, 1987; Baharith, 1989). Prior to the work described here there was little information on the Auchenorrhyncha of the Deeps at Collyweston except for a few casual records (Kirby, pers. comm.). Davis (1986) described the fauna associated with *Helianthemum nummularium* (L.) Miller at the Deeps, and other sites in the Stamford area, which included two species of leafhopper (*Bactracomorpha irroratus* Lewis and *Arboridea parvula* Boheman).

2.2 The study site

The site on which most of my work was based is an area (6.32 ha.) of unimproved limestone grassland at Easton-on-the-Hill near Stamford (Grid ref.: TF 004038) known either as the Deeps or Collyweston Quarries (Fig. 2.1 and Plate 2.1) (hereafter referred to as the Deeps). The grassland is an S.S.S.I. owned by Burghley Estate and the Easton-on-the-Hill Parish Council and is leased to the Northamptonshire Wildlife Trust as a Trust nature reserve. Permission to work on the site was obtained from both the Trust and English Nature.

Collyweston is well known for the roofing slates obtained from a limestone bed quarried in the area. This bed consists of a siliceous, shaley limestone, 0.3m to 3m deep, and lies at an average depth of 10m beneath the overlying Lincolnshire



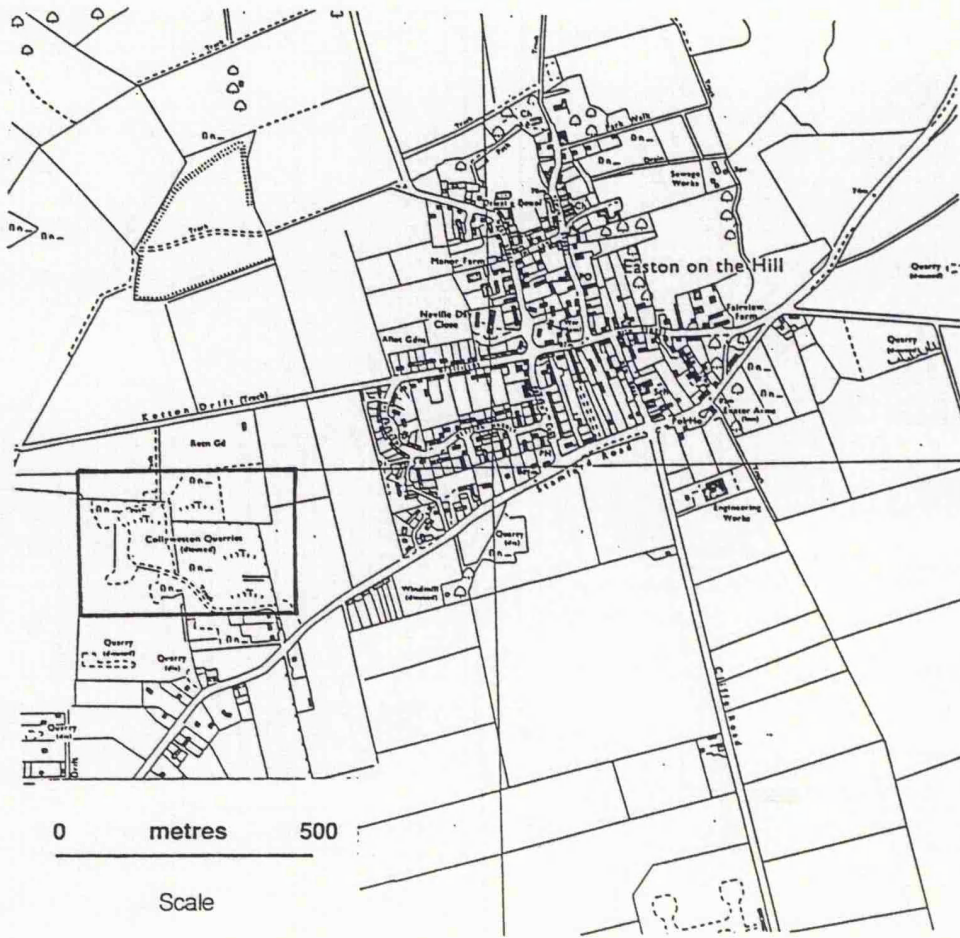
Fig. 2.1 Map showing the location of the study site (the Deeps or Collyweston Quarries).

Plate 2.1

Plate 2.1

Above: Aerial photograph of the Deeps, showing position of sampling sites 1 and 2.

Below: Map showing position of the Deeps (Collyweston Quarries - enclosed in the box), in relation to the village of Easton on the Hill.



0 metres 500

Scale

Limestone (Inferior Oolite) which is also quarried for building stone. According to Hepburn (1955), the Deeps was quarried for limestone on an open cast basis for at least 250 years until the end of the 19th century when the demand for limestone products declined and the cost of removing the overburden became prohibitive. Slate alone was then mined on a small scale until 1935 and again more recently between 1950 and 1970. Some of the mine shafts can still be seen on the western edge of the area just outside the reserve boundary. An Enclosure Award dated 1839 shows much of the area was rough grassland at the time and sporadic grazing seems to have been the only form of management since then. Since 1985 the Northamptonshire Wildlife Trust has introduced winter sheep grazing (October - February) to maintain the botanical interest of the grassland.

As a result of past quarrying the topography of the Deeps is very irregular, consisting of a mosaic of low hills and shallow depressions. The soil varies considerably in its depth and composition. Hepburn (*op. cit.*) found that over much of the area the soil depth was about 20cm but less in stony places, the CaCO₃ content varied between 31% and 2.5% with an average value of 16%. The pH was generally between 7 and 7.4 with a few sandy areas giving a value of 6.8.

Hepburn's (*op. cit.*) vegetation survey of the Deeps provides an estimate of the percentage frequency (shown in parentheses below) of the commoner species, based on 50 1m² quadrats. Plant nomenclature in this study follows Clapham, Tutin and Moore (1987) and the names given by Hepburn have been changed as necessary. The grassland is dominated by *Bromus erectus* Hudson (92) and *Brachypodium pinnatum* (Hudson) Beauv. (78). Other common grasses are *Festuca ovina* L. (64)¹, *Briza media* L.(20), *Trisetum flavescens* (L.) Beauv. (14), *Arrhenatherum elatius* (L.) Beauv. ex J. & C. Presl. (10) and *Avenula pubescens* (Hudson) Dumort. (4). Grasses classed by Hepburn as occasional (o) or rare (r) are: *Alopecurus myosuroides* Hudson (o), *Anthoxanthum oderatum* L. (o),

¹ Although *Festuca rubra* L. is now more abundant than *F. ovina* in the Deeps, the species is not mentioned by Hepburn (1955)

Avenula pratensis (L.) Dumort.(r), *Cynosurus cristatus* L.(r), *Dactylis glomerata* L.(r), *Holcus lanatus* L. (o), *Koeleria macrantha* (Ledeb.) Schultes (o) and *Phleum pratense* L. (r).

The dicotyledonous flora is extremely rich and includes the following local species: *Aceras anthropophorum* (L.) Aiton f., *Anacamptis pyramidalis* (L.) Richard, *Campanula glomerata* L., *Genista tinctoria* L. (abundant), *Gymnadenia conopsea* (L.) R.Br., *Filipendula vulgaris* Moench, *Helianthemum nummularium* (L.) Miller (abundant), and *Orobanche elatior* Sutton. The grassland falls into the type CG4 of the National Vegetation Classification (NVC) (Rodwell, 1992).

2.3 Preliminary Survey of Auchenorrhyncha

2.3.1 Methods

The survey of Auchenorrhyncha was carried out between April and September 1987. Two contrasting sites within the grassland were chosen for sampling (Fig. 2.2). Site 1 is an area of relatively low vegetation (height: 10 - 20 cm) on a shallow soil, overlying what was probably a spoil heap of limestone 'slate' fragments, dominated by *Bromus erectus*, *Festuca rubra* and *Festuca ovina*. Other grasses present include *Arrhenatherum elatius*, *Avenula pubescens*, *Koeleria macrantha*, *Briza media* and *Trisetum flavescens*. Site 2 is an area of ranker vegetation (height 50 - 70 cm) on a deeper soil, typical of the majority of the grassland, dominated by *Brachypodium pinnatum*, *Bromus erectus* and *Festuca rubra*. Other grasses include *Arrhenatherum elatius* and *Dactylis glomerata*. The results of a plant survey, based on 25 randomly placed quadrats for each site, are given in Table 2.1.

Each site was sampled every two weeks from April 22 to September 9 by means of both an Univac vacuum sampler (Arnold, Needham & Stevenson 1973) and a sweep net. The vacuum sampler was used in conjunction with a metal cylinder 60 cm high and 50 cm diameter (1963.5 cm² in cross-sectional area). This

Table 2.1 Frequency of plant species in sites 1 and 2 at the Deeps, Collyweston.

Plant Species	Frequency in 25 (0.5m x 0.5m) quadrats per site		Plant species	Site 1	Site 2
	Site 1	Site 2			
<i>Achillea millefolium</i>	13	3	<i>Helianthemum nummulari</i>	16	9
<i>Arabis hirsuta</i>	1	1	<i>Hieracium pilosella</i>	4	1
<i>Arenaria serpyllifolia</i>	17	0	<i>Koeleria cristata</i>	1	1
<i>Arrhenatherum elatius</i>	3	10	<i>Lathyrus pratensis</i>		
<i>Avenula pratense</i>	1	1	<i>Luzula campestris</i>	3	
<i>Avenula pubescens</i>	2	1	<i>Medicago lupulina</i>	4	
<i>Brachypodium pinnatum</i>	6	24	<i>Phleum pratense</i>	3	1
<i>Briza media</i>	2		<i>Pimpinella saxifraga</i>	18	14
<i>Bromus erectus</i>	22	21	<i>Plantago lanceolata</i>	13	12
<i>Bryonia dioica</i>		1	<i>Poa pratensis</i>		2
<i>Capsella bursa-pastoris</i>	1		<i>Potentilla reptans</i>	2	
<i>Carex flacca</i>		1	<i>Primula veris</i>		12
<i>Centaurea nigra</i>	2	11	<i>Quercus robur</i>		1
<i>Centaurea scabiosa</i>	4	11	<i>Ranunculus bulbosus</i>	1	1
<i>Cirsium acaulon</i>		2	<i>Rosa canina</i>		1
<i>Convolvulus arvensis</i>	12		<i>Rumex acetosa</i>	2	9
<i>Convolvulus monogyna</i>		3	<i>Sanguisorba minor</i>	7	18
<i>Crepis sp</i>	14		<i>Senecio jacobaea</i>	5	
<i>Cuscuta epithymum</i>	1		<i>Silene vulgaris</i>	1	
<i>Dactylis glomerata</i>	2	4	<i>Thymus drucei</i>	1	
<i>Festuca ovina</i>	21	3	<i>Tragopogon pratensis</i>		3
<i>Festuca rubra</i>	20	18	<i>Trifolium campestre</i>	3	1
<i>Galium verum</i>	12	5	<i>Trifolium pratense</i>	1	
<i>Galium aparine</i>		1	<i>Trisetum flavescens</i>	1	
<i>Gallium mullago</i>		2	<i>Veronica officinalis</i>	1	
<i>Genista tictoria</i>	7	3	<i>Vicia sativa</i>		12
<i>Geranium molle</i>	2	5	<i>Vicia sepium</i>		2

was placed at random over the vegetation and the area within the cylinder was swept with the hose of the suction sampler for approximately two minutes, starting at the top of the vegetation and working down to ground level. A muslin cover was placed over the top of the cylinder immediately after it was positioned to prevent escapes prior to suction sampling. Four samples were taken in this way from each site on each sampling occasion, care being taken to order the samples in such a way that the vegetation was not disturbed prior to sampling. The samples, consisting of one Univac bag from each site, were sorted as soon as possible after collection so that the majority of leafhoppers were still alive and easier to see among the debris. Representatives of all species were carded and the remainder stored in 70% ethanol prior to identification and counting. Species were identified using keys to the Auchenorrhyncha by Le Quesne (1960, 1965, 1969), Le Quesne & Paine (1981) and Ossiannilsson (1978, 1981, 1983). Nomenclature is in accordance with the check-list of British Auchenorrhyncha in Le Quesne & Paine (1981).

After vacuum sampling the sites were sampled with a sweep net. Ten sweeps were taken in each site by walking through the vegetation in the direction of the sun and taking one sweep per pace. All Auchenorrhyncha were taken from the net with a pooter and preserved as above.

Auchenorrhyncha were also sampled on two occasions (July 28-30 and August 15-18) by sticky traps. These consisted of 60cm lengths of plastic piping, 5 cm in diameter, covered with white bin-liner polythene. Ecotak (supplied by Oecos Ltd.), a sticky non-drying resin, was smeared over the polythene. Each trap, one per site on each sampling occasion, was held in place in the grassland by a wooden stake placed inside the tube and driven into the ground. Plants close to the traps were cut back so that leaves did not stick to the Ecotak. Auchenorrhyncha caught by the traps were removed with forceps and stuck onto card, the Ecotak remaining on them serving as an adhesive. No attempt was made to remove the Ecotak as it did

not hinder identification (if anything it made dissection of the aedeagus easier).

Two other sites were sampled in August 1988. One was an area of *Brachypodium pinnatum* dominated grassland on an abandoned limestone quarry at Ketton (Grid Ref.: SK 975056), a few miles from Collyweston (Fig 2.1, p. 22). The other was an area of limestone grassland in Longdale NNR, Derbyshire (Grid Ref.: SK 202597), which consisted of a steep grazed slope dominated by *Festuca* spp. with a range of smaller grasses including *Avenula pratensis*. Although these surveys were brief they are included for the information they provide on a few species that are common at the Deeps.

2.3.2 Results

A list of Auchenorrhyncha recorded at the Deeps is given in Table 2.2. Most of these species were recorded during the survey, but for completeness species found subsequently are also included.

There were few adult Auchenorrhyncha present in the grassland before mid June. During earlier months four delphacids (*Criomorpus albomarginatus*, *Hyledelphax elegantulus*, *Javesella pellucida* and *Stenocranus minutus*) and two cicadellids (*Euscelis incisus* and *Mocydia crocea*) were caught in low numbers as adults, together with a greater number of cicadellid nymphs. Between June and September the cercopids *Neophilaenus lineatus* and *Phileanus spumarius* were dominant in most of the samples (Univac and sweep). The most abundant cicadellids were *Diplocolenus abdominalis* and *Turrutus socialis*. *D. abdominalis* developed relatively early in the season, reaching a peak in late June and July, while *T. socialis* was abundant from late July to September. A total of 32 species was found in the samples (4 cercopids, 23 cicadellids, including two species only caught by sticky traps, and 5 delphacids). The final total for the site was increased to 40 species during the work that followed this survey.

Table 2.2 Auchenorrhyncha recorded at the Deeps

Cercopidae

- Aphrophora alni* (Fallen, 1805)
- Cercopis vulnerata* Illiger in Rossi, 1807
- Neophilaenus lineatus* (Linnaeus, 1758)
- Philaenus spumarius* (Linnaeus, 1758)

Cicadellidae

- Adarrus multinotatus* (Boheman, 1847)
- Agallia ribauti* Ossiannilsson, 1938
- Agallia venosa* (Fallen, 1806)
- Aphrodes albifrons* (Linnaeus, 1758)
- Aphrodes bifasciatus* (Linnaeus, 1758)
- Aphrodes bicinctus* (Schrank, 1776)
- Aphrodes flavostriatus* (Donovan, 1799)
- Arthaldeus pascuellus* (Fallen, 1826)
- Bactracomorpha irroratus* Lewis, 1834
- Dikranuera variata* Hardy, 1850
- Diplocolenus abdominalis* (Fabricius, 1803)
- Doratura stylata* (Boheman, 1847)
- Elymana sulphurella* (Zetterstedt, 1828)
- Euscelis incisus* (Kirschbaum, 1858)
- Graphocraerus ventralis* (Fallen, 1806)
- **Macrosteles sexnotatus* (Fallen, 1806)
- Macustus griseus* (Zetterstedt, 1828)
- Megophthalmus scanicus* (Fallen, 1806)
- Mocycdia crocea* (Herrich-Schaeffer, 1836)
- **Mocycdiopsis attenuata* (Germar, 1821)
- Paluda adumbrata* (C. Sahlberg, 1842)
- **Paluda flaveola* (Boheman, 1845)
- **Psammotettix confinis* (Dahlbom, 1850)
- Rhytistylus proceps* (Kirschbaum, 1868)
- Streptanus aemulans* (Kirschbaum, 1868)
- Streptanus sordidus* (Zetterstedt, 1828)
- Turrutus socialis* (Flor, 1861)
- **Zyginidia scutellaris* (Herrich-Schaeffer, 1838)

Delphacidae

- Criomorpha albomarginatus* Curtis, 1833
- **Delphacinus mesomelas* (Boheman, 1850)
- **Dicranotropis hamata*, (Boheman 1847)
- **Eurysa lineata* (Perris, 1857)
- Hyledelphax elegantulus* (Boheman, 1847)
- Javesella pellucida* (Fabricius, 1794)
- Kelisia vittipennis* (Sahlberg, 1868)
- Stenocranus minutus* (Fabricius, 1787)

* = species found after the survey

The numbers of Auchenorrhyncha caught by suction and sweep sampling are recorded in Table 2.3. Some species were caught more frequently by the Univac (e.g. *Aphrodes bifasciatus*, *Adarrus multinotatus*, *Bactracomorpha irroratus* and cicadellid nymphs) and others more frequently by sweeping (e.g. *Doratura stylata*, *Euscelis incisus* and *Turrutus socialis*). This may reflect the strata in which the adults of these species generally occur; those that occur higher in the vegetation being more abundant in sweep samples and those that occur lower down being more abundant in Univac samples. *Adarrus multinotatus* and *Aphrodes bifasciatus* were frequently seen at the bases of plants and were rarely caught by sweeping. On the other hand the differences may be due to the differential mobility of the various species.

A comparison of Sites 1 and 2 is shown in Table 2.4. for the combined Univac and sweep samples. Twenty two species were caught in the *Bromus erectus* / *Festuca rubra* dominated vegetation of Site 1 and 23 species in the ranker *Brachypodium pinnatum* / *Bromus erectus* dominated vegetation of Site 2. Most of the more common species were clearly more abundant in one or other of the sites. *Adarrus multinotatus*, *Aphrodes bifasciatus*, *A. flavostriatus*, *Mocydia crocea* and *Stenocranus minutus* were characteristic of Site 2, while *Doratura stylata*, *Euscelis incisus*, *Graphocraerus ventralis*, *Paluda adumbrata*, *Rhytistylus proceps* and *Turrutus socialis* were characteristic of Site 1. Although caught in low numbers during the survey, casual observations and samples from the sticky traps (see below) indicated that *A. multinotatus* was one of the dominant species in Site 2. The sticky traps caught a total of 18 species in the two sites and although the numbers were generally low, the distribution patterns, shown in Table 2.5 were very similar to those for the Univac and sweep samples shown in Table 2.3. The relative numbers of the species caught were, however, quite different. The only species caught in any quantity was *A. multinotatus*. Two species, *Streptanus aemulans* and *S. sordidus*, were recorded for the first time. Nearly 80% of the *Adarrus multinotatus* on the sticky traps were caught below 15 cm from the ground

Table 2.3 Numbers of Auchenorrhyncha caught by Univac and sweep net.
(Numbers combined for sites 1 and 2)

	Adults		Nymphs	
	Univac	Sweep Net	Univac	Sweep Net
Cercopidae				
<i>Aphrophora alni</i>		3		
<i>Cercopis vulnerata</i>		1		
<i>Neophilaenus lineatus</i>	73	36	*	*
<i>Philaenus spumarius</i>	35	30	*	*
Cicadellidae				
<i>Adarrus multinotatus</i>	7	2		
<i>Agallia ribauti</i>	5	1	5	1
<i>A. venosa</i>	2	3		
<i>Aphrodes albifrons</i>	1			
<i>A. bifasciatus</i>	13	1	40	0
<i>A. bicinctus</i>	4			
<i>A. flavostriatus</i>	5		12	1
<i>Arthaldeus pascuellus</i>	2			
<i>Bactracomorpha irroratus</i>	21	1	10	
<i>Dikraneura variata</i>	1			
<i>Diplocolenus variatus</i>	19	16	9	23
<i>Doratura stylata</i>	2	14		1
<i>Elymana sulphurella</i>		2		
<i>Euscelis incisus</i>	3	25	2	10
<i>Graphocraerus ventralis</i>	2	1	6	2
<i>Megophthalmus scanicus</i>	1			
<i>Macustus grisescens</i>	1			
<i>Mocydia crocea</i>	1	7	1	15
<i>Paluda adumbrata</i>	11	2	1	3
<i>Rhytistylus proceps</i>	8	2	1	1
<i>Turrutus socialis</i>	15	49	7	6
Delphacidae				
<i>Criomorpha albomarginatus</i>	2			
<i>Hyledelphax elegantulus</i>		2		
<i>Javesella pellucida</i>	1	2		
<i>Kelsia vittipennis</i>	3			
<i>Stenocranus minutus</i>	12	1	3	
Unidentified cicadellid nymphs			6	4
Unidentified delphacid nymphs			4	2

* The nymphs of *Neophilaenus lineatus* and *Philaenus spumarius* were present in the samples but not collected.

Table 2.4 Comparison of Auchenorrhyncha from sites 1 and 2
(Numbers from Univac and sweep net combined)

	Site 1		Site 2	
	Adults	Nymphs	Adults	Nymphs
Cercopidae				
<i>Aphrophora alni</i>	2		1	
<i>Cercopis vulnerata</i>			1	
<i>Neophilaenus lineatus</i>	49	*	60	*
<i>Philaenus spumarius</i>	38	*	27	*
Cicadellidae				
<i>Adarrus multinotatus</i>			9	
<i>Agallia ribauti</i>	5	6		
<i>A. venosa</i>	6			
<i>Aphrodes albifrons</i>	1			
<i>A. bifasciatus</i>	5	12	9	28
<i>A. bicinctus</i>	3		1	
<i>A. flavostriatus</i>	3	1	2	12
<i>Arthaldeus pascuellus</i>			2	
<i>Bactracomorpus irroratus</i>	15	7	7	3
<i>Dikraneura variata</i>			1	
<i>Diplocolenus abdominalis</i>	10	23	25	9
<i>Doratara stylata</i>	16	1		
<i>Elymana sulphurella</i>			2	
<i>Euscelis incisus</i>	28	12		
<i>Graphocraerus ventralis</i>	1	6	2	2
<i>Megophthalmus scanicus</i>			1	
<i>Macustus grisescens</i>			1	
<i>Mocycia crocea</i>	2	2	6	14
<i>Paluda adumbrata</i>	11	4	2	
<i>Rhytistylus proceps</i>	10	2		1
<i>Turrutus socialis</i>	61	12	3	1
Delphacidae				
<i>Criomorpus albomarginatus</i>			2	
<i>Hyledelphax elegantulus</i>	1		1	
<i>Javesella pellucida</i>	3			
<i>Kellsia vittipennis</i>	1		2	
<i>Stenocranus minutus</i>	1		12	3
Unidentified cicadellid nymphs		3		7
Unidentified delphacid nymphs		2		4

* The nymphs of *Neophilaenus lineatus* and *Philaenus spumarius* were present in the samples but not collected.

Table 2.5 Auchenorrhyncha caught on sticky traps in sites 1 and 2. (One trap per site for two sampling periods; 28-30 July and 15-18 August)

Auchenorrhyncha	Site 1	Site 2
Cercopidae		
<i>Neophilaenus lineatus</i>	1	
<i>Philaenus spumarius</i>	4	1
Cicadellidae		
<i>Adarrus multinoctatus</i>	1	16
<i>Agallia vercosa</i>	3	
<i>Aphrodes bifasciatus</i>		1
<i>A. bicinctus</i>	1	2
<i>Bactracomorphus irroratus</i>	3	
<i>Diplocolenus abdominalis</i>		1
<i>Doratura stylata</i>	1	
<i>Elymana sulphurella</i>		2
<i>Euscelis incisus</i>	3	
<i>Moecydia crocea</i>	1	1*
<i>Rhyttistylus proceps</i>	5	
<i>Streptanus aemulans</i>		1
<i>S. sordidus</i>		1
<i>Turrutus socialis</i>	3	
Delphacidae		
<i>Hyalephax elegantulus</i>	1	
<i>Javesella pellucida</i>	3	

* Nymph

Table 2.6 Auchenorrhyncha from Longdale and Ketton (Data from sweep net samples).

Auchenorrhyncha	Longdale	Ketton
Cercopidae		
<i>Neophilaenus exclamationis</i>	*	
<i>Neophilaenus lineatus</i>	*	*
<i>Philaenus spumarius</i>	*	
Cicadellidae		
<i>Adarrus multinoctatus</i>		a
<i>Aphrodes albifrons</i>	*	
<i>A. bicinctus</i>	*	
<i>Acrocephalus punctum</i>	*	
<i>Cicadula aurantipes</i>	a	*
<i>Euscelis incisus</i>		*
<i>Eupteryx notata</i>	*	
<i>Evancanthus interruptus</i>		*
<i>Hardya melanops</i>	a	
<i>Megophthalmus scabripennis</i>	*	
<i>Moecydia crocea</i>		*
<i>Paluda adumbrata</i>	*	
<i>Streptanus aemulans</i>	*	
<i>S. sordidus</i>	*	*
<i>Turrutus socialis</i>	a	
Delphacidae		
<i>Kelisia guttula</i>	a	
<i>K. perspicillata</i>	*	

* = species present, a = species abundant

surface in vegetation that was generally over 60 cm tall, indicating that this species is active in the lower strata of the vegetation. Numbers of other species caught were too low to reveal any pattern.

The Auchenorrhyncha found at Ketton and Longdale are listed in Table 2.6 (p. 34). At Ketton where *Brachypodium pinnatum* was abundant, *A. multinotatus* was the dominant leafhopper. Both of these species were absent at Longdale, where *Turrutus socialis* was the dominant leafhopper on the grazed bank and *Cicadula aurantipes* (Edwards) was abundant in the longer vegetation at the top of the bank. *Hardya melanopsis* (Hardy) was also abundant on the grazed bank; Le Quesne (1969, p. 102) described this species as being 'local, on fine grasses on alkaline heaths'.

2.3.3 Discussion

Thirty two species of Auchenorrhyncha were recorded during the preliminary survey of the Deeps consisting of 4 cercopids, 23 cicadellids and 5 delphacids. If the species list for the Deeps is compared to those published for other sites (Whittaker, 1969; Waloff & Solomon, 1973; Morris, 1971a, 1973, 1990c; Hollier, 1987; Baharith, 1989) it appears reasonably typical of lists for chalk and limestone grassland. All published lists, of which I am aware, for British grassland sites that provide information on the rank order of the most abundant 9 - 15 species, are given in Table 2.7, together with that for the Deeps. Waloff (1981) considers that a comparison of lists from acid and calcareous grasslands reveals no dramatic differences but a range of common species which occur in different proportions in different grasslands (hence the variation in the lists given in Table 2.7) and a few species that are more or less confined to a particular type of grassland. On the basis of comparisons between the fauna of Silwood Park and that of Upper Seeds, Wytham (Whittaker, 1969) and Barton Hills (Morris, 1971a), Waloff suggests that *Bactracomorpha irroratus*, *Mocycdia crocea*, *Mocycdiopsis attenuata*, *Neophilaenus campestris* (Fallen), *N. exclamatoris* (Thunberg), *Turrutus socialis* and *Ulopa trivialis*

Table 2.7. Auchenorrhyncha from British Grasslands

The table shows the most abundant 9 - 15 species from each site, listed in rank order.

Acid to Neutral Grasslands			
1. Waloff & Solomon 1973	2. Hollier 1987	3. Baharith 1989	4. Morris 1980
<i>Psammotettix confinis</i>	<i>Psammotettix confinis</i>	<i>Stenocranus minutus</i>	<i>Psammotettix confinis</i>
<i>Jassargus distinguendus</i>	<i>Neophilaenus lineatus</i>	<i>Javesella pellucida</i>	<i>Deltocephalus pulicaris</i>
<i>Arthaldeus pascuellus</i>	<i>Adarrus ocellaris</i>	<i>Macrosteles sexnotatus</i>	<i>Macrosteles laevis</i>
<i>Balclutha punctata</i>	<i>Cicadula persimilis</i>	<i>Euscelis lineolatus</i>	<i>Euscelis incisus</i>
<i>Javesella pellucida</i>	<i>Jassargus distinguendus</i>	<i>Arthaldeus pascuellus</i>	<i>Javesella pellucida</i>
<i>Adarrus ocellaris</i>	<i>Graphocraerus ventralis</i>	<i>Psammotettix confinis</i>	<i>Aphrodes serratulae</i>
<i>Macrosteles laevis</i>	<i>Streptanus sordidus</i>	<i>Adarrus ocellaris</i>	<i>Hyledephax elegantulus</i>
<i>Euscelis incisus</i>	<i>Arthaldeus pascuellus</i>	<i>Aphrodes bicinctus</i>	<i>Neophilaenus lineatus</i>
<i>Streptanus sordidus</i>	<i>Neophilaenus campestris</i>	<i>Streptanus sordidus</i>	<i>Streptanus aemulans</i>
<i>Neophilaenus lineatus</i>	<i>Philaenus spumarius</i>	<i>Zyginidia scutellaris</i>	
<i>Muirodelphax exiguus</i>	<i>Dicranotropis hamata</i>	<i>Neophilaenus lineatus</i>	
<i>Hyledephax elegantulus</i>	<i>Eupelix cuspidata</i>	<i>Aphrodes fivostratus</i>	
<i>Struebingianella dalei</i>	<i>Delphacinus mesomelus</i>	<i>Cicadula persimilis</i>	
<i>Doratura stylata</i>	<i>Cicadula persimilis</i>	<i>Conomelas anceps</i>	
<i>Macrosteles viridigriseus</i>	<i>Euscelis incisus</i>	<i>Aphrodes albifrons</i>	
Calcareous grasslands			
5. Whittaker 1969	6. Morris 1971	7. Morris 1973 & 1990	8. Morris 1981 & 1990
<i>Stenocranus minutus</i>	<i>Turrutus socialis</i>	<i>Zyginidia scutellaris</i>	<i>Zyginidia scutellaris</i>
<i>Philaenus spumarius</i>	<i>Zyginidia scutellaris</i>	<i>Arocephalus punctatum</i>	<i>Dikraneura variata</i>
<i>Neophilaenus lineatus</i>	<i>Dikraneura variata</i>	<i>Turrutus socialis</i>	<i>Arthaldeus pascuellus</i>
<i>Cicadula persimilis</i>	<i>Eupteryx notata</i>	<i>Paluda adumbrata</i>	<i>Adarrus multinotatus</i>
<i>Hyledephax elegantulus</i>	<i>Mocydia crocea</i>	<i>Rhytistylus proceps</i>	<i>Arboridia parvula</i>
<i>Arthaldeus pascuellus</i>	<i>Neophilaenus exclamationis</i>	<i>Arboridia parvula</i>	<i>Javesella pellucida</i>
<i>Aphrodes albifrons</i>	<i>Javesella pellucida</i>	<i>Eupteryx notata</i>	<i>Mocydia crocea</i>
<i>Mocydia crocea</i>	<i>Kelsia guttula</i>	<i>Hyledephax elegantulus</i>	<i>Stenocranus minutus</i>
<i>Emelyanoviana mollicula</i>	<i>Forcipata citrinella</i>	<i>Agallia venosa</i>	<i>Mullerianella fairmairei</i>
<i>Megophthalmus scanicus</i>	<i>Paluda adumbrata</i>	<i>Neophilaenus exclamationis</i>	<i>Hyledephax elegantulus</i>
<i>Javesella pellucida</i>	<i>Kosswigianella exigua</i>	<i>Javesella pellucida</i>	
<i>Aphrophora alni</i>	<i>Euscelis incisus</i>	<i>Dikraneura variata</i>	
<i>Arboridia parvula</i>	<i>Arboridia parvula</i>	<i>Stenocranus minutus</i>	
<i>Recilia coronifera</i>	<i>Criomorpus albomarginatus</i>	<i>Kosswigianella exigua</i>	
<i>Evacanthus interruptus</i>	<i>Neophilaenus campestris</i>	<i>Mocydiopsis attenuata</i>	
The Deeps	The Deeps (cont.)		
<i>Neophilaenus lineatus</i>	<i>Paluda adumbrata</i>		
<i>Philaenus spumarius</i>	<i>Stenocranus minutus</i>		
<i>Turrutus socialis</i>	<i>Rhytistylus proceps</i>		
<i>Euscelis incisus</i>	<i>Mocydia crocea</i>		
<i>Diplocolenus abdominalis</i>	<i>Adarrus multinotatus</i>		
<i>Bactracomorpus irroratus</i>	<i>Agallia venosa</i>		
<i>Doratura stylata</i>	<i>Agallia ribauti</i>		
<i>Aphrodes bifasciatus</i>			

- Silwood Park** (Berkshire). Acid grassland with *Agrostis tenuis*, *Festuca rubra*, *Holcus mollis* & *Dactylis glomerata*. Sampling method: sweep net; sampling period: 1968 - 1970.
- Mitcham Common** (Surrey). Acid grassland with grasses as above plus *Arrhenatherum elatius* & *Molinia caerulea*. Sampling method: sweep net; sampling period: May - June 1984
- Cleppa Park** (S. Wales). Neutral grassland. Sampling method: sweep net; sampling period: May - Oct. 1985
- Park Grass plots, Rothamstead** (Hertfordshire). Acid subplots, cut for hay in June. Sampling method: suction; sampling period: July - Sept., 1977; Aug - Sept., 1978
- Upper Sands, Wytham** (Oxfordshire). Limestone grassland with *Brachypodium pinnatum*. Sampling method: suction & sweep; sampling period: 1964 - 1965
- Barton Hills** (Bedfordshire). Chalk grassland with *Bromus erectus*, *Festuca ovina*, *Koeleria cristata* & *Avenula pratense*. Sampling method: suction; sampling period: 1967 - 1969
- Aston Rowant** (Oxfordshire). Chalk grassland. Sampling method: suction; sampling period: 1969 - 1971
- Castor Hanglands** (Cambridgeshire). Limestone grassland dominated by *Arrhenatherum elatius*. Sampling method: suction; sampling period: 1972 - 1975.

German, appear to be typical of calcareous grasslands while *Adarrus ocellaris* (Fallen), *Macrosteles sexnotatus*, *M. viridigriseus* (Edwards), *Mocydiopsis parvicauda* Ribaut, *Psammotettix confinis*, *Ribautodelphax angulosus* (Ribaut) and *Struebingianella dalei* (Scott) are acid grassland species. Comparisons based on the information now available, including that from the Deeps, indicates that *Adarrus multinotatus*, *Aphrodes bifasciatus*, *Paluda adumbrata* and *Rhytistylus proceps* may also be confined to, or much more abundant on, calcareous grasslands. *Zyginidia scutellaris* was very abundant in calcareous grassland sites sampled by Morris (1971a, 1973, 1981, 1990). It was not found during the survey of the Deeps, but was found later on in this study, although not in large numbers.

The factors determining the distribution of the species of Auchenorrhyncha are at present largely unknown although tentative suggestions can be made for a few species. *Turrutus socialis* is a common and often dominant species of calcareous grasslands in England but relatively scarce in the limestone grasslands of the Burren, Eire, where the dominant species is *Jargassus distinguendus* (Flor), (Morris, 1974). Most of the English samples taken by Morris were from eastern and central areas where rainfall did not exceed 900 mm and was less than 625 mm for many sites. The Burren, however, has an oceanic climate with rainfall in the range 1170 - 1650 mm, and it is possible that this has a limiting effect on *T. socialis* (Morris, *op. cit.*). Rainfall does not explain its absence from acid grasslands in England.

Adarrus multinotatus has not been recorded in Eire (Morris, *op. cit.*) and in England is confined to eastern and central areas (Le Quesne, 1969). The host plant of *A. multinotatus* in Germany is *Brachypodium pinnatum*. (Schiemenz, 1969). Although there is no information on the host plants of *A. multinotatus* in this country it is possible that it is closely associated with *Brachypodium pinnatum*, which has an eastern and central distribution in England, occurs only sporadically in Eire, and is mainly found in calcareous grasslands (Perring & Walters, 1976; Grime, Hodgson & x

Hunt, 1988).

X

Although the numbers of Auchenorrhyncha caught during the survey were generally low, most of the more abundant species appeared to show a preference for one or other of the sites. *Bactracomorphus irroratus*, *Doratura stylata*, *Euscelis incisus*, *Paluda adumbrata*, *Rhytistylus proceps* and *Turrutus socialis* were characteristic of Site 1 and *Adarrus multinotatus*, *Mocycdia crocea* and *Stenocranus minutus* were characteristic of Site 2. This pattern was similar for both nymphs and adults. There is some correspondence between these results and those of Morris (1990b) who found that on his sown plots at Royston, Herts., *Criomorphus albomarginatus*, *Dikraneura variata*, *E. incisus*, *P. adumbrata*, *R. proceps* and *T. socialis* showed a preference for fine-leaved grasses and *M. crocea* and *S. minutus* showed a preference for coarse-leaved grasses. Only two specimens of *C. albomarginatus* were caught during the survey, both in Site 2. This species was sampled in greater numbers in 1990 - 92 during work described later and was virtually confined to Site 2. Although site 1 was dominated by fine-leaved, and site 2 by coarse-leaved grasses, they were not exactly comparable to those of Morris (*op. cit.*). Both sites contained a mixture of fine and coarse grasses. Another delphacid, *Hyledelphax elegantulus*, was also found much larger numbers during field work in 1990. Whether or not this was a real variation in numbers or a consequence of different sampling techniques is unknown. Whittaker (1969) found great variation in this species from one year to the next at Upper Sands, Wytham.

The abundance of a host plant, rather than mere presence, may be an important factor in determining the distribution of plant feeding insects as Davis & Jones (1986) have shown for the fauna associated with *Helianthemum nummularium* on limestone grassland sites in eastern England. They sampled a large number of calcareous grassland sites and found the full compliment of species that were specific to *H. nummularium* only at the Deeps, Collyweston, the site where the plant was most abundant. *Bactracomorphus irroratus* is a member of this fauna and

is one of the few grassland cicadellids that is host specific to a forb.

Climate and host plants, in addition to other factors, must influence the distribution of Auchenorrhyncha on both regional and local scales. An important additional factor in the local variation of Auchenorrhyncha communities (as between Sites 1 and 2 at the Deeps) is vegetation structure. The abundance of many grassland species is reduced if the vegetation is either cut or grazed (Morris, 1971, 1973, 1981). On limestone grassland plots at Castor Hanglands, *A. multinotatus* numbers were severely reduced by cutting (Morris, 1981) and at Barton Hills *T. socialis* was adversely affected by grazing although it remained relatively abundant on grazed plots (Morris, 1971a). At the Deeps *A. multinotatus* was confined to rank grassland dominated by *B. pinnatum* and *B. erectus*, while *T. socialis* was confined to shorter vegetation dominated by *F. rubra* and *B. erectus*. At Longdale *A. multinotatus* was absent as was *B. pinnatum*, but *T. socialis* was abundant on the grazed slope and apparently absent from the rank grassland at the top of the slope. It seems likely that a complex of factors is involved in determining the distribution and abundance of these and other Auchenorrhyncha which includes the abundance and structure of their host plants. The requirement by an insect for a particular host plant in a particular state is illustrated by the Lulworth Skipper (*Thymelicus acteon* Rottemburg) which although specific to *B. pinnatum*, will only lay eggs on the plant if it is growing in a rank sward (Smith, 1980).

Grassland Auchenorrhyncha are vertically stratified within the grass sward; some species occur at or near ground level and others higher in the vegetation (Andrejewska, 1965; Whittaker, 1969). The position occupied by a single species usually changes as it develops from a nymph to an adult; most nymphs occurring lower in the vegetation. As a taller sward has a more complex architecture (Lawton, 1978) it is likely to provide a greater number of habitats for Auchenorrhyncha and therefore contain a greater number of species than a shorter sward (Morris, 1971b). Information on the vertical stratification of different species

can be obtained by comparing vacuum and sweep samples (Andrejewska, *op.cit.*, Whittaker, *op.cit.*). Vacuum sampling is the best method for recording the absolute abundance of Auchenorrhyncha (Tormala, 1982), while sweeping provides relative estimates of abundance and is effective only for those species that occupy the upper strata of the vegetation. Although the numbers obtained by the two methods are not comparable, the absence of a species from sweep samples and its presence in vacuum samples indicates that it may occupy the lower strata of the vegetation while relatively high numbers in sweep samples would suggest that it either spreads widely or occupies the upper strata of the vegetation. Low numbers in net samples may also be due to a species' ability to leap away from a moving net (Whittaker, 1969). The information obtained from the survey of the Deeps (Table 2.3, p. 31) indicates that *Adarrus multinotatus*, *Aphrodes bifasciatus*, *A. flavostriatus*, *Bactracomorpus irroratus*, *Paluda adumbrata* and *Rhytistylus proceps* are active low in the vegetation and that *Diplocolenus abdominalis*, *Doratura stylata*, *Euscelis incisus*, *Mocydia crocea* and *Turrutus socialis* are active throughout the vegetation or mainly in the upper stratum. Data obtained from the sticky traps supports the suggestion that *A. multinotatus* is active low in the vegetation; used on a larger scale this technique could provide useful information on the activity patterns and abundance of grassland Auchenorrhyncha.

Two species of leafhoppers, *Adarrus multinotatus* and *Turrutus socialis* provide striking contrasts. They are closely related (both were originally classified as *Deltocephalus* Boheman) and are both confined to calcareous grassland. *A. multinotatus* is a species of rank grassland, active in the lower stratum of the vegetation, and, in Germany at least, is associated with *Brachypodium pinnatum*. *T. socialis* is found in shorter vegetation, is active in the upper strata, and is probably associated with fine grasses (Morris, 1990b). In some of the work described in the following chapters, special attention was given to these two species.

3. LIFE HISTORIES AND ECOLOGY OF THE MORE COMMON SPECIES OF AUCHENORRHYNCHA AT THE DEEPS

3.1 Introduction

The information available, prior to this study, on the life histories and ecology of the more common species of Cicadellidae and Delphacidae recorded at the Deeps is reviewed below.

3.2 Cicadellidae

Adarrus multinotatus (Boheman)

This species is described by Le Quesne (1969) as being "local, near the base of taller grasses, usually in calcareous areas". *A. multinotatus* overwinters in the egg stage and in central Europe is bivoltine (Schiemenz, 1969b, cited in Ossiannilsson, 1983). The nymph is described by Vilbaste (1982). Whittaker (1969) recorded *A. multinotatus* from limestone grassland in Upper Seeds, Wytham Woods, and described it as a species of the field layer in grassland and the ground zone in woodland glades. Morris (1973, 1981) recorded the species from chalk grassland at Aston Rowant and limestone grassland at Castor Hanglands. On the latter site where it was the fourth most abundant species it was much more abundant on uncut than cut grassland but its distribution was uneven on the uncut plots. *A. multinotatus* does not appear to have been recorded from acid grassland (see Waloff & Solomon, 1973 and Hollier, 1987). In Germany the host plant of this species is *Brachypodium pinnatum*, (Schiemenz, 1969). Le Quesne (*op. cit.*) describes the distribution of *A. multinotatus* in the British Isles as being north to Yorkshire and west to Staffordshire. It is absent from the limestone grassland in the Burren, Eire (Morris, 1974).

Aphrodes albifrons (L.)

This is one of the most abundant of the *Aphrodes* species in this country and is common in grassland, usually near ground level (Le Quesne, 1969). Waloff & Solomon (1973) found it to be one of the more abundant species on the acid grassland at Silwood Park where it was univoltine and overwintered in the egg stage. They found *Holcus* spp. and *Dactylis glomerata* to be the main host plants and in the field. They bred *A. albifrons* in relatively large numbers from a range of grasses brought in from the field and kept in an out-door insectary, especially *Holcus mollis* and *Agrostis capillaris*. Morris (1973, 1974, 1981, 1990) recorded *A. albifrons* from a number of limestone and chalk grasslands, where it was sometimes abundant and showed a marked preference for ungrazed and uncut plots. Whittaker (1969) describes it as being a species of the ground layer in limestone grassland at Wytham where it was the most abundant *Aphrodes* species. In the Netherlands *A. albifrons* is a species of dry localities where it is associated with a range of grasses including *Agrostis capillaris*, *Anthoxanthum odoratum*, *Luzula* sp. and *Holcus mollis* (Gravestain, 1965, cited in Ossiannilsson, 1983). Whitcomb (1953), working in N. America hatched one nymph of *A. albifrons* from *Elymus repens* and quotes Osborn (1939) as reporting it from *Phleum pratense*.

Aphrodes bifasciatus (L.)

The male of this species is very distinctive with black and white bands on the forewings. It is generally found in dry habitats (Le Quesne, 1969; Ossiannilsson, 1983) although a variety with a broken anterior white band on the forewings is associated with marshy habitats (Le Quesne, 1969). It has not been recorded on acid grasslands (Waloff & Solomon, 1973; Hollier, 1987) and appears to be characteristic of the Auchenorrhyncha community of calcareous grasslands, although often found in low numbers (Whittaker, 1969, 1977; Morris, 1971a, 1973). Morris (1971a) found it almost exclusively in ungrazed grassland at Barton Hills and Whittaker (1977) recorded it from sugar limestone grassland in the Cow Green area of Upper Teasdale. *A. bifasciatus* overwinters in the egg stage (Ossiannilsson

1983).

Arthaldeus pascuellus (Fallen)

This is a widely distributed species that is found mainly in drier habitats (Le Quesne, 1969). It is common in both acid and calcareous grasslands (Whittaker, 1969; Waloff & Solomon, 1973; Morris 1971a, 1973, 1974, 1981; Hollier, 1987) and is more abundant on ungrazed than on grazed grassland (Morris, 1971a). *A. pascuellus* is bivoltine and overwinters in the egg stage (Waloff & Solomon, 1973; Ossianniilsson; 1983) Waloff & Solomon give *Agrostis capillaris* as the host plant at Silwood Park but also found that it was abundant on *Festuca rubra*. They found that *A. pascuellus* only hatched from these two grasses out of a range of grass species brought in from the field. Also at Silwood Park, Prestidge & McNeill (1981) found that *A. pascuellus* was neither host specific nor polyphagous but mainly associated with *Lolium perenne* and *Festuca pratensis*. Waloff describes this species as an active flier which she caught in relatively high numbers in suction traps and Morris (1990a) found that it was an early coloniser of sown grassland plots on calcareous soil at Royston, Herts.

Doratura stylata (Boheman)

This species is widespread in various types of grassland (Le Quesne, 1969; Waloff & Solomon, 1973; Whittaker, 1969; Hollier, 1987). Waloff & Solomon (1973) found it to be one of the more common species at Silwood Park where it was primarily associated with *A. capillaris*, although also reared on *F. rubra*. Prestidge (1982a), also at Silwood Park, found that both *A. capillaris* and *F. rubra* were host plants. In Germany *D. stylata* is associated with "Molinietum typic. Var. v. *Nardus stricta*" (Marchland, 1953, cited in Ossianniilsson, 1983, p. 644). This species has been introduced into North America where it has been found associated with *Poa pratensis* (Whitcomb, 1953). Records from calcareous grasslands suggest that it is one of the less common species in these habitats (Whittaker, 1969; Morris, 1973). *D. stylata* displays alary polymorphism; it is normally brachypterous with the hind

wings missing, but fully winged forms occur in low numbers (Waloff, 1973). It is univoltine and overwinters in the egg stage.

***Diplocolenus abdominalis* (Fab) *juvencus* (Hardy)**

(*Verdanus abdominalis* (Fab) in Ossiannilsson (1983))

This is a common species that has been recorded from a range of grasslands, both acidic and calcareous. Whittaker (1969) describes *D. abdominalis* as a species of the field layer in limestone grassland in Upper Seeds, Wytham, where it occurred in low numbers. At Silwood Park, Waloff & Solomon (1973) found it to be one of the less common species and closely associated with *Holcus mollis*. It is univoltine and overwinters in the egg stage (Waloff & Solomon, 1973; Ossiannilsson, 1983), the eggs being laid at the base of grass hosts in dead leaf sheath tissue (Thompson, 1978). *D. abdominalis* is a spring developing species that feeds when grass levels of amino acids are high; females feed preferentially on flower stems (Hill, 1982). Prestidge (1982a) found that it responded negatively to nitrogen fertiliser being more abundant on plots at Silwood Park that were unfertilised. Hill (*op. cit.*) reported that *D. abdominalis* is a phloem feeder.

***Euscelis incisus* (Kirschbaum)**

A common species that has been recorded from acid and calcareous grassland (Whittaker, 1969; Waloff & Solomon, 1973; Morris 1971a, 1973, 1981; Hollier, 1987). Whittaker (1969) describes *E. incisus* as a field layer species and Waloff & Solomon (1973) found it predominately in areas dominated by *A. capillaris* and *F. rubra*. Prestidge & McNeill (1981, 1983) found that *E. incisus* was a generalist feeder with respect to grass species, although showing a preference for *L. perenne*, *F. pratensis* and *Poa pratensis*, but a specialist with respect to nitrogen levels. Females fed from grasses with higher nitrogen levels during their oviposition period. *E. incisus* is predominantly a xylem feeder (unlike many cicadellids) but may feed from the phloem and produces copious quantities of watery excreta (Port, 1972; Hill 1982). Prestidge (1982a) found that it was able to

extract nitrogen from its food more efficiently than the phloem feeders *Dicranotropis hamata* and *Elymana sulphurella* and the mesophyl feeder *Zyginidia scutellaris*.

Morris reported *E. incisus* to be more abundant on ungrazed than grazed chalk grassland at Barton Hill, but subsequently (Morris, 1981) found it to be more abundant on plots cut in May and June than on uncut controls at Castor Hanglands. In sown plot experiments at Royston (Morris, 1990b), *E. incisus* was more common on plots sown with a fine grass mixture than on those sown with coarse grasses. It overwinters mainly as a nymph, but with a small percentage of diapausing eggs, and has two morphologically distinct generations a year (Muller, 1981, cited in Ossiannilsson, 1983).

***Graphocraerus ventralis* (Fallen)**

A local species (Le Quesne, 1969) that occurs in a range of grassland types, usually in low numbers (Whittaker, 1969; Waloff & Solomon, 1973; Hollier, 1987). It was not recorded from the calcareous grasslands at Barton Hills and Aston Rowant (Morris, 1973) but was one of the more common species in the *Arrhenatherum elatius* dominated acid grassland at Mitcham Common (Hollier, 1987).

Ossiannilsson (1983) cites the following references to grasses hosts and habitat; "on *Poa pratensis* and *Anthoxanthum odoratum* (Schaefer, 1973)" and "in the *Arrhenatherum*" (Schwoerbel, 1957). Waloff (1973) caught young adult *G. ventralis* in low numbers in suction traps at Silwood Park. The species overwinters in the egg stage and has one generation per year (Remane, 1958; Schiemenz, 1969; both cited in Ossiannilsson 1983).

***Milocydia crocea* (Herrich - Schaeffer)**

M. crocea is a typical species of calcareous grassland and rare in acid grassland (Waloff, 1981). Le Quesne gives possible host grasses as *Brachypodium pinnatum*, *Bromus erectus* and *Dactylis glomerata*. Whittaker (1969) recorded *M. crocea* from *B. pinnatum* at Upper Seeds. It has been taken occasionally on the acid

grasslands at Silwood Park (Waloff & Solomon, 1973; Prestidge, 1982a). Morris (1971, 1973, 1981) found it on a range of calcareous grassland sites where it was often abundant (rank 6 at Barton Hills, rank 7 at Castor Hanglands). *M. crocea* was a coloniser of sown grassland plots of Royston where it occurred almost exclusively on plots sown with coarse, as opposed to fine, grasses, although in low numbers (Morris, 1990b). Muller (1987) described six differently coloured nymphal forms of *M. crocea* and their response to a range of plant hosts. He found the main hosts to be *Brachypodium pinnatum*, *Bromus erectus*, *Dactylis glomerata* and *Lolium perenne*. It is a bivoltine species, overwinters as an adult (Morris, 1981), has a distribution in England north to Yorkshire and has been recorded from Wales (Pembrokeshire) and Ireland (Le Quesne, 1969).

***Rhytistylus proceps* (Kirschbaum)**

This species is also characteristic of calcareous grasslands (Le Quesne, 1969). Waloff & Solomon (1973) found it in low numbers at Silwood Park where it was confined to areas dominated by *F. rubra*. *R. proceps* was reasonably abundant on the chalk at Barton Hills, and rank 5 in abundance at Aston Rowant (Morris, 1971, 1973). On both sites it was more abundant on ungrazed or uncut areas. On sown grassland plots at Royston it was associated with fine grasses (Morris, 1990b). The following plant associates are quoted by Ossiannilsson (1983, p. 692): "On *Corynephorus canescens* and *Nardus stricta* (Kuntze, 1937)", "in the Corynephorum (Marchland, 1953)", and "larvae and imagines common on *Carex arenaria* (Trolle, in litt.)". *R. proceps* is univoltine and overwinters in the egg stage (Ossiannilsson, *op. cit.*).

***Turrutus socialis* (Flor)**

T. socialis appears to be confined to calcareous grasslands (Waloff, 1981). At Upper Seeds, Whittaker (1969) recorded it as a species of open ground. It was one of the most abundant species in the chalk grassland at Barton Hills (Morris, 1971a) where, although it showed a preference for ungrazed plots, it was relatively

frequent on grazed grassland. Out of 222 samples taken from over 60 chalk and limestone grassland sites in England *T. socialis* occurred in 88% (Morris, 1974). It colonised sown grassland plots at Royston within 18 months (in low numbers) and was significantly more abundant on plots sown with fine grasses (Morris, 1990b). It was the most abundant species of Auchenorrhyncha collected in pit-fall traps at Weeting Heath, Norfolk (Le Quesne & Morris, 1971). The site had a soil of chalky sand, pH about 7, and was dominated by *Festuca rubra* and *F. ovina* with *Avenula pratense* and *Koeleria macrantha* occasional. *T. socialis* is bivoltine and overwinters in the egg stage (Sheimenz, 1969, cited in Ossianniilsson, 1983).

Zyglidia scutellaris (Herrich-Schaeffer)

This is a widespread and often abundant grassland species. Whittaker (1969) found it most frequently on *Brachypodium pinnatum* at Upper Seeds. *Z. scutellaris* was abundant at Silwood Park (rank 10 in 1974), where the main hosts were *Holcus* spp. and *Dactylis glomerata* although it was also bred from *Agrostis capillaris* and found associated with this grass in the field (Waloff & Solomon, 1973). According to Le Quesne & Payne (1981, p. 33) it is "common in grass, mainly associated with *Dactylis glomerata* and *Festuca rubra*". It is sometimes a dominant species in calcareous grassland and on sown plots at Royston was generally associated with coarse grasses (Morris, 1990b). Prestidge & McNeill (1983) found this species to be a generalist feeder but closely associated with high grass nitrogen levels during the ovipositional period. *Z. scutellaris* is multivoltine and overwinters as an adult (Morris, 1981).

3.3 Delphacidae

Criomorpus albomarginatus (Curtis)

A common species in a range of grasslands. It occurred in low numbers at Upper Seeds where it was characteristic of the field layer (Whittaker, 1969). Waloff & Solomon (1973) gave *Holcus* spp. as the host plants, although they also bred it from *F. rubra*. Waloff (1973) took a few macropterous specimens of this generally

brachypterous species in suction traps at Silwood Park and from a field sample recorded 2% macropters. In calcareous grassland Morris (1971a, 1973, 1981) found that *C. albomarginatus* was particularly sensitive to grazing and cutting, being adversely affected by both. It colonised sown plots at Royston in low numbers and was only recorded on fine grasses (Morris, 1990b). In Finland specimens in cages have reproduced on *Avena sativa* and *Festuca pratensis* and fed on *Poa pratensis*, *Phleum pratense*, *Elymus repens* and *Deschampsia cespitosa* (Raatikainen & Vasarainen, 1976). *C. albomarginatus* is univoltine and overwinters as a nymph (Waloff & Solomon, 1973).

***Hyledelphax elegantulus* (Boheman)**

A common species, especially of dry grassland habitats (Le Quesne, 1969). At Upper Seeds, it was the second most abundant species in suction samples in 1964, but entirely absent from the samples in 1965 (Whittaker, 1969).

H. elegantulus was one of the more abundant species (rank 6 - 10) at Silwood Park, where its host plant was *F. rubra*. It was bred from field samples of this grass in relatively large numbers (Waloff & Solomon, 1973). It is a mainly brachypterous species in which long winged forms are uncommon; at Silwood Park, Waloff (1973) caught a few macropterous specimens in suction traps and found 0.1 - 0.3% in field samples. *H. elegantulus* was a common species (rank 1) at Aston Rowant, where it was most abundant on ungrazed plots but fairly tolerant of winter and summer grazing, and at Castor Hanglands (rank 10) where it was severely affected by cutting. Ossiannilsson (1978, p. 128) gives the following account (citing Strubing in Muller, 1957, Remane, 1958); "a heliophilous species apparently associated with *Deschampsia flexuosa* on moors and heaths with *Calluna*, also in wood glades with *Vaccinium* etc." *H. elegantulus* is bivoltine and overwinters as a nymph (Waloff & Solomon, 1973).

4. THE NYMPHS OF THE MORE COMMON SPECIES OF CICADELLIDAE RECORDED AT THE DEEPS

4.1 Introduction

In the introduction to his key to the nymphs of Delphacidae of North Europe, Vilbaste (1968) states that up to that date the nymphs of Auchenorrhyncha were considered to be undeterminable. Since then a number of authors, including Vilbaste (1982), have published descriptions and keys to the nymphs of Cicadellidae. Brief descriptions of nymphs are given for a number of species by Ossiannilsson (1981, 1983) some of which are based on Vilbaste (1982). Other keys to cicadellid nymphs are those of Wilson (1978) on woodland Typhlocybinae, Walter (1975 & 1978) on the Euscelini and Kathirithamby (1971) on 22 species of cicadellids from acid grassland at Silwood Park. Descriptions of the nymphs of individual species are given by May (1971) for *Stenocranus minutus* and by Muller (1987) for *Mocydia crocea*. A number of authors have included nymphs in their work on various aspects of cicadellid ecology, although they give no detailed descriptions (Claridge, Reynolds & Wilson, 1977; Coupe & Schulz, 1968; Drosopoulos, 1977; Gustin & Stoner, 1968; Waloff & Solomon, 1973). Gustin & Stoner provide diagrams of the five nymphal instars of *Deltocephalus sonorus*.

During the development of cicadellid nymphs, which generally takes between 30 and 66 days, they normally pass through 5 instars (DeLong, 1971; Kathirithamby, *op. cit.*; Vilbaste, 1982). The instars are most easily identified by the development of mesothoracic wing pads (Vilbaste, 1968, 1982).

Identification of the nymphs of the more common cicadellid species at the Deeps formed an essential part of the work described in later chapters. Although keys referred to above were used to identify the nymphs of some species, most species were identified by rearing nymphs collected from the field. As very few delphacid

nymphs were encountered during the study they have not been included.

4.2 Methods

Identification of cicadellid nymphs was a continuing part of this research and took place over an extended period. The majority of identifications were made by rearing nymphs, mostly collected from the field, in clip cages (described in Chapter 7; see Plate 7.1, p. 136) in the greenhouse. Identifications of *Turrutus socialis* and *Adarrus multinotatus* nymphs were made from specimens reared from grasses in the greenhouse during the host choice experiments described in Chapter 5. Live nymphs were photographed, using a Nikon trinocular stereo microscope (SMZ-2T) and a Pentax ME Super camera, as they recovered after being anaesthetised with CO₂. Shadows were difficult to eliminate in photographs taken with nymphs resting directly on a background card. In later photographs this problem was overcome by placing the nymphs on a glass plate supported a few centimetres above the background card. Freehand drawings were made from the same microscope, fitted with a gridded eye-piece graticule, onto tracing paper backed by a sheet of graph paper.

The key to nymphs given below is based primarily on firsthand observations, but includes some information given by Vilbaste (1982) and Ossiannilsson (1983). The preliminary keys to subfamilies and tribes are based on Vilbaste. Descriptions apply to 4th or 5th instar nymphs. Earlier instars are generally similar to the later, although some characteristic features may not be so well developed.

**4.3 A key to nymphs of the common calcareous grassland
Cicadellidae found at the Deeps**

4.3.1 Key to the subfamilies of Cicadellidae (4th & 5th instars)

- 1 Ocelli absent, or indistinct. They are never present on the vertex, or on the transition between the vertex and face..... 2
Ocelli present on the vertex, or on the transition between the vertex and face (Figs 4.4 & 4.5).....3
- 2 Lora (Fig. 4.1) indistinct and rounded. Transition between vertex and face distinctly angled. Head without stout setae. Abdomen much longer than its width towards the base. **Typhlocybinae** (p. 51)

Lora distinct (clearly differentiated from genae (Fig. 4.1)) and elongate. Transition between vertex and face smoothly rounded. Head covered in stout setae. Length of abdomen less than its width towards the base. **Agallinae** (p. 52)

- 3 Ocelli on vertex, set well back from the anterior margin of the head. Abdomen uniformly covered with small hairs or almost bare. Transition between vertex and face either angular or narrowly rounded. (Figs 4.4, 4.9, 4.10) **Aphrodinae** (p. 52)
Ocelli on the transition between vertex and face (Fig. 4.5). Abdomen usually with four rows of hairs. Transition between vertex and face rounded. **Deltocephalinae** (p. 53)

4.3.2 Species of Typhlocybinae

Only two species of Typhlocybinae were recorded at the Deeps; *Dikraneura variata* and *Zyginidia scutellaris*, and only the nymph of the

latter species was found (Plate 4.1). They belong to the tribes Dikraneurini and Erythroneurini respectively, which may be separated in the nymphal stages by the form of the frontal sutures (Wilson, 1978; Vilbaste, 1982). In the Dikraneurini, the frontal sutures unite anteriorly on the frons, while in the Erythroneurini (and other tribes) they extend only to the antennal pits.

4.3.3 Species of Agallinae

Distinctive small, squat nymph covered by very stout longish setae (Fig. 4.2). Frontal sutures unite on the face and continue to the upper side of the head as single 'coronal' suture. Lora elongate (not approximately semicircular as in Aphrodinae and Deltocephalinae) (Fig. 4.7). One genus.

Agallia sp. (Plate 4.1)

4.3.4 Key to the species of Aphrodinae

1 Transition between vertex and face in side view narrowly rounded and sharply defined (Fig. 4.9). Abdomen light to dark brown and covered with clear whitish spots. *Aphrodes bifasciatus*

Transition between vertex and face in side view more broadly rounded and less angular in side view (Fig. 4.9).....2

2 Nymph almost uniform light brown with few dark markings.

*Aphrodes albifrons** (Plate 4.1)

Nymph light brown with darker brown markings. Markings on dorsal surface generally consist of two narrow longitudinal central bands separated by narrow pale mid band, dark patches on the wing pads, the sides of abdominal tergites and on the front of the vertex

*Aphrodes flavostriatus** (Plate 4.1)

* The markings on these two species are variable and the nymphs are not always easy to separate. Vilbaste (1982) does not separate them in his key, referring to the nymphs of both species as having a faint, often barely visible, pattern.

4.3.5 Key to the tribes of Deltocephalinae

- 1 Vertex with distinct concavity before apex (Fig. 4.6).

Doraturini (p. 53)

Vertex without concavity before apex.....2

- 2 Vertex more or less horizontal and as long, or longer, than width between the eyes. Nymphs may lack bands and be more or less uniform in colour, but they are often clearly banded on the dorsal surface. The pattern generally consists of four broad longitudinal bands, which may be fainter on the head and thorax than on the abdomen.

Paralimnini (p. 53)

Vertex often convex and usually much shorter than the width between the eyes.....3

- 3 Bands on dorsal surface may or may not be present. If present, bands consist of two narrow central bands on either side of a narrow pale median line plus broader lateral bands or lateral bands only.

Athysanini (p.54)

4.3.6 Species of Doraturini

Brown to dark brown nymph with characteristic lighter patches on head, thorax and abdomen. Vertex with characteristic pattern (Fig. 4.7) and abdomen with light area on abdominal tergites 1V and V. One species.

Doratura stylata (Plate 4.1)

4.3.7 Key to the species of Paralimnini

- 1 Vertex much longer (x 1.5) than width between the eyes. Body pale yellow brown with four brown longitudinal bands on the dorsal surface. In living specimens the body may have a greenish tinge and

the eyes are green. No markings on the face.

Adarrus multinotatus (Plate 4.1)

Vertex less than 1.5 x as long as wide between the eyes.

Longitudinal bands may or may not be clearly visible.....2

- 2 Pattern of arched lines on the frontoclypeus and dark markings at the base of the eye on the genae form a border to a characteristic pale triangular area on the lower face (Fig. 4.12). Two dark, diverging lines at the tip of the vertex. Four brown to dark brown strongly demarcated longitudinal bands present on dorsal surface.

Turrutus socialis (Plate 4.1)

Pattern of markings on the frontoclypeus not as above.....3

- 3 Ventral surface heavily marked with black. Hind legs predominantly black. Dorsal surface pale green with four faint to well defined longitudinal bands. Abdomen usually darker. Face heavily marked, usually with central pale patch (Fig. 4.13). Anteclypeus with broad central longitudinal band.

Diplocolenus abdominalis

Ventral surface without dark markings.....4

- 4 Vertex pale greenish yellow or yellow brown, with pale mid line which generally continues down the length of the body. Wedge shaped pale area on the lower part of the frontoclypeus (Fig. 4.14) Thorax with four faint longitudinal bands which become darker on the abdomen.

Arthaldeus pascuellus (Plate 4.1)

4.3.8 Key to the species of Athysanini

- 1 Dorsal surface unbanded or with lateral bands only. Central area of dorsal surface without dark markings.....2

- Dorsal surface with dark bands close to the mid-line.....3
- 2 Nymph green with few markings. Thorax, especially wing pads may be yellowish green. Abdomen with small black spots on the sides of tergites V to V111 which increase in size towards V111. The face is unmarked. *Graphocraerus ventralis*
Nymph yellow with sharply contrasting black or dark brown lateral bands. Bands continue in front of the eyes as four black or dark brown patches on the transition between the vertex and the face. Face and rest of the body without markings .
Miocydia crocea (Plate 4.1)
- 3 Nymph yellow with sharply contrasting dark brown lateral bands and two thin, irregular, narrowly separated central bands. Face unmarked, or with light brown markings on the frontoclypeus.
Paluda adumbrata (Plate 4.1)
Nymph not yellow. Face with dark markings.....4
- 4 Markings on frontoclypeus and genae produce a characteristic broad, dark brown, transverse band (Fig. 4.11). Body colour off-white to cream with two brown or dark brown, irregular, narrowly separated central bands and brown lateral bands. The lateral bands may be poorly defined on the thorax. In living specimens the body has a very characteristic whitish bloom, which is soon lost in dead specimens. *Rhytistylus proceps* (Plate 4.1)
Frontoclypeus with transverse brown bands marked with dark brown spots which extend onto the unbanded lower part of the frons (Fig. 4.15). Colour variable, from light brown to grey / blue. Characteristic markings include two dark brown central bands, which are broader on the thorax than on the abdomen and separated by narrow pale

mid-band, and the pattern of brown markings on the vertex (Fig. 4.16). (Early instars usually lack markings in the central area of the dorsal surface and have lateral bands only).

Euscelis incisus (Plate 4.1)

(N.B. The presence of lateral hairs only on the posterior angle of tergite V111 distinguishes *E. incisus* from other *Euscelis* species (Vilbaste 1982)).

Figs 4.1 - 4.5

Figs 4.1 - 4.5

4.1 Face of deltocephaline nymph

4.2 - 4.5 Outline examples of nymphs of cicadellid subfamilies.

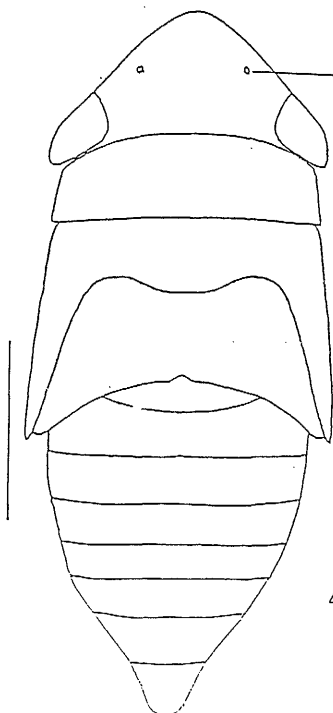
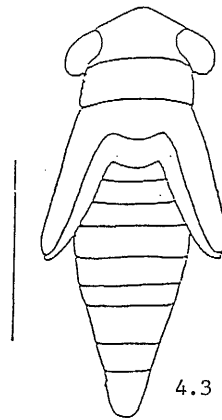
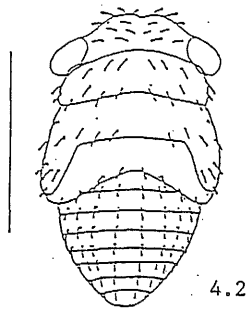
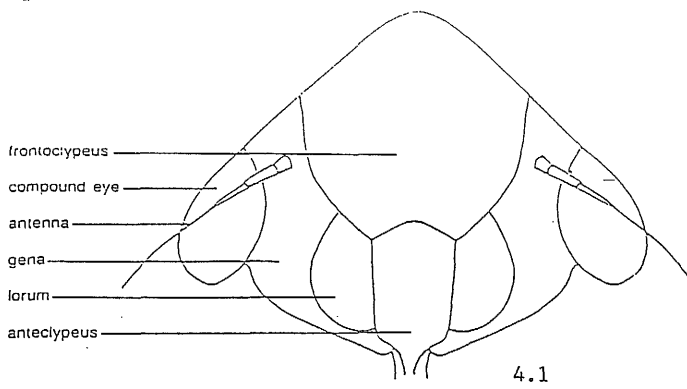
4.2 Agallinae (4th instar *Agallia* sp.)

4.3 Typhlocybinae (5th instar *Zyginidia scutellaris*)

4.4 Aphrodinae (5th instar *Aphrodes bifasciatus*)

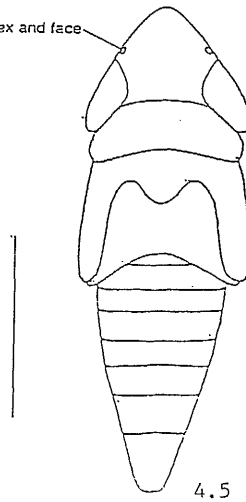
4.5 Deltocephalinae (5th instar *Turrutus socialis*)

N.B. Setae are only shown on the diagram of Agallinae, in which subfamily they are especially stout and characteristic.



Ocellus placed well back on vertex

Ocellus on the transition between the vertex and face



All scale lines equivalent to 1 cm

Figs 4.6 - 4.16

Figs 4.6 - 4.16

4.6 *Doratura stylata*: head in side view

4.7 *Doratura stylata*: vertex

4.8 *Agallia* sp.: face

4.9 *Aphrodes bifasciatus*: head in side view

4.10 *Aphrodes albifrons*: head in side view

4.11 *Rhytistylus proceps*: face

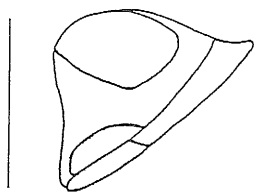
4.12 *Turrutus socialis*: face

4.13 *Diplocolenus abdominalis*: face

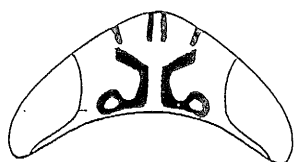
4.14 *Arthaldeus pascuellus*: face

4.15 *Euscelis incisus*: face

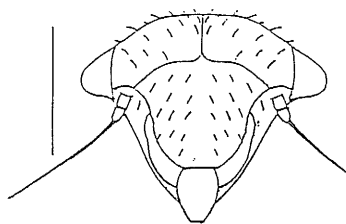
4.16 *Euscelis incisus*: vertex



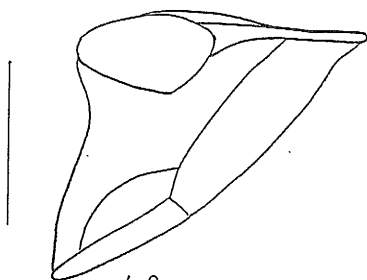
4.6



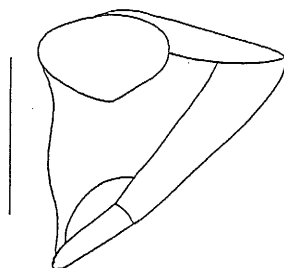
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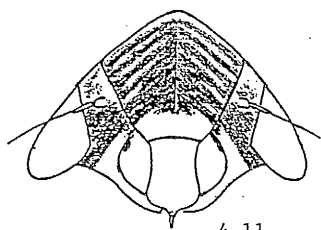
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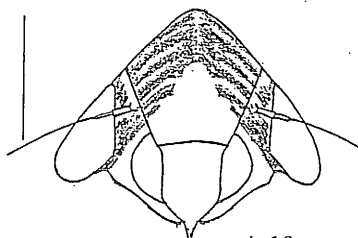
4.9



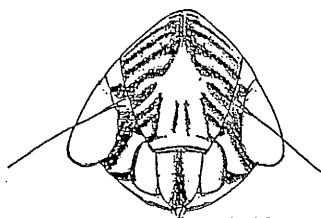
4.10



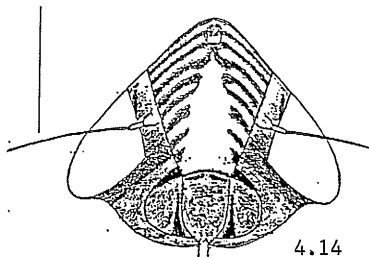
4.11



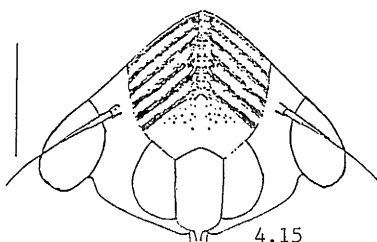
4.12



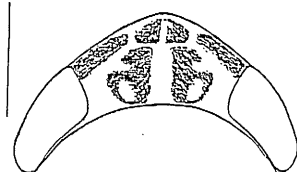
4.13



4.14



4.15



4.16

Plate 4.1



Agallia sp.



Aphrodes albifrons



Aphrodes flavostriatus



Zyginidia scutellaris



Doratura stylata



Euscelis incisus



Rhytistylus proceps



Paluda adumbrata



Mocydia crocea



Adarrus multinotatus



Turrutus socialis



Arthaldeus pascuellus

5. THE HOST PLANTS OF THE MORE COMMON AUCHENORRHYNCHA AT THE DEEPS

5.1 Introduction

The information available on the host plants of British grassland Auchenorrhyncha, which comes mainly from work on acid grasslands, suggests that the majority of species in any community will have a range of host plants, and that specific Auchenorrhyncha / plant host associations will be uncommon. More data are required before it is possible to assess the general applicability of this view. The object of the work described in this chapter was to obtain data on the grass hosts of calcareous grassland Auchenorrhyncha. Although a few authors have succeeded in collecting Auchenorrhyncha from named grasses in the field (Den Bieman, 1987; Whitcomb, Kramer, Coan & Hicks, 1987) it is often difficult to obtain unambiguous records because grasses usually grow as an intimate mixture of species (Whitcomb *et al. op. cit.*) and many grassland Auchenorrhyncha are extremely mobile. An attempt was made to overcome these problems by setting up choice experiments, in a greenhouse and in the field, in which potential host grasses were grown in pots, so making it easier to collect Auchenorrhyncha from them.

5.2 Greenhouse Choice experiments

5.2.1 Methods

The grasses for the greenhouse choice experiments were collected from the Deeps in autumn 1987 and planted in 127 mm plastic pots in soil taken from mole hills on the site. As nutrient levels in grasses grown in pots with "natural" soil decline rapidly (Ratcliffe, pers. comm.), a small quantity of bonemeal (approximately 50g to 5kg of soil) was added to offset this. The species chosen, which included the dominant and common grasses at the Deeps, were: *Arrhenatherum elatius*, *Avenula pubescens*, *Brachypodium pinnatum*, *Briza media*, *Bromus erectus*, *Dactylis glomerata* and *Festuca rubra*. The potted plants were kept outside during

the winter and brought into a greenhouse in the early spring. The grasses were divided and repotted to give 12 pots of each species and then placed on a tray-like bench, 4 m long, 80 cm wide and 20 cm deep which ran the length of the south facing side of a small greenhouse. The bench was divided into 7 compartments each of which was lined with heavy duty polythene and filled to a depth of about 4 cm with fine gravel. (The compartments were included to facilitate the separation of grass species for the hatching experiment described later (p. 64)). The gravel, which was kept damp, provided a bed for the pots, which were watered as necessary and fed with a 1 g litre^{-1} NH_4NO_3 every three to four weeks. The grasses were occasionally trimmed back to a height of about 20 cm to encourage new growth and to maintain them at a suitable size for handling in the choice experiment, but otherwise were left to grow until required for the choice experiment which was carried out in August 1988.

Prior to the experiment the grasses were arranged on the bench in 14 groups, each group consisting of 6 pots of the same species. These were arranged so that groups of the same species were well separated and one group of each species was on the lighter side of the bench next to the south facing side of the greenhouse. To prevent the escape of leafhoppers the whole bench was enclosed on all sides with a white muslin cage, the roof of which was 70 cm from the base of the bench, high enough to allow easy access to all pots (see Plate 5.1). The presence of the cage created, incidentally, a more equitable environment for the grasses and leafhoppers by reducing the temperature on hot days. Nothing was done, other than this, to control the conditions within the cage.

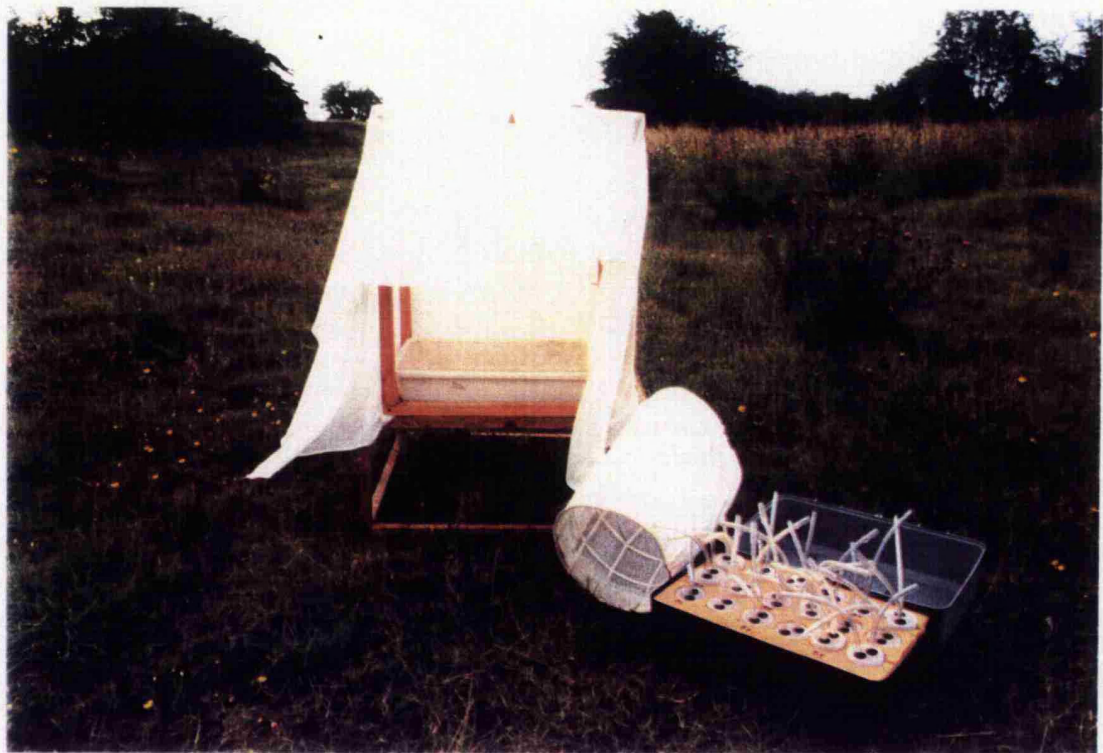
Two species of cicadellid were used in the choice experiment; *Adarrus multinotatus* and *Turrutus socialis*. They were chosen because the results of the preliminary survey indicated they were abundant species with contrasting distribution patterns. Initially approximately 150 *A. multinotatus* and 100 *T. socialis* were collected from the Deeps by sweeping and searching. They were caught with a pooter, the base

Plate 5.1

Plate 5.1

Above: The greenhouse, showing the divided bench on the left and shelves with pots covered by nylon mesh sleeves on the right. For the greenhouse choice tests the bench was completely enclosed in a white muslin cage; only the side of the cage is in place in the photograph. To record the nymphs emerging from the grasses in the year following the choice tests each compartment was separated within the cage by vertical white muslin partitions. The small muslin covered cage in which the leafhoppers were removed from the grasses is shown at the back of the greenhouse.

Below: The equipment used to remove leafhoppers from grasses in the field choice experiment. The grasses in pots were enclosed by the muslin cylinder and transferred to the white muslin cage, which was supported by a wooden frame. The grasses were brushed over the white tray, and the leafhoppers collected in pooters. A different pooter was used for each species of grass (and for the fertilised and unfertilised plants within each species as described in chapter 6)



of which was lined with damp tissue to minimise damage to the insects and transferred at intervals to a larger container, which contained damp tissue and a small quantity of grass, to avoid over-crowding. The leafhoppers were transferred after a maximum of four hours in this container to the greenhouse choice chamber by scattering them over the grasses. The initial collection was made over a period of four days (August 13-17) as a number of visits to the site was necessary to obtain sufficient numbers. The leafhoppers were left to settle in the choice chamber for a further 3 days after August 17 before the numbers of each species on the different plants were recorded. Two days later an additional 50 *T. socialis* were introduced and one week after this another count was made.

Direct counts of the leafhoppers on the plants in the choice chamber were difficult to make as they were hard to see and easily disturbed. Instead, the counts were made by carefully transferring each plant to be examined from the choice chamber to a white tray inside a small muslin cage (open on one side) on a nearby bench (see Plate 5.1). The plant was then brushed thoroughly over the tray and the leafhoppers recorded as they were collected with a pooter from the tray or the muslin sides of the cage. This procedure was carried out early in the morning (starting at about 0700 hr) when the temperature in the greenhouse was relatively low and the leafhoppers inactive. Very few leafhoppers were seen to leave the plants as they were transferred from the bench to the cage. To minimise disturbance the plants were kept trimmed so that leaves did not extend far beyond the circumference of the pot and intertwine with those of adjacent plants.

In order to obtain information on oviposition the leafhoppers were kept in the choice chamber following this experiment until they died in November. In April of the following year the plants were rearranged so that each species occupied a different compartment on the bench. The compartments were separated from each other with white muslin to ensure that any nymphs that hatched from the plants in May or June would remain on the same host species. Nymphs were first observed

on the grasses on May 25 and a few were collected with a pooter and transferred to clip cages (described in chapter 7) in which they were reared to adults to confirm their identity. On June 14 the experimental plants were examined for leafhoppers in the way described above.

5.2.2 Results.

The results of the greenhouse choice experiments are shown in Table 5.1. Under 50% of the animals introduced into the choice chamber were collected from the plants. Some may have died soon after they were introduced, others may have escaped or have been off the plants at the time they were examined. A few may have been lost during the transfer of the plants from the choice chamber to the collecting tray. Nevertheless, the two species of leafhopper had contrasting distribution patterns on the potential host plants. Chi-squared tests on the results showed that in both choice experiments the distribution of *A. multinotatus* among the grass species departed significantly from the expected ($P < .001$), indicating a strong association with *Brachypodium pinnatum*. *Turrutus socialis* spread more widely among the grasses and showed no clear preference for a single host. In the first choice experiment (August 21) a chi-squared test showed a significant departure from the expected distribution, indicating a preference by *T. socialis* for *Avenula pubescens* and *Festuca rubra*. In the second (August 31), a 7x1 chi-squared test showed no significant departure from the expected distribution ($P > 0.2$) although twice as many *T. socialis* were found on *F. rubra* than on any other species. However, when the numbers found on *A. pubescens* and *F. rubra* were combined and compared with the combined numbers found on the remaining species, a chi-squared test showed significant heterogeneity ($0.01 > P < 0.02$).

The results of the experiment on oviposition and subsequent hatching are shown in Table 5.2. *A. multinotatus* nymphs were found only on *B. pinnatum*, a distribution that departed significantly from the expected ($P < 0.001$). A chi-squared test on the *T. socialis* distribution also showed a significant departure from

Table 5.1 Numbers of *Adarrus multinotatus* and *Turrutus socialis* found on different grass species in the greenhouse choice test. The table shows the number of leafhoppers caught on each grass species (numbers caught on individual plants given in parentheses).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>D. glomerata</i>	<i>F. rubra</i>	Chi-squared
Date: 21.8.88*								
<i>T. socialis</i>	8 (1.3.2.2)	12 (1.2.2.1.4.1)	3 (1.1.1)	8 (2.3.1.1.1)	2 (1.1)	5 (1.1.1.1.1)	13 (1.2.2.1.1.5)	(7x1) 14.64 P < 0.05
<i>A. multinotatus</i>	1		48 (3.4.1.2.2. 4.3.5.6.2.4.3)		1		1	(7x1) 272.9 P < 0.001
Date 31.8.88*								
<i>T. socialis</i>	4 (2.2)	6 (1.1.2.1.1)	4 (2.2)	4 (1.1.2)	3 (1.1.1)	5 (1.2.2)	12 (1.1.4.2.1. 2.1)	(2x1) 6.57 P < 0.02
<i>A. multinotatus</i>			25 (2.1.3.5.6. 1.1.3.2.1)	1				(2x1) 170.6 P < 0.001

*22.8.88 150 *Adarrus multinotatus* and 100 *Turrutus socialis* introduced into choice chamber 13-17.8.88

*31.8.88 Additional 50 *Turrutus socialis* introduced 23.8.88

Table 5.2 Numbers of *Adarrus multinotatus* and *Turrutus socialis* nymphs collected from overwintered grasses following the greenhouse choice tests.

	<i>A. elatus</i> *	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>D. glomerata</i>	<i>F. rubra</i>	Chi-squared
<i>T. socialis</i>	0	22	0	1	4	0	18	(7x1) 83.5 P < .001
<i>A. multinotatus</i>	0	0	12	0	0	0	0	(2x1) 72.3 P < .001

*This species did not overwinter well in pots and was generally in poor condition

the expected ($P < 0.001$) indicating that *A. pubescens* and *F. rubra* were the grasses preferred for oviposition. *Arrhenatherum elatius* was, however, in poor condition after overwintering in pots and this may have affected the survival of eggs or nymphs on this grass.

5.3 Field Host Choice Experiments

5.3.1 Methods

Attempts were made to obtain information on the host grasses of Auchenorrhyncha at the Deeps by direct observation in the field, but this proved very difficult and time consuming. It quickly became apparent that some form of experimental manipulation was required to look at host relationships in the field but the method generally used, that of sowing plots of different grass species on site was not possible in the circumstances (the site is a SSSI and it is open to the public). An alternative was to set up a grid of grasses grown in pots and sample leafhoppers from these. This was done with the permission of English Nature and the Northamptonshire Wildlife Trust.

Eight species of grasses and one sedge were used in the first field choice experiment. Six of these species were used in the greenhouse choice tests described above and the same grasses were divided and potted on in late autumn 1989. In the summer of that year two other grasses and one sedge were taken from the Deeps and transplanted to pots. All soil used in these and subsequent plantings was taken from molehills on site and mixed with a small quantity (0.01%) of bonemeal. The species used for the choice experiment in 1990 were:

Gramineae:

Tribe Aveneae:	Tribe Brachypodieae:	Tribe Poeae
<i>Arrhenatherum elatius</i>	<i>Brachypodium pinnatum</i>	<i>Briza media</i>
<i>Avenula pubescens</i>	Tribe Bromeae	<i>Festuca ovina</i>
<i>Trisetum flavescens</i> *	<i>Bromus erectus</i>	<i>Festuca rubra</i>

Cyperaceae:

Carex flacca *

* Species not used in previous greenhouse choice test

These species were chosen because they were common at the Deeps and represented a cross-section of different tribes. *Dactylis glomerata*, which was used in the greenhouse experiments was replaced by *F. ovina*, which was characteristic of Site 1 and other similar areas of the Deeps. *T. flavescens* was added to the list because it also was reasonably common in the grassland. *Carex flacca* was included as a contrast to the grasses and because some delphacids feed on Cyperaceae (Le Quesne, 1969).

In April 1990, pots of the the 9 plant species, each replicated 8 times were placed in a grid on Site 1. This site was chosen for the main field experiment because it was the habitat of *Turrutus socialis*, a species on which more data was needed, and it was less susceptible to trampling than the longer grass site. There was little to choose between the two sites on the basis of the numbers of leafhoppers found during the initial survey. A smaller scale experiment was, however, set up on Site 2 in June 1990 (see below).

On Site 1 the pots were arranged in a grid of six rows, each row consisting of six pairs of pots. The pots were sunk into the ground so that the rims were more or less flush with the ground surface. The plants of a pair were the same species and the distance between them was 50 cm. The distance between the different pairs of pots was 3 m. Pairs of pots were positioned randomly along the rows in replicates, one replicate consisting of one pair of each species (and, therefore, taking up one and a half rows). The rows ran approximately north to south. The paired arrangement was chosen primarily for the nitrogen treatments described in the following chapter.

The pots were sampled every two to three weeks between April 26 and October 17, except for the period between July 19 and August 22 when the pots were returned to the greenhouse because very dry conditions made it difficult to maintain the plants in the field and caused a severe decline in the number of leafhoppers caught on the experimental grasses.

Leafhoppers were collected from a plant by quickly covering it with a light muslin covered cylinder (38 cm high, 22 cm diameter) and lifting the pot out of the ground and into the same muslin covered cage that was used in the greenhouse choice experiments. The cage was supported 30 cm off the ground by a separate wooden frame to provide a convenient working height and reduced contamination by *Auchenorrhyncha* from surrounding vegetation. Once transferred the grass was thoroughly brushed by hand over a white tray that covered the base of the cage and *Auchenorrhyncha* were collected from the tray or muslin sides of the cage with a pooter. This procedure was carried out while kneeling by the open side of the cage. The grid was always sampled in the morning, usually between 7 and 11 am, by moving along the rows from west to east so that shadows were never cast on the plants prior to collecting. Before collecting, the cage was positioned about 1 m to the west of a pair of pots so that the muslin covered rear side faced the direction of the sun. Leafhoppers were rarely lost through the open side of the cage as this was mostly shielded by my upper body as I collected from the pots. The sampling apparatus is shown in Plate 5.1 (p. 66).

The efficiency with which the *Auchenorrhyncha* were removed from the grasses by the technique described above was checked during one sampling session by enclosing one plant of each grass species within a fine mesh white nylon hood (shown in Plate 5.1) as soon as they had been examined in the field, and returning them to the greenhouse. There they were examined thoroughly on two occasions during the following week before being returned to the field. No further *Auchenorrhyncha* were obtained from any of these plants on either occasion.

The two main problems encountered while using the pot technique in the field were rabbit grazing and drought. Rabbits soon found the pots and grazed the grasses selectively, preferring *Festuca* spp. and *Bromus erectus* and avoiding *Brachypodium pinnatum* and *Avenula pubescens*. In very dry periods, when much of the grass on the site had died back they were less selective. The contrast between a heavily grazed pot of *B. erectus* and a more or less untouched pot of *A. pubescens* is shown in Plate 5.2. Protecting the pots with netting was not possible because of the risk of vandalism. (Following vandalism to some of the pots soon after they were first put in place, all the pots were camouflaged by covering the exposed rims with dead vegetation. After taking this precaution, they were not interfered with).

1990 was a very dry year and the pots had to be watered more frequently than anticipated. Care was taken to give each pot the same amount of water, which was limited on any occasion by the amount that could be carried to the site by car. None of the grasses died while out in the field although some wilted in very dry weather. They were always watered a few days prior to sampling to make sure they were in a suitable condition for Auchenorrhyncha. The pots drained freely into the bed of limestone shale on which they rested. By the end of May 1990, following a very dry month, Site 1 was almost completely brown with only a few patches of green vegetation on pockets of deeper soil and in the pots. The site recovered in June but was again severely affected by drought in July and August. It is likely that the unfavourable conditions reduced the numbers of leafhoppers on the site and hence the number caught from the experimental grasses.

Disturbance of the leafhoppers as the pots were approached prior to sampling and contamination of the samples by leafhoppers from the vegetation surrounding the pots were potential problems. Disturbance was minimised by sampling early in the morning when temperatures were low and the leafhoppers relatively inactive. During periods of drought, temperatures rose rapidly in the morning and some

Plate 5.2

Plate 5.2

Above: An *Avenula pubescens* plant used in the field choice experiment.

This species was not grazed by rabbits.

Below: A *Bromus erectus* plant used in the field choice experiment. This

species was grazed by rabbits, sometimes heavily.



for the site to 40 species. Table 5.3 compares the rank orders of the species obtained from sites 1 and 2 using the survey techniques of vacuum sampling and sweeping with those obtained from the pot experiment. The lists have most of their species in common but the rank orders are different. Compared with the 1987 survey, the forb feeding species *Bactracomorpha irroratus* and *Philaenus spumarius* were recorded in low numbers using the pot technique as was *Neophilaenus lineatus*, a species that feeds on both grasses and forbs. The delphacid *Hyledelphax elegantulus* was caught in relatively high numbers from the pots on Site 1 in 1990 but was not recorded in the survey. The ground living *Aphrodes* spp. were relatively more abundant in the pot samples, *A. bifasciatus* being more common on Site 1 and *A. flavostriatus* more common on Site 2. The differences between the survey and pot experiment results are probably due partly to the methods used and partly to changes in the abundance of the species.

Site 1

The total numbers of Auchenorrhyncha caught from the different grasses and the sedge on Site 1 during 1990 and 1991 are shown in Fig 5.1 (p. 79). (See also Appendix 1a and 1c.) The higher totals came from *Avenula pubescens*, *Festuca ovina* and *F. rubra*, while the remaining species yielded similar numbers, with the exception of *Carex flacca*. Despite the fact that *C. flacca* was only included in the 1990 experiment, the low numbers caught from this plant probably indicate that it was a less suitable host than the grasses for most of the Auchenorrhyncha. Over four times as many Auchenorrhyncha were caught from the potted grasses in 1990 as in 1991 (1194 and 259 respectively), and if the *C. flacca* total of 69 for 1990 is adjusted proportionally to produce an estimated catch for both years the total rises to 84; still considerably below that for any of the grasses.

Although no attempt was made to measure the amount of vegetation that the different plants provided for leafhopper colonisation it appeared, from a subjective assessment, that the overall yield from grasses that either grew sparsely in pots or

disturbance could not be avoided; in these conditions a few leafhoppers were seen to leave the grasses before they were enclosed by the muslin cylinder. In order to reduce the possibility of contaminating the samples with leafhoppers from the vegetation immediately surrounding the pots this vegetation was periodically clipped to ground level.

In June 1990 a smaller grid of potted grasses was set up in Site 2. The species used were the dominant grasses on the site; *Brachypodium pinnatum*, *Bromus erectus* and *Festuca rubra*. Details were as described above except that each species was replicated four times and the grid consisted of two rows with three pairs of pots in each.

The field pot experiment was repeated on Site 1 in 1991 (May 24 - August 19). To cut down sampling time only the grasses were used and *Carex flacca* was excluded. It was felt that sufficient information on this plant had been obtained in 1990. Rabbit grazing and drought were again problems, the drought being so severe during the summer that the sampling programme was cut short and finished in August. In 1992 the grid was again set up on Site 1 (with the exception of *Trisetum flavescens* which failed in the pots during the winter of 1991-1992) but the grasses were soon found and severely grazed by rabbits. The full grid was relocated to Site 2 on May 10 where rabbit grazing was less intense. Leafhoppers were collected from the grasses every week between May 18 and June 25.

5.3.2 Results

Thirty four species of Auchenorrhyncha were collected from sites 1 and 2 using the pot technique. *Aphrophora aini*, *Cercopis vulnerata* and *Streptanus sordidus*, species recorded in the 1987 survey, were not found during any of the choice experiments. *Dicranotropis hamata*, *Eurysa lineata*, *Macrosteles sexnotatus*, *Mocycdiopsis attenuata*, *Paluda flaveola* *Psammotettix confinis* and *Zyginidia scutellaris* were recorded for the first time during this period, bringing the total list

Table 5.3 The rank orders of the 15 most abundant species, in descending order, collected from sites 1 & 2 during the survey (1987) and the pot experiments (1990)

Site 1

Pot Experiment

Turrutus socialis
Hyledelphax elegantulus
Diplocolenus abdominalis
Aphrodes bifasciatus
Rhytistylus proceps
Euscelis incisus
Mocydia crocea
Psammotettix confinis
Graphocraerus ventralis
Doratura stylata
Aphrodes albifrons
A. flavostriatus
Arthaldeus pascuellus
Kelisia vittipennis
Criomorphus albomarginatus

Survey

Turrutus socialis
Neophilaenus lineatus
Philaenus spumarius
Euscelis incisus
Diplocolenus abdominalis
Bactracomorpus irroratus
Aphrodes bifasciatus
Doratura stylata
Paluda adumbrata
Agallia venosa
Rhytistylus proceps
Graphocraerus ventralis
Mocydia crocea
Aphrodes flavostriatus
Aphrodes bicinctus

Site 2

Pot Experiment

Mocydia crocea
Arthaldeus pascuellus
Adarrus multinotatus
Criomorphus albomarginatus
Hyledelphax elegantulus
Diplocolenus abdominalis
Aphrodes flavostriatus
Neophilaenus lineatus
Javesella pellucida
Paluda adumbrata
Stenocranus minutus
Elymana sulphurella
Psammotettix confinis
Dicranotropis hamata
Zyginidia scutellaris

Survey

Neophilaenus lineatus
Aphrodes bifasciatus
Diplocolenus abdominalis
Philaenus spumarius
Mocydia crocea
Stenocranus minutus
Aphrodes flavostriatus
Bactracomorpus irroratus
Adarrus multinotatus
Turrutus socialis
Graphocraerus ventralis
Elymana sulphurella
Paluda adumbrata
Criomorphus albomarginatus
Arthaldeus pascuellus

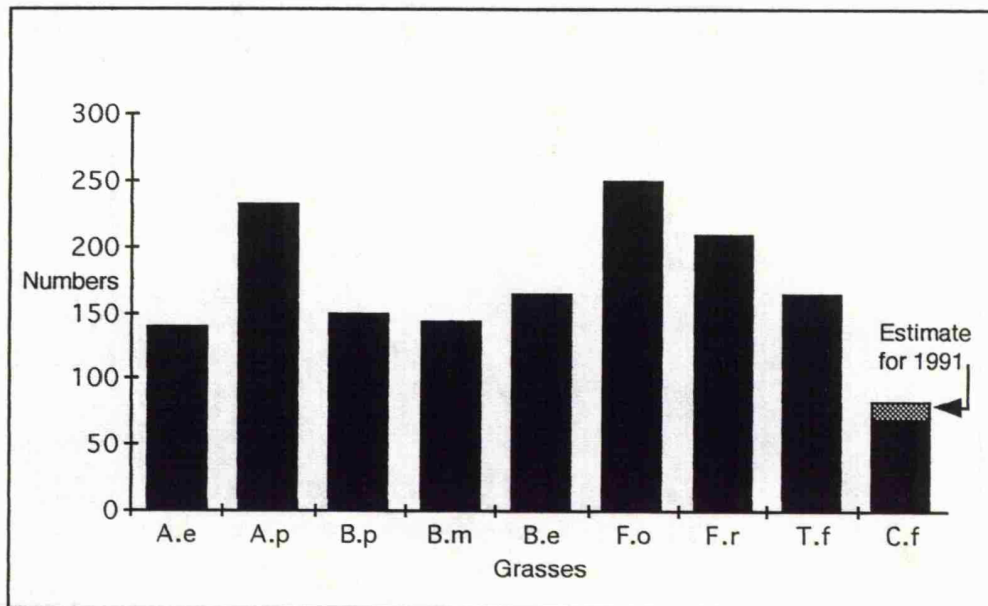


Fig 5.1 Total numbers of Auchenorrhyncha caught from experimental grasses on site 1 during 1990 and 1991.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
 B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*
 Sedge: C.f = *Carex flacca* (As *C. flacca* was not included in the field choice experiment in 1992, an estimate is given for this year)

were more heavily grazed by rabbits was not noticeably reduced. Most of the grasses grew well in pots but *Trisetum flavescens* and *Arrhenatherum elatius* never formed very substantial plants. Grazing by rabbits reduced the biomass of some species, especially *Bromus erectus*, *F. ovina*, *F. rubra* and *A. elatius*. *Avenula pubescens*, *Brachypodium pinnatum*, *Briza media* and *C. flacca* were generally only lightly grazed, although in very dry periods rabbits became less selective and grazed these species more heavily, especially *B. media*. At certain times, when a particular species was severely reduced by grazing, noticeably fewer Auchenorrhyncha were caught from it. As none of the grasses yielded particularly low numbers of leafhoppers and most appeared to have at least one species of associated Auchenorrhyncha it seems reasonable to suggest that differences in plant architecture did not play an overriding role in determining colonisation. With the exception of *Carex flacca*, the lowest number of Auchenorrhyncha was obtained from *Briza media*, a grass that grew well in pots and which was generally only lightly grazed.

Although the numbers of Auchenorrhyncha caught over the two years from the pots in Site 1 were low for the majority of species (less than 30 individuals per species) there was considerable variation in the proportions of the different species collected from the eight grasses. Taking the distributions of the 8 most abundant Auchenorrhyncha species, a chi-squared analysis of the resulting 8 X 8 contingency Table (Table 5.4) shows significant heterogeneity ($P < 0.01$). (Just over 15% of the cells in Table 5.4 contain expected values of less than 5, which is well within the upper limit of 20% recommended by some authors for a reliable chi-squared test (Siegel & Castellan 1988).)

Chi-squared tests on the individual distributions of the 10 most abundant species of Auchenorrhyncha among the grasses show significant heterogeneity for all except *Diplocolenus abdominalis* (Table 5.5). These tests were performed over all eight grass species for those Auchenorrhyncha caught in numbers of 40 or

Table 5.4 Data for Chi-squared test on the 8 most abundant Auchenorrhyncha species caught on Site 1 in 1990 and 1991.
(Expected values in parentheses)

Gramineae:	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. erectus</i>	<i>B. media</i>	<i>B. pinnatum</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	Sub-totals
Auchenorrhyncha									
Cicadellidae									
<i>Aphrodes bifasciatus</i>	5 (12.9)	18 (22.7)	26 (15)	19 (12)	13 (12.9)	18 (21.8)	23 (18.1)	9 (15.5)	131
<i>Diplocolenus abdominalis</i>	14 (13.5)	22 (23.8)	21 (15.7)	10 (12.5)	21 (13.6)	21 (22.8)	17 (18.9)	11 (16.2)	137
<i>Euscelis incisus</i>	6 (10)	17 (17.5)	12 (11.6)	15 (9.2)	3 (10)	5 (16.8)	4 (13.9)	39 (12)	101
<i>Graphacraerus ventralis</i>	9 (3.2)	10 (5.7)	2 (3.8)	1 (3)	1 (3.3)	0 (5.5)	1 (4.5)	9 (3.9)	33
<i>Mocytia crocea</i>	2 (4.1)	4 (7.3)	11 (4.8)	2 (3.8)	16 (4.2)	2 (7)	2 (5.8)	3 (5)	42
<i>Rhytidistylus proceps</i>	9 (13.6)	3 (24)	1 (15.8)	6 (12.6)	10 (13.7)	79 (23)	28 (19)	2 (16.4)	138
<i>Turrutus socialis</i>	45 (50.3)	99 (88.8)	55 (58.7)	44 (46.8)	61 (50.8)	65 (85.3)	70 (70.6)	73 (60.7)	512
Delphacidae									
<i>Hyalociphax elegantulus</i>	37 (19.4)	51 (34.2)	20 (22.6)	21 (18)	3 (19.5)	25 (32.8)	33 (27.2)	7 (23.3)	197
Sub-totals	127	224	148	118	128	215	178	153	Grand Total = 1291

Chi-Squared = 340 P < 0.005

more (so giving expected chi-squared values of 5 or more for each cell) and over three grass tribes (see below) for those that were less abundant but found in sufficient numbers to give expected chi-squared values of 5 or more. In the latter case the grasses were grouped into the Aveneae, the Poeae and *Brachypodium pinnatum* plus *Bromus erectus* (both placed in the Brachypodieae by Clapham, Warburg & Tutin, 1962). The observed numbers of Auchenorrhyncha on *Arrhenatherum elatius* and *Trisetum flavescens* were generally less than the expected values calculated for the chi-squared tests; this may have been due to their poorer or sparser growth combined, especially in the case of *A. elatius*, with rabbit grazing. However, *Hyledelphax elegantulus* occurred more frequently than expected on *A. elatius*, as did *Euscelis incisus* on *T. flavescens* and *Graphocraerus ventralis* on both grasses.

A chi-squared test reveals the presence of any significant heterogeneity in the distribution of a species among potential host plants, but does not provide a measure of host specificity. An index of host specificity based on chi-squared, but not providing any measure of significance, was used by Prestidge & McNeill (1981) in their work on the Auchenorrhyncha of Silwood Park. The advantage of this index, compared with the simple 'coefficient of oligophagy' described by Whitcomb *et al.* (1987) (see p. 7), is that it is based on the number of occurrences of a species on all potential hosts. The 'coefficient of oligophagy' is based entirely on the number of animals occurring on the preferred host.

The index of Prestidge & McNeill (*op. cit.*) was used in the study and was calculated by taking the numbers of a species found on each type of grass and expressing these as a percentage of the total number of that species caught. The deviation of these percentages from those calculated for an uniform distribution was assessed as a chi-squared which was then divided by the maximum possible value for chi-squared. The maximum value is calculated by assuming the species is completely specific to one host category, and varies according to the number of

host categories involved. The index varies between 0 (complete generalist) and 1 (complete specialist). An example is worked out below for *Aphrodes bifasciatus* in Table 5.6 below.

Table 5.6 An example of the procedure for working out the specificity index

Numbers of <i>A. bifasciatus</i> on different grasses	Observed % abundance	Expected % abundance for uniform distribution
5	3.8	12.5
18	13.7	12.5
13	9.9	12.5
19	14.5	12.5
26	19.9	12.5
18	13.7	12.5
23	17.6	12.5
9	6.9	12.5

Chi-squared values ((O-E) ² / E)	Maximum chi-squared value for 8 host species = 700
6.06	
.12	
.54	
.32	
4.38	
.12	
2.10	
<u>2.51</u>	
16.19	

Specificity index for *A. bifasciatus* = 16.19 / 700 = .023

Specificity indices have been calculated for the adults plus nymphs of those species whose combined total for 1990 + 1991 exceeded 15 and for one or two species which fell below this but show associations with grasses that are corroborated elsewhere in this work. Indices for adults alone and nymphs alone have also been calculated where possible. The results, based on numbers per host species, are shown in Table 5.7. The calculations have also been done for the numbers of Auchenorrhyncha species per plant tribe, again combining *Brachypodium pinnatum* and *Bromus erectus* to form a third group. Because this method of calculating specificity indices requires the expected values to be the same for each plant group the numbers of Auchenorrhyncha found on the

Table 5.7 Specificity indices based on numbers of Auchenorrhyncha on individual plant species
Data from site 1, 1990 & 1991.

Cicadellidae	Specificity Indices			Main host plant species
	Adults	Nymphs	Adults + Nymphs	
<i>Aphrodes bifasciatus</i>	0.03	0.04	0.02	<i>Bromus erectus</i>
<i>Arthaldeus pascuellus</i>	0.17	- *		<i>Festuca ovina</i>
<i>Diplocolenus abdominalis</i>	0.03	0.01	0.01	<i>Avenula pubescens</i>
<i>Doratura stylata</i>	0.09	0.31	0.19	<i>Festuca rubra</i>
<i>Euscelis incisus</i>	0.12	0.1	0.09	<i>Trisetum flavescens</i>
<i>Graphocraerus ventralis</i>	0.14	0.23	0.14	<i>Avenula pubescens</i>
<i>Mocycdia crocea</i>	0.16	0.14	0.13	<i>Brachypodium pinnatum</i>
<i>Psammotettix confinis</i>	0.09	-		<i>Briza media</i>
<i>Rhytistylus proceps</i>	0.13	0.44	0.29	<i>Festuca ovina</i>
<i>Turrutus socialis</i>	0.02	0.01	0.01	<i>Avenula pubescens</i>
Delphacidae				
<i>Criomorphus albomarginatus</i>	0.58	-		<i>Festuca rubra</i>
<i>Hyledelphax elegantulus</i>	0.05	-		<i>Avenula pubescens</i>
<i>Kelisia vittipennis</i>	1	-		<i>Carex flacca</i>

* - = No, or very few, individuals in that group

The Wilcoxon signed ranks test (Siegel & Castellan 1988) on the eight species for which adult and nymphal specificity indices could be calculated, showed no significant difference between the two sets of indices ($P > 0.27$).

Table 5.8 Specificity indices based on numbers of Auchenorrhyncha on grass tribes.
Data from site 1, 1990 & 1991.

Cicadellidae	Specificity Indices			Main host tribes
	Adults	Nymphs	Adults + Nymphs	
<i>Aphrodes bifasciatus</i>	0.02	0.06	0.03	Poeae
<i>Arthaldeus pascuellus</i>	0.05	- *		Poeae
<i>Diplocolenus abdominalis</i>	0.03	0.005	0.009	
<i>Doratura stylata</i>	0.11	0.5	0.29	Poeae
<i>Euscelis incisus</i>	0.08	0.19	0.15	Aveneae
<i>Graphocraerus ventralis</i>	0.43	0.75	0.58	Aveneae
<i>Mocycdia crocea</i>	0.29	0.27	0.31	Bromeae / Triticeae
<i>Psammotettix confinis</i>	0.21	-		Poeae
<i>Rhytistylus proceps</i>	0.06	0.81	0.45	Poeae
<i>Turrutus socialis</i>	0.01	0.01	0.005	Aveneae
Delphacidae				
<i>Criomorphus albomarginatus</i>	0.6	-		Poeae
<i>Hyledelphax elegantulus</i>	0.07	-		Aveneae

* - = No, or very few, individuals in that group.

The Wilcoxon signed ranks test on the eight species for which adult and nymphal specificity indices could be calculated, showed no significant difference between the two sets of indices ($0.05 < P < 0.055$).

B. pinnatum / *B. erectus* group were multiplied by 1.5 to bring them into line with the Aveneae and Poeae, each of which were represented by three species. This expedient was considered justifiable as, in the vast majority of cases, it served to lower the index. Very few species occurred more frequently on *B. pinnatum* or *B. erectus* than on the other grasses and the only species that showed a significant association with both was *Mocycdia crocea*. In this case it could be argued that the index may be slightly higher than it might have been had a third grass species been included in this group. The results are shown in Table 5.8 (p. 85).

Based on these results and the chi-squared analyses there is reasonable evidence to suggest that a number of the Auchenorrhyncha species were associated with a particular grass or group of grasses. The specificity indices also demonstrate the importance of looking at the distribution of the nymphs, as in some cases this appeared to be quite different to that of the adults. x

Rhytistylus proceps was closely associated with the Poeae and especially with *Festuca ovina*, but only the nymphs, which were caught in relatively high numbers, showed this host specificity. There was a very large difference between the specificity indices of the adult and nymphs (0.06 and 0.81 respectively for the indices based on grass tribes). *Doratura stylata* and *Graphocraerus ventralis* also had relatively high indices as nymphs but much lower as adults. *D. stylata* was associated with *F. rubra* and *G. ventralis* with the Aveneae. *G. ventralis* showed a clearer association with a tribe, in that it occurred with equal frequency on all three grass species, than any other leafhopper. Although *Brachypodium pinnatum* and *Bromus erectus* are no longer classified in the same tribe they are probably more closely related to each other than to the other grasses used in the experiment (Clayton & Renvoize, 1986). Both adults and nymphs of *Mocycdia crocea* showed an association with these two grasses. Wilcoxon's matched pairs test showed no significant difference between the specificity of adults and nymphs to grass tribes (Table 5.8, p. 85) for the eight species for which the indices could be calculated

($P = 0.055$). Although some of the differences between adult and nymphal specificity were very small, the level of significance was close to $P = 0.05$ and markedly higher than that obtained for the differences between the indices calculated for the separate grass species ($P > 0.27$) (Table 5.7, p. 85).

Three of the common cicadellids on Site 1, *Aphrodes bifasciatus*, *Diplocolenus abdominalis* and *Turrutus socialis* showed no association with any particular grass species or tribe and had very low specificity indices. Adult *T. socialis* were caught in large enough numbers to allow a comparison of males and females on the experimental grasses. The specificity index for females (0.12) was more than twice that for the males (0.05), due mainly to a greater proportion of females on *Avenula pubescens* and *Festuca rubra* (see Fig. 5.9, p. 98). Chi-squared tests showed that only on *F. rubra* was the number of females significantly greater than the number of males ($P < 0.01$). Adults of the other two species were not caught in large enough numbers to allow a comparison of male and female specificity indices.

Paluda adumbrata was caught in very low numbers, but only from *F. ovina*. Combined with data from Site 2, described below, this indicates an association with *F. ovina* and *F. rubra* in this species.

Very few delphacid nymphs were caught from the grasses and so data on host preferences are available only for adults in this group. *Hyledelphax elegantulus* was abundant in 1990 but scarce in 1991. It showed no clear host preference and had very low specificity indices for both grass species and tribes. The specificity index for the females (0.06) was similar to that for the males (0.05). *Criomorpus albomarginatus*, by contrast, was scarce on Site 1 but strongly associated with *F. rubra*. This association is supported by data from site 2. *Kelisia vittipennis* was the only species with a specificity index of 1; it was found only on *Carex flacca*.

Site 2

Host plant data for Site 2 was obtained from a small scale experiment with 3 grass species performed in 1990 (see Appendix 1b), and the large scale experiment (but without *Trisetum flavescens*) performed in 1992 (see Appendix 1d). For species common to sites 1 and 2 the data obtained generally supported the findings described in the previous section.

In 1990 the experimental plants in Site 2 were untouched by rabbits while in 1992 grazing did occur and most species were affected to some extent, especially *Briza media* (which was one of the least affected species on site 1 in 1990 & 91). Chi - squared analyses of the distributions of the more abundant species recorded in 1990 (*Adarrus multinotatus*, *Arthaldeus pascuellus*, *Mocycdia crocea* and *Criomorphus albomarginatus*) showed significant heterogeneity in all cases (Table 5.9). *A. multinotatus* occurred most frequently on *B. pinnatum* ($P < 0.02$), *A. pascuellus* on *F. rubra* ($P < 0.01$), *M. crocea* on *B. erectus* ($P < 0.01$) and *C. albomarginatus* on *F. rubra* ($P < 0.001$). The three specimens of *Paluda adumbrata* that were caught came from *F. rubra*. This finding, in conjunction with the data from site 1, suggests an association with *Festuca* spp.

The numbers of Auchenorrhyncha obtained from the full-scale experiment on Site 2 in 1992 were disappointingly small (Table 5.10). Only *Criomorphus albomarginatus* and *Diplocolenus abdominalis* were caught in reasonable numbers. Chi-squared analyses over all the experimental grass species showed the distribution of *C. albomarginatus*, which occurred almost entirely on *F. rubra*, departed significantly from the expected ($P < 0.001$) while that of *D. abdominalis* did not ($P > 0.05$). Although only caught in low numbers, *M. crocea* occurred only on *B. pinnatum* and *B. erectus*, *P. adumbrata* on *F. rubra* and *Rhytistylus proceps* on *F. ovina*. *A. multinotatus* occurred predominantly on *B. pinnatum*. Specificity indices were not calculated from the data because of the low numbers.

Table 5.9 Auchenorrhyncha (adults + nymphs) from field pot experiment on Site 2, June 6 - Oct 17 1990 (Totals from 7 sampling occasions)

Gramineae:	<i>B. pinnatum</i>	<i>B. erectus</i>	<i>F. rubra</i>	Chi-squared
Cicadellidae:				
<i>Adarrus multinodeatus</i>	14	5	4	7.92 0.01 < P<.02
<i>Aphrodes flavostriatus</i>	1	2	5	*
<i>Arthaleus pascuellus</i>	6	4	18	12.29 0.001 < P<.01
<i>Dikraneura variata</i>	2			*
<i>Diplocolenus abdominalis</i>	3	7	2	*
<i>Elymana sulphurella</i>		1		*
<i>Mocycia crocea</i>	17	26	8	9.52 0.001 < P<.01
<i>Paluda adumbrata</i>			3	*
<i>Psammotectix confinis</i>			1	*
Unidentified nymphs		3		*
Delphacidae:				
<i>Criomorpus albomarginatus</i>			17	34.02 P<.001
<i>Dicranotropis hamata</i>	1			
<i>Hyledelphax elegantulus</i>	1	7	2	*
<i>Javesella pellucida</i>	1	2		*
<i>Stenocranus minutus</i>	2			*
Unidentified nymphs	1	2	9	
Cercopidae:				
<i>Neophilaenus lineatus</i>	3		3	*
<i>Philaenus spumarius</i>		1		*

* = Insufficient data for valid Chi-squared test

Table 5.10 Distribution of Auchenorrhyncha (adults & nymphs) on experimental grasses in Site 2. May 18th - June 26th 1992. (Totals from 5 sampling occasions.)

Gramineae:	<i>A. elatius</i>	<i>B. pinnatum</i>	<i>A. pubescens</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	Chi-squared (7x1)
Cicadellidae:								*
<i>Adarrus multinodeatus</i>		7				2	2	*
<i>Aphrodes bifasciatus</i>	3	3			3	2	3	*
<i>A. flavostriatus</i>		6	1	2	5	7	5	*
<i>Aphrodes sp.</i>		1				2		*
<i>Diplocolenus abdominalis</i>	3	9	7	3	3	8	12	12.43 0.05 < P<.01
<i>Doratura stylata</i>		1			1			*
<i>Mocycia crocea</i>		3			2		1	*
<i>Paluda adumbrata</i>							3	*
<i>Rhyttistylus proceps</i>						6		*
<i>Turrutus socialis</i>							1	*
Delphacidae:								
<i>Criomorpus albomarginatus</i>		1		1	1		40	218 P<.001

* = Insufficient data for valid chi-squared test

The results obtained from the field choice experiments on sites 1 & 2 are summarised in Figs 5.2 - 5.11 (pages 91 - 100).

5.4 Oviposition on Grass Hosts in the Field

5.4.1 Methods

To obtain data on the grass hosts used for oviposition by the Auchenorrhyncha at the Deeps the plants used in the 1990 and 1991 field experiments on Site 1 and in the 1990 experiment on Site 2 were transferred to the greenhouse in the autumn following the field experiments. They were overwintered on shelves which had been made into shallow troughs by nailing narrow strips of wood to the sides. The troughs were lined with heavy duty polythene and filled to a depth of 2-3 cm with fine gravel which was kept damp to prevent the plants drying out. The arrangement is shown in Plate 5.1 (p. 66).

In early May of each of the following years (1991 & 1992) every plant was covered by a fine nylon gauze hood (mesh size approx. 0.03 mm²), which was secured round the top of the pot with a rubber band, to prevent the escape of any nymphs which hatched from eggs (Plate 5.1). The pots were first examined for nymphs in late May or early June by removing the hood and brushing each plant over the white tray inside a muslin covered cage described previously for the greenhouse choice tests (Plate 5.1). Nymphs were collected with a pooter, anaesthetised with carbon dioxide (delivered from "sparklets" through a small screw operated valve) and returned to the plant in clip cages for future identification. The plants were examined again later in June, although this second examination yielded very few additional specimens in 1991, and none in 1992. Nymphs were identified mainly from the results of clip cage rearings that had been carried out in previous years. Nymphs not already encountered, or those over which there was still some doubt were reared through to adults in the clip cages. Additional information was obtained from keys by Vilbaste (1968, 1982).

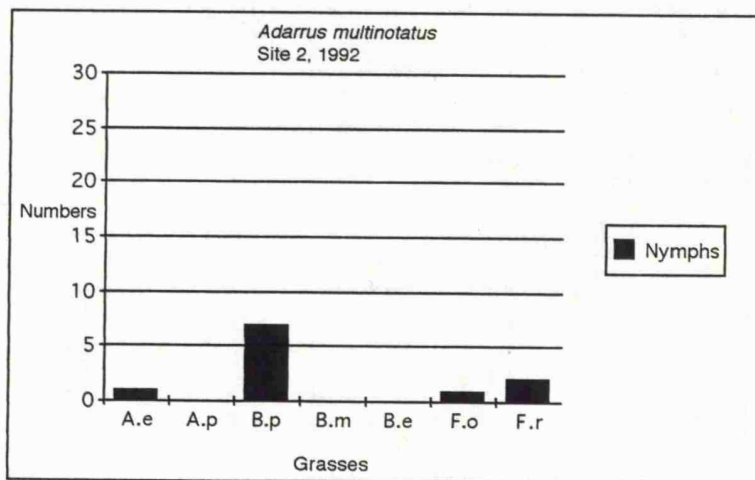
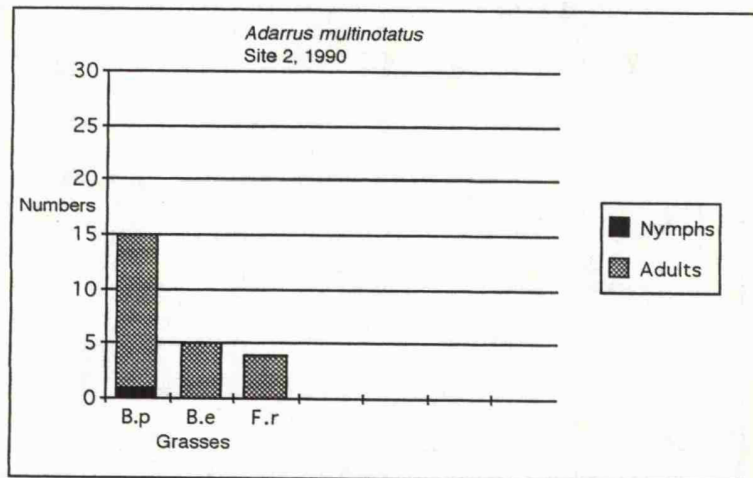


Fig 5.2 Distribution of *Adarrus multinotatus* among grasses in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*, B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*. T.f = *Trisetum flavescens*

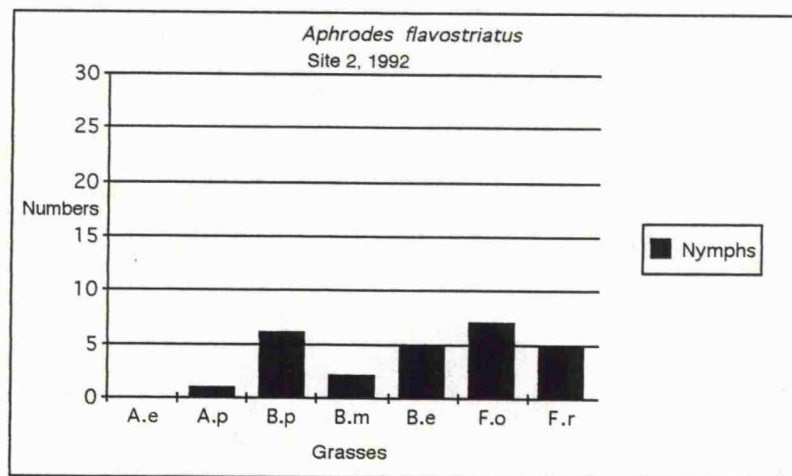
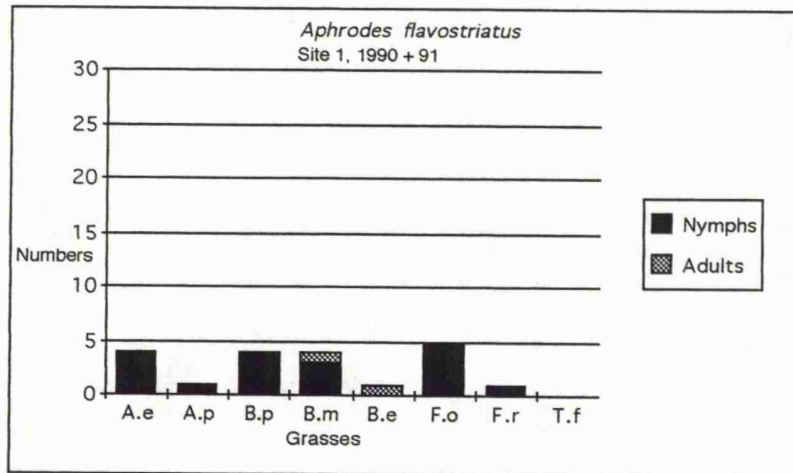


Fig 5.3 Distribution of *Aphrodes flavostriatus* among grasses in field choice experiments

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

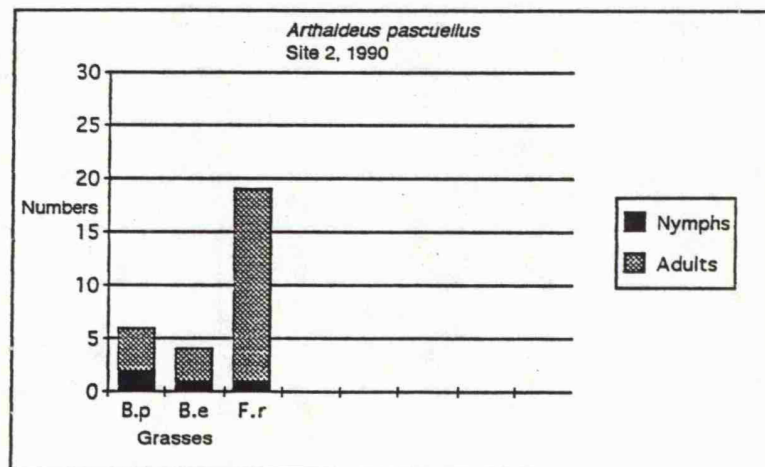
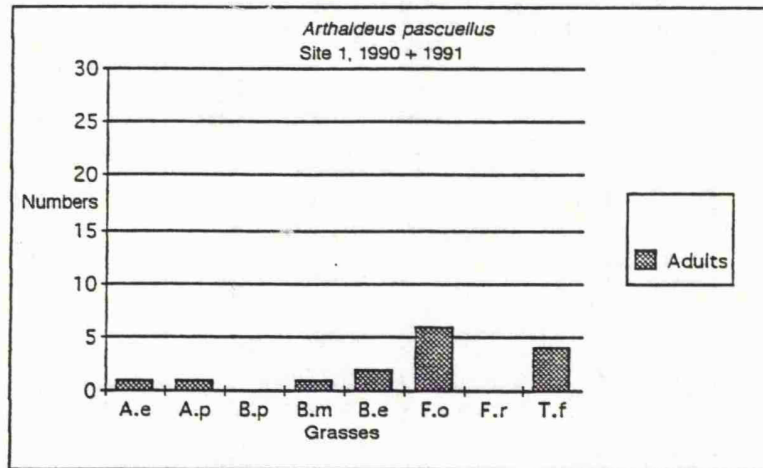


Fig 5.4 Distribution of *Arthaleus pascuellus* among grasses in fields choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avena pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

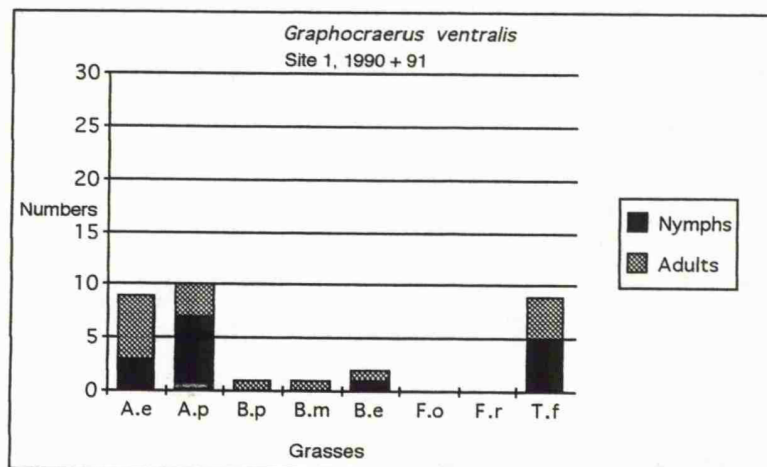
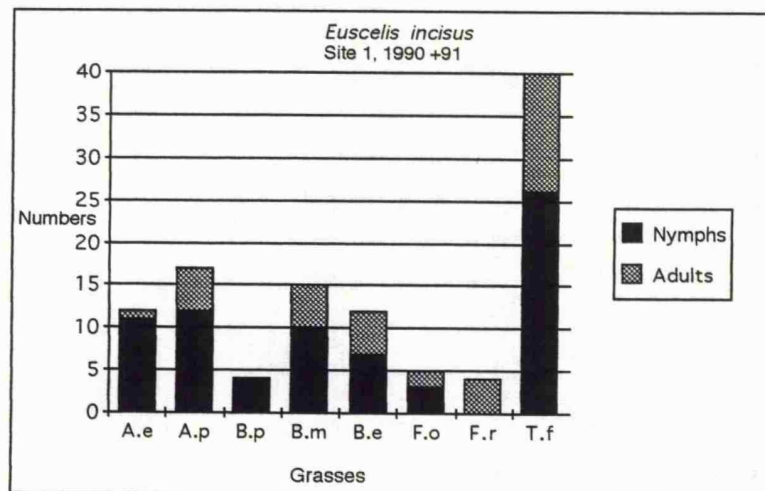
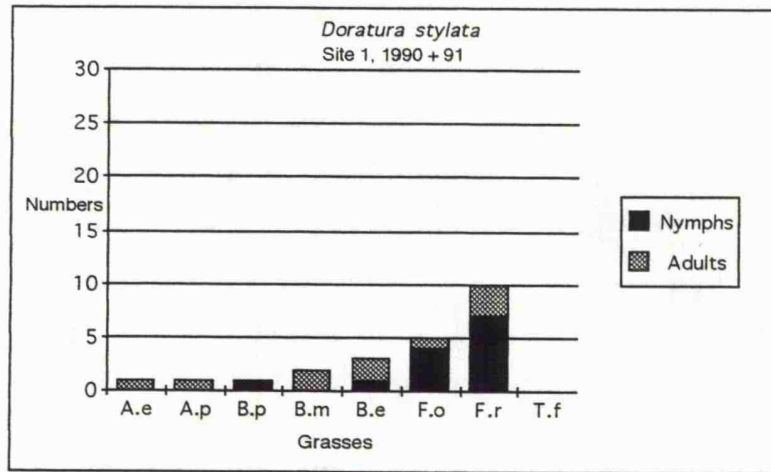


Fig 5.5 Distribution of *Doratura stylata*, *Euscelis incisus* and *Graphocraerus ventralis* among grasses in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

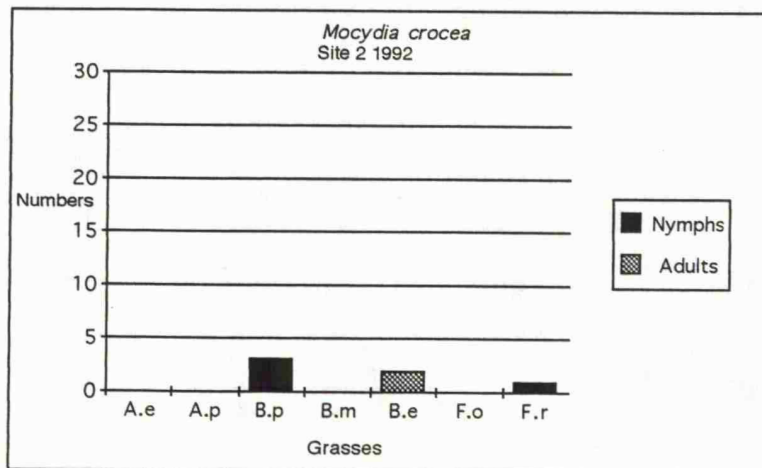
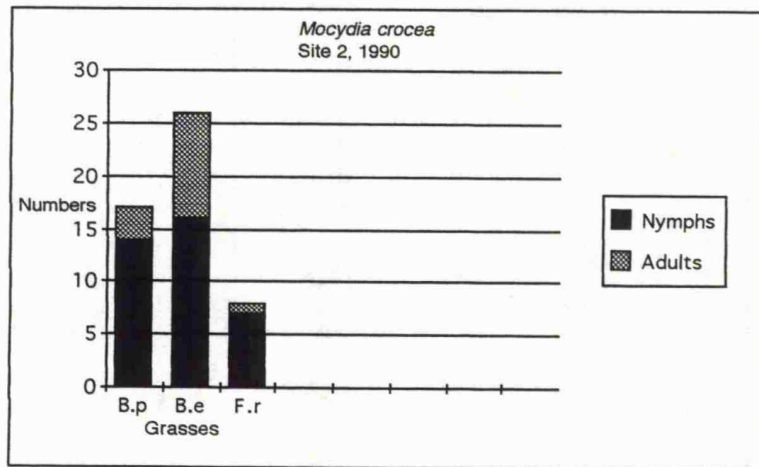
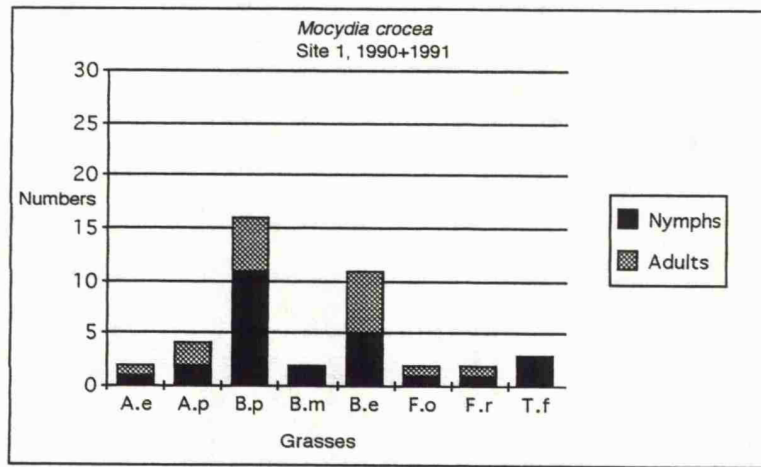


Fig 5.6 Distribution of *Mocydia crocea* among grasses in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

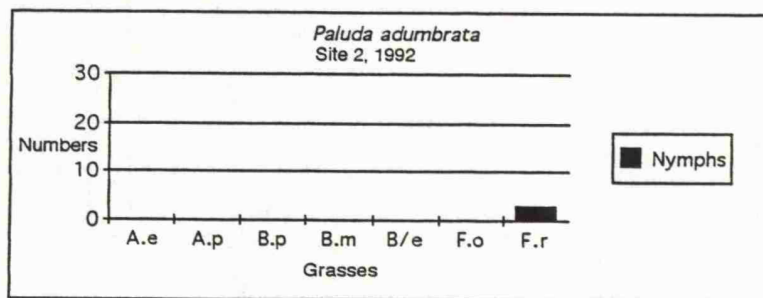
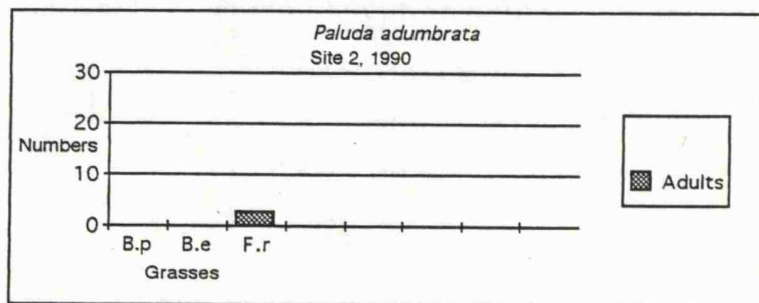
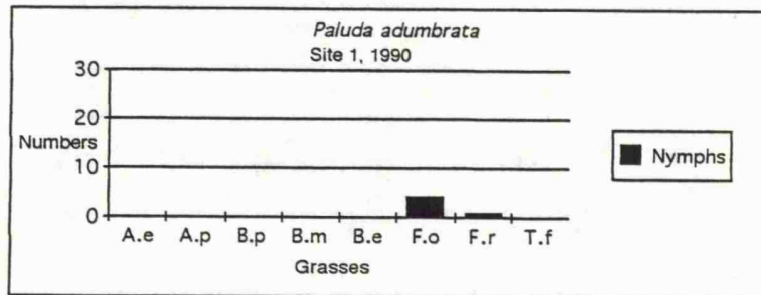


Fig 5.7 Distribution of *Paluda adumbrata* among grasses in field choice experiments. (NB *P. adumbrata* is included despite low numbers because of the consistent results).

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

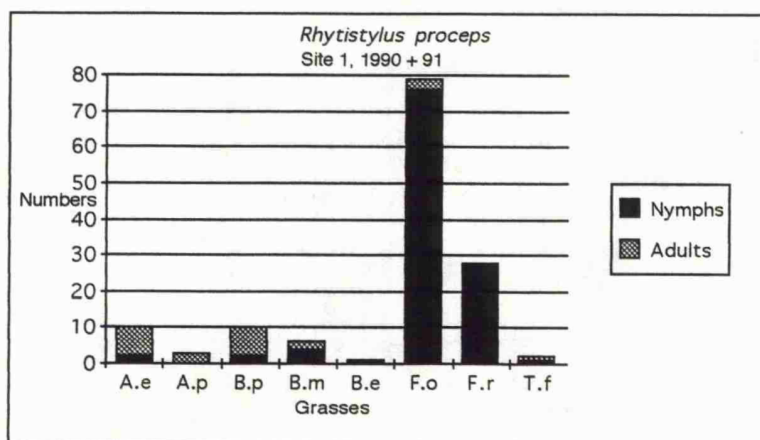
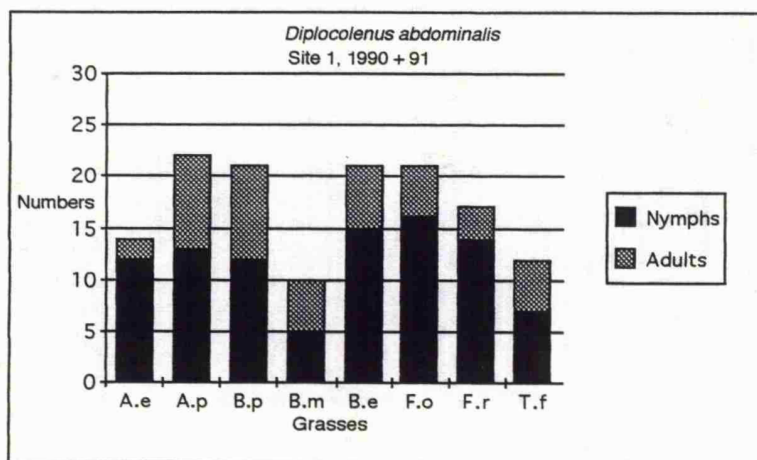
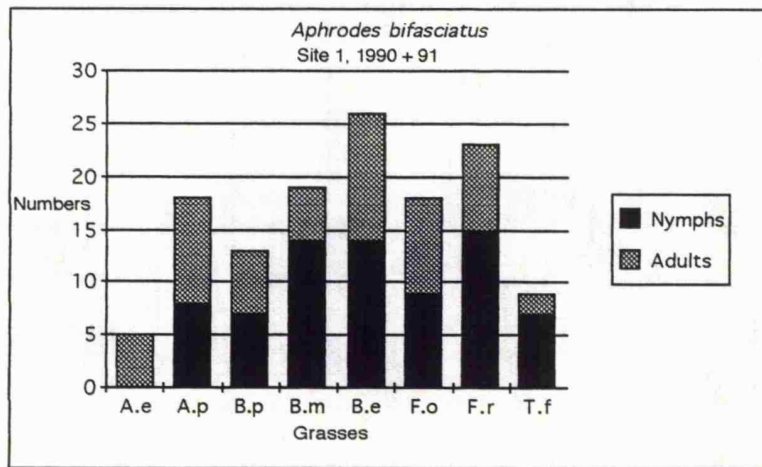


Fig 5.8 Distribution of *Aphrodes bifasciatus*, *Diplocolenus abdominalis* and *Rhytistylus proceps* among grasses in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

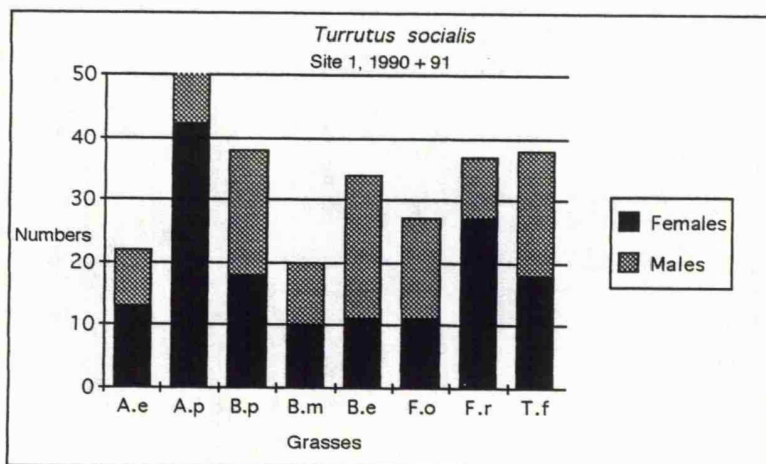
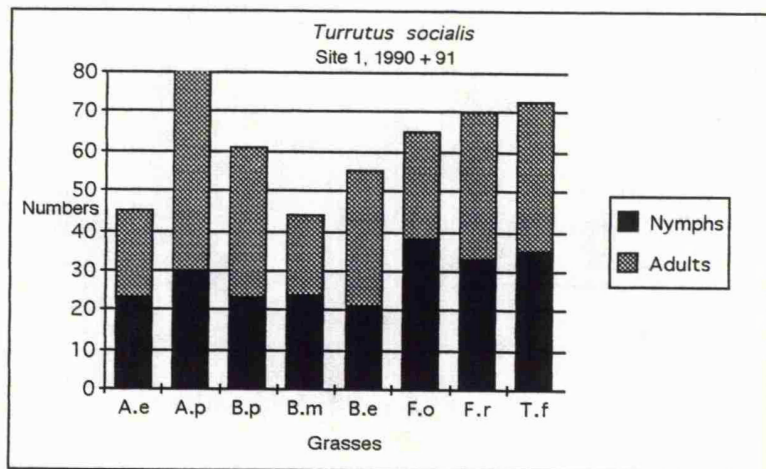


Fig 5.9 Distribution of *Turrutus socialis* among grasses in field choice experiments

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
 B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

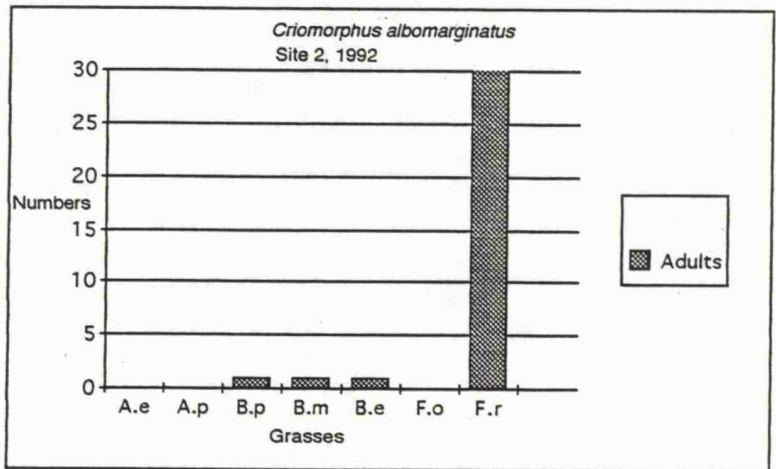
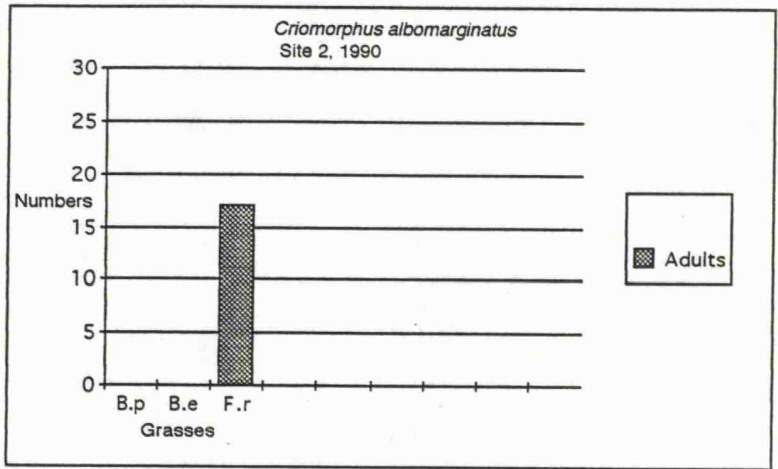
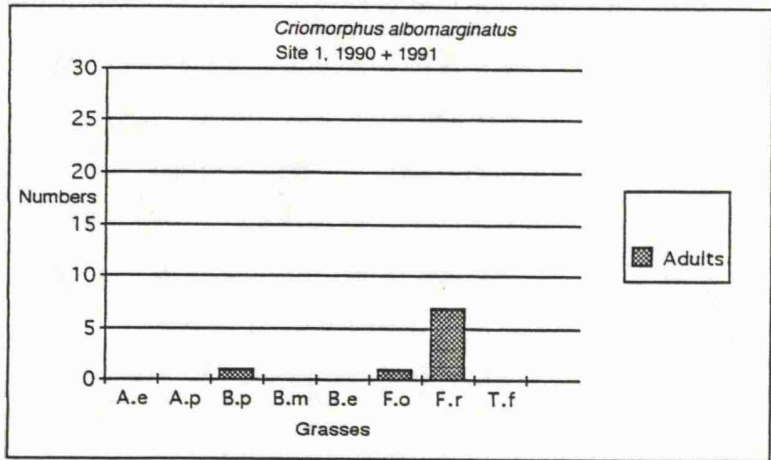


Fig 5.10 Distribution of *Criomorpus albomarginatus* among grasses in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*, B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*

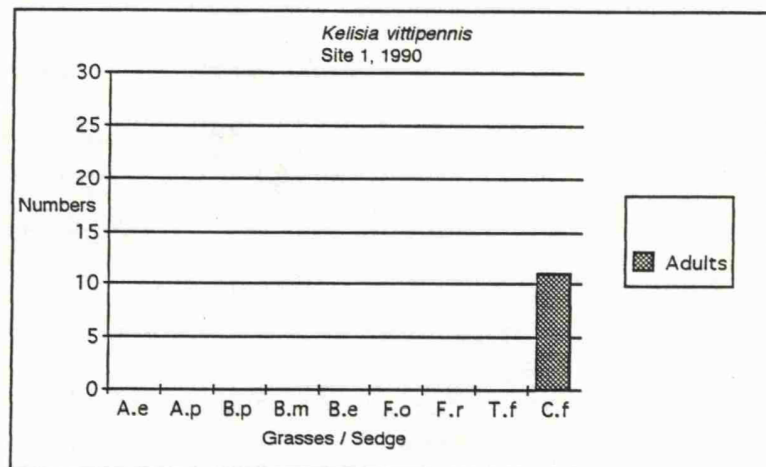
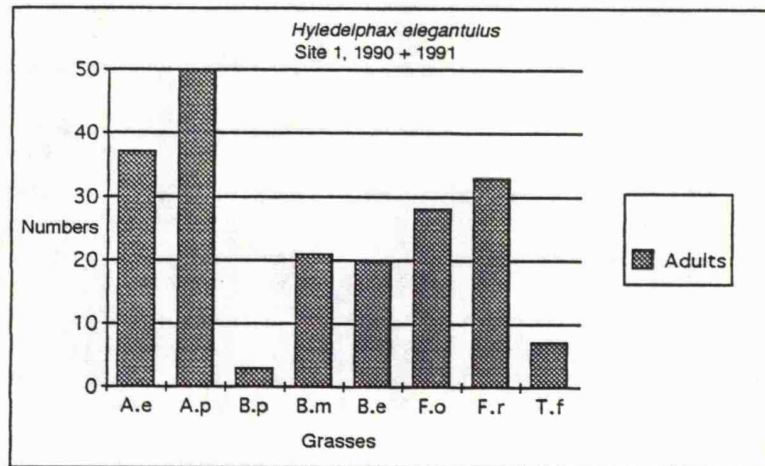


Fig 5.11 Distribution of *Hyledephax elegantulus* and *Kelisia vittipennis* on grasses and sedge used in field choice experiments.

Grasses: A.e = *Arrhenatherum elatius*, A.p = *Avenula pubescens*, B.p = *Brachypodium pinnatum*
B.m = *Briza media*, B.e = *Bromus erectus*, F.o = *Festuca ovina*, F.r = *F. rubra*, T.f = *Trisetum flavescens*, C.f = *Carex flacca*

During 1990-91 *Arrhenatherum elatius* failed to overwinter in the pots and had to be discarded. *Trisetum flavescens* did not overwinter well and two out of the eight plants failed leaving six to be included in the experiment. Two *Carex flacca* plants also failed. In 1991-92 *T. flavescens* failed completely, while all *A. elatius* plants survived. The other species overwintered well in both years.

5.4.2 Results

The dominant species hatching from the overwintered Site 1 plants in 1991 were *Aphrodes albifrons* and *Zyginidia scutellaris* (Table 5.11). They showed significant heterogeneity in their distribution among the grasses ($P < 0.001$ for both species). Almost twice as many *A. albifrons* hatched from *Festuca ovina* as from any other plant and *Z. scutellaris* was recorded mainly from broad leaved grasses, especially *Briza media*. Of the other species, *Mocycdia crocea* was found only on *Bromus erectus* and *Turrutus socialis* mainly on *Brachypodium pinnatum* and *Festuca rubra*. Smaller numbers of leafhoppers were obtained from the Site 2 grasses (Table 5.12), *Aphrodes flavostriatus* was recorded mainly from *Festuca rubra* and *Mocycdia crocea* from *Brachypodium pinnatum* and *Bromus erectus*.

Low numbers were also obtained in 1992 from the full set of grasses (minus *T. flavescens*) used in the 1991 field experiment (Table 5.13). *Aphrodes albifrons* again came predominantly from *F. ovina*, and 4 out of the 5 *Turrutus socialis* obtained were found on *Avenula pubescens*.

Table 5.11 Leafhoppers hatched from plants used in the Site 1 field experiment and overwintered in the greenhouse. (Collected June 9 - 11, 1991). Numbers of plants from which leafhoppers were collected are given in parenthesis.

	Gramineae:	A. pubescens	B. pinnatum	B. media	B. erectus	F. ovina	F. rubra	T. flavescens	Carex flacca	Chi-squared (7x1)*
Cicadellidae:										
Aphrodes albifrons	1	14 (5)	6 (4)			23 (6)	7 (6)	3 (2)	1	55.3 (P<0.001)
A. flavostriatus	1						1			-
Doratura stylata										-
Euscelis incisus										-
Mocycia crocea					17 (2)					-
Turrutus socialis			4 (3)		1	1	3 (2)			-
Zyginidia scutellaris	3 (1)	14 (5)	36 (6)	12 (5)				2 (1)		112.2 (P<0.001)

* Results for *Carex flacca* not included in the chi-squared analysis.
 -- = Insufficient data for valid chi-squared analysis

Table 5.12 Leafhoppers hatched from plants used in Site 2 field experiment in 1990. (Collected June 9 - 11th 1991).

	Gramineae:	B. pinnatum	B. erectus	F. rubra
Cicadellidae:				
Aphrodes albifrons	2 (1)	1	2 (2)	
A. flavostriatus		1	8 (3)	
Arthaldeus pascuellus			1	
Mocycia crocea	1	2 (2)		

Table 5.13 Leafhoppers hatched from plants used in Site 2 field experiment 1991. (Collected May 28 - June 1, 1992).

	Gramineae:	A. elatius	A. pubescens	B. erectus	B. media	B. pinnatum	F. ovina	F. rubra
Cicadellidae								
Aphrodes albifrons	4 (2)						10 (4)	2 (1)
Euscelis incisus						1		
Turrutus socialis	1	4 (2)						

5.5 Discussion

The results obtained from the greenhouse and field choice experiments provide useful information on the host plants of the Auchenorrhyncha of the Deeps. They indicate a significant degree of host specialism (monophagy or oligophagy) among many of the species recorded as well as a wide host range in a number of the common species. The data support or add to published information in some cases, but contradict previous findings in others.

There is no published information on the host plants of *Adarrus multinotatus* in this country, but the results obtained in this study support those of Schiemenz (1969), who found from field observations in Germany that *A. multinotatus* was associated with *B. pinnatum*. The greenhouse choice tests provided good evidence that this species is specific to *Brachypodium pinnatum* at the Deeps. This conclusion is supported by the field choice experiments, although *A. multinotatus* was only caught in small numbers from the experimental grasses, and by the initial survey in which *A. multinotatus* was only found in association with *B. pinnatum*.

The results indicated that some Auchenorrhyncha species were closely associated with *Festuca* spp. *Rhytistylus proceps* was one of the more abundant species on Site 1 and the nymphs were caught in relatively high numbers in the field choice experiment from *F. ovina* and *F. rubra*, especially the former. Although the adults, which were caught in low numbers, showed little host preference, the nymphs had one of the highest specificity indices recorded. This is in partial agreement with the findings of Waloff & Solomon (1973), who found main host plant was *F. rubra*, and with Morris (1990b) who found that *R. proceps* was associated with fine-leaved grasses. Other cicadellids that possibly showed a preference for *Festuca* spp. were *Doratura stylata* and *Paluda adumbrata*; however, because of the small numbers caught in the field experiment, the evidence is less reliable. In both cases the nymphs occurred almost exclusively on either *F. ovina* or *F. rubra*. Waloff & Solomon (*op. cit.*) found *D. stylata* to be associated with *Agrostis capillaris* and

F. rubra at Silwood Park, while Prestidge & McNeill (1983) gave only *A. capillaris* as the host. Port (1981) found that on motorway verges *P. adumbrata* only occurred where *F. rubra* was present.

The results obtained from the smaller scale field experiment on Site 2 showed *Arthaldeus pascuellus* was significantly more abundant on *F. rubra* than on the two broad leaved grasses *B. pinnatum* and *B. erectus*. Morris (1990b) was unable to draw any conclusions as to the host preferences of *A. pascuellus*, owing to its varied occurrence on his experimental plots.

Euscelis incisus was one of the more abundant species sampled during the field experiments and showed a marked preference for *Trisetum flavescens*, despite the relatively sparse growth of this grass in pots. Morris (*op. cit.*) found that *E. incisus* showed a preference for fine-leaved grasses but Prestidge & McNeill (1981) found that it had a low specificity index and showed no preference for *Agrostis capillaris*, the only fine grass included in their grass plots that was also used by Morris.

Adults of the delphacid *Criomorpha albomarginatus* were caught in relatively high numbers from Site 2 in 1992 and occurred almost exclusively on *F. rubra*. This species provided one of the clearest examples of host specificity in the adult stage (the others were *A. multinotatus* and *Kelisia vittipennis*). Morris (1990b) found *C. albomarginatus* was associated with fine grasses, but Waloff & Solomon (*op. cit.*) gave *Holcus* spp. as the host plants. Another delphacid *Kelisia vittipennis* was specific to *Carex flacca* and was the only species that had a specificity index of one. This was partly due to the fact that only one species of sedge was included in the experiment but is nevertheless an indication of specificity to sedges in this species. This is in agreement with Le Quesne (1960) and Ossiannilsson (1978), although the latter also cites Linnavuori (1952) who found *K. vittipennis* associated with *Eriophorum vaginatum* in bogs.

Data from the field choice experiments indicated that some of the Auchenorrhyncha were associated with particular groups of grasses. Although the numbers caught were not large, *Graphocraerus ventralis* clearly showed a preference for *Arrhenatherum elatius*, *Avenula pubescens* and *Trisetum flavescens* and occurred on each of these species in about equal numbers. These grasses belong to the tribe Aveneae and this result is the clearest indication obtained in this study of an association between a leafhopper and a grass tribe. Although *G. ventralis* has been recorded by researchers at Silwood Park (Waloff & Solomon, 1973; Prestidge & McNeill, 1983; Prestidge 1982a) no host plant was given. Ossiannilsson (1983) quotes the 'Arrhenatheretum' as a plant association in which *G. ventralis* has been found (Schwoerbel, 1957) and *Poa pratensis* and *Anthoxanthum odoratum* as possible host plants (Schaefer, 1973).

The adults and nymphs of *Mocycdia crocea* were associated with *Brachypodium pinnatum* and *Bromus erectus*. The field evidence is backed up by the results obtained from the follow-up work on oviposition in which nymphs of *M. crocea* were found entirely on *B. erectus*, except for one on *B. pinnatum*. Whittaker (1969) gave *B. pinnatum* as the host plant of *M. crocea*, and Le Quesne (1969) gave *B. pinnatum*, *B. erectus* and *Dactylis glomerata*. Muller (1987) found that these grasses, together with *Lolium perenne*, were the main host plants of *M. crocea* nymphs and that semi-arid grassland in the Onobrychido - Brometum was the typical habitat of *M. crocea* in continental Europe. *M. crocea* is a calcareous grassland species in Britain (Waloff, 1980).

Apart from *M. crocea*, the nymphs that emerged from eggs on overwintered plants in 1991 were predominantly those of *Aphrodes albifrons* and *Zyginidia scutellaris*, two species that were only caught in low numbers from the field in the preceding year. Both species showed significant heterogeneity in their choice of plants for oviposition (assuming that the numbers of nymphs were an indication of the numbers of eggs laid). *Z. scutellaris* nymphs hatched from broad leaved grasses,

especially *Briza media*, and *A. albifrons* from a range of grasses but especially *F. ovina*. Published information on the host plants of *Z. scutellaris* includes *B. pinnatum* (Whittaker, *op. cit.*), *Holcus* spp. and *D. glomerata* (Waloff & Solomon, 1973), *D. glomerata* and *F. rubra* (Le Quesne & Payne, 1981) and coarse grasses (Morris, 1990b). This generally supports the findings of this study in that all these species, with the exception of *F. rubra*, are broad leaved grasses. The published host plants for *A. albifrons* are; *B. pinnatum* (Whittaker, *op. cit.*) *Holcus* spp. and *D. glomerata* (Waloff & Solomon *op. cit.*). The last-named authors found *A. albifrons* to be the most abundant species (out of 23) that hatched from grasses on which eggs had been laid by field populations despite the fact that sweep-net samples indicated it was one of the less abundant species on the site.

Three of the more abundant species on Site 1, *Aphrodes bifasciatus*, *Diplocolenus abdominalis* and *Hyledelphax elegantulus* gave little indication of host preference. *A. bifasciatus* occurred in similar numbers on most of the experimental grass species. The significant heterogeneity in the distribution of this species was mainly due to low numbers on *Arrhenatherum elatius* and *Trisetum flavescens*, two grasses which provided relatively low amounts of vegetation for Auchenorrhynchan colonisation. There is no published information, of which I am aware, on the host plants of this calcareous grassland species. *D. abdominalis* was the only common species that did not show significant heterogeneity in its distribution among the grasses. It is a species that has featured frequently in work based on the Silwood Park grasslands (Thompson, 1978; Hill, 1982; Prestidge, 1982a) where it has been found to be closely associated with *Holcus* spp., especially *H. lanatus*. Neither *Holcus* spp. was present on the study sites at the Deeps and *H. lanatus* was, according to Hepburn (1955), only occasional on the grassland as a whole. My own observations suggest that it is now an uncommon grass at the Deeps.

Hyledelphax elegantulus was the most abundant species early in the season on Site 1 in 1990, but virtually absent from the site in 1991. In 1991 it showed

significant heterogeneity in its distribution among the experimental grasses. Expected and observed numbers were more or less equal for *Briza media*, *Bromus erectus*, and *Festuca ovina*, while observed numbers were lower than expected on *Brachypodium pinnatum*, which grew well in the pots and was little affected by grazing, and on *Trisetum flavescens*. The result for the last-named species was probably due to its poor growth early in the season. Observed numbers were higher than expected on *Avenula pubescens* and *Festuca rubra*. This is in partial agreement with Waloff & Solomon (1973) who gave *F. rubra* as the host plant for this species.

Data on the grass hosts of *Turrutus socialis*, the most abundant species on Site 1, were obtained from greenhouse and field choice experiments. The results from the greenhouse experiments, especially on oviposition and subsequent emergence of nymphs, indicated that this species has a preference for *A. pubescens* and *F. rubra*. In the field both nymphs and adults occurred in relatively large numbers on most of the experimental grass species, the nymphs showing no more specificity than the adults. There was, however, significant heterogeneity in the distribution of *T. socialis* among the grasses, due mainly to a high number on *A. pubescens* and low numbers on *Arrhenatherum elatius* and *Briza media*. The numbers on *Festuca rubra* were little different from those on *Brachypodium pinnatum*, *Festuca ovina* and *Trisetum flavescens*. However, the proportion of female to male *T. socialis* was highest on *A. pubescens* and *F. rubra* and only on *F. rubra* were there significantly more females than males. This finding is of interest in that the behaviour of ovipositing females may be an important determinant of host specificity (Claridge, Reynolds & Wilson, 1977). Sowaga & Pathak (1970) found that the males of *Niliparvata lugens* showed more variance in host plant preference than females.

The technique of using potted grasses in the field to sample Auchenorrhyncha and to obtain information on host preferences was less effective than it might have been in this study because of the influence of drought and rabbit grazing. In more

favourable climatic conditions and in situations where control of grazing is possible the numbers of Auchenorrhyncha would probably have been much larger. Pots which carry their own reservoir of water ('self- watering' pots) have been used in the field (McNeill, pers. comm.) and would have been useful in overcoming the problems of drought at the Deeps.

As with sown plots, the pot technique allows individual grass species to be sampled. It has the advantage of mimicking the natural situation more closely (grasses often grow in scattered patches), of allowing a thorough search of all parts of a plant, right down to the soil surface, and of being a more practical approach in situations where resources are limited. The major disadvantage (apart from drought and grazing) is that only a small amount of vegetation is available for sampling a group of insects that is often highly mobile, especially in the adult stage. The nymphal stages of Auchenorrhyncha are less mobile than the adults and this may, at least in part, explain why they showed a greater degree of host specificity.

One of the useful outcomes of this aspect of the study is that it demonstrated the importance of including the nymphs in research on the host plants of grassland Auchenorrhyncha.

6. THE ROLE OF NITROGEN IN THE SELECTION OF GRASS HOSTS BY AUCHENORRHYNCHA

6.1 Introduction

The importance of nitrogen in insect plant relationships has been emphasised by a number of authors (e.g. McNeill & Southwood, 1978; Strong, Lawton & Southwood, 1984). Various studies have shown a correlation between insect performance and the nitrogen content of the plant food source. These include studies on the aphids *Brevicoryne brassicae* L. and *Myzus persicae* Sulz (Van Emden & Bashford, 1971), the mirid *Leptoterna dolabrata* (McNeill, 1973) and various Auchenorrhyncha (Hill, 1982; Prestidge 1982b).

Although plant nitrogen quality is undoubtedly important in insect / plant relationships, the extent to which it is a determining factor in host selection by grass feeding Auchenorrhyncha is still uncertain. There is good evidence that some species select their hosts on the basis of their nitrogen (or amino acid) content (Prestidge, 1982b; Prestidge & McNeill, 1983) but it has yet to be shown whether or not this is the case in the majority of species. The aim of this part of the study was to obtain information on the response of calcareous grassland Auchenorrhyncha to variation in the total leaf nitrogen of potential host plants.

6.2 Methods

6.2.1 Preliminary nitrogen analyses

Measurements of nitrogen in plants may be made for total nitrogen, soluble nitrogen (which gives an approximate indication of nitrogen in the phloem), and individual amino acids. Although soluble nitrogen and amino acid analyses would probably give the best indication of the nutrients available to Auchenorrhyncha, the techniques involved are more elaborate and time consuming than those required

for the measurement of total nitrogen. In the following investigations only total leaf nitrogen was measured.

The aim of the preliminary analyses was to obtain background information on nitrogen levels of grasses grown in pots, in a greenhouse, as compared with those in the field. Grasses grown in pots show a rapid decline in nutrient levels if unfertilised (Ratcliffe pers. comm.) and to counter this the greenhouse plants were fed with ammonium nitrate. Information on the response of grasses to a given concentration of NH_4NO_3 was needed for planning a field choice experiment with potted grasses. It was also necessary to develop a suitable procedure for dealing with the grass nitrogen determinations that were to be performed during the field experiment.

The three commonest grasses at the Deeps, *Brachypodium pinnatum*, *Bromus erectus* and *Festuca rubra* were used for the preliminary analyses. The greenhouse grasses were those that had been used for choice tests in the previous year (see Chapter 5). From March 16 until May 25 1989, three pots of each species were fed with 100 cm³ per pot of NH_4NO_3 at a concentration of 1g litre⁻¹ every two weeks. Leaf samples of *B. pinnatum* were taken from the greenhouse and the field (on the same day) on five occasions between the end of March and mid July. For *B. erectus* and *F. rubra* samples were taken on four occasions between early May and mid July. On each sampling occasion between 5 g and 10 g fresh weight of each species were collected. The leaves cut from the plants were fully expanded and showed no signs of senescence. The greenhouse samples were taken from all three plants of each species and the field samples were taken at random from two areas of the grassland. The leaves were dried to constant weight at 80°C, milled in an electric mill and stored in polythene bags prior to nitrogen determination. Nitrogen levels in grasses grown in pots with a small quantity of bone meal mixed with soil at the time of potting as the only nutrient supplement were not measured during the preliminary analyses.

Total nitrogen was measured by means of a micro-Kjeldahl digestion (Benton Jones 1987) followed by colorimetric determination. In the preliminary analyses 0.2 g of a milled sample was placed in a round bottomed flask with 5 cm³ concentrated sulphuric acid and a tablet composed of 1 g Na₂SO₄ and 0.05 g Se. (The selenium is a catalyst and the sodium sulphate raises the temperature of the digestion). Each sample was duplicated. The flasks were heated on a heating rack in a fume cupboard at a relatively low temperature (approximately 100° C) for one hour to avoid bumping and then, once the solution had cleared, at a higher temperature (approximately 300° C) for a further hour. The digestion of the vegetation oxidises carbon compounds to CO₂ and converts all forms of organic-nitrogen to ammonium-nitrogen. Following the digestion the flasks were allowed to cool before the contents were transferred to 100 cm³ volumetric flasks and made up to volume with deionised water.

For the colorimetric determination of ammonium, 100 microlitres of the diluted digest were transferred to a sterile screw top plastic tube and mixed with 5 cm³ salicylate reagent and 5 cm³ cyanurate standard (added in that order). The screw top was replaced immediately after adding these reagents to avoid loss of ammonia. The bottles were left to stand for 30 minutes to allow the colour (emerald green) to develop. Standard solutions were made up by digesting NH₄Cl in the same background as that used for the grass samples (concentrated H₂SO₄ plus selenium tablet). The concentrations of NH₄Cl used to make up the standards were 1 mM, 3 mM and 5 mM. These solutions were treated as described above for the grass samples and used to calibrate a Beckman spectrophotometer. Absorbance was read at 677 nm. The concentration of nitrogen in the grass leaf digests was then read on the spectrophotometer in mM and converted to % nitrogen (dry weight).

6.2.2 Analysis of total leaf nitrogen in the field choice experiment

To obtain data on the responses of leafhoppers to the nitrogen content of potential

host plants, samples were taken from the grasses used in the field choice experiment in 1990 every four weeks between April 11 and September 11 and analysed for total nitrogen.

The species of grass used and the way they were prepared and placed in the field has been described in the previous chapter. The paired arrangement of grasses in the grid was adopted so that a comparison could be made between fertilised and untreated plants. Approximately every two weeks from June 18 onwards, the more easterly plants of each pair were fed with 100 cm³ of 1g litre⁻¹ of NH₄NO₃. To ensure that all plants received the same amount of water, the untreated plant of a pair was given 100 cm³ of water. Otherwise water was given to all plants equally when required (i.e. during dry spells of weather).

In April and May, before treatment with NH₄NO₃ started, samples of fully expanded, non-senescent leaves were taken from all plants and pooled for each species for nitrogen determination. The first nitrogen determination was made as soon as the grasses were put out in the field on April 11, but poor weather delayed the first *Auchenorrhyncha* sample to 26 April. Two further determinations were made during this period on May 17 and June 13. From June 26 onwards samples from the four treated and four untreated plants of each species were collected and analysed separately. Four determinations were made during this period on dates approximately mid-way between additions of NH₄NO₃ (June 26, July 23, August 16 and September 11). This experimental design was adopted so that the response of *Auchenorrhyncha* to nitrogen variation within a grass species as well as between grass species could be investigated.

The micro Kjeldahl digestion technique used for the preliminary analyses was modified in order to process more samples. A smaller quantity of milled grass (0.1g) was weighed on a beam balance and placed in a tall Pyrex boiling tube

(15 cm tall and 1.9 cm in diameter). To this was added 3 cm³ H₂SO₄ and a digestion tablet. A glass bulb drawn out into a narrow tube on one side was used as a stopper and rested on the top of the boiling tube with the drawn out glass extending downwards to provide stability; this prevented the loss of acid during heating. Unused grass material from the preliminary analyses was analysed using this modified technique as a check on the methods.

6.2.3 Oviposition and Grass Nitrogen

As described in the previous chapter, the grasses used in the 1990 field choice experiment were taken into the greenhouse in late October and overwintered. In April of the following year they were each covered by a fine nylon hood (Plate 5.1, p. 66) to contain any nymphs which hatched from eggs laid during the previous year. In addition to the results described in the previous chapter data were obtained on the numbers of nymphs hatching from treated and untreated grasses. Overwintering eggs would have been laid later in the season, well after the beginning of treatment with NH₄NO₃ on June 18.

6.3 Results

6.3.1 Preliminary analyses

The mean values for total leaf nitrogen of the three grass species used in the preliminary analyses are shown in Table 6.1 below.

Table 6.1 Mean % dry weight of total leaf nitrogen in greenhouse and field grasses, based on 5 determinations between March and July 1989

Grass:	% Nitrogen (dry wt.)	
	Field samples	Greenhouse samples (NH ₄ NO ₃ treated)
<i>Brachypodium pinnatum</i>	2.58	2.67
<i>Bromus erectus</i>	1.92	2.89
<i>Festuca rubra</i>	1.59	2.76

All grasses fed with NH_4NO_3 in the greenhouse had higher mean nitrogen contents than those from the field although in the case of *Brachypodium pinnatum* the difference was small. The effect of adding nitrogen to the grasses was to maintain total leaf nitrogen at a fairly constant level; in the field grasses the nitrogen showed a steady decline from March to July (Fig 6.1). As the results showed that feeding the grasses grown in pots with 100 cm^3 of 1 g litre^{-1} NH_4NO_3 every two weeks maintained total leaf nitrogen at levels that were generally well above those of grasses in the natural field situation, it was decided that this level of feeding would be suitable for the field choice experiment. Although nitrogen levels in grasses grown in pots without the addition of NH_4NO_3 were not measured at this stage, it was assumed that the contrast between NH_4NO_3 fed and unfed potted grasses would be suitable for the field choice experiment.

6.3.2 Grass nitrogen in the field choice experiment

The modified micro-Kjeldahl technique used to assess the total leaf nitrogen in the field choice experiment gave very similar results to those obtained using the original method when tested with spare material from the preliminary analyses. The results are shown in Table 6.2.

Table 6.2 Comparison of flask and tube micro-Kjeldahl methods for determining total nitrogen. Values for one sample, taken from greenhouse grasses 10.7.89

Grass	Nitrogen (% dry wt.)	
	Flask method	Tube method
<i>Brachypodium pinnatum</i>	2.40	2.32
<i>Bromus erectus</i>	2.68	2.62
<i>Festuca rubra</i>	2.43	2.40

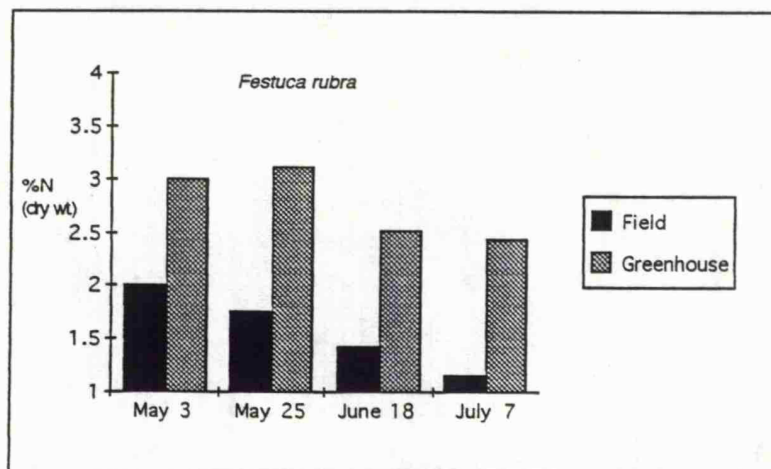
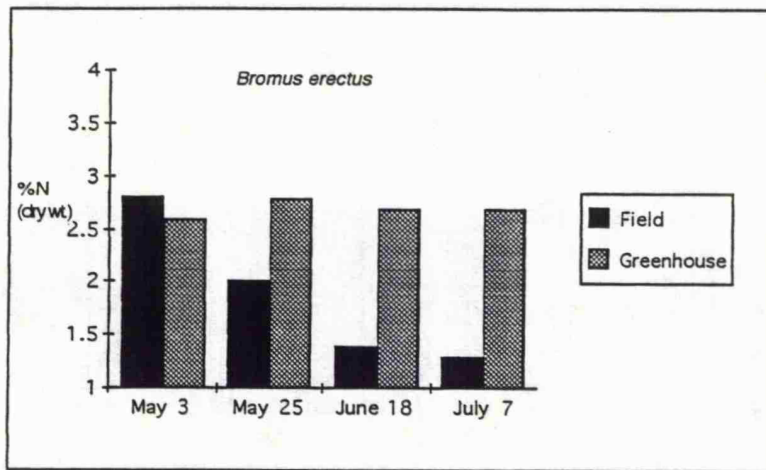
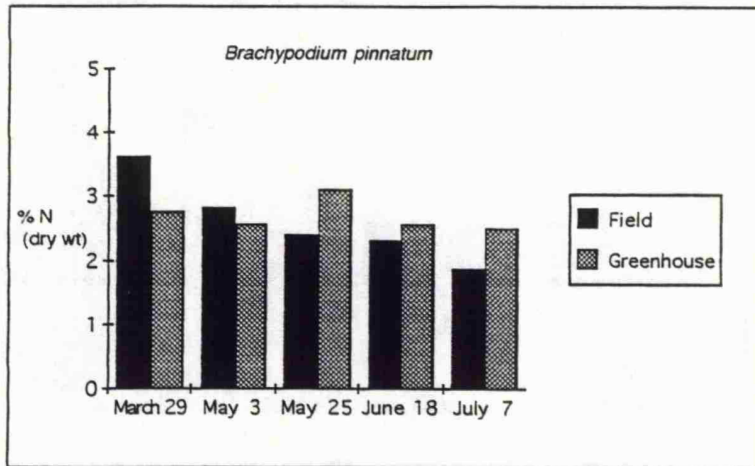


Fig 6.1 Changes in the total leaf nitrogen of grasses in the greenhouse and the field.

There was considerable variation in the total leaf nitrogen of the different grass species used in the field choice experiment. The mean values for the grasses not treated with NH_4NO_3 are given for the April - September sampling period in Table 6.3. The values ranged from 2.3% nitrogen (dry wt.) in *Festuca ovina* to 3.7 % in *Trisetum flavescens*.

The changes in nitrogen values during the sampling period are shown for each grass species in Figs 6.2 - 6.4 (pp. 117-119). There was a general decline in leaf nitrogen in most of the untreated grasses as the season progressed. In some cases the decline was steady and in others more erratic. *Arrhenatherum elatius* showed a decline in leaf nitrogen followed by a sharp increase early in the season before a regular decline set in from June 26. *A. elatius* was the species most heavily grazed by rabbits and this may have been the cause of the irregular changes in nitrogen early in the season. The highest spring values (> 4% nitrogen) were found in the Aveneae (*A. elatius*, *Avenula pubescens* and *Trisetum flavescens*) and the lowest in *Briza media* and *Festuca ovina*. The grasses fed with NH_4NO_3 from June 18 all showed a marked increase in total leaf nitrogen as compared with the untreated set. Anomalous results were obtained for *A. elatius* on June 26 and *Bromus erectus* August 16 when untreated grasses gave the same nitrogen value as the treated (Figs 6.2 and 6.3) and for *Brachypodium pinnatum* on June 26 when the untreated grasses gave a higher nitrogen value than the treated. The value for treated *Trisetum flavescens* on August 16 was, like *B. erectus*, much less than the values measured before and after that date. As there seems to be no biological reason why these anomalous values should have occurred, it is most likely they were due to experimental error.

The mean nitrogen values for the treated and untreated grasses for the period June 26 - September 11 are given in Table 6.4. The greatest response to NH_4NO_3 was shown by *F. ovina* (48% increase in mean nitrogen content) followed by *F. rubra* (20%) and the smallest response by *Carex flacca* (7%).

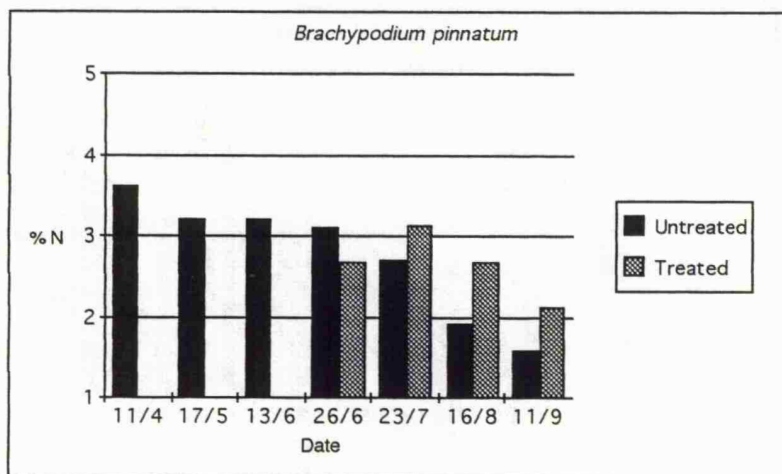
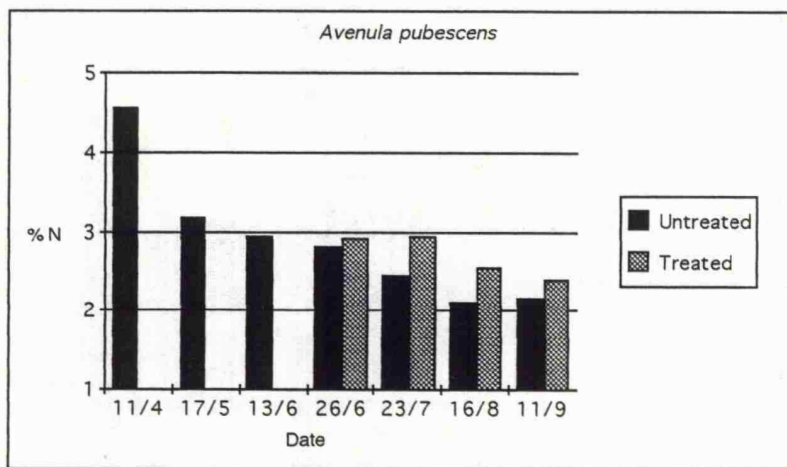
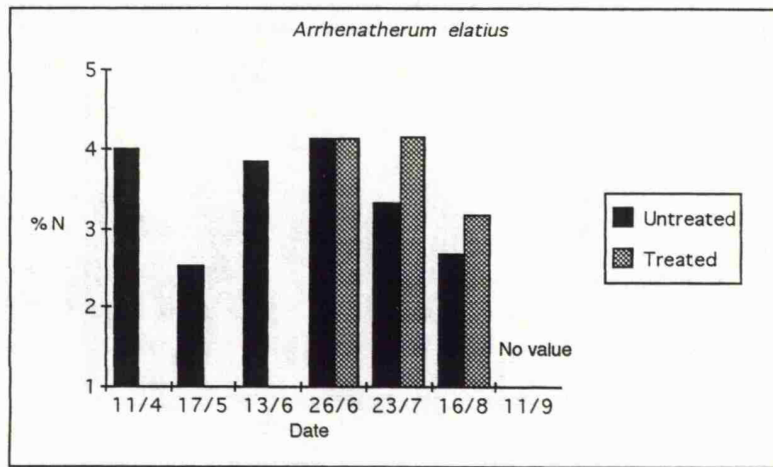


Fig 6.2. Comparison of changes in total nitrogen (% dry wt.) in untreated and treated grasses during the 1990 field choice experiment.

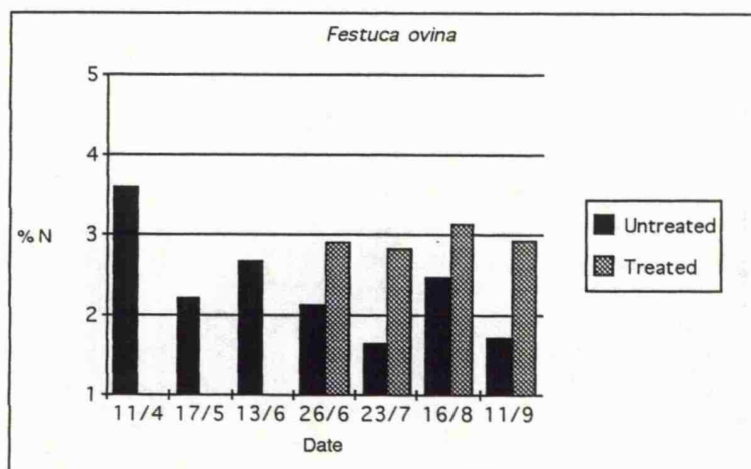
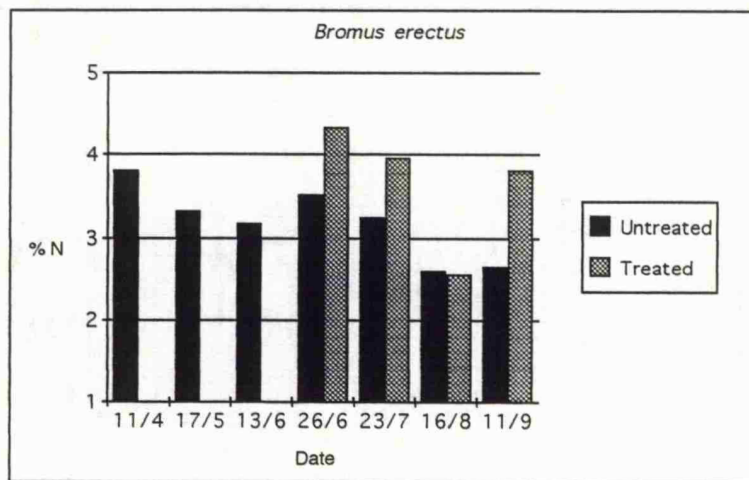
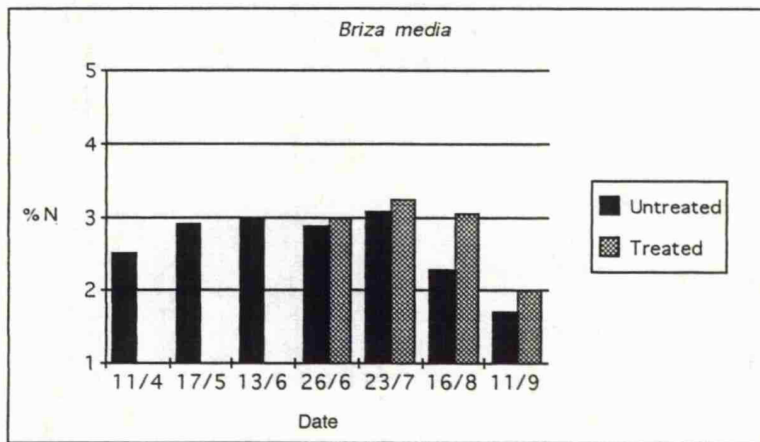


Fig. 6.3. Comparison of changes in total nitrogen (% dry wt.) in treated and untreated grasses during the 1990 field choice experiment.

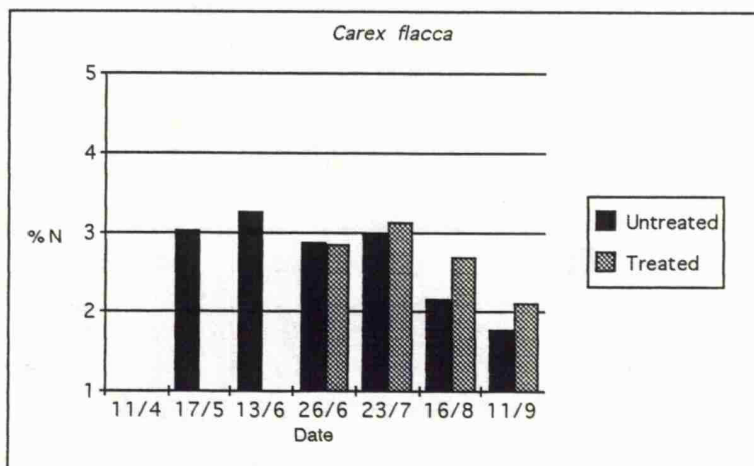
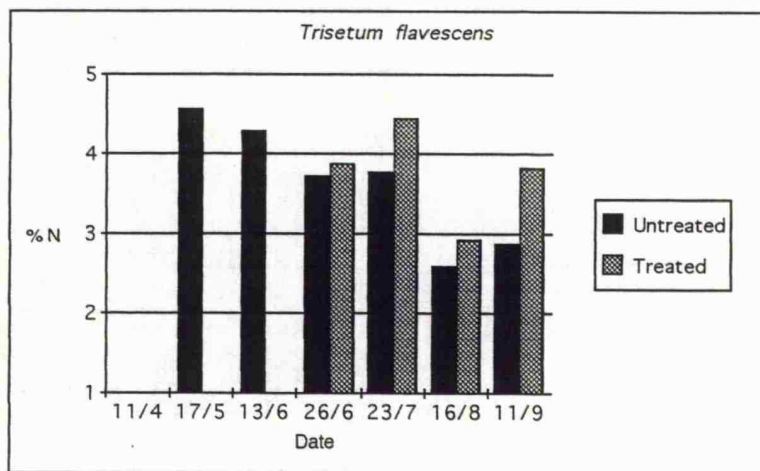
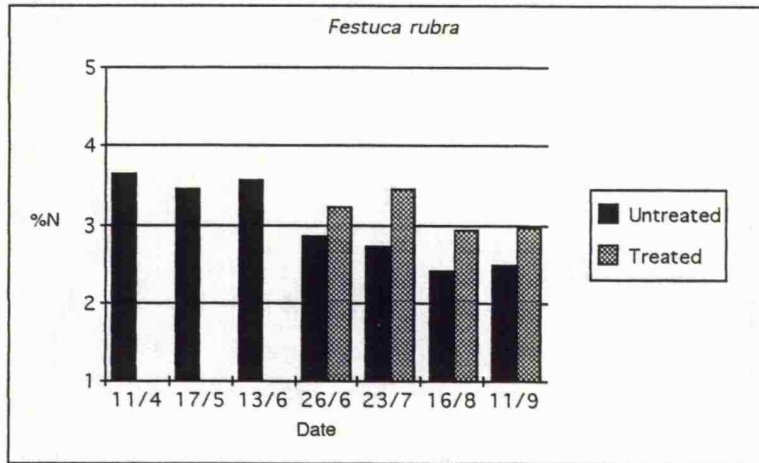


Fig. 6.4. Comparison of changes in total nitrogen (% dry wt.) in treated and untreated grasses during the 1990 field choice experiment.

Table 6.3 Mean total leaf nitrogen for the period 11.4.90 - 11.9.90, for grasses not treated with ammonium nitrate (7 determinations)

Plants	% Nitrogen (dry wt.)
<i>Arrhenatherum elatius</i>	3.4
<i>Avenula pubescens</i>	2.9
<i>Brachypodium pinnatum</i>	2.7
<i>Briza media</i>	2.6
<i>Bromus erectus</i>	3.2
<i>Festuca ovina</i>	2.3
<i>Festuca rubra</i>	3.0
<i>Trisetum flavescens</i>	3.7
<i>Carex flacca</i>	2.7

Table 6.4 Comparison of means of total leaf nitrogen in fed and unfed grasses for the period 2.6.90 - 11.9.90 (4 determinations)

Plants	% Nitrogen (dry wt.)	
	Untreated	Treated
<i>Arrhenatherum elatius</i>	3.38	3.81
<i>Avenula pubescens</i>	2.38	2.70
<i>Brachypodium pinnatum</i>	2.33	2.65
<i>Briza media</i>	2.49	2.83
<i>Bromus erectus</i>	3.00	3.66
<i>Festuca ovina</i>	1.99	2.94
<i>Festuca rubra</i>	2.63	3.15
<i>Trisetum flavescens</i>	3.24	3.77
<i>Carex flacca</i>	2.44	2.61

6.3.3 The response of Auchenorrhyncha to grass nitrogen

The numbers of leafhoppers on paired grasses in the field choice experiment prior to nitrogen treatment

Prior to nitrogen treatment each grass plant of a pair in the field grid at the Deeps was treated in exactly the same way except that one was 50 cm to the west of its partner and was always sampled first. (It was the eastern partner that was treated with NH_4NO_3 from 18.6.90). It is very unlikely that the position of the pots would have affected the catch of leafhoppers, but it is possible that leafhoppers on the eastern plant of a pair were disturbed while the western one was being sampled, despite the care taken to avoid casting shadows on unsampled pots. Wilcoxon signed ranks tests (Siegal & Castellan, 1988) showed no significant difference between the catches from eastern and western plants on any of the four sampling occasions prior to nitrogen treatment. The pooled results also showed no significant difference ($P > 0.25$) (Table 6.5).

The response of Auchenorrhyncha to grass hosts treated with nitrogen (Responses to nitrogen variation within grass species)

Auchenorrhyncha were collected from the potted grasses on six occasions during the treatment with NH_4NO_3 . Wilcoxon signed ranks tests showed a significant difference ($P < 0.05$) in the total number of Auchenorrhyncha caught from the treated (eastern) as compared with the untreated (western) pots on only one occasion (6.9.90). There was also a significant difference between the two categories when the totals for the six sampling occasions were tested. ($P < 0.02$) (Table 6.6)

Turrutus socialis was the dominant leafhopper caught during the treatment period. Significantly more adults of this species were caught on treated than on untreated grasses ($P < 0.01$) (Table 6.7). The results obtained for all species of

Table 6.5

Comparison of Auchenorrhyncha caught from paired plants (referred to as western and eastern plants) in the field choice experiment during the period prior to nitrogen treatment. There were four plants of each species in each category. Totals of four sampling occasions

Plants	Western plants	Eastern plants
<i>Arrhenatherum elatius</i>	28	50
<i>Avenula pubescens</i>	62	40
<i>Brachypodium pinnatum</i>	23	21
<i>Briza media</i>	27	28
<i>Bromus erectus</i>	23	50
<i>Festuca ovina</i>	58	79
<i>Festuca rubra</i>	61	51
<i>Trisetum flavescens</i>	32	31
<i>Carex flacca</i>	2	15
Totals	316	365

Wilcoxon signed ranks statistic = 29 ($0.3 > P > 0.25$)

Table 6.6

Comparison of Auchenorrhyncha caught from treated (eastern) and untreated plants in the field choice experiment. Totals of 6 sampling occasions.

Plants	Untreated	Treated
<i>Arrhenatherum elatius</i>	26	13
<i>Avenula pubescens</i>	37	53
<i>Brachypodium pinnatum</i>	31	45
<i>Briza media</i>	27	43
<i>Bromus erectus</i>	35	30
<i>Festuca ovina</i>	28	65
<i>Festuca rubra</i>	26	47
<i>Trisetum flavescens</i>	32	52
<i>Carex flacca</i>	22	33
Totals	264	381

Wilcoxon signed ranks statistic = 41 ($0.01 > P > 0.02$)

Table 6.7. Numbers of *Turrutus socialis* adults and nymphs caught from treated and untreated plants in field choice experiment. Data from 6 sampling occasions during period 21.6.90 - 28.9.90.

Plants	Adults		Nymphs	
	Untreated	Treated	Untreated	Treated
<i>Arrhenatherum elatius</i>	8	6	2	2
<i>Avenula pubescens</i>	17	24	5	7
<i>Brachypodium pinnatum</i>	9	21	4	2
<i>Briza media</i>	3	11	5	3
<i>Bromus erectus</i>	11	10	7	4
<i>Festuca ovina</i>	3	17	4	9
<i>Festuca rubra</i>	4	19	6	11
<i>Trisetum flavescens</i>	13	18	5	11
<i>Carex flacca</i>	5	13	2	2
Totals	73	139	40	51
Wilcoxon signed ranks statistic	42 (0.005<P<0.01)		20 (P>0.5)	

Table 6.8 Numbers of *Euscelis incisus* and *Rhytistylus proceps* caught from treated and untreated grasses during field choice experiment. Data from six sampling occasions during the period 21.6.90 - 28.9.90.

Plants	<i>Euscelis incisus</i>		<i>Rhytistylus proceps</i>	
	Untreated	Treated	Untreated	Treated
<i>Arrhenatherum elatius</i>	2	1	0	0
<i>Avenula pubescens</i>	2	6	1	1
<i>Brachypodium pinnatum</i>	2	2	2	2
<i>Briza media</i>	4	4	1	4
<i>Bromus erectus</i>	3	4	0	0
<i>Festuca ovina</i>	1	3	6	11
<i>Festuca rubra</i>	2	4	4	5
<i>Trisetum flavescens</i>	8	14	1	2
<i>Carex flacca</i>	1	1	0	1
Totals	25	39	15	26
Wilcoxon signed ranks statistic	19.5 (0.02<P<0.05)		10 (0.05<P<0.1)	

Auchenorrhyncha (Table 6.6) were largely due to *T. socialis*. The nymphs of *T. socialis* showed no preference for treated plants, but few were caught during the treatment period (Table 6.7). The differences in the numbers of adult *T. socialis* caught from untreated and treated plants varied considerably. There were, for instance, relatively large differences in the numbers caught from the two categories of *Brachypodium pinnatum* and both *Festuca* spp., while from *Arrhenatherum elatius* and *Bromus erectus* (two grasses more severely affected by rabbit grazing) there was very little difference (in fact, slightly more *T. socialis* were caught from the untreated grasses). The possibility that these differences were related to the response of the grasses to NH_4NO_3 , in terms of increased leaf nitrogen, was tested by calculating the Spearman rank-order correlation coefficient between the percentage difference in the numbers caught on the two treatments and the percentage increase in leaf nitrogen shown by treated grasses. There was no significant correlation ($P > 0.1$).

Few species of Auchenorrhyncha at the Deeps, other than *Turrutus socialis*, were caught in sufficient numbers during the treatment period to justify an analysis of their responses to treated and untreated grasses. Two of the more abundant leafhoppers, *Euscelis incisus* (which occurred most abundantly on *Trisetum flavescens*) and *Rhytistylus proceps* (which occurred most abundantly on *Festuca ovina*) were caught more frequently on the treated plants of their preferred host. The numbers of these two species (adults plus nymphs) caught on all the experimental grasses during the treatment period is shown in Table 6.8 (p. 123). Wilcoxon signed ranks test showed a significant difference in the numbers of *E. incisus* on treated and untreated plants, but no significant difference in the case of *R. proceps* ($P > 0.05$). (Chi-squared analyses on the totals of these species caught from treated and untreated grasses gave values of 3.06 for *E. incisus* and 2.95 for *R. proceps*, showing no significant difference in either case ($P < 0.1$)).

Responses of Auchenorrhyncha to the variation in nitrogen content between different grass species

The response of all species of Auchenorrhyncha to the variation in leaf nitrogen between the different grass species was analysed for both the pretreatment and treatment periods. For the pretreatment (April 26 - June 18) period the correlation (Spearman rank-order) between the numbers of adult Auchenorrhyncha caught from the different grass species and the mean nitrogen content of the grasses (the mean of three determinations made between April 11 (see p. 112) and June 13) was not significant ($r_s = 0.61$, $P < 0.1$). If, however, the results for *Carex flacca* and *Trisetum flavescens* were excluded from the analysis on the grounds that the former is a sedge and the latter showed very poor growth at the beginning of the season, the correlation was significant ($r_s = 0.89$, $P < 0.05$) (Fig. 6.5a). This result, and all other results in this section, must be treated with caution as the mean nitrogen values of five of the grasses (*A. elatius*, *A. pubescens*, *B. pinnatum*, *B. erectus* and *F. rubra*) are very similar. No significant correlation was found when nymphs were included in the analysis ($r_s = 0.29$, $P > 0.5$).

The correlation between numbers of adult Auchenorrhyncha and leaf nitrogen for the pretreatment period was largely due to the abundant delphacid *Hyledelphax elegantulus*, the adults of which had more or less died out by the time treatment with NH_4NO_3 was started. When *Carex flacca* and *Trisetum flavescens* were again excluded from the analysis, there was a significant correlation between the adult numbers of *H. elegantulus* and the nitrogen content of the grasses ($r_s = 0.79$, $P < 0.05$) (Fig 6.5b). The most abundant cicadellids during the pretreatment period were nymphs of *Diplocolenus abdominalis*, *Rhytistylus proceps* and *Turrutus socialis*. *R. proceps* was confined to *Festuca ovina* and *F. rubra* and neither of the other species showed a significant correlation with grass nitrogen (for *D. abdominalis* $r_s = 0.13$, $P > 0.5$, and for *T. socialis* $r_s = -0.36$, $P > 0.2$).

For the treatment period, the relationship between Auchenorrhyncha numbers and

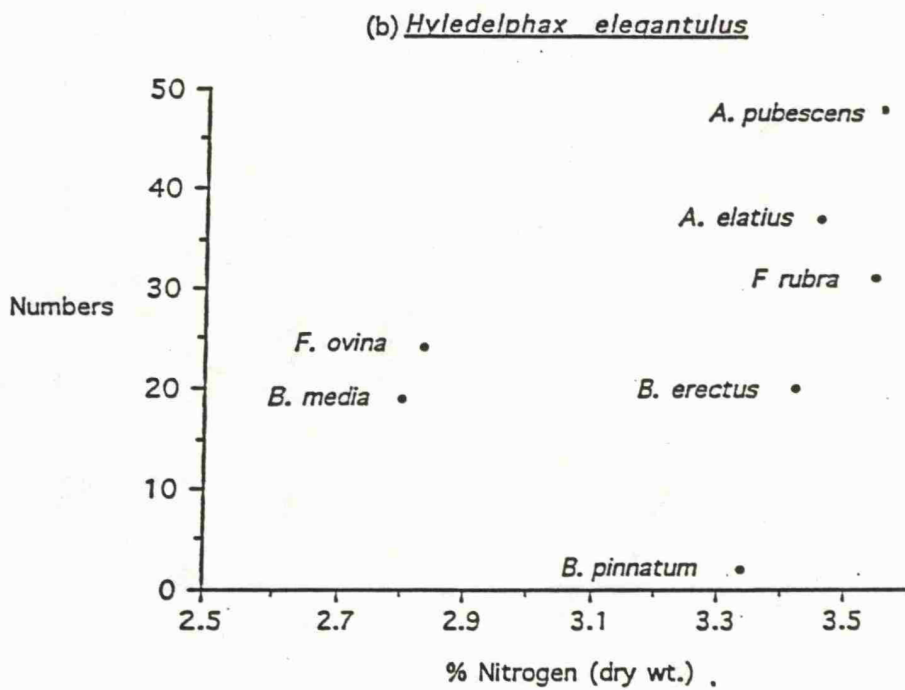
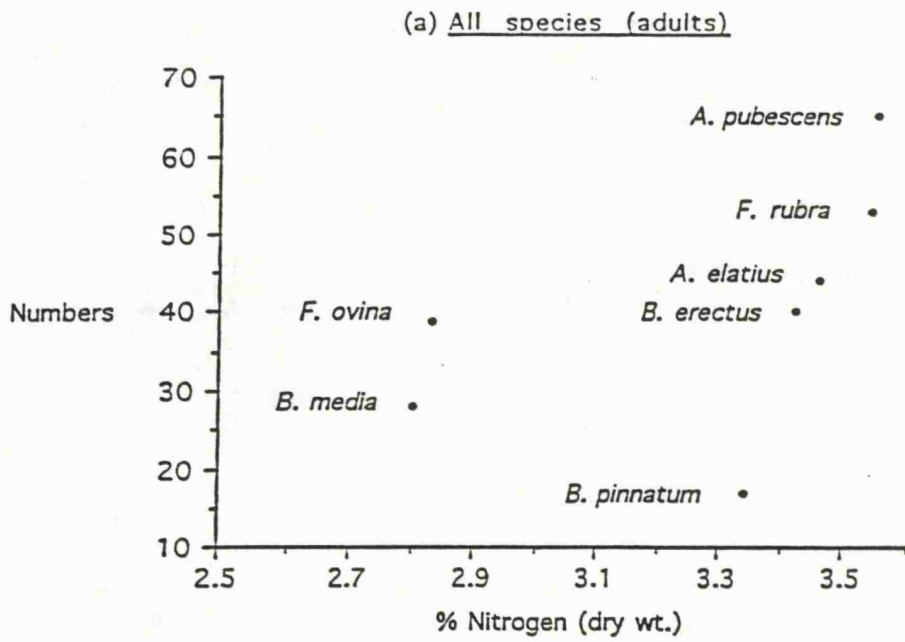


Fig 6.5 Relationship between a) all species of Auchenorrhyncha and b) *Hyledelphax elegantulus* and grass nitrogen levels during the pretreatment period (24.4.90 - 18.6.90). For a) $r_s = 0.89$, ($0.02 < P < 0.05$), and for b) $r_s = 0.79$, ($0.02 < P < 0.05$).

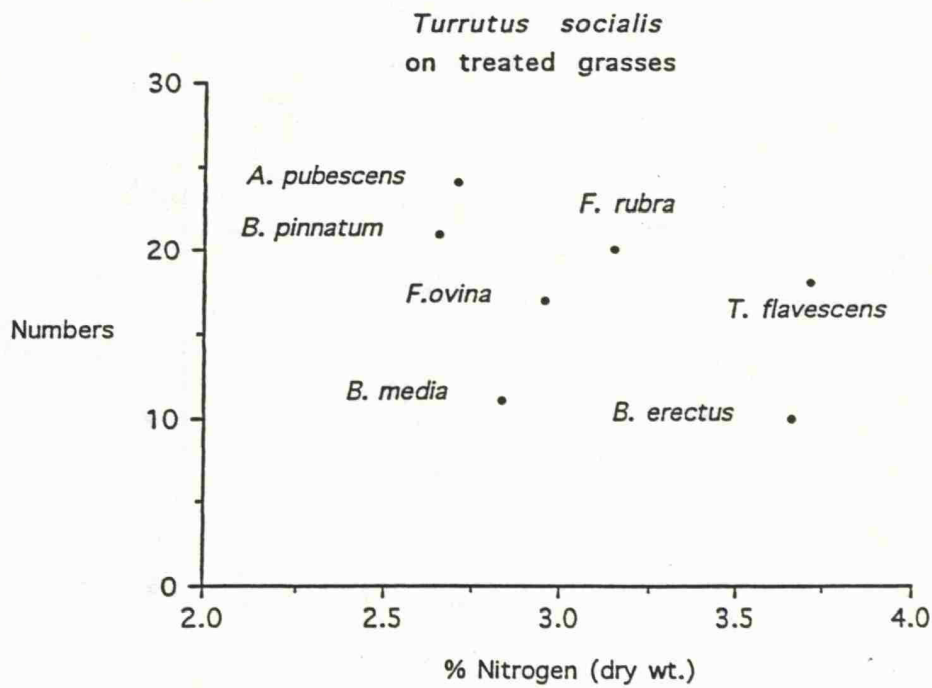
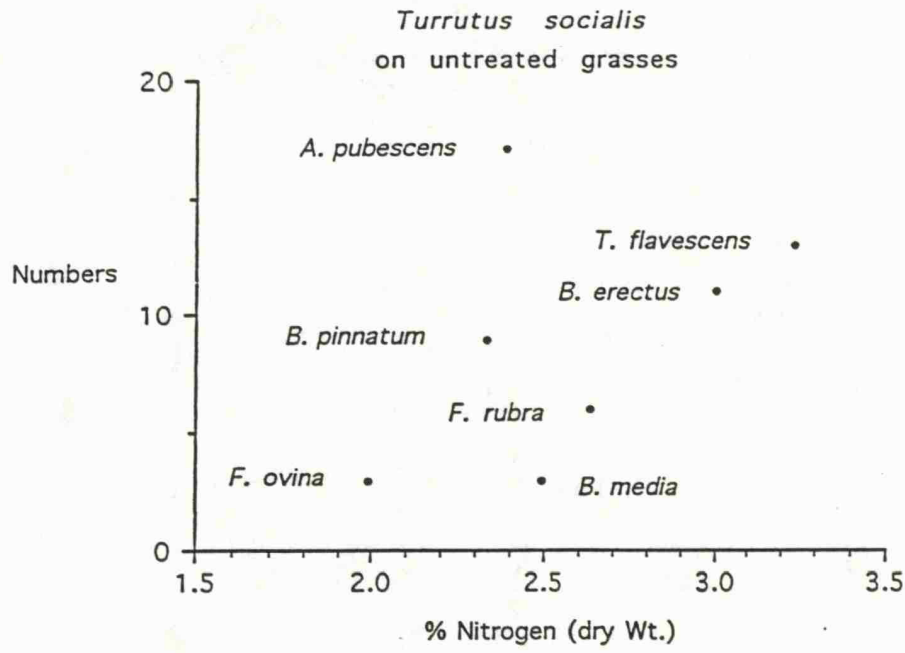


Fig 6.6 Relationship between numbers of adult *Turrutus socialis* and grass nitrogen in untreated and treated grasses. For untreated $r_s = 0.42$ ($0.5 > P > 0.2$), and for treated $r_s = -0.54$ ($0.5 > P > 0.2$).

grass nitrogen was analysed separately for the treated and untreated grasses. *Arrhenatherum elatius* was excluded from the analyses, because by this time it had been severely reduced by rabbit grazing. *Carex flacca* was also excluded but *T. flavescens* was included as during this period it grew well in the pots. There was no correlation between total numbers of adult Auchenorrhyncha and mean grass nitrogen levels (based on four determinations between 26.6.90 and 11.9.90) in either treated or untreated sets of grasses ($r_s = -0.5$, $P > 0.2$ and $r_s = 0.29$, $P > 0.5$ respectively). The most abundant leafhopper caught during the period was *Turrutus socialis*. The numbers of adults of this species recorded on the different grasses showed no significant correlation with nitrogen. There was, however, a large difference in the correlation coefficients for the untreated and treated grasses. In the former category the scatter of points showed a positive trend ($r_s = 0.42$, $P > 0.2$), (Fig 6.6a) while in the latter category the trend was negative ($r_s = -0.54$, $P > 0.2$) (Fig 6.6b).

6.4.4 Oviposition and Grass Nitrogen

The numbers of Auchenorrhyncha that hatched from the experimental grasses in May and June 1991 are shown in Table 6.9 (p.128). The total number of Auchenorrhyncha that hatched from those plants that had been treated with NH_4NO_3 was significantly greater than the number from plants that had not been treated ($P < 0.05$). This was due almost entirely to two species that hatched in significantly larger numbers from treated plants; *Aphrodes albifrons* ($P < 0.001$) and *Mocycdia crocea* ($P < 0.001$). The typhlocybine *Zyginidia scutellaris* was, however, significantly more abundant on untreated grasses ($P < 0.01$).

Table 6.9 Numbers of Auchenorrhyncha hatching in May and June 1991 from treated (with NH_4NO_3) and untreated grasses used in the 1990 field experiment.

Gramineae:	Total Auchenorrhyncha		<i>Aphrodes albifrons</i>		<i>Zyginidia scutellaris</i>		<i>Mocycdia crocea</i>	
	Treated	Untreated	Treated	Untreated	Treated	Untreated	Treated	Untreated
<i>Avenula pubescens</i>	2	3	1	0	0	3		
<i>Brachypodium pinnatum</i>	20	14	13	1	3	11		
<i>Briza media</i>	16	26	5	1	11	25		
<i>Bromus erectus</i>	23	7	0	0	6	6	17	0
<i>Festuca ovina</i>	19	5	19	4				
<i>F. rubra</i>	5	5	4	2				
<i>Trisetum flavescens</i>	2	1	1	0				
Totals	87	61	43	8	20	45	17	0

Chi-squared values (for Totals) 4.6 (0.01 < P < 0.05) 24 (P < 0.0001) 9.6 (0.001 < P < 0.01) 17 (P < 0.001)

6.4 Discussion

Despite the shortcomings of this aspect of the study (see below) data were obtained which were useful in the interpretation of the observed host preferences of some of the Auchenorrhyncha species of the Deeps.

There was quite clear evidence, of a general nature, that the nitrogen content of host plants can influence the distribution of plant feeding insects. *Turrutus socialis*, one of the commonest leafhoppers on the site, was more abundant in the adult stage on plants that were treated with NH_4NO_3 than on those that were not.

Aphrodes albifrons and *Mocycdia crocea* hatched in significantly larger numbers from treated plants; evidence that females of these species had oviposited in the previous season on grasses with a higher nitrogen content. (However, the possibility that this preference was due to a change in the structure of the plant following fertilization cannot be ruled out). *Zyginidia scutellaris*, on the other hand, hatched in significantly greater numbers from plants that had not been treated. In the case of *M. crocea*, there is field evidence (described in the previous chapter) of host specificity to *Brachypodium pinnatum* and *Bromus erectus* and the results from overwintered plants suggest selection by ovipositing females for higher nitrogen within a host species.

Tentative evidence was found for selection of host species on the basis of leaf nitrogen by the delphacid *Hyledelphax elegantulus*. This is in agreement with Prestidge (1982a) who suggested that those Auchenorrhyncha, like the delphacids, that overwinter as late instar nymphs and reproduce during the spring flush, when food quality is high, are more likely to have a higher requirement for nitrogen. This is in contrast to many cicadellids that reproduce later in the year. The cicadellid *Euscelis incisus*, which, like the delphacids, also overwinters as a nymph, was found in this study to have a clear preference for *Trisetum flavescens* (Chapter 5, Fig. 5.5, p. 94). This grass, together with *Arrhenatherum elatius*, had the highest mean leaf nitrogen content. The latter species was severely grazed in the

second half of the season when *E. incisus* was relatively abundant and this may explain why few *E. incisus* were found on it. High leaf nitrogen may have also played a part in the host choice of the early season cicadellid *Graphocraerus ventralis*, which occurred with equal frequency on all three members of the Aveneae (Chapter 5, Fig. 5.5, p. 94). *Avenula pubescens*, however, did not have particularly high nitrogen levels.

Although adult *Turrutus socialis* showed a significant preference for treated grasses the numbers caught showed no correlation with the nitrogen content of particular host species. There was a more even distribution of *T. socialis* among the treated grasses than among the untreated, suggesting that the increase in leaf nitrogen made some species (like *F. ovina*) relatively more acceptable. There was a consistent, although marginal, preference for *A. pubescens* by *T. socialis* in both sets of grasses.

The problem of nitrogen and host selection in grass feeding Auchenorrhyncha can be resolved into two extreme alternatives. Host selection may be determined solely by the quantity or quality of plant nitrogen or it may be determined entirely by other factors (secondary chemicals, plant structure, etc), although in the latter case selection of suitable plants within host species may be made on the basis of plant nitrogen. In most species the mechanism of host selection must lie somewhere along a spectrum between these alternatives, some being close to one of the extremes.

Prestidge & McNeill (1981) have shown that some species in acid grassland select their hosts largely on the basis of the quality of plant nitrogen. A larger scale field study than that described here, in which the problems discussed in the previous chapter (grazing, small sample size etc) were overcome, relevant nitrogen compounds like amino acids were assayed in detail, account was taken of plant architecture and a greater range of leaf nitrogen concentrations was introduced (by

fertilisation), would help to elucidate the mechanisms of host selection prevalent in calcareous grassland species.

It should also be noted that apart from indicating a response by some species of Auchenorrhyncha to higher nitrogen contents in potential host plants, this study has also shown that grasses with low mean nitrogen values, like *Festuca ovina*, may support host specific species in large numbers. Although this does not necessarily mean that nitrogen is unimportant in this situation (Prestidge & McNeill (*op. cit.*) have demonstrated that Auchenorrhyncha may select hosts on the basis of particular concentrations or particular types of nitrogen compounds, especially amino acids) it seems likely that other factors play a part in host selection.

7. CLIP-CAGE EXPERIMENTS ON SURVIVAL AND OVIPOSITION

7.1 Introduction

Data from field collections and choice tests in which the presence of an insect on a plant is used as a measure of host preference provides essential information on the host plants of insects, but cannot reveal the reasons for the associations. Host specificity, for instance, may be due to the physiological or microclimatic requirements of nymphs or adults, the need for particular oviposition sites or for protection from predators. Information on some of these details may be obtained from laboratory studies in which insects are caged on plants. Such studies provide an essential back-up to the results of field experiments which, especially in the case of leafhoppers and other very mobile insects, may be difficult to interpret. To quote Whitcomb, Cramer, Coan & Hicks (1987, p.168) "supplementation of field data with observations of insects confined on host plants in the laboratory gives important insights into the breadth of food plant tolerances of cicadellids".

The work described in this chapter concentrated mainly on the survival and oviposition behaviour of *Adarrus multinotatus* and *Turrutus socialis* when confined on a range of possible host grasses. These two common cicadellids were shown by work described in the preceding chapters to have different distribution patterns and degrees of host specificity. Choice tests showed clearly that *A. multinotatus* was associated with *Brachypodium pinnatum*, but the results for *T. socialis* were far from clear. They indicated that it was polyphagous, with a possible preference for *Avenula pubescens* and *Festuca rubra*. The main aim of the clip-cage experiments was to obtain more information on the response of these two species to potential host grasses.

Data were also obtained on the survival of *Criomorpus albomarginatus* on *Festuca ovina* and *F. rubra*. Field choice experiments indicated that this species

occurs almost exclusively on *F. rubra* at the Deeps, avoiding the closely related *F. ovina* and a clip-cage experiment was performed to compare the survival of *C. albomarginatus* on these two grasses.

In addition to the more extensive investigations on the ovipositional behaviour of *A. multinotatus* and *T. socialis*, smaller scale clip-cage experiments were performed on a number of other species (*Doratura stylata*, *Euscelis incisus*, *Mocydia crocea* and *Rhytistylus proceps*) to obtain information on the sites used for oviposition. As oviposition requirements may be an important factor governing host selection I considered that any data obtained might contribute to the interpretation of the results obtained from the field choice experiments.

7.2 Survival and oviposition in *Adarrus multinotatus*

7.2.1 Methods

The host plants used in the experiments on *A. multinotatus* were *Brachypodium pinnatum* (B.p.), *Bromus erectus* (B.e.) and *Festuca rubra* (F.r.). These were the predominant grasses in the ranker areas of the Deeps where *A. multinotatus* occurred. The experiment was performed in 1990 and the grasses were prepared in the same way as those used in the field choice experiment in the same year (i.e. plants used in previous experiments were divided and potted on during the winter of 1989 - 90 in plastic 127 mm pots with soil collected from molehills at the Deeps to which was added approximately 0.01% by weight of bonemeal). Three pots of each of the three species were placed in one of the gravel based compartments of the greenhouse in three rows, and arranged (non-randomly) as shown below:

South side of greenhouse

B.p.	F.r.	B.e.
B.e.	B.p.	F.r.
F.r.	B.e.	B.p.

Nymphal survival

Nymphs of *Adarrus multinotatus* were collected from the Deeps between May 14 and May 27, 1990. As they occurred at the base of the vegetation, in areas dominated by *B. pinnatum*, the nymphs were most effectively collected by lying in the grass, parting the vegetation to ground level, and catching them with a pooter once they revealed themselves by moving. They were identified by their characteristic rapid movement and general appearance (see chapter 4) and only occasionally were nymphs of other species, usually *Mocycdia crocea*, collected in error. The pooter was lined with slightly dampened tissue to minimise damage to the nymphs and to prevent desiccation. Within three hours of capture they were taken to the greenhouse and confined individually on the experimental plants in small clip-cages (Honeyborne, 1969; Adams & van Emden, 1972). The nymphs were transferred from pooter to cage with a very fine damp brush, pared down to a few hairs, whilst anaesthetised with CO₂.

The clip-cages (Plate 7.1) were made from two 7 mm lengths of perspex tubing, external diameter 40 mm and internal diameter 36 mm, each with one side covered by a fine nylon gauze with a mesh size that was approximately 1 x 0.5 mm. The rim of the other side was lined with a thin layer of foam rubber which formed a seal when the halves of the cage met. The halves of the cage were held together and hinged by a stainless steel hair clip, the ends of which were glued into small holes made in the perspex.

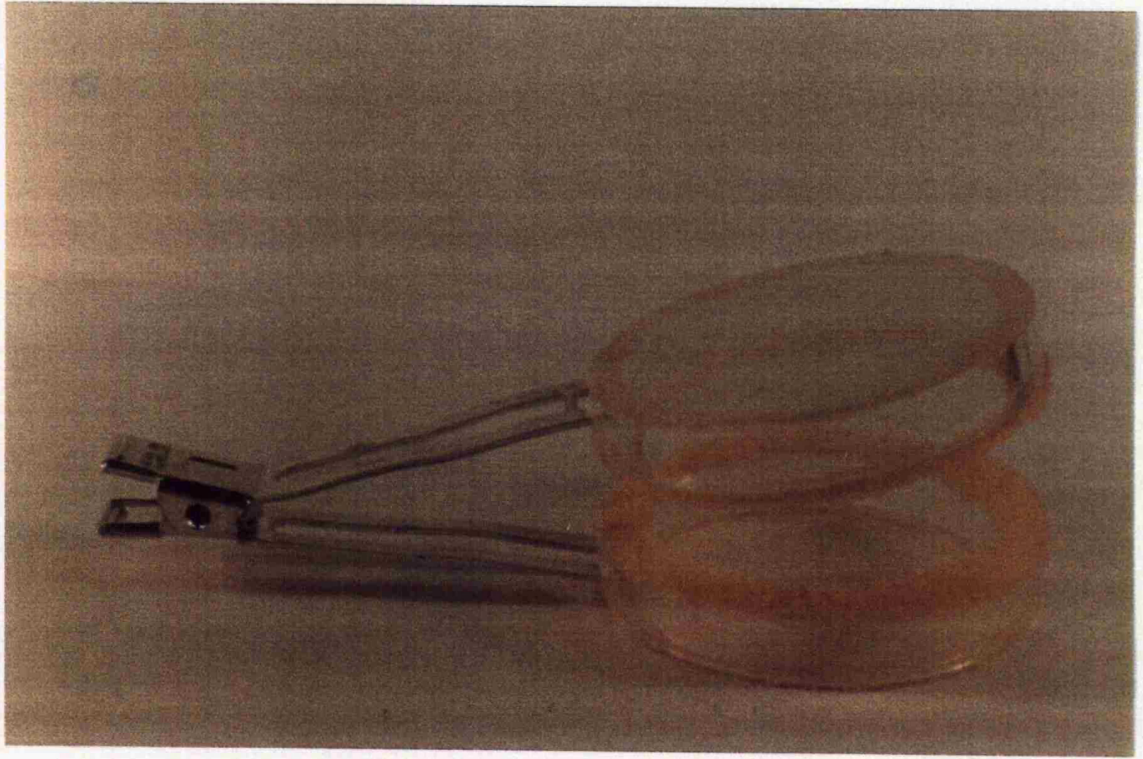
Over a period of two weeks (May 14 - May 27) fifteen individually caged nymphs were placed on each species of grass, five per plant. Each cage was clipped to a grass shoot fairly low down in the tuft of grass so that it contained a section of leaf stem and sheath and two or three leaves. A few nymphs were lost during inspections or were found to be the wrong species, but about ten nymphs remained on each host species until they either matured or died. The nymphs were inspected every few days (the period between inspections was nearly always 5 days or less).

Plate 7.1

Plate 7.1

Above: A clip-cage

Below: Clip-cages in position



Although the duration of different instars, marked by the production of exuviae, was considered as a measure of host suitability, this was rejected in favour of straight survival and development to maturity because of the mixture of instars used and the variable time periods between inspections.

Survival and oviposition in adult females

Male and female *A. multinotatus* were reared in the greenhouse on *Brachypodium pinnatum*. Some were obtained from the survival experiment with nymphs (all nymphs caged on *B. pinnatum* developed into adults) but most were reared from additional nymphs collected from the Deeps and caged on other *B. pinnatum* plants grown in the same way as the experimental plants described above. The experimental hosts were the same as those used for the nymphs. Between June 13 and June 26 eight pairs of virgin males and females were placed in separate clip-cages on each species of grass, two or three cages being attached to each plant in the same way as described for the nymphs. Earlier observations indicated that *A. multinotatus* laid eggs in dead leaf sheaths and so a stem enclosed by a dead sheath was included in all clip-cages except for two on *B. pinnatum*. These two exceptions were deprived of dead sheath material for over two months of the experiment in order to see if they would oviposit in living tissue.

Although mating probably occurred within the first day of confinement (Coupe & Schulz, 1968), the males were left in the cages with the female for approximately one week and then removed. (In most leafhopper species, one mating is sufficient to fertilise the eggs of a female during her lifetime (DeLong 1971)). To minimise the loss of caged insects all transfers were performed once they had been anaesthetised with CO₂. Survival was monitored and the plant material enclosed by the cages was examined for eggs at intervals that varied between a few days at the beginning of the experiment (June 13 - 28) and one to three weeks for the remaining period (June 28 - December 4). The experiment continued until December 4, by which time all the leafhoppers had died.

Each time plant material was examined for eggs, the clip-cages were removed from the plants by cutting the shoots below the cages with scissors. The leaves protruding from the tops of the cages were also cut so that only the sections within the cages were left. This plant material was searched for eggs under a Nikon SMZ - 2T trinocular microscope. At first, all the plant material, living and dead, was examined, but subsequently, when it became apparent that only dead sheaths were used for oviposition, living tissue was only searched occasionally as a check. The eggs were easily seen and counted within the dead sheaths.

7.2.2 Results

Survival of *Adarrus multinotatus* nymphs

The results of the experiment on nymphal survival are summarised in Table 7.1 below and shown in detail in Table 7.2.

Table 7.1 Survival of *Adarrus multinotatus* nymphs on potential host grasses (+/- standard error)

	<i>B. pinnatum</i>	<i>B. erectus</i>	<i>F. rubra</i>
Number of nymphs caged	11	12	11
Number surviving to maturity	11	0	1
Mean development time in days	24.9 +/- 2.2	0	44.5
Mean survival time of nymphs that died	-	6.8 +/- 1.3	19.8 +/- 4.6

Clearly, the nymphs only developed successfully on *Brachypodium pinnatum*. On this grass all the experimental insects developed to the adult stage after a mean period of 24.9 days, while on *Bromus erectus* none reached maturity and on *Festuca rubra* all except one of the nymphs died before reaching the adult stage. Survival on *B. erectus* and *F. rubra* provided an interesting contrast; although the mortality was high on *F. rubra* the mean survival time was much longer (19.8 days)

Table 7.2 Survival of *Adarrus multinotatus* nymphs on potential host grasses
(Symbols used: N = nymph placed on plant, + = nymph alive, D = dead, M = male, F = female)

a) Survival on *Brachypodium pinnatum*

	Nymphs										
	1	2	3	4	5	6	7	8	9	10	11
Date											
May 14 1990	N	N	N								
May 17	+	+	+	N	N	N	N	N	N	N	
May 22	+	+	+	+	+	+	+	+	+	+	
May 24	+	+	+	+	+	+	+	+	+	+	
May 27	+	+	+	+	+	+	+	+	+	+	N
May 31	+	+	+	+	+	+	M	+	+	+	+
June 5	+	+	+	+	+	M		+	+	+	+
June 8	+	+	+	+	M			+	+	+	+
June 15	M	F		F				+	+	+	+
June 19			M					F	M	+	M
June 23										+	
June 28										F	
Development time in days	28.5	28.5	30.5	25.5	20.5	16.5	12	25.5	25.5	39.5	21

b) Survival on *Bromus erectus*

	Nymphs											
	1	2	3	4	5	6	7	8	9	10	11	12
Date												
May 14 1990	N	N	N	N								
May 17	+	+	+	+	N	N	N	N	N	N		
May 22	+	D	D	D	+	+	D	D	+	D		
May 24	+				+	+			+		N	N
May 27	+				+	D			D		+	+
May 31	D				D						D	+
June 5												+
June 8												D
Survival in days	15	4.5	4.5	4.5	12	7.5	2.5	2.5	7.5	2.5	5	13.5

c) Survival on *Festuca rubra*

	Nymphs										
	1	2	3	4	5	6	7	8	9	10	11
Date											
May 14 1990	N										
May 17	+	N	N	N	N	N	N	N	N		
May 22	+	+	+	+	+	+	+	+	+		
May 24	+	+	+	+	+	+	+	+	+		
May 27	+	+	+	+	D	+	+	+	D	N	N
May 31	+	D	+	+		+	D	D		+	+
June 5	+		+	+		+				+	+
June 8	+		+	+		+				+	D
June 15	+		+	+		+				+	
June 19	+		+	+		D				D	
June 23	+		+	+							
June 28	D		+	+							
July 3			D	M							
Survival in days	42.5	12	44.5	44.5*	7.5	31	12	12	7.5	22	6.5

* Development time

and the one nymph which reached the adult stage took 44.5 days to do so. Two of the nymphs that died on *F. rubra* also survived for over forty days. On *B. pinnatum* the longest development time was 39.5 days. While some of this variation may have been due to the mixture of instars originally placed onto the plants, the results, nevertheless, show marked differences in the response of *A. multinotatus* to the three grass species.

Survival and oviposition of adult females

The results of the experiments on female *Adarrus multinotatus* survival and oviposition corresponded with those described above for the nymphs. The results are summarised in Table 7.3 below and are shown in detail in Table 7.4.

Table 7.3. Survival and oviposition in female *Adarrus multinotatus* on potential host grasses

	(+/- standard error)		
	<i>B. pinnatum</i>	<i>B. erectus</i>	<i>F. rubra</i>
Number of females caged	8	8	8
Mean survival time (days)	118 ^a +/- 14.65	5.7 +/- 0.96	21.3 +/- 9.01
Number of females that laid eggs	7	0	2
Mean number of eggs ovipositing female ⁻¹	100.5 ^b +/- 16.58	0	7.5

(^a mean for 7 females, 1 escapee excluded)

(^b mean for 4 females; 2 deprived of dead leaf sheaths excluded)

On *Bromus erectus* survival was short and there was no oviposition. On *Festuca rubra* survival was better, but only 15 eggs were laid by two females. On *Brachypodium pinnatum* the majority of females survived for over 100 days in the clip-cages and the mean number of eggs laid per ovipositing female (excluding the two deprived of dead leaf sheaths) was 100.5. The two females that were deprived of dead leaf sheaths until August 20 (see Table 7.4 a) laid no eggs up to that date but did oviposit once this material was included in the clip-cages.

Table 7.4. Survival and oviposition of *Adarrus multinotatus* on potential host grasses. (Numbers in table = number of eggs laid. Symbols used: F + M = virgin female and male, + = female alive, D = dead). Males were removed after approximately one week. Survival of females was estimated from 2nd day in the clip-cage to mid-way between date on which last observed alive and following date when dead.

a) Survival and oviposition on *Brachypodium pinnatum*

Date	Females						
	1	2	3	4	5	6	7
June 13 1990	F + M						
June 15	+	F + M					
June 19	+	+	F + M				
June 20	+	+	+	F + M			
June 26	+	+	+	+	F + M	F + M	
June 27	+	+	+	+	+	+	M + F
July 12	+	+	+	+	+	+	+
July 19	+	+	+	35	10	7	23
Aug. 8	+	+	D	10	52	43	30
Aug. 20	+*	+*		17	23	+	8
Sept. 7	37	20		7	31	1	+
Sept. 28	13	D		2	20	8	33
Oct. 19	+			1 D	12	27	2
Nov. 6	D				D	+	+
Nov. 26						+	D
Dec. 4						D	
Survival (days)	149	94.5	46	110.5	124	157	145
Number of eggs	50	20	0	72	148	86	96

* Females 1 and 2 deprived of dead leaf sheath material until Aug 20th
(Number of females reduced from 8 to 7 due to an escape)

b) Survival and oviposition on *Bromus erectus*

Date	Females							
	1	2	3	4	5	6	7	8
June 13 1990	F + M							
June 15	+							
June 19	D	F + M	F + M					
June 20		+	+	F + M				
June 23		+	+	+	F + M			
June 26		+	+	+	+	F + M	F + M	F + M
June 28		D	D	D	D	+	+	+
July 3						D	+	D
July 4							+	
July 12							D	
Survival (days)	4	6.5	6.5	5.5	2.5	4.5	11.5	4.5
Number of eggs	0	0	0	0	0	0	0	0

c) Survival and oviposition on *Festuca rubra*

Date	Females							
	1	2	3	4	5	6	7	8
June 15	F + M							
June 19	+	F + M	F + M					
June 20	+	+	+	F + M				
June 23	+	+	+	+	F + M			
June 26	+	+	+	+	+	F + M	F + M	F + M
June 28	+	D	+	D	+	+	+	+
July 3					D	+	D	D
July 12	+		D			+		
July 19	8					+		
Aug. 8	5					1		
Aug. 20	D					1		
Sept. 7						D		
Survival (days)	60	6.5	18.5	5.5	7.5	64	4.5	4.5
Number of eggs	13	0	0	0	0	2	0	0

The Kruskal-Wallis one way analysis of variance (Siegel & Castellan 1988) performed on adult survival and oviposition showed there was a highly significant difference in the responses to *B. pinnatum* and the other two grasses (for survival, $P < 0.001$, and for oviposition, including only those 5 females on *B. pinnatum* that were supplied with dead leaf sheaths, $P < 0.005$).

7.3 Survival and oviposition in *Turrutus socialis*

7.3.1 Methods

Nymphal survival and adult female survival and oviposition were investigated in *Turrutus socialis*. The experiments on female *T. socialis* were carried out in 1991. For these experiments nymphs were collected from the Deeps in June and confined individually in clip-cages on *Festuca rubra*, in the greenhouse, until they matured to adults. *F. rubra* was chosen as a suitable rearing plant on the basis of previous greenhouse and field choice experiments. Virgin female and male *T. socialis* were then confined in pairs on potential host plants. The number of grass species used in these experiments was increased to six, as, unlike *A. multinotatus*, previous work indicated that *T. socialis* had a wide host range. The species of grasses were; *Avenula pubescens* (Ap), *Brachypodium pinnatum* (Bp), *Briza media* (Bm), *Bromus erectus* (Be), *Festuca ovina* (Fo) and *F. rubra* (Fr). All of these species were among the host plants used in the field choice experiment on Site 1 at the Deeps and occurred on the site naturally. (Site 1 was the type of habitat at the Deeps where *T. socialis* was abundant). The plants were prepared in the same way as for the *A. multinotatus* experiments. Two plants of each species were arranged non-randomly on a gravel based compartment of the greenhouse as shown below:

South side of greenhouse

A.p	B.p	B.m
B.e.	F.o	F.r.
B.m	A.p	B.p.
F.r.	B.e.	F.o

Eight female / male pairs were clipped on to each species, four per plant. These

could not all be put in place at once, but were placed on the different grass species in rotation as the adults became available. Survival and oviposition were recorded at intervals which were generally between one and two weeks. The experiment started on July 12 and continued until the last female died on December 18.

The experiment on nymphal survival was performed in 1992. The same six grass species used for female survival and oviposition (divided and repotted over the winter) were used in this experiment. Nymphs were collected from the Deeps in early June 1992 with a sweep net and pooter and confined within three hours on the experimental grasses in the greenhouse, which were arranged in the same way as described above. As the nymphs of *T. socialis* were not particularly abundant in that year, it was difficult to obtain sufficient numbers for the experiment and a fairly wide spread of instars (mainly 2 to 4) had to be used. Nymphal survival was recorded at weekly intervals or less between June 13 and July 2.

7.3.2 Results

Survival of *Turrutus socialis* nymphs

The results of the nymphal survival experiment are summarised in Table 7.5 below and given in detail in Table 7.6.

Table 7.5 Survival of *Turrutus socialis* nymphs on potential host plants

(Grasses: A.p = *Avenula pubescens*, B. p = *Brachypodium pinnatum*, B. m = *Briza media*, B. e = *Bromus erectus*, F. o = *Festuca ovina*, F. r = *F. rubra*)

	A.p	B.p.	B.m	B.e.	F.o	F.r.
Number of nymphs caged	11	9*	11	8*	11	8*
Number that died before maturing	0	0	10	1	3	0
Number that matured but died before the end of the experiment	0	6	1	2	3	0
Number of adults alive at the end of the experiment	11	2	0	4	5	7
Number of nymphs alive at the end of the experiment	0	1	0	1	0	1

* Number of nymphs reduced by parasitism and escapes.

Table 7.6 Survival and development of *Turrutus socialis* nymphs on potential host grasses
(Symbols used: N = nymph placed on plant, + = nymph or adult alive, D = dead, M = male, F = female)

a) Survival on *Avenula pubescens*

	Nymphs										
Date	1	2	3	4	5	6	7	8	9	10	11
June 13	N	N	N	N	N	N	N				
June 16	+	+	+	+	+	+	+				
June 18	+	+	+	+	+	+	+	N	N	N	N
June 23	F	M	+	M	+	+	+	+	+	+	+
July 2	+	+	M	+	F	F	F	F	F	M	F

b) Survival on *Brachypodium pinnatum*

	Nymphs								
Date	1	2	3	4	5	6	7	8	9
June 13	N	N	N	N	N	N			
June 16	+	+	+	+	+	+			
June 18	+	+	M	+	M	+	N	N	N
June 23	+	M	+	M	+	+	+	+	F
July 2	FD	D	D	D	+	F	MD	+	D

(N.B. Number of nymphs reduced from 11 to 9 due to escapes)

c) Survival on *Briza media*

	Nymphs										
Date	1	2	3	4	5	6	7	8	9	10	11
June 13	N	N	N	N	N	N	N				
June 16	+	D	+	+	D	D	D				
June 18	+	+	+	+				N	N	N	N
June 23	D		D	+				F	+	D	+
July 2				D				D	D		D

d) Survival on *Bromus erectus*

	Nymphs						
Date	1	2	3	4	5	6	7
June 13	N	N	N	N	N	N	
June 16	+	+	+	+	+	+	
June 18	+	+	+	+	+	+	N
June 23	+	+	M	+	+	+	+
July 2	FD	MD	+	M	+	D	M

(N.B. Of the 10 nymphs placed on *B. erectus*, 2 were parasitised and 1 escaped)

e) Survival on *Festuca ovina*

	Nymphs										
Date	1	2	3	4	5	6	7	8	9	10	11
June 13	N	N	N	N	N	N	N	N			
June 16	+	+	+	+	+	+	+	+			
June 18	+	+	+	+	+	+	+	+	N	N	N
June 23	+	+	+	+	F	MD	+	M	D	+	+
July 2	F	MD	F	M	+		D	D		D	M

f) Survival on *Festuca rubra*

	Nymphs							
Date	1	2	3	4	5	6	7	8
June 13	N	N	N	N	N			
June 16	+	+	+	+	+			
June 18	+	+	+	+	+	N	N	N
June 23	+	+	+	+	+	+	+	+
July 2	M	M	M	M	F	+	M	M

(N.B. Of the 10 nymphs placed on *F. rubra*, 2 were parasitised)

As interpretation of this experiment was limited by the range of instars initially caged on the plants the time taken for nymphs to develop into adults was not included in the analysis. However, the number of nymphs that developed into adults on the different grass species showed marked variation, as did the survival of the adults following emergence. *Briza media* was clearly the least suitable host; all but one of the nymphs caged on it died before reaching maturity and the single adult that emerged died before the end of the experiment. On *Festuca ovina* 3 out of 11 nymphs died before maturing, and 3 out of the 8 adults that emerged died before the end of the experiment. On the other grasses all the nymphs survived and most became adults. Only on *Avenula pubescens* and *Festuca rubra* were all the adults that emerged alive at the end of the experiment. Out of all the 64 nymphs caged on all the grasses 4 (6.25%) were parasitised. One hymenopteran parasite was successfully reared from a pupa found in a clip cage but has still to be identified. Of the 41 adults that emerged in the clip cages, 25 (61%) were male.

Survival and oviposition in female *Turrutus socialis*

The results of the experiment on survival and oviposition are summarised below in Table 7.7 and given in detail in Table 7.8.

Table 7.7 Survival and oviposition of *Turrutus socialis* on potential grass hosts
(Grasses: A.p = *Avenula pubescens*, B. p = *Brachypodium pinnatum*, B. m = *Briza media*, B. e = *Bromus erectus*,
F. o = *Festuca ovina*, F. r = *F. rubra*) (+/- standard error)

	A.p	B.p.	B.m	B.e.	F.o	F.r.
Numbers of females caged	6*	7*	9	6*	8	7*
Mean survival time in days	90.8 +/- 20.0	105 +/- 21.2	12.1 +/- 3.3	40.2 +/- 13.2	8.9 +/- 3.2	81.4 +/- 12.7
Number of females that laid eggs	6	7	4	5	1	7
Mean number of eggs per ovipositing female	53.3 +/- 8.2	23.7 +/- 5.0	5.5 +/- 2.4	36.2 +/- 14.5	5	79.0 +/- 11.1
Mean time (days) taken to lay first egg(s)	17.4 +/- 2.8	17.9 +/- 2.6	15.0 +/- 5.3	14.0 +/- 2.5	24.5	5.6 +/- 1.1

*Numbers reduced from starting figure of 8 because of escapes

Table 7.8 Survival and oviposition of *Turrutus socialis* on potential host grasses.

(Numbers in table = number of eggs laid. Symbols used: F + M = virgin female and male, + = female alive, D = dead). Males were removed after approximately one week. Survival of females was estimated from 2nd day in the clip-cage to mid-way between date on which last observed alive and following date when dead.

a) Survival and oviposition on *Avenula pubescens*

Date	Females					
	1	2	3	4	5	6
July 12 1991	F + M	F + M				
July 15	+	+	F + M			
July 30	+	+	+	F + M	F + M	F + M
Aug 6	+	27	17	+	+	+
Aug 13	12	1	2	9	6	+
Aug 21	6	1	12	19	15	2
Aug 27	18	12	3	13	12 D	1
Sept 3	7	18	+	15		6
Sept 12	D	9	4	9		6
Sept 20		2	+	8		3
Sept 26		6	D	1		4
Oct 3		+		+		5
Oct 21		4		+		11
Nov 11		+		+		8
Nov 26		D		+		4
Dec 18				D		2
Survival (days)	49.5	129.5	70	130	25	141
Number of eggs	43	80	38	74	33	52

(N.B. Number of females reduced from 8 to 6 due to escapes)

b) Survival and oviposition on *Brachypodium pinnatum*

Date	Females						
	1	2	3	4	5	6	7
July 12 1991	F + M	F + M					
July 15	+	+	F + M				
July 30	+	+	+	F + M	F + M	F + M	F + M
Aug 6	2	5	3	+	3	+	+
Aug 13	3	2	5	+	5	+	+
Aug 21	+	5	+	3	+	2	+
Aug 27	3	+	10	5	9	1	12 D
Sept 3	+	11	8	+	+	D	
Sept 12	8	1	1	3	+		
Sept 20	+	+	6	3	4		
Sept 26	1	+	+	+	+		
Oct 3	1	2	2	6	5		
Oct 21	+	9	+	1	3		
Nov 11	6	6	+	D	+		
Nov 26	+	+	+		4		
Dec 18	D	D	+		D		
Survival (days)	148	148	156	93.5	130	31.5	25
Number of eggs	24	41	35	21	30	3	12

(N.B. Number of females reduced from 8 to 7 due to an escape)

c) Survival and oviposition on *Briza media*

Date	Females								
	1	2	3	4	5	6	7	8	9
July 12 1991	F + M	F + M							
July 15	+	+	F + M	F + M					
July 29	+	D	+	D					
July 30	+		+		F + M	F + M	F + M	F + M	F + M
Aug 6	+		2		5	D	D	+	D
Aug 13	2 D		4 D		7			2 D	
Aug 21					D				
Survival (days)	28.5	8.5	25.5	7	18	3.5	3.5	10.5	3.5
Number of eggs	2	0	6	0	12	0	0	2	

Table 7.8 (cont.) Survival and oviposition of *Turrutus socialis* on potential host grasses. (Numbers in table = number of eggs laid. Symbols used: F + M = virgin female and male, + = female alive, D = dead.) Males were removed after approximately one week. Survival of females was estimated from 2nd day in the clip-cage to mid-way between date on which last observed alive and following date when dead.

d) Survival and oviposition on *Bromus erectus*

Date	Females					
	1	3	3	4	5	6
July 12 1991	F + M					
July 15	+	F + M				
July 29	+	+				
July 30	+	+	F + M	F + M	F + M	F + M
Aug 6	13	D	+	+	D	+
Aug 13	+		8	15		14
Aug 21	1		1	10		13 D
Aug 27	+		5	12		
Sept 3	2		8	9		
Sept 12	+		2 D	12		
Sept 20	9			21		
Sept 26	+			6		
Oct 3	3			4 D		
Oct 21	3D					
Survival (days)	92	19	38	63.5	3.5	25
Number of eggs	31	1	24	89	0	36

(N.B. Number of females reduced from 8 to 6 due to escapes)

e) Survival and oviposition on *Festuca ovina*

Date	Females							
	1	2	3	4	5	6	7	8
July 12 1991	F + M							
July 15	+	F + M	F + M	F + M				
July 29	D	D	D	D				
July 30					F + M	F + M	F + M	F + M
Aug 6					D	D	D	+
Aug 13								+
Aug 21								+
Aug 27								5
Sept 3								D
Survival (days)	8.5	7	7	7	3.5	3.5	3.5	31.5
Number of eggs	0	0	0	0	0	0	0	5

f) Survival and oviposition on *Festuca rubra*

Date	Females						
	1	2	3	4	5	6	7
July 12 1991	F + M	F + M					
July 15	+	+	F + M	F + M			
July 29	5	2	7	4			
July 30	+	+	+	+	F + M	F + M	F + M
Aug 6	11	19	2	6	14	3	22
Aug 13	13	18	3	17	12	7	10
Aug 21	+	10	13	20	10	13	16
Aug 27	8	5	+	+	5	2	7
Sept 3	10	6	20	9	15	13	11
Sept 12	10	15	3 D	1	7	4	9
Sept 20	2	17		5	1 D	1	12
Sept 26	D	6		+		+	18 D
Oct 3		10		1		5	
Oct 21		12		11		23	
Nov 11		12		D		D	
Nov 26		+					
Dec 18		D					
Survival (days)	73	148	54.5	89	48	93.5	64
Number of eggs	59	132	48	74	64	71	105

(N.B. Number of females reduced from 8 to 7 due to an escape)

Survival of female *T. socialis* was good on *A. pubescens*, *B. pinnatum* and *F. rubra* (mean > 80 days), intermediate on *B. erectus* (mean 40.2 days) and poor on *B. media* and *F. ovina* (mean < 13 days). Oviposition was highest on *A. pubescens* and *F. rubra* (mean number of eggs 53.3 and 79 respectively), intermediate on *B. pinnatum* and *B. erectus* (mean number of eggs 23.7 and 36.2 respectively) and lowest on *B. media* and *F. ovina* (mean number of eggs 5.5 and 5 respectively). Although the estimates of the mean time to lay the first eggs are very dependent on the length of the time periods between observations, it is noteworthy that this was much shorter on *F. rubra* than on the other grasses. Like *Adarrus multinotatus*, *T. socialis* oviposited in dead leaf sheaths although very occasionally living sheaths or leaves were used.

The Kruskal-Wallis one way analysis of variance by ranks showed that for both survival and oviposition there were significant differences in the response of female *T. socialis* to the different grass species (for survival $K = 28.6$, $P < 0.001$ and for oviposition $K = 25$, $P < 0.001$). Using an extension of the Kruskal-Wallis test (Siegel & Castellan 1988), multiple comparisons between treatments (for $P = 0.05$) showed that oviposition on *B. media* and *F. ovina* was significantly less than on *A. pubescens* and *F. rubra* and that survival on *B. media* and *F. ovina* was significantly shorter than on *A. pubescens*, *B. pinnatum* and *F. rubra*.

7.4 Survival of *Criomorphus albomarginatus* on *Festuca ovina* and *F. rubra*

7.4.1 Methods

Field choice experiments gave a strong indication that the delphacid, *Criomorphus albomarginatus*, was specific to *Festuca rubra*. A small scale clip-cage experiment was carried out on *C. albomarginatus* to compare its survival on the host plant with that on the closely related *Festuca ovina*. Ten females, collected from the field, were caged individually on each species of grass between May 18 and May 29 1992. The clip-cages were distributed between 3 plants of each species that were

prepared in the same way as described above for the other clip-cage experiments and placed on the gravel based greenhouse bench. Survival was recorded at intervals which varied between a few days and two weeks.

7.4.2 Results

The results of the clip-cage experiment with *C. albomarginatus* are shown in Table 7.9. On the field host plant, *F. rubra*, mean survival time was 18.9 days and on *F. ovina* 4.6 days. A Mann-Whitney U test showed that the median survival times (17.5 and 4.5 respectively) were significantly different ($P < 0.05$). The survival time of *C. albomarginatus* on its host plant was relatively short, probably because the experiment was conducted quite late in the adult season of this species. *C. albomarginatus* overwinters as a nymph and becomes adult early in the year.

7.5 Observations on oviposition

7.5.1 Methods

Information on oviposition behaviour was obtained for a number of species, in addition to those used in the experiments described above, by confining females on host grasses in clip cages. Host grasses were chosen on the basis of the results of the field choice experiments and a variety of plant tissue was included in the clip-cages (grass stems enclosed in live and dead sheaths, and sections of live and dead leaves). Females were confined in the cages with males for about a week to ensure they were fertile, although for these observations adults were brought in direct from the field and not bred from nymphs. The grasses were grown in pots as described for the survival and oviposition experiments and kept on the gravel based greenhouse bench. Plant material was examined for eggs, and the eggs were photographed, using a Nikon trinocular microscope and Pentax ME Super camera. Most of the observations were made in 1990 and 1991.

Table 7.9 Survival of female *Criomorpha albomarginatus* on *Festuca ovina* and *F. rubra*.
 (Symbols used: F = female placed on plant, + = alive, D = dead)
 Survival was estimated from the 2nd day (first full day) in the clip cage to mid-way between the date on which last observed alive and following date when dead.

a) Survival on *Festuca ovina*

	Females									
	1	2	3	4	5	6	7	8	9	10
Date										
May 18	F	F	F	F						
May 21	+	+	+	+	F	F	F	F		
May 23	+	D	D	D	+	+	+	+		
May 29	D				D	D	D	D	F	F
June 9									D	D
Survival (days)	7.5	3.5	3.5	3.5	4.5	4.4	4.5	4.5	5	5

Mean survival time (+/- standard error) = 4.6 +/- 0.37.

b) Survival on *Festuca rubra*

	Females							
	1	2	3	4	5	6	7	8
Date								
May 18	F	F	F	F				
May 21	+	+	+	+	F	F	F	
May 23	+	+	+	+	+	+	+	
May 29	D	D	+	+	+	+	D	F
June 9			+	+	+	+		D
June 23			D	+	+	+		
Survival (days)	7.5	7.5	27.5	35	32	32	4.5	5

(N.B. Out of the original 10 *C. albomarginatus* placed on *F. ovina*, 2 escaped)

Mean Survival time (+/- Standard error) = 18.9 +/- 4.87

7.5.2 Results

Oviposition in *Adarrus multinotatus*

The eggs of *A. multinotatus*, like most of the cicadellid eggs observed, were approximately 1 mm long, 0.2 mm wide in the middle and shaped like a slightly curved cylinder with bluntly pointed ends. They had a smooth unsculptured surface and were translucent white. They were first found on dead leaf sheaths of *Brachypodium pinnatum* plants that had been overwintered in the greenhouse between 1988 and 1989 during the choice experiments described earlier. Later clip cage experiments, described earlier in this chapter, indicated that they would only lay on dead leaf sheaths, or, occasionally, on dead leaves. The eggs were always inserted through the leaf sheath, so that they rested between the sheath and the grass stem, and stuck by one end to its inner surface. They were never lodged between the outer and inner epidermis of the sheath. As the dead sheaths (and leaves) were generally tightly rolled the eggs rested within a tough cylinder (Plate 7.2 (a)).

Criomorphus albomarginatus

One female confined in a clip cage laid 2 eggs side by side into a young tightly rolled leaf of *Festuca rubra*. The eggs were pushed through the outer sheath and lodged horizontally in slits made in opposite sides of the rolled leaf.

Doratura stylata

One female placed on *F. rubra* laid eggs on three separate green leaf sheaths, always in the same position at the top of the sheath just below the transition to the leaf. They were generally laid side by side, angled across the long axis of the sheath and were all embedded between the outer and inner epidermis. (Plate 7.2 (b))

Euscellis inclisus

One female placed on *Arrhenatherum elatius* laid 6 eggs in a green leaf sheath.

Holes on the outside of the sheath suggested that during oviposition the eggs were pushed through the outer surface. Some of the eggs were pushed through the inner epidermis and so were exposed on the inside of the sheath, one end being embedded in the sheath. Other eggs were lodged between the outer and inner epidermis and, like the eggs of *D. stylata*, could be seen clearly through the inner surface of the sheath.

Mocycdia crocea

Females of the autumn generation of this species were caged on *Brachypodium pinnatum* in August 1990 and August 1991. In 1990, eggs were not observed until early November, and in 1991 until late October. This was the only species among those examined that laid eggs exclusively in living leaf tissue. No eggs were observed in leaf sheaths or dead tissue of any sort. Eggs were laid through slits made in the adaxial surface of the leaf. Some protruded from the slits while others were entirely embedded and only visible as a bulge in the leaf surface.

Rhytistylus proceps

In 1990 4 female *R. proceps* were placed on *Festuca ovina* in separate clip-cages. Despite including living and dead stems and leaves and varying the position of the clip-cages no eggs were laid, although the females survived well on the grass. This was surprising in view of the very close association between *R. proceps* nymphs and *F. ovina* revealed by the field choice experiments. In 1991, females were caged on *Arrhenatherum elatius* as well as *F. ovina* as this was a grass that adult *R. proceps* preferred in field choice experiments. Again, no eggs were laid despite good survival on both species. A dead flowering stem was then included in one of the cages on *A. elatius* and when after about two weeks this was slit open it was found to be packed with eggs (Plate 7.2 (c)). Following this, dead flowering stems were added to cages on *F. ovina* and again oviposition occurred within the stems. Barely visible slits were present on the outer surface of the stems where eggs had been inserted.

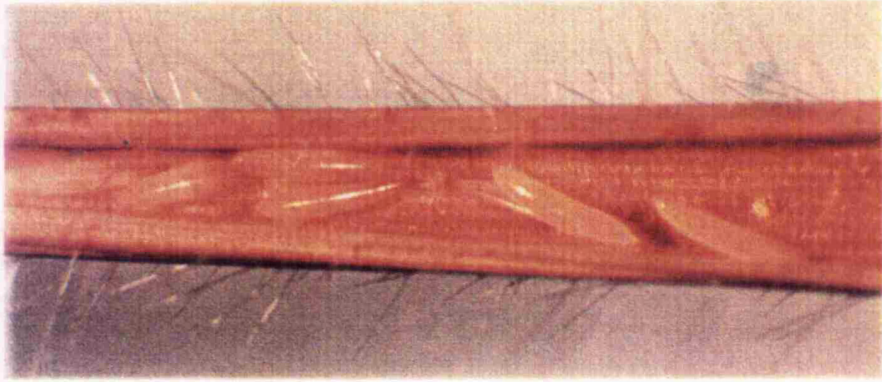
Plate 7.2

Plate 7.2

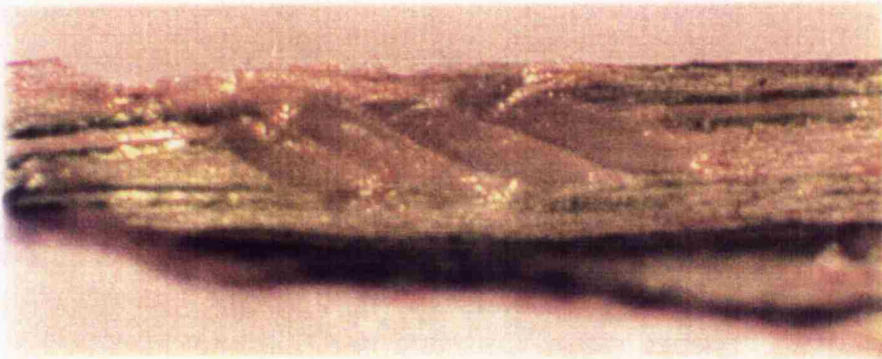
- a) Eggs of *Adarrus multinotatus* on inner surface of dead leaf sheath of *Brachypodium pinnatum*.
- b) Eggs of *Doratura stylata* in a living leaf sheath of *Festuca rubra*.
- c) Dead flowering stem of *Arrhenatherum elatius* split open to reveal eggs of *Rhytistylus proceps*.
- d) Eggs of *Turritus socialis* in a dead leaf sheath of *Avenula pubescens*, showing eggs attached to the inner surface of the sheath only by one end, and eggs embedded in the sheath.

N.B. All the eggs are approximately 1mm long

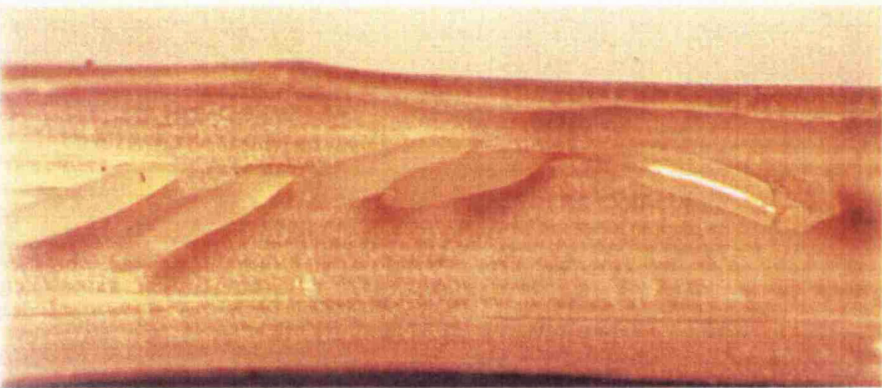
a



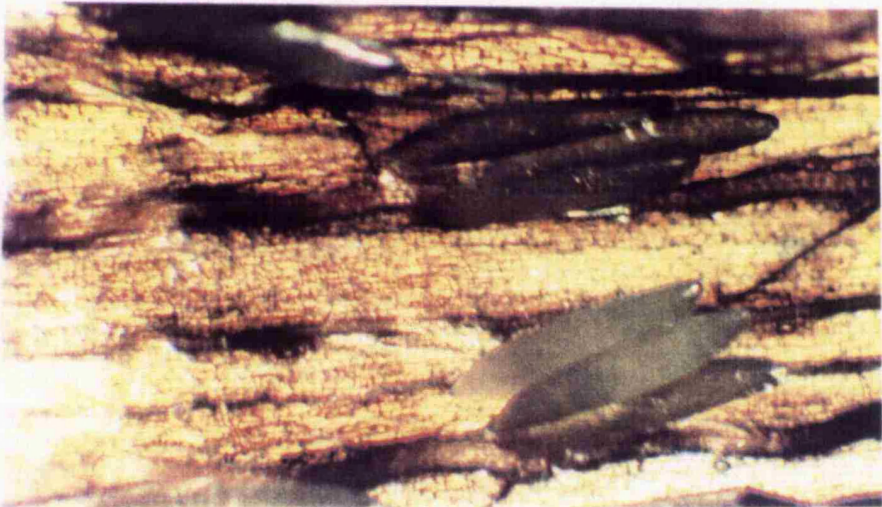
b



c



d



Turrutus socialis

In 1990, some time before the survival and oviposition experiments with *T. socialis* described earlier, females confined on *Avenula pubescens* and *Festuca rubra* laid eggs on both grasses. Eggs were always laid in dead leaf sheaths (Plate 7.2 (d)). As in *Doratura stylata* and *Euscelis incisus* the eggs were often lodged between the outer and inner epidermis where they were clearly visible through the thin inner lining of the sheath. Less frequently eggs were inserted through both surfaces with one end firmly embedded in the sheath. The oviposition experiments confirmed this egg laying behaviour but showed that very occasionally *T. socialis* would lay eggs in living leaf and sheath tissue.

7.6 Discussion

The experiments described in this chapter were based on plants grown in pots in a greenhouse. It could be argued that because plants grown in this way would differ in nutrient status and growth form from those growing naturally in the field such experiments may give a false picture of host suitability (Gibson, 1976). Any experimental manipulation will differ from the natural situation; if in this study insects had been caged on plants in the field (an alternative that was logistically impossible) the artificial microclimate within the cage and their confinement to one position would have been almost as unnatural. As all the plants in the greenhouse were treated in the same way it is reasonable to argue that the no-choice experiments provided a relative measure of host suitability.

Experiments in which an insect is confined to different potential host plants test its physiological potential to survive on those plants. The potential host range as measured by no-choice tests is generally greater than that observed in field or laboratory choice experiments although preference is usually shown for the field host or hosts (Drosopoulos, 1977; den Bieman, 1987). Field and laboratory choice tests on *Adarrus multinotatus* described in previous chapters provided clear evidence of specificity to *Brachypodium pinnatum* and the results of the no-choice

tests strongly support this. All the nymphs of *A. multinotatus* tested on *B. pinnatum* matured to adults while on *Festuca rubra*, although survival was good, only one nymph matured after a long development time. Survival on *Bromus erectus* was very poor. The responses of adult females corresponded with those of the nymphs.

The poor survival of *A. multinotatus* on *B. erectus* as compared with that on *F. rubra* does not correspond with the structural similarities or taxonomic relationships between these grasses and the field host *B. pinnatum*. (Clayton & Renvoize, 1986). Drosopoulos (*op. cit.*) found that the host specific delphacid *Muellerianella brevipennis* failed to survive on *Deschampsia flexuosa*, a cogener of its field host *D. cespitosa*, although females survived and reproduced on two other species less closely related to the field host.

Drosopoulos (*op. cit.*) also found that nymphs of *M. brevipennis* confined with *Holcus lanatus*, the host plant of the closely related *M. fairmairei*, had a mean survival time of 3.22 days, only a little longer than the survival time of 2.64 days on moist filter paper. Drosopoulos suggested that lack of proper nutrition was the main factor causing nymphal mortality. The poor survival of *A. multinotatus* on *B. erectus* and its failure to mature on *F. rubra* may well be due to nutritional factors, although this explanation does not seem entirely satisfactory. (That *A. multinotatus* actually fed upon *B. erectus* was not confirmed by looking for feeding marks on the plant tissue, but as the mean survival time of *A. multinotatus* nymphs was 6.8 days and adults 5.7 days it may be inferred that some feeding took place.) *Turrutus socialis* survived well on *B. erectus* (see below), both in the nymphal and adult stages, and it seems unlikely that the basic nutritional requirements of this species would be very different from those of *A. multinotatus*. Deficiencies in particular nutrients may prolong development, or reduce reproduction (Hill, 1976; McNeill & Southwood, 1978; Cheng & Pathak, 1972) but the rapid mortality of *A. multinotatus* on *B. erectus* suggests that other factors, including chemical or physical barriers to successful long term feeding, may be involved. Closely related plant species may

differ in one or two secondary chemicals, just as closely related herbivorous insects may differ in their ability to detoxify them (Harborne, 1988).

The results obtained from the no-choice experiments on *Turrutus socialis* confirmed the ability of this species to utilise a fairly wide range of host grasses. Although the experiment on nymphal survival was based on the performance of late instars only (earlier instars may have been more host specific), there was marked variation in the numbers of nymphs that matured on the different host plants. This corresponded with the performance of the adult females. Both nymphs and adults performed best on *Avenula pubescens* and *Festuca rubra*, adding to the evidence from choice tests that these two grasses may be important hosts. Survival of nymphs and adults and oviposition were significantly lower on *Briza media* and *Festuca ovina*. The short survival times of adult females on these two grasses may be due to chemical or physical deterrents, as discussed above in relation to *A. multinotatus* on *B. erectus*. The significant difference in the response of *T. socialis* to *F. ovina* and *F. rubra* again demonstrates that taxonomic affinity in grasses is not necessarily an indication of their suitability as hosts for particular species of Auchenorrhyncha.

The short experiment on the survival *Criomorpus albomarginatus* on *F. ovina* and *F. rubra* demonstrated a clear preference for *F. rubra*, to which it was specific in the field. More information is needed on the survival of this, and other species found at the Deeps, on a range of possible host grasses. In this study, physical evidence of feeding, in the form of puncture marks in the leaf, was not recorded. If similar experiments were to be repeated, such evidence would be useful in interpreting the results.

In the experiments on *A. multinotatus* and *T. socialis*, females were reared from nymphs that were caged on *B. pinnatum* and *F. rubra* respectively, following collection from the field. As the adult females performed well on the grasses on

which they were caged as nymphs, it could be argued that the experience of the nymphs had some influence on subsequent behaviour. The Hopkins Host Selection Principle or theory of larval memory postulates that female insects prefer to oviposit on plant species that they fed upon as larvae (Claridge & Wilson, 1978). Claridge & Wilson found that nymphs of tree feeding cicadellids were less host specific than females and considered female oviposition behaviour to be an important determinant of host specificity. They also cited work by Wiklund (1974) and Chew (1977) as further evidence against the idea that oviposition behaviour is influenced by conditioning of immature stages. There is also evidence that in tree-living leafhoppers, oviposition preferences and the behaviour associated with oviposition are species specific inherited characteristics (Claridge & Reynolds, 1972).

It was considered unlikely that nymphal conditioning influenced the results of the no-choice experiments performed in this study, although this cannot be completely discounted. *T. socialis* performed as well on *A. pubescens* as on *F. rubra*, the grass used to rear the females from nymphs, which suggests that conditioning did not influence this species.

There is little information available on the oviposition behaviour of those species of Auchenorrhyncha found at the Deeps. Thompson (1978) described the oviposition sites of five Auchenorrhyncha species on their host plants, *Holcus lanatus* and *H. mollis*, in acid grassland. (Three of these species, *Dicranotropis hamata*, *Diplocolenus abdominalis* and *Elymana sulphurella* also occurred at the Deeps.) He found that *D. abdominalis* laid the majority of its eggs in dead leaf sheath tissue, mainly towards the base of the plant. Two other cicadellids, *Adarrus ocellaris* and *Recilia coronifera* also laid mostly in leaf sheaths but utilised living and dead tissue equally. In the fourth cicadellid, *Elymana sulphurella* egg distribution was divided equally between leaf blades and leaf sheaths, but oviposition occurred only in living tissue. The only delphacid in Thompson's study, *Dicranotropis hamata*, laid

most of its eggs in grass stems. The cicadellids and the delphacid differed in the way in which eggs were positioned; *D. hamata* inserted eggs vertically into stems or rolled, developing, leaves while the majority of the cicadellid eggs were laid between the upper and lower epidermis of leaf tissue. Thompson suggested that utilisation of different parts of their host plants for oviposition may be a factor that enables these species to coexist.

The range of oviposition behaviour found by Thompson (*op. cit.*) was also found in Auchenorrhyncha from the Deeps. The data obtained was limited by the clip-cage method used to investigate oviposition; species confined on the wrong part of a plant in a clip-cage may not have exhibited typical egg laying behaviour, even though a range of plant structures was presented to them. Most species preferred leaf sheath tissue for oviposition. Living tissue was used by *Doratura stylata* and *Euscelis incisus*, and dead tissue by *A. multinotatus* and *T. socialis*. Clip-cage experiments showed that *A. multinotatus* would only lay in dead leaf sheath tissue of *B. pinnatum*. Two females provided with only living tissue for oviposition laid no eggs for over two months. They both laid immediately after dead leaf sheath material was included in their clip-cages. Once dead, the leaf sheaths of *B. pinnatum* became very tough and tightly rolled, presumably providing secure sites for overwintering eggs. The toughness of the dead sheaths may also explain why, unlike other species that laid in sheaths, *A. multinotatus* did not embed eggs in the tissue but inserted them through the sheath into the space between the sheath and the stem, securing them at one end to the inner surface of the sheath (see Plate 7.2 (a)).

T. socialis embedded the majority of its eggs between the inner and outer epidermis of dead leaf sheaths (Plate 7.2 (d)) on all hosts used for oviposition with the exception of *B. pinnatum*. On this grass eggs were frequently attached to the inner surface of the leaf sheath or, occasionally, partially embedded in it. A few eggs in the latter group actually ruptured during the examination of the leaf sheath,

due to the pressure exerted on the eggs by the tough tissue. Although *T. socialis* also laid eggs mainly in the dead leaf tissue of its hosts, it occasionally laid in living tissue. This occurred although there was unutilised dead tissue available in the clip-cages.

The observations made on oviposition in *Rhytistylus proceps* clearly indicate an obligatory requirement for dead flowering stems. For a period of over two months females were caged on different parts of *Festuca ovina*, a plant they survived well on and which choice experiments had indicated was an important host, but no eggs were laid. Only when dead flowering stems were provided would this species oviposit. It is possible that a completely cylindrical structure (as opposed, for instance, to a rolled leaf) of a particular diameter is required by *R. proceps* because of the mechanics of oviposition. If, for instance, it oviposits by "hugging" the stem to obtain the necessary leverage to pierce the stem tissue with the ovipositor; the rigidity and diameter of the stem may be critical. It is possible that *R. proceps* not only oviposits on hosts with suitable flower stems, but also utilises particular sections of the stems. Different species of grass bugs (Stenodemini; Miridae) have been shown by McNeill (pers. comm.) to oviposit at different heights in grass flower stems.

Mocydia crocea was the only cicadellid, among the six observed, that oviposited consistently in living leaf tissue. This species laid eggs in clip-cages on *B. pinnatum* and *B. erectus*, but was not tested on any other species of grass. However, in field choice tests it showed a clear preference for these two host species. It is possible that species like *M. crocea*, that embed eggs in leaves may have a requirement for leaves of a particular width or thickness.

Oviposition was only observed once in the delphacid *Criomorphus albomarginatus* and only tested on its host plant, *Festuca rubra*. The method of oviposition appeared to be very similar to that described by Thompson (1978) for *Dicranotropis*

hamata. Two eggs were found inserted into a living stem of *F. rubra*, at right angles to the long axis of stem.

Attempts to overwinter eggs of *A. multinotatus* and *T. socialis* by placing leaf sheath tissue containing eggs in clip-cages on the respective host plants in the greenhouse failed. This may be an indication of the critical conditions required for the successful development of leafhopper eggs. Simply caging a leaf sheath containing eggs close to the position on a plant from which it came probably did not duplicate the natural conditions closely enough. The humidity to which the eggs are exposed is probably a critical factor in their development (McNeill, pers. comm.) and the variety of plant structures (rolled leaf sheaths, within leaf tissue, dead flower stems, etc) used by different species of Auchenorrhyncha for oviposition may reflect the very precise conditions required for successful development. As well as ensuring suitable physical conditions, the varied types of oviposition behaviour may have evolved to reduce the risks of attack by predators and parasites on eggs (Claridge & Reynolds, 1972). Further work with clip-cages could provide useful data on the relationship between oviposition requirements and host choice.

The successful development of a certain proportion of eggs on a particular host is essential to the establishment and survival of an insect population. Although *A. multinotatus* and *T. socialis* were successfully reared from overwintered eggs laid on host plants in the greenhouse, the difficult task of estimating the number of eggs originally laid on the different grasses was not attempted. A detailed assessment of host suitability would require life tables of fecundity and mortality for each species on each potential host plant.

8. GENERAL DISCUSSION

In this study, the Auchenorrhyncha of an area of calcareous grassland in the East Midlands were described and an attempt made to determine the host preferences of these grass feeding-insects by using grasses grown in pots for choice experiments in the field and greenhouse. Cicadellid nymphs formed an important part of the samples obtained during the choice experiments and they were identified, mainly by greenhouse rearing, and described. No-choice tests were used to examine the response of a few of the commoner species of Auchenorrhyncha to a range of possible hosts.

The results of the field choice experiments indicate that, at the Deeps, a group of species was confined to, or showed a marked preference for, one species or genus of grass, another small group was associated with a particular range (tribe) of grasses, and a third group of species had little or no overall host preference. Information on host preference was obtained for 16 out of the 40 species recorded from the site. This information complements or supports published data in some cases but is contradictory in others. Before discussing the relationships between grassland Auchenorrhyncha and their plant hosts with reference to the findings of this study, the information now available on the host preferences of the species found at the Deeps is summarised below.

Cicadellidae

Adarrus multinotatus

This was a common species at the Deeps and only found in areas dominated by *Brachypodium pinnatum*. Choice tests in the field and greenhouse and no-choice tests provided strong evidence of specificity to *B. pinnatum*. This is in agreement with Schiemenz (1969) who, in a survey of the Auchenorrhyncha of dry grassland sites in Germany, found that *A. multinotatus* was associated with *B. pinnatum*. This

is the only reference to the host plant of this species of which I am aware.

Aphrodes albifrons

Although only caught occasionally during the field choice experiments, this was one of the most abundant species to hatch from grasses brought into the greenhouse following the field choice experiments. *A. albifrons* hatched from a range of grasses but most abundantly from *Festuca ovina*. Significantly more *A. albifrons* hatched from plants that had been treated with ammonium nitrate in the field. Published accounts of this species (see chapter 3) indicate a wide host range although there is no reference to *F. ovina* or *F. rubra* as host plants.

Aphrodes bifasciatus

This was the most abundant of the *Aphrodes* spp. caught in the field choice experiments but it showed no clear association with any of the grasses. None of the eight references to *A. bifasciatus*, reviewed in chapter 3, gives any information on host plants. It appears to be typical of calcareous grassland.

Arthaldeus pascuellus

At the Deeps this species was more common on Site 2 where it showed a significant preference for *F. rubra* in the small scale choice experiment based on *Brachypodium pinnatum*, *Bromus erectus* and *F. rubra*. It occurred on Site 1 in low numbers, where it was recorded mainly on two fine leaved grasses, *F. ovina* and *T. flavescens*, but not from *F. rubra*. Although there is some evidence for an association between *A. pascuellus* and fine leaved grasses (Waloff & Solomon, 1973; Morris, 1990b), it has also been found on *Lolium perenne* and other broad leaved grasses (Prestidge & McNeill, 1981; Morris, *op. cit.*). Prestidge & McNeill (1983) found that this species was not significantly influenced by grass nitrogen levels.

Doratura stylata

This species was characteristic of Site 1 at the Deeps, and in the choice experiments nymphs were caught mainly from *F. ovina* and *F. rubra*, especially the latter. In clip-cages it oviposited in living leaf sheaths of *F. rubra*. At Silwood park *D. stylata* was found on *Agrostis capillaris* and *F. rubra* (Waloff & Solomon, 1973; Prestidge & McNeill, 1982). In continental Europe, Marchland (1953) (cited by Ossiannilsson, 1983) recorded *D. stylata* from *Nardus stricta* grassland and in North America it has been found on *Poa pratensis* (Whitcomb, 1953).

Diplocolenus abdominalis

This was one of the more abundant species at the Deeps, and occurred on both study sites. It was the only species which showed no significant heterogeneity in the numbers caught from experimental grasses on Site 1. Despite the apparently wide host range at the Deeps, *D. abdominalis* was found to be closely associated with *Holcus* spp. in the acid grassland at Silwood Park (Waloff & Solomon, *op. cit.*). *H. lanatus* was recorded by Hepburn (1955) as occasional at the Deeps, although he did not record it in 50 1m² quadrat samples taken at random over the grassland. The grass was not present in the sites used in this study and I have only seen it occasionally along the edges of paths in other parts of the grassland.

Euscelis incisus

E. incisus was caught in relatively high numbers from a range of grass species but showed a marked preference for *Trisetum flavescens*, a plant that did not grow very vigorously in pots. *T. flavescens* did, however, have a higher average nitrogen content than any other grass used in the choice experiments, which may explain the association with *E. incisus*. Prestidge & McNeill (1983) found that *E. incisus* was a generalist feeder with respect to grass species (although it showed some preference for *Lolium perenne*, *Festuca pratensis* and *Poa pratensis*), but a specialist with respect to nitrogen levels. As *E. incisus* overwinters as a nymph and matures early in the season, breeding females may have a relatively high

requirement for nitrogen (Prestidge, 1982a). However, the association between *E. incisus* and *T. flavescens* was mainly due to the numbers of nymphs caught in June and July. Morris (1990b) found that *E. incisus* was more common on plots sown with fine grasses.

Graphocraerus ventralis

Although caught in fairly low numbers during the choice experiments on Site 1, this species showed an association with the Aveneae (*Arrhenatherum elatius*, *Avenula pubescens* and *T. flavescens*). There is little published information on this species; it was one of the more common species in the *A. elatius* dominated grassland at Mitcham Common (Hollier, 1987), and in continental Europe has been found on *Poa pratensis* and *Anthoxanthum odoratum* and "in the *Arrhenatheretum*" ((Schaefer, 1973; Schwoerbel, 1957; both cited in Ossiannilsson 1983). At Silwood Park it was found on sites dominated by *F. rubra* and *Agrostis capillaris* (Waloff & Solomon, *op. cit.*).

Mocycdia crocea

The results of both field choice experiments and hatchings from grasses brought into the greenhouse following the 1990 choice experiments, gave a strong indication of an association between *M. crocea* and the two dominant grasses of the Deeps *Brachypodium pinnatum* and *Bromus erectus*. The evidence from the hatchings suggested that *B. erectus* may be the more important host. Le Quesne (1969) gave *B. pinnatum*, *B. erectus* and *Dactylis glomerata* as host grasses for *M. crocea*, and Whittaker (1969) recorded it from *B. pinnatum*. Morris (1990b) found that it occurred almost exclusively, although in low numbers, on plots sown with coarse, as opposed to fine, grasses (which included *D. glomerata*, but not *B. pinnatum* or *B. erectus*). Muller (1987) described six 'larval forms' of *M. crocea* in mid-European semi-arid grassland (Onobrychido-Brometum) and reported that the main host grasses were *B. pinnatum*, *B. erectus*, *D. glomerata* and *Lolium perenne*.

Rhytistylus proceps

The nymphs of this species were found in relatively high numbers almost exclusively on *Festuca* spp., especially *F. ovina*. The adults, however, which were caught in much lower numbers, showed little specificity. *R. proceps* would only oviposit in dead flowering stems when confined on *F. ovina* in clip-cages, and also laid in the dead flowering stems of *Arrhenatherum elatius*. Waloff and Solomon (*op. cit.*) found *R. proceps* only in areas dominated by *F. rubra*. On sown grassland plots it was associated with fine grasses (Morris, *op. cit.*) and Ossiannilsson (1987) gave *Corynephorus canescens* and *Nardus stricta* (citing Kuntze, 1937), the Corynephoretum (citing Marchland, 1953) and *Carex arenaria* (citing Trolle *in litt.*) as possible host plants. Both *C. canescens* and *N. stricta* are fine leaved grasses.

Turrutus socialis

As this species appears to be confined to calcareous grassland (see chapter 3) an association with a calcicolous grass (as in the case of *A. multinotatus*) would not have been surprising. The results of both choice and no-choice experiments generally showed a marked lack of specificity although *T. socialis* may have a preference for *Avenula pubescens* and *F. rubra*, especially for oviposition. *T. socialis* is one of the dominant species in calcareous grasslands in England (Morris, 1974), but there is little information available on host plants. Morris (1990b) found that it was significantly more abundant on plots sown with fine grasses, which included *F. rubra*.

Zyginidia scutellaris

This was one of the species that hatched in relatively large numbers from grasses used in the 1990 field choice experiment on Site 1, although it was rarely caught in any of the field samples. *Z. scutellaris* hatched only from the broader leaved grasses and among those showed a preference for *Briza media*. It hatched in significantly larger numbers from grasses that had not been treated with ammonium nitrate in the field experiment. *Z. scutellaris* has been found in

association with *B. pinnatum* (Whittaker 1969), *Holcus* spp., *D. glomerata* and *A. capillaris* (Waloff & Solomon *op. cit.*) and with coarse grasses (Morris, 1990b). According to Le Quesne & Payne (1981) it is mainly associated with *D. glomerata* and *F. rubra*. Prestidge & McNeill (1983) found it to be a generalist feeder but closely associated with high nitrogen levels during the ovipositional period. Although it has been found to overwinter as an adult (Prestidge, 1982a), it is almost certain that *Z. scutellaris* overwintered in the egg, or early nymph, stage on the grasses kept in the greenhouse following the field choice experiment.

Other cicadellids

Little information was obtained during this study on any of the other cicadellids recorded at the Deeps. During 1990, when Site 1 was severely affected by drought, *Psammodettix confinis* and *Macrostelus sexnotatus* were caught from a number of the experimental grasses species in low numbers. *P. confinis* is an opportunist and probably responds positively to habitat disturbance (Prestidge & McNeill, 1983). Prestidge & McNeill found that it was not significantly influenced by grass nitrogen levels. It is also one of the most common species of acid grassland (Waloff & Solomon, *op. cit.*; Morris, 1980; Hollier, 1987) where it appears to be particularly associated with *Agrostis capillaris*. It is quite possible that the occurrence of *P. confinis* at the Deeps was opportunistic and that it is not a characteristic member of the Auchenorrhyncha community. The same may apply to *M. sexnotatus*; which is also an opportunistic species (Morris, 1984). *Paluda adumbrata* nymphs were caught in low numbers during the field choice experiments exclusively from *Festuca* spp. Port (1981) found that, on roadside verges, this species only occurred where *F. rubra* was present.

Delphacidae

Criomorpha albomarginatus

This species was almost exclusively associated with *Festuca rubra* in the field choice experiments, occurring most abundantly in the ranker type of vegetation of

Site 2. In clip-cages *C. albomarginatus* survived markedly longer on *F. rubra* than on *F. ovina*. In acid grassland Waloff & Solomon (1973) found that *C. albomarginatus* was mainly associated with *Holcus* spp., but they also bred it from *F. rubra*. *C. albomarginatus* colonised sown grassland in low numbers at Royston, Hertfordshire, where it was only recorded on fine-leaved grasses (Morris 1990b). In Finland, specimens in cages reproduced and fed on a variety of grasses (Raatikainen & Vasarainen, 1973).

Hyledelphax elegantulus

H. elegantulus was found abundantly during the choice experiment on Site 1. It appeared to have a wide host range, although it avoided *B. pinnatum*. There was some evidence from the nitrogen study that the number of *H. elegantulus* found on a particular grass was positively correlated with total nitrogen content, but this result must be treated with caution because of the small differences found in the total leaf nitrogen between some of the grass species. Waloff & Solomon (*op. cit.*) found that the main host plant of this delphacid in acid grassland was *F. rubra* and Ossiannilsson (*op. cit.*), citing both Strubing in Muller (1957) and Remane (1958) gave *Deschampsia flexuosa* as a possible host.

Kelisia vittipennis

This species was found only on *Carex flacca*. Linnavuori (1952) recorded it in bogs on *Eriophorum vaginatum* and Dolling (1991) suggested that *K. vittipennis* is confined to this host. According to Le Quesne (1960) it is found on sedges both on dry hillsides and in peat bogs.

Other delphacids

The other delphacids present at the Deeps were only recorded in very low numbers during the field choice experiments. *Javesella pellucida* has been fairly well studied, and has been found to have a wide host range within the Gramineae (Raatikainen, 1967; Prestidge, 1982a). In acid grassland it has been found to be

closely associated with high grass nitrogen levels (Prestidge & McNeill, 1983) *Dicranotropis hamata* is closely associated with *Holcus* spp. in acid grassland (Waloff & Solomon, *op. cit.*). Only one specimen of this species was found during the entire study. There is substantial evidence to suggest that *Stenocranus minutus* is monophagous on *Dactylis glomerata* (Waloff & Solomon, *op. cit.*; May, 1971; Prestidge & McNeill, 1981; Prestidge, 1982a). During my preliminary survey of the Deeps *S. minutus* was caught in larger numbers than any other delphacid, despite the rarity of *D. glomerata* on the site (Hepburn, 1955), suggesting that another host for this species may exist on calcareous grassland.

Although the data available on the grass hosts of the Auchenorrhyncha at the Deeps is far from comprehensive there is an indication from the above summary that a degree of host specialism (feeding on one species, one genus or one tribe; (Crawley, 1983)) is not uncommon. Those species that are generalists (feeding on a range of grass tribes) may in some cases be restricted to grasses with a particular morphology, i.e. fine-leaved or broad-leaved grasses, for at least a part of their life cycle. Although the quantity and quality of particular nutrients is undoubtedly an important factor in the choice of plant hosts by grassland Auchenorrhyncha the assumption that the majority of species are, in other respects, opportunists, as suggested by Crawley (1983), should be questioned. It seems very probable that host choice may be determined by a number of factors, and these are discussed below in relation to the findings of this study.

The results of the no-choice tests showed that both a host specialist (*Adarrus multinotatus*) and generalist (*Turrutus socialis*) had a very limited survival period on some of the grass species on which they were caged. *A. multinotatus* survived for an average of 5.7 days on *Bromus erectus* and *T. socialis* for 12.1 days on *Briza media* and 8.9 days on *Festuca ovina*. On some of the other hosts, both species were able to survive for over 90 days in clip-cages. As argued in Chapter 6, it is likely that feeding took place on the unsuitable hosts and possible that the

relatively rapid mortality was due to secondary chemicals present in the grasses. It is of interest in this respect that Whitcomb, Kramer, Coan & Hicks (1987) considered that a grass host was suitable for survival if the majority of a sample of adult cicadellids of a given species survived on it in experimental conditions for 5-7 days. This seems a very short period over which to determine host suitability.

Although grasses generally seem to have a limited range of secondary chemicals in low concentrations (Gibbs, 1974; Harborne & Williams, 1976), it has been shown that flavonoid and hydroxamic acids are present in a number of species (Harborne & Williams, *op. cit.*; Argandona et al., 1980, 1981, 1985). Harborne & Williams (*op. cit.*) found a range of flavonoids among the 274 grass species they analysed from temperate and tropical sub-families. Of the grasses used in this study, Harborne & Williams analysed *Arrhenatherum elatius*, *Briza media*, *Bromus erectus* and *Festuca rubra*. They also analysed species closely related to the other grasses used, i.e. *Brachypodium sylvaticum*, *Avenula pratense* and *Trisetum spicatum*. Flavone C-glycosides and tricetin were found to be the major flavonoids present, occurring in 93% of the samples including all the above named species. On the other hand the flavonols kaempferol and quercetin were present in only 3% and 5% respectively of all the samples. They were both present in *B. media*, but absent from all the other above named species. Quercetin glycosides have been shown to deter feeding in insects (Harborne, 1988). Harborne & Williams found luteolin (a flavone O-glycoside) was present in 15% of the tribe Poeae, 43 % of the Triticeae, 43% of the Agrostideae but absent from the Aveneae. It occurred only in *Bromus erectus* among the above named species. In general there was a marked variation in the flavonoid content of different species and genera within a tribe.

In addition to flavonoids the hydroxamic acid DIMBOA (2,4-Dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one) is present in many grasses (Harborne, *op. cit.*) and has been shown to act as an insect antifeedant in a variety of cereals (Argandona et al., 1980, 1981, 1985). Oxalic acid in some resistant varieties of *Oryza sativa* has

(Argandona *et al.*, 1980, 1981, 1985). Oxalic acid in some resistant varieties of *Oryza sativa* has been shown to inhibit feeding by the brown plant hopper *Nilaparvata lugens* (Yoshihara, Sowaga, Pathak, Juliano & Sakamura, 1980). It has also been found that resistance of *O. sativa* to *N. lugens* may be due to the chemical composition of the wax surface, the effective agents being the hydrocarbon and carbonyl-containing fractions of the wax (Woodhead & Padgham, 1988). Secondary chemicals in plants may not only deter feeding in insects but also act as feeding and oviposition stimulants (Harbourne, 1988). Using a Y-shaped olfactometer, Hopkins & Young (1990) showed that the grasshopper *Melanoplus sanguinipes* was strongly attracted to volatile chemicals given off by *Lolium perenne* and *Triticum aestivum*. It seems probable that secondary chemicals play a variety of roles in the choice of host grasses by Auchenorrhyncha.

There is a considerable body of evidence to show that the chemical nature of grasses in terms of their nutrient quality plays an important role in host selection by Auchenorrhyncha (McNeill & Southwood, 1978; Prestidge & McNeill, 1981, 1983; Prestidge, 1982b). Data collected in this study indicates that two species, *Euscelis incisus* and *Hyledelphax elegantulus*, showed a preference for hosts with a higher total nitrogen content. Another species, *Turrutus socialis*, occurred more abundantly on the set of experimental grasses treated with ammonium nitrate than on the untreated set, although it showed no significant preference for particular grass species with higher total nitrogen contents. One of the aims of the work on leaf nitrogen and host preference in this study was to attempt to distinguish between Auchenorrhyncha that select their hosts mainly on the basis of nutrient quality (selection between species) and those that are limited in their host range for other reasons but may still select plants within particular species on the basis of nutrient quality. Due to the small scale and short term nature of the fertilization experiments, sufficient data for a comparison of the responses of a range of species was not obtained.

The work on nitrogen did, however, provide feasible explanations for some of the results obtained from the field choice experiments, especially the marked preference of *Euscelis incisus* for *Trisetum flavescens*. (Prestidge & McNeill (1983) found that this species was a nitrogen specialist in acid grassland.) It also indicated that certain species, like *Mocydia crocea*, may discriminate between plants of different nutrient quality when ovipositing. *Zyginidia scutellaris* on the other hand laid fewer eggs on grasses that had been fertilised. Prestidge (1982) found that the oviposition rate in *Dicranotropis hamata*, *Elymana sulphurella*, *E. incisus* and *Z. scutellaris* increased when they were fed on *Holcus lanatus* that had been fertilised with ammonium nitrate. A similar response has been found in other groups of insects. For instance, ovipositing females of *Pieris rapae* have been shown to discriminate between host plants that have been subjected to different fertiliser regimes (Myers, 1985).

The nitrogen analysis showed that *Festuca ovina*, the plant from which the highest number of individuals of a specialist species (*Rhytistylus proceps*) was caught, had the lowest nitrogen content of any of the grasses used. Specialist grassland Auchenorrhyncha are probably less dependent on particular nitrogen levels in their food than those species with other strategies (Prestidge & McNeill, 1981). However, total nitrogen is a fairly crude measure of nutrient quality; as Prestidge & McNeill have shown grassland Auchenorrhyncha may respond to the concentrations of particular amino acids in their host plants.

In his work on the colonisation of sown grasslands by Heteroptera and Auchenorrhyncha, Morris (1990a) gave no reasons for his choice of coarse and fine-leaved grass mixtures other than that they provided contrasting habitats. Neither did he suggest any reasons for the occurrence of certain Auchenorrhyncha almost exclusively on one or other of the grasslands. Some of these species may have been host specific and have simply colonised the grassland which contained their host. It is also possible that some of the species that colonised the plots were

not host specific, but, nevertheless, required grasses with a particular morphology; i.e. they were morphological specialists.

Support for this idea comes from some of the information on the species found at the Deeps given earlier in this chapter. *Doratura stylata* has been found associated with the fine-leaved grasses *Agrostis capillaris*, *Festuca rubra*, *Nardus stricta* and *Poa pratensis*. The last named grass was used by Morris (1990a) in his fine-leaved mixture. *Rhytistylus proceps* has been found on *Corynephorus canescens*, *Festuca ovina* and *F. rubra* and *Nardus stricta*. It was found by Morris (1990 b) to be confined to fine-leaved grasses. *Mocydia crocea* appears to be confined to broad-leaved grasses such as *Brachypodium pinnatum*, *Bromus erectus*, *Dactylis glomerata* and *Lolium perenne*. *M. crocea* and *Zyginidia scutellaris* were found by Morris to be colonists of coarse(broad)-leaved grassland although the latter species has been reported from some fine-leaved grasses. In this study, however, *Z. scutellaris* hatched exclusively from broad-leaved grasses. It is also clear from the host plant summaries given earlier in this chapter that there are a number of species that do not fit in with this fine-leaved / broad-leaved distinction (e.g. *Arthaldeus pascuellus* and *Turrutus socialis*).

Morphological specialisation by grass-feeding Auchenorrhyncha, whether based on the fine-leaved / broad-leaved distinction, or other characteristics, could be due to one or more requirements which are related to the structure of their hosts. As shown by Thompson (1978), and by this study, grassland Auchenorrhyncha may be exacting in their oviposition requirements, only laying in a particular type of tissue. Apart from the use of *Juncus* spp. for laying overwintering eggs (but not for feeding) by *Muellerianella fairmairei* (Drosopoulos, 1977) I am unaware of any grass-feeding Auchenorrhyncha that have been shown to require a particular host or range of hosts for oviposition. The relationship between plant structure and oviposition preference would repay further study. Claridge *et al.*(1977) concluded from their work on tree-living *Oncopsis* spp. that adult oviposition behaviour was

the primary determinant of host specificity observed in the field. Oviposition sites must not only provide developing eggs with a suitable microclimate, but also protect them from parasitoidism and predation. There also appears to be no evidence as yet to suggest that predators or parasitoids affect host selection in grass feeding Auchenorrhyncha. Claridge & Reynolds (1972) speculated that avoidance of mymarid parasites might influence the choice of oviposition sites in tree living *Oncopsis* spp. Thompson (1988) suggested that an insect's performance on a plant species may be influenced as much by enemies as by plant characteristics. Certain structural features of host plants may provide a refuge, or 'enemy-free space' (Lawton, 1978), for particular phytophagous insects.

Mechanical barriers to feeding have been shown to limit the range of feeding sites available to the nymphs of the spittle bug *Philaenus spumarius* on the host plants *Anaphalis margaritacea* and *Medicago sativa* (Hoffman & McEvoy, 1986). The limitations were due to trichomes and tissue hardness, both of which prevented stylet penetration to the xylem. The ability of nymphs to penetrate through trichomes and hard tissue increased with size and so the range of feeding sites increased with instar. Tingey (1985) has reviewed the role of trichomes in the resistance to leafhoppers of a number of commercially important dicotyledonous plants. There appears to be no evidence as yet to show that the host range of grass-feeding Auchenorrhyncha may be limited by physical barriers, although it has been suggested that the high silica content of *B. pinnatum* may deter feeding by some insects including certain plant-sucking Stenodemini (Miridae) (Gibson, 1976). The possibility that such barriers influence host choice in grass feeding Auchenorrhyncha cannot be ruled out.

Whitcomb, Kramer, Coan & Hicks (1987) found that many grass-feeding cicadellids had host ranges that reflected the taxonomic relationships of their host plants. Their analysis was based on 2000 collections from grassland sites throughout North America. This study was based largely on one site and so allows little comment on

whether or not this may be the case in British grassland. In view of variation in the chemistry and structure of closely related species, there is perhaps no good *a priori* reason for expecting the relationship found by Whitcomb *et al.* As they have pointed out, their collections came from species of grass belonging to three sub-families (Chloridoideae, Panicoideae and Pooideae), while North European species belong predominantly to one (Pooideae). In this study only one species of Auchenorrhyncha, *Graphocraerus ventralis* appeared to be associated with a grass tribe (the Aveneae). *Mocydia crocea* was associated with two relatively closely related species (*Brachypodium pinnatum* and *Bromus erectus*) and those species that occurred on *Festuca* spp. (*Rhytistylus proceps*, *Doratura stylata* and *Paluda adumbrata*) generally occurred on both *F. ovina* and *F. rubra*. There was no evidence of a species occurring both on *Festuca* spp. and *Briza media*, the other member of the Poeae used in the choice experiments. It is quite likely that the pattern of host selection in these species (with the possible exception of *G. ventralis*) is due to chemical or structural features that these plants have in common which are not necessarily shared by other members of their wider taxonomic group. As *F. ovina* and *F. rubra* were the only species used in the study that belonged to the same genus it is not surprising that they had a number of predators in common. The difference between them is perhaps of more interest ; *Rhytistylus proceps* showed a very marked preference for *F. ovina* and *Criomorphus albomarginatus* an exclusive preference for *F. rubra*.

For a number of the species sampled during the field choice experiments at the Deeps, the evidence for host specificity came largely from the behaviour of the nymphs, which showed a greater degree of specificity than the adults. The difference was especially marked in *Doratura stylata*, *Graphocraerus ventralis* and *Rhytistylus proceps*. This demonstrated the importance of sampling the nymphs, which, because of their greater numbers and lower mobility, may give a better indication of host specificity than the adults. It is possible that in some species the adults may feed more widely than the nymphs which, due perhaps to a greater

sensitivity to plant defences, are confined to particular hosts. According to Eastop (1973), many Auchenorrhyncha spend a considerable part of their adult life feeding on plants on which they do not oviposit. Pitre (1967) found that the nymphs of the leafhopper *Dalbulus maidus* (DeLong & Walcott) would develop only on *Zea mays* although the adults survived well on a wide range of graminaceous species. Curiously, a large number of grass species were also acceptable for oviposition by *D. maidus*. Claridge & Wilson (1977), on the other hand, found that adult oviposition behaviour was more discriminating than nymphal feeding behaviour in tree-living *Oncopsis* spp. In this study female *Turrutus socialis* had a higher specificity index than either males or nymphs due to their relatively high numbers on *Avenula pubescens* and *Festuca rubra*. The greenhouse no-choice experiments showed that these two grasses were preferred by *T. socialis* for oviposition. It may be that in this species oviposition requirements determine host range.

The relationship between the preference of ovipositing females and the performance of the resulting offspring is a major problem in the study of insect / plant relationships (Thompson, 1988). Thompson suggests that in some cases natural selection could favour oviposition on the plant host that is best for egg survivorship and development of early instars, although the performance of later instars is best on other plant species. The host plant relationships of grassland Auchenorrhyncha are obviously complex, and the degree of host specificity in any species may vary in different stages of the life cycle. Even in apparently polyphagous species, a much narrower host range may be required during a critical part of the life cycle.

There was a reasonable degree of correspondence between the published information on the host preferences of Auchenorrhyncha found at the Deeps and the information obtained by this study. There were also some noteworthy differences. *Diplocolenus abdominalis* was associated with *Holcus lanatus* in the acid grassland at Silwood Park (Waloff & Solomon, 1973; Hill, 1982; Prestidge,

1982) and so was *Criomorpha albomarginatus* (Waloff & Solomon, *op. cit.*). Both species were abundant at the Deeps despite the scarcity of *H. lanatus* on the site as a whole and its absence from the sampling sites. *D. abdominalis* showed no clear host preference, but *C. albomarginatus* showed very marked specificity for *Festuca rubra*. *Hyledelphax elegantulus* was also common at Silwood Park, where it was associated with *Festuca rubra* (Waloff & Solomon, *op. cit.*), while at the Deeps it showed no preference for this grass, although caught in larger numbers than *Criomorpha albomarginatus*.

There are a number of possible explanations for these findings. *Diplocolenus abdominalis* may have shown a preference for *H. lanatus* had this grass been included in the field choice experiment. Whether this would have been the case or not, it seems unlikely that *D. abdominalis* was dependent on *H. lanatus* at the Deeps, in view of the scarcity of this grass. It also seems unlikely that the population was maintained by migration from nearby overwintering sites where *H. lanatus* may have been present, as a relatively large number of early instar nymphs were caught early in the year during the choice experiments. Drosopoulos (1977) suggested that *Muellerianella fairmairei* may, in some situations, make local migrations to sites containing *Juncus effusus*, the main host for overwintering eggs. The host specificity of *D. abdominalis* at Silwood Park may have been due to a lack of suitable alternative hosts, which were present at the Deeps. It is also possible that *D. abdominalis* was a host specialist at the Deeps but that the sampling methods did not provide sufficient data to show this. Information on adult and nymphal survival and oviposition on a range of hosts is needed before the requirements of this species can be better understood. The same arguments apply to *Hyledelphax elegantulus*, although in the case of this species the acid grassland host was used in the choice tests at the Deeps but was apparently no more attractive than a number of other potential hosts.

Criomorpha albomarginatus showed a high degree of specificity to *F. rubra* at the

Deeps and was also found to be associated with fine grasses by Morris (1990b) on his chalk grassland site at Royston. At Silwood Park, although *F. rubra* was fairly common (Waloff & Solomon, 1973), *C. albomarginatus* was associated with *H. lanatus*. It is possible that this grass is the preferred host, but that due to its absence at the Deeps *C. albomarginatus* switched to the only appropriate alternative. The dissimilarity between *H. lanatus* and *F. rubra* both structurally and taxonomically make them surprising alternative hosts for a species which appears to be so specific. Fox & Morrow (1981) have emphasised the importance of scale in the diet of herbivores. They consider that ; "...specialization is often a flexible attribute of a population that is responding to features of its particular community, rather than an attribute of a particular species throughout its geographical range" (p. 887). An insect herbivore may feed on a variety of plants over its geographical range, but be a specialist at the community level. This may be because the herbivore occurs in a greater range of habitats than particular plant hosts, as in the case of *C. albomarginatus*, *D. abdominalis* and, possibly, *H. elegantulus*.

Fox & Morrow (*op. cit.*) also discuss situations in which herbivores only feed on one or a few hosts, although a larger number of potential hosts may be available in the community. Such selective behaviour may be determined by the relative densities of host plants, the presence of other herbivores, the presence of predators and / or parasitoids (see also Claridge & Reynolds, 1972), or the effects of abiotic factors. Host selection has a strong genetic basis (Booij, 1982; Claridge *et al.*, 1977; Den Bieman, 1987; Fox & Morrow, *op. cit.*) and genetic changes in Auchenorrhyncha populations may be the cause of local shifts in host preference. It would be very interesting to compare experimentally the host preferences of populations of grassland Auchenorrhyncha species which, like *C. albomarginatus*, show different patterns of host selection in different parts of their range.

Cobben (1987) reviewed the current state of knowledge on host selection in Auchenorrhyncha and concludes that it amounted to "precious little" (p. 81). He

summarised the information available on host specificity in the Delphacidae and Cicadellidae and found that monophagy (feeding on one host species) and oligophagy *sensu stricto* (feeding on 2 - 4 species in one genus) was widespread. He questioned the idea that in grassland communities plant architecture has a more important effect on Auchenorrhyncha than the plant species themselves as suggested, for instance, by Morris (1971b) and Waloff & Solomon (1973) and the idea that host specificity in grassland is less common than it is in woodland (Claridge & Wilson, 1976, 1978; Port, 1978). On the basis of over 2,000 collections from North American grasslands, Whitcomb, Hicks, Lynn *et al.* (1987) considered that host specificity was a major determinant of diversity in Cicadellidae. Clearly, much more data is needed on the field host preferences of grassland Auchenorrhyncha on this side of the Atlantic.

The findings of this study suggest that, in calcareous grassland, Auchenorrhyncha which may reasonably be described as grass specialists are nearly as common as grass generalists. The specialists are those species that are clearly confined to a single species or genus of grass (strict specialists) or to a broader but well defined group of grasses (e.g. a tribe). The generalists are those Auchenorrhyncha that showed no clear preference for any of the grasses used in this study. The information now available on the host plants of the Cicadellidae and Delphacidae found at the Deeps is summarised in Table 8.1 (p. 182) and where possible they are tentatively categorised as either specialist or generalist.

Four of the Auchenorrhyncha listed in the Table 8.1; *Adarrus multinotatus*, *Paluda adumbrata*, *Rhytistylus proceps*, and *Criomorphus albomarginatus* were closely associated with a single species or genus of grass at the Deeps. Although no information was obtained on the host of *S. minutus* at the Deeps, there is strong evidence from work on the acid grassland at Silwood Park for its specificity to *D. glomerata*. Whittaker (1969), on the other hand, considered the main host plant on calcareous grassland at Wytham, Oxfordshire, to be *B. pinnatum*. I have frequently

Northamptonshire and it seems probable that *S. minutus* was associated with this grass, or with *B. pinnatum*, at the Deeps. If *S. minutus* is included, the above five species could reasonably be called 'strict specialists'. (*Bactracomorphus irroratus* and *Kelisia vittipennis* are probably also 'strict specialists', but not on grasses.) *Doratura stylata* may also be a strict specialist at the Deeps, but the low numbers of this species obtained during this study make this designation problematical; it has however, been classed as a specialist (on fine grasses at least) in Table 8.1 on the basis of the evidence available. Although *Paluda adumbrata* was obtained in low numbers at the Deeps, its consistent association with *Festuca* spp., together with published information (Port, 1981), is considered justification for its designation as a strict specialist. Two species of Auchenorrhyncha, *Graphocraerus ventralis* and *Mocycdia crocea* have been classed as specialists in table 8.1 because of their association with a well defined group of grasses.

It seems reasonable to suggest, in the light of the previous discussion, that host choice in these specialist species is likely to be governed by the secondary chemical or physical characteristics of grasses. However, the potential flaw in this argument is revealed by *Euscelis incisus*, a species also designated as a specialist on the basis of its preference for *Trisetum flavescens*. It is possible that the high total leaf nitrogen in *T. flavescens* was the reason for this association. More detailed analyses of grass nutrient quality may have revealed characteristics in other species that made them particularly suitable hosts for other specialists. If *E. incisus* is included, a total of nine species in Table 8.1 have been designated specialists.

Nine species have been designated generalists in Table 8.1. Some species may have been included in this latter group by default and further studies could reveal particular host preferences. It is in this group, however, that the opportunistic Auchenorrhyncha that select their hosts primarily on the basis of food quality (Crawley, 1983) are likely to be found.

(Crawley, 1983) are likely to be found.

A relatively high proportion of specialist grass-feeding Auchenorrhyncha may be characteristic of ancient semi-natural grassland like the Deeps. This type of habitat is now relatively rare in lowland Britain where much of the grassland is recent in origin or severely modified by disturbance. Auchenorrhyncha with opportunistic feeding strategies are likely to predominate in disturbed habitats.

Table 8.1. Summary of host-plant relationships of the commoner Auchenorrhyncha found at the Deepes.

Cicadellidae	Preferred host or hosts at the Deepes	Additional information	Apparent status at the Deepes	Qualifying remarks
<i>Adarus multinotatus</i>	Associated with <i>Brachypodium pinnatum</i>	Associated with <i>B. pinnatum</i> in Germany (1)	Specialist	
<i>Aphrodes albifrons</i>	Wide host range. Oviposition preference for <i>Festuca ovina</i>	Associated with a range of broad-leaved grasses (2,3)	Generalist	
<i>Aphrodes bifasciatus</i>	Wide host range	No information	Generalist	
<i>Aphrodes flavostriatus</i>	Wide host range	No information	Generalist	
<i>Arthaleus pascuellus</i>	Possibly associated with <i>Festuca</i> spp.	Wide host range (3,4,5); possible association with fine-leaved grasses in calcareous grassland (6).	Uncertain	
<i>Bactracomorphus irroratus</i>	No information	Associated with <i>Helianthemum nummularium</i> (7)	Specialist	
<i>Diplocolenus abdominalis</i>	Wide host range	Associated with <i>Holcus lanatus</i> in acid grassland (3)	Generalist	
<i>Doratura stylata</i>	Associated with <i>Festuca</i> spp., especially <i>Festuca rubra</i>	Associated with fine-leaved grasses (3,4,12)	Specialist	May be a morphological specialist
<i>Euscelis incisus</i>	Associated with <i>Trisetum flavescens</i>	Wide host range (4); preference for fine-leaved grasses in calcareous grassland (6); nitrogen specialist in acid grassland (4)	Nitrogen specialist	

Table 8.1. cont.

Cicadellidae	Preferred host or hosts at the Deepes	Additional information	Apparent status at the Deepes	Qualifying remarks
<i>Graphoaraenus ventralis</i>	Associated with the Aveneae	No information	Specialist	May be confined to the Aveneae
<i>Mocystia crocea</i>	Associated with <i>Brachypodium pinnatum</i> & <i>Bromus erectus</i>	With broad-leaved grasses, especially <i>B. pinnatum</i> , <i>B. erectus</i> and <i>Dactylis glomerata</i> (2,7,8)	Specialist	May be a morphological specialist
<i>Paluda adumbrata</i>	Associated with <i>Festuca</i> spp.	Associated with <i>Festuca rubra</i> (9)	Specialist	
<i>Psammetitix confinis</i>	Wide host range	Wide host range although may be associated with <i>Agrostis capillaris</i> in acid grassland (3,4)	Generalist	
<i>Rhyssalus proceps</i>	Strongly associated with <i>Festuca</i> spp., especially <i>F. ovina</i>	Associated with <i>Festuca rubra</i> and other fine grasses (3,4,6,10)	Specialist	May be a morphological specialist
<i>Turritus socialis</i>	Wide host range, but possible preference for <i>Avenula pubescens</i> and <i>F. rubra</i>	Associated with fine grasses in calcareous grassland (6)	Generalist	
<i>Zyginidia scutellaris</i>	Oviposition preference for broad-leaved grasses	Associated with broad-leaved grasses (6); nitrogen specialist in acid grassland (4)	Generalist	May be a morphological specialist

Table 8.1. cont.

Delphacidae	Preferred host or hosts at the Deeps	Additional information	Apparent status at the Deeps	Qualifying remarks
<i>Critomorphus albomarginatus</i>	Associated with <i>F. rubra</i>	With <i>Holcus lanatus</i> in acid grassland (2); with fine grasses in calcareous grassland (6)	Specialist	
<i>Hydelphax elegantulus</i>	Wide host range	With <i>Festuca rubra</i> in acid grassland (2); with <i>Deschampsia flexuosa</i> on heaths (5)	Generalist	May be a nitrogen specialist
<i>Javesella pellucida</i>	Wide host range	Wide host range (11); nitrogen specialist (4)	Generalist	
<i>Kelisia vittipennis</i>	Associate with <i>Carex flacca</i>	With <i>Carex</i> spp. and <i>Eriophorum vaginatum</i> (5,7)	Specialist	
<i>Stenocranius minutus</i>	No information	Associated with <i>Dactylis glomerata</i> (3-4), with <i>Brachypodium pinnatum</i> (2) and with coarse grasses (6)	Uncertain	Probably a specialist, as in acid grassland

Authors:

- 1) Schiemenz, (1969); 2) Whittaker, (1969); 3) Waloff & Solomon, (1971); 4) Prestidge & McNeill, (1983); 5) Ossiannilsson, (1983); 6) Morris, (1990b); 7) Le Quesne, (1969); 8) Muller, (1987); 9) Port, (1981); 10) Kuntze, (1937) (in Ossiannilsson, (1983)); 11) Raatikainen, (1967); 12) Marchland, 1953 (in Ossiannilsson, (1983)).

SUMMARY

1) The Auchenorrhyncha of the Deeps, an area of calcareous grassland in Northamptonshire, were surveyed. Two contrasting sites within grassland, one with taller (50 - 70 cm) vegetation dominated by *Brachypodium pinnatum* and the other with shorter (10 - 20 cm) vegetation dominated by *Festuca* spp., were sampled with both an Univac vacuum sampler and a sweep net between April 22 and September 9, 1987. On two occasions sticky traps were also used. Most of the commoner species showed a marked preference for one or other of the sampling sites. The majority of the 40 species of Auchenorrhyncha recorded from the site during the entire study was found during the survey.

2) The nymphs of the commoner species of Cicadellidae encountered during the study were identified and described. Most of the identifications were made by rearing the nymphs to maturity by confining them in clip-cages on grasses, which were grown in plastic pots in a greenhouse. A key to the nymphs, illustrated by drawing and photographs, was constructed.

3) Choice experiments were conducted in a greenhouse on two of the common species of cicadellid recorded at the Deeps; *Adarrus multinotatus* and *Turrutus socialis*. Adult specimens of the two species were collected from the field and released into a cage with seven species of the commoner grasses found at the Deeps. Collections of the leafhoppers made from the grasses indicated that *A. multinotatus* was specific to *Brachypodium pinnatum* and *Turrutus socialis* had a wide host range, with a preference for *Avenula pubescens* and *Festuca rubra*.

4) Choice experiments were conducted in the field over a three year period (1990 - 1992). Replicated grass species, grown in plastic pots, were sunk into the ground in both the sites initially surveyed at the Deeps. Auchenorrhyncha were collected from the grasses at intervals by carefully removing pots from the ground and

brushing the plant inside a muslin cage. Auchenorrhyncha removed from the grasses in this way were collected from the cage with pooters. The data obtained from this aspect of the study indicated that a number of species of Auchenorrhyncha were specific to one grass species or genus, a few species were associated with a well defined range of grasses and a third group (the largest) had a wide host range.

5) During the first year of the field choice experiments an investigation into the role of plant nitrogen in host selection by Auchenorrhyncha was undertaken. The response of Auchenorrhyncha to the 'natural' range of total leaf nitrogen found in unfertilised grasses grown in pots and their response to grasses fertilised with NH_4NO_3 were studied. Total leaf nitrogen was measured using a micro-Kjeldahl digestion. Although this aspect of the study was limited, the results indicated that only a few species at the Deeps selected plant hosts with a high nitrogen content.

6) Greenhouse no-choice experiments were conducted on the survival and oviposition of *Adarrus multinotatus* and *Turrutus socialis* and the survival of *Criomorpha albomarginatus* on a range of potential host grasses. The survival and oviposition of specimens contained in clip-cages on potential host grasses grown in plastic pots was monitored. The results obtained supported the results of the choice experiments, indicating that *A. multinotatus* was specific to *B. pinnatum*, *T. socialis* had a wide host range, and *C. albomarginatus* was specific to *F. rubra*.

7) Observations were made on the oviposition behaviour of a number of species, in addition to those described in 6) above, which were confined on host plants in clip-cages. Dead or living leaf sheaths were most commonly used for oviposition, although flower stems and leaves were also used. Generally, the species observed appeared to be specific in their choice of oviposition site.

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Appendices

Auchenorrhyncha caught on different sampling occasions during the 1990 field choice experiment on Site 1.

Table 1: 26.4.1990 (all pots). Symbols used: f = female, m = male, n = nymph

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:									
<i>Aphrodes albifrons</i>			1f						
<i>A. bifasciatus</i>				2n		1n	3n		
<i>Dikraneura variata</i>	1f								
<i>Diplocolenus abdominalis</i>	1n		1n		3n				
<i>Euscelis incicus</i>				1f	1f	1f	1f		
<i>Mocystia crocea</i>		1f	1f		1f				
Unidentified nymphs							1		
Delphacidae:									
<i>Hyalodelphax elegantulus</i>	5f + 1m	4f		2f + 2m	2f + 3m	8f + 7m	1f + 2m + 1n		1m
<i>Javesella pellucida</i>			1f + 1m						

Table 2: 11.5.1990 (all pots).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:									
<i>Aphrodes albifrons</i>									
<i>A. bifasciatus</i>		1n		1n					
<i>Dikraneura variata</i>									
<i>Diplocolenus abdominalis</i>	1n	4n		1n	2n	3n	6n	1n	
<i>Euscelis incicus</i>		1f			1f				1f
<i>Graphocrærus ventralis</i>		2n						2n	
<i>Macustus griseus</i>					1f				
<i>Mocystia crocea</i>			2f		1f	1f	1f		
<i>Turrutus socialis</i>		1		1		1			
Unidentified nymphs						2n			
Delphacidae:									
<i>Cromorphus albomarginatus</i>							1f		
<i>Hyalodelphax elegantulus</i>	7f + 5m	18f + 3m	2f	4f + 3m	7f + 5m	5f + 1m	9f + 6m	1f	
<i>Javesella pellucida</i>						1f			

Appendix 1a (cont.)

Table 3: 23.5.1990 (all pots). Symbols used: f = female, m = male, n = nymph

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:										
<i>Aphrodes albifrons</i>										
<i>A. bifasciatus</i>			2n	1m + 1n	5n	2n	1n	6n	2n	1n
<i>Dikraneura variata</i>						1f				
<i>Diplocolenus abdominalis</i>		8n	5n	5n	2n	9n	7n	5n	4n	1n
<i>Doratura stylata</i>				1n						
<i>Euscelis incicus</i>		1f + 1n	1f + 3n		2f + 2n			1n	4f	
<i>Graphocraerus ventralis</i>			3n						3n	
<i>Macustus griseus</i>						1f				
<i>Mecydia crocea</i>										
<i>Rhytistylus proceps</i>							3n	7n		
<i>Turrutus socialis</i>		6n	2n	4n	5n		11n	4n	10n	
Unidentified nymphs			1	1	1	1	2			
Delphacidae:										
<i>Crionomorphus albomarginatus</i>							1f			
<i>Hydeolaphax elegantulus</i>		7f + 6m	19f + 2m		6f	3f	3f	3f + 6m	6f	
<i>Javesella pellicida</i>										
Cercopidae										
<i>Neophilaenus lineatus</i>									1n	

Table 4: 7.6.1990 (all pots).

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:										
<i>Aphrodes albifrons</i>										
<i>A. bifasciatus</i>		1m	3f + 1m + 1n	1m + 1n	1m	1f + 1n	1f + 1n	1f + 3m + 2n	5n	1m
<i>A. flavostriatus</i>				1n						
<i>Arthaleus pascuellus</i>					1f	1f	3f + 1m			1f
<i>Dikraneura variata</i>							1f			
<i>Diplocolenus abdominalis</i>		1f + 1n	1f + 1m	3f + 2m + 3n	1f + 1n	1f + 2m	1f + 1m + 4n	2f + 1n	1f + 2m + 1n	2n
<i>Doratura stylata</i>							4n	5n		
<i>Euscelis incicus</i>		4n	1f + 1n		1n	2n		1f + 1n	2f + 4n	
<i>Graphocraerus ventralis</i>		2m + 1n	1n			1m + 1n		1f	3m + 1f	
<i>Mecydia crocea</i>		1n				1n		1n	1n	
<i>Paluda adumbrata</i>							2n			
<i>Psammotettix confinis</i>			1f							
<i>Rhytistylus proceps</i>							44n	9n		
<i>Turrutus socialis</i>		1f + 9n	2f + 2m + 8n	4m + 5n	1m + 7n	3f + 4m + 7n	1f + 3m + 9n	1f + 4m + 4n	1f + 2m + 4n	6n
Unidentified nymphs		1	1			1			1	1
Delphacidae:										
<i>Crionomorphus albomarginatus</i>								4f + 2m	1f	
<i>Hydeolaphax elegantulus</i>		5f + 1m	2f	1f + 1m				3f + 1m		1f
<i>Stenocranus minutus</i>			1f							

Appendix 1a (cont.)

(Nitrogen treatment on half the pots began on 18.6.1990)

Table 5a: 21.6.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:										
<i>Aphrodes albifrons</i>										
<i>A. bifasciatus</i>	2m	1f		2m	1n		1m	1n	1m + 1n	1f + 3m + 1n
<i>A. flavostriatus</i>										
<i>Arthaleus pascuellus</i>	1f									
<i>Diplocolenus abdominalis</i>	1m						1n			1n
<i>Doratura stylata</i>	1n	1m						1n		
<i>Euscelis incicus</i>	2n			1n				2n	1n	
<i>Graphocraerus ventralis</i>				1m						
<i>Rhytistylus proceps</i>				1n			4n	3n		
<i>Turrutus socialis</i>	1f	1n		2m + 2n	2n	2f + 2m + 3n	1n	3n	1f + 3m + 2n	1m + 1n
<i>Zyginidia scutellaris</i>						1				
Unidentified nymphs					2n		1n			
Delphacidae										
<i>Eurysa lineata</i>				1m						
<i>Javesella pallucida</i>				1f						

Table 5b: 21.6.1990 (treated pots).

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:										
<i>Agallia</i> sp.			1n							
<i>Aphrodes bifasciatus</i>				2m	1f + 2n	2f + 2m	2f + 1n			
<i>A. flavostriatus</i>				1n						
<i>Arthaleus pascuellus</i>						1f				
<i>Diplocolenus abdominalis</i>			2f + 1m	1f		2m	2m			
<i>Euscelis incicus</i>	1n	1f + 1m + 1n	1f	1n			1n	1n	1m	
<i>Graphocraerus ventralis</i>				1f + 1n			1n			
<i>Mecydia crocea</i>						1f	2n	1n		
<i>Paluda adumbrata</i>					3n		6n	5n		
<i>Rhytistylus proceps</i>				1n			2f + 2m = 4n	2f + 1m + 4n		
<i>Turrutus socialis</i>	1n	1f + 1m + 3n		1f + 3m + 2n	1f + 3n	1m + 2n	2f + 1m + 4n	3f + 1m + 3n	1f + 4m + 1n	
<i>Zyginidia scutellaris</i>		1f					1			
Unidentified nymphs				1						

Appendix 1a (cont.)

Table 6a: 6.7.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

	Gramineae	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:										
<i>Adarus multinotatus</i>				1f						
<i>Agallia ribauti</i>								1f		
<i>Aphrodes albifrons</i>								2m		
<i>A. bifasciatus</i>			1m + 1n					1f		
<i>A. flavostriatus</i>				2n	1n		1n			
<i>Arthaldus pascuellus</i>							1f			
<i>Diplocolenus abdominalis</i>							1f	1m		1f
<i>Euscelis incicus</i>				1n	1n	1n				
<i>Graphoaeus ventralis</i>			1f		1f					1f
<i>Mocydia crocea</i>				1n		1n			1n	
<i>Rhytistylus proceps</i>							1n			
<i>Turrutus socialis</i>		1m + 1n	6f + 1m + 2n	1f + 1m + 1n	1m + 1n	in			2m + 1n	1f
Delphacidae										
<i>Hyalelphax elegantulus</i>			1n							

Table 6b: 6.7.1990 (treated pots).

	Gramineae	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:										
<i>Aphrodes bifasciatus</i>			1m + 1n	1n		1f		2f		
<i>A. flavostriatus</i>					1n		2n			
<i>Diplocolenus abdominalis</i>			1f + 1m	1f + 1m					1m	
<i>Doratura stylata</i>				1m						
<i>Euscelis incicus</i>			2n		1n	2n			5n	
<i>Mocydia crocea</i>			1n							
<i>Rhytistylus proceps</i>		1m					1m + 2n		1n	
<i>Streptanus aemulans</i>			1m							
<i>Turrutus socialis</i>		1f	3m + 2n	3f + 4m		1n	1f + 4m	2f + 1m	1f + 1m + 1n	
<i>Zyginidia scutellaris</i>					1f					
Delphacidae										
<i>Hyalelphax elegantulus</i>							1n			

Appendix 1a (cont.)

Table 7a. 18.7.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

Gramineae	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Achirus multirotatus</i>			1m						
<i>Aphrodes bifasciatus</i>		1f	1n		1f	1f		1f	
<i>A. flavostriatus</i>	2n	1n			1f				
<i>Bactracomorpha irroratus</i>						1f			
<i>Dikraneura variata</i>				1m					
<i>Diplocolenus abdominalis</i>					1m				
<i>Doratura stylata</i>				1f+1n	1n			1m+1n	
<i>Euscelis incicus</i>				1m	1n				
<i>Mocodya crocea</i>				1m	1n				
<i>Rhytistylus proceps</i>		1f				1f+1n			
<i>Turrutus socialis</i>	1m	1f+1m	1m		1f+2m		1f	1n	
<i>Zygnidia scutellaris</i>						1f			
Unidentified nymphs			1					1	
Delphacidae									
<i>Hyalodelphax elegantulus</i>		1f							

Table 7b. 18.7.1990 (treated pots).

Gramineae	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Aphrodes albifrons</i>									
<i>A. bifasciatus</i>			1f	1m	1f	1m+1n			1f
<i>A. flavostriatus</i>				1f+1n		1n			
<i>Diplocolenus abdominalis</i>			1m	2f+1m	1m				
<i>Doratura stylata</i>							1f		
<i>Euscelis incicus</i>	1n	1n		1n	1n		1f+1n	1f+2n	
<i>Mocodya crocea</i>									
<i>Paluda flaveola</i>									
<i>Rhytistylus proceps</i>						1m+1n			
<i>Turrutus socialis</i>		1f+4m		1m	1m	3m	2f	1f+2n	
Delphacidae									
<i>Hyalodelphax elegantulus</i>			1f+1n	1m		1n			

Appendix 1a (cont.)

Table 8a: 22.8.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:									
<i>Aphrodes bifasciatus</i>					1f				
<i>Arthaleus pascuellus</i>					1f				
<i>Bactracomorphus irroratus</i>					1f				1n
<i>Euscelis incicus</i>						1m			
<i>Macrostelus sexnotatus</i>									
<i>Mocycdia crocea</i>			1m						
<i>Psammetetix confinis</i>				1f		1m	1f		1f + 1m
<i>Turrutus socialis</i>	1m + 1n	1f	1f + 1n	1m + 1n	3n	1f + 3n	1f + 1n	1f + 1m + 1n	1f + 1n
<i>Zyginidia scutellaris</i>	1m	1m		2f					
Delphacidae									
<i>Hyalodelphax elegantulus</i>				1m					
<i>Javesella pellucida</i>	1f								
<i>Kelsia vittipennis</i>									1m

Table 8b: 22.8.1990 (treated pots).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. fiacca</i>
Cicadellidae:									
<i>Agallia ribauti</i>		1m			1f				1m
<i>Aphrodes albifrons</i>				1f				1f	
<i>A. bisinctus</i>						1f		1f	
<i>A. bifasciatus</i>									
<i>Arthaleus pascuellus</i>		1m				1f			
<i>Deratura stylata</i>						1f		1f	
<i>Elymana sulphurella</i>								1m + 1n	
<i>Euscelis incicus</i>				1f		1f			
<i>Psammetetix confinis</i>	1f + 1m			1f		1m	1f		
<i>Rhytistylus proceps</i>		1f	1f					1f	
<i>Turrutus socialis</i>	1m + 1n	3f + 2n		1f + 1m	2m	2f + 3n	1f + 4n	1f + 5n	1f + 1n
<i>Zyginidia scutellaris</i>				1f + 1m					
Delphacidae									
<i>Kelsia vittipennis</i>									7f + 1m
Cercopidae									
<i>Neophilaenus lineatus</i>	1f								

Appendix 1a (cont.)

Table 9a: 6.9.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Macrostelus sexnotatus</i>								1f	
<i>Psammotettix confinis</i>	1m			1f	2m				3f
<i>Rhytistylus proceps</i>			1f					1f	
<i>Turrutus socialis</i>	3f	6f + 1m	1f	1f	4m	1f + 1m	1f + 1m + 1n	1f + 1m	1f + 1m
Delphacidae									
<i>Hyalophax elegantulus</i>						1f			

Table 9b: 6.9.1990 (treated pots).

	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Aphrodes albifrons</i>				1m					
<i>Arthaleus pascuellus</i>						1m	1f	4m	2f
<i>Doratura stylata</i>				1f					1m
<i>Euscelis incisus</i>						1n	1m	2f	1f
<i>Macrostelus sexnotatus</i>						1f			
<i>Psammotettix confinis</i>	1m			2m	1m	4f + 1m	1m		1f
<i>Rhytistylus proceps</i>									1f
<i>Turrutus socialis</i>	2f + 2m	6f + 4m	6f + 3m	4f + 3m	2f + 4m	2f + 1m + 1n	3f + 2m + 3n	4f + 4m + 2n	4f + 1m
Delphacidae									
<i>Kelsia vittipennis</i>									2m
Cercopidae									
<i>Philaenus spumarius</i>			1m						

Appendix 1a (cont.)

Table 10a: 28.9.1990 (untreated pots). Symbols used: f = female, m = male, n = nymph

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Aphrodes flavostriatus</i>			1f						
<i>Euscelis incicus</i>		1n	2n		1f	1n		1f + 1n	
<i>Macrostelus sexnotatus</i>	1m								
<i>Turrutus socialis</i>	1f		1f			1n		1f + 1m	
Delphacidae									
Unidentified nymphs	1								

Table 10b: 28.9.1990 (treated pots).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Euscelis incicus</i>				1n				1n	
<i>Psammatettix confinis</i>				1f		1f			
<i>Turrutus socialis</i>		1f	1f			5f			

Table 11a: 17.10.1990 (untreated pots).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Euscelis incicus</i>						1n		3n	2n
<i>Psammatettix confinis</i>	1f			1f					
<i>Turrutus socialis</i>	1n					2f			

Table 11b: 17.10.1990 (treated pots).

	<i>A. elatus</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>	<i>C. flacca</i>
Cicadellidae:									
<i>Adarus multipunctatus</i>									
<i>Euscelis incicus</i>	2n	2n	1f		2n				
<i>Psammatettix confinis</i>							1m		
<i>Turrutus socialis</i>						1f			
Delphacidae									
Unidentified nymphs		1							

Appendix 1b

Auchenorhyncha caught on different sampling occasions during the 1990 field choice experiment on site 2.

Table 1: 23.6.1990. Symbols used: f = female, m = male, n = nymph

	Gramineae	B. pinnatum	B. erectus	F. rubra
Cicadellidae:				
<i>Adarrus multinctatus</i>		1f + 1m		1m
<i>Arthaleus pascuellus</i>		2m		3f + 5m
<i>Diplocolenus abdominalis</i>		1n		1m
<i>Mocycia crocea</i>		2f + 2n	3n	
Unidentified nymphs			2	
Delphacidae:				
<i>Cromorplus albomarginatus</i>				4f + 3m
<i>Hyledephax elegantulus</i>		1f		
Cercopidae				
<i>Neophilaenus lineatus</i>				1f

Table 2: 10.7.1990.

	Gramineae	B. pinnatum	B. erectus	F. rubra
Cicadellidae:				
<i>Adarrus multinctatus</i>		3f	3f + 2m + 1n	1f
<i>Arthaleus pascuellus</i>		2f	1f + 1m	2f + 1m
<i>Dikraneura variata</i>		1f		
<i>Diplocolenus abdominalis</i>		2m	1f	
<i>Psanmotettix confinis</i>				1f
<i>Mocycia crocea</i>		1f + 9n	6n	7n
Delphacidae:				
<i>Cromorplus albomarginatus</i>			1	
Unidentified nymphs		1	1	6f + 2m
Cercopidae				
<i>Neophilaenus lineatus</i>		1f		2

Table 3: 19.7.1990

	Gramineae	B. pinnatum	B. erectus	F. rubra
Cicadellidae:				
<i>Adarrus multinctatus</i>		1f	1f	
<i>Aphrodes flavostriatus</i>		1n	1n	4n
<i>Arthaleus pascuellus</i>			1f	1f
<i>Diplocolenus abdominalis</i>		1m	5f + 1m + 1n	
<i>Elymana sulphurella</i>			1f	
<i>Mocycia crocea</i>		8n	2n	1m
Delphacidae:				
<i>Cromorplus albomarginatus</i>				1f + 1m
<i>Dicranotropis hamata</i>		1f		
<i>Hyledephax elegantulus</i>		1f	2f	2f
<i>Javesella pellucida</i>		1f	1f	
Unidentified nymphs			1	1

Table 4: 23.8.1990

	Gramineae	B. pinnatum	B. erectus	F. rubra
Cicadellidae:				
<i>Adarrus multinctatus</i>			1f	1m
<i>Arthaleus pascuellus</i>		1n	1n	1n
<i>Diplocolenus abdominalis</i>				1f
<i>Mocycia crocea</i>		1f + 4m	2m	1m
<i>Zygnidia scutellaris</i>		1f		
Delphacidae:				
<i>Hyledephax elegantulus</i>				1f + 1m
<i>Javesella pellucida</i>			3f	
Cercopidae				
<i>Neophilaenus lineatus</i>		1f + 1m		1m

Appendix 1c

Auchenorrhyncha caught during the 1991 field choice experiment on Site 1.
(No pots were fertilised during this experiment.)

Table 1: 24.5.1991 (all pots). Symbols used: f = female, m = male, n = nymph

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>
Cicadellidae:									
<i>Agallia</i> sp.						1n			
<i>Aphrodes bifasciatus</i>				1n				1n	
<i>Diplocolenus abdominalis</i>			2n	3n		1n			
<i>Euscelis incicus</i>			1f						
<i>Graphocraerus ventralis</i>		1n				2f			
<i>Mocycdia crocea</i>		1f					1m		
<i>Mocycdiopsis attenuata</i>									1n
<i>Turrutus socialis</i>				1n					
Delphacidae:									
<i>Criomoropus albomarginatus</i>							1m		

Table 2: 7.6.1991 (all pots).

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>
Cicadellidae:									
<i>Aphrodes bifasciatus</i>			1n	2n	3n	9n	3n	2n	
<i>Diplocolenus abdominalis</i>		1n	2n		1n			2n	
<i>Doratura stylata</i>							1n		
<i>Graphocraerus ventralis</i>		1n		1n					
<i>Rhytistylus proceps</i>		1n			1n		2n		
<i>Turrutus socialis</i>			1n		3n		1n	2n	1n
Unidentified nymphs					1		1		

Table 3: 29.6.1991 (all pots).

	Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>
Cicadellidae:									
<i>Agallia</i> sp.									1n
<i>Aphrodes bifasciatus</i>			1m + 1n	1f + 1n	1m	1f + 1m + 1n	1f + 1m	1n	1f
<i>A. albifrons</i>		1n						1n	
<i>Doratura stylata</i>						1n			
<i>Euscelis incicus</i>									
<i>Graphocraerus ventralis</i>			1m						
<i>Mocycdia crocea</i>									
<i>Rhytistylus proceps</i>		1n					9n	2n	
<i>Turrutus socialis</i>		1n	1n			1n		3n	1n
Unidentified nymphs								1	1

Appendix 1c (cont.)

Table 7: 19.8.1991 (all pots). Symbols used: f = female, m = male, n = nymph

Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>	<i>T. flavescens</i>
Cicadellidae:								
<i>Aphrodes bifasciatus</i>								1f
<i>Euscelis inlicus</i>								1n
<i>Mocycia crocea</i>			1n					
<i>Rhyssalus proceps</i>			1f					
<i>Turrutus socialis</i>	1f	4f	1f	1f	1f + 1m		2f	1m + 1n

Appendix 1d

Auchenorrhyncha caught during the 1992 choice experiment on Site 2

Table 1: 18.5.1992 (all pots). Symbols used: f = female, m = male, n = nymph

Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>
Cicadellidae:							
<i>Aphrodes flavostriatus</i>							
<i>Diplocolenus abdominalis</i>	1n		3n	1n		1n	5n
Delphacidae:							
<i>Criomorpha albomarginatus</i>			1m	1f	1f		6f + 7m

Table 2: 21.5.1992 (all pots).

Gramineae	<i>A. elatius</i>	<i>A. pubescens</i>	<i>B. pinnatum</i>	<i>B. media</i>	<i>B. erectus</i>	<i>F. ovina</i>	<i>F. rubra</i>
Cicadellidae:							
<i>Diplocolenus abdominalis</i>	1n	5n	1n	1n	3n	3n	4n
<i>Mocycia crocea</i>					2f		
<i>Paluda adumbrata</i>							1n'
Unidentified nymphs		2					
Delphacidae:							
<i>Criomorpha albomarginatus</i>							7f + 5m + 1n

Appendix 1d (cont.)

Table 3: 28.5.1992 (all pots). Symbols used: f = female, m = male, n = nymph

	Gramineae	A. elatus	A. pubescens	B. pinnatum	B. media	B. erectus	F. ovina	F. rubra
Cicadellidae:								
<i>Aphrodes bifasciatus</i>		1n		1n		2n		
<i>A. flavostriatus</i>						1n		
<i>Diplocolenus abdominalis</i>				4n	1n	1n	2n	2n
<i>Mocytia crocea</i>				2n				
<i>Rhytistylus proceps</i>							2n	
Unidentified nymphs		1		1			1	
Delphacidae:								
<i>Criomorplus albomarginatus</i>								5f + 6m

Table 4: 10.6.1992 (all pots).

	Gramineae	A. elatus	A. pubescens	B. pinnatum	B. media	B. erectus	F. ovina	F. rubra
Cicadellidae:								
<i>Adarrus multinotatus</i>				4n			1n	1n
<i>Aphrodes bifasciatus</i>		2n		2m			1n	1n
<i>A. flavostriatus</i>				1n	1n	2n	4n	2n
<i>Diplocolenus abdominalis</i>		1f	1n	1f + 1m			2n	1n
<i>Graphocraerus ventralis</i>								1m
<i>Mocytia crocea</i>				1n				1n
<i>Paluda adumbrata</i>								1n
<i>Rhytistylus proceps</i>							3n	
<i>Turrutus socialis</i>								1n
Delphacidae:								
<i>Criomorplus albomarginatus</i>								1f + 1m

Table 5: 25.6.1992 (all pots).

	Gramineae	A. elatus	A. pubescens	B. pinnatum	B. media	B. erectus	F. ovina	F. rubra
Cicadellidae:								
<i>Adarrus multinotatus</i>		1n		3n			1m	1n
<i>Aphrodes bifasciatus</i>						1m	2n	1m + 1n
<i>A. flavostriatus</i>			1n	5n	1n	2n	2n	3n
<i>Diplocolenus abdominalis</i>			1f					
<i>Doratura stylata</i>		1n		1n		1n		
<i>Graphocraerus ventralis</i>								
<i>Mocytia crocea</i>				1n				
<i>Paluda adumbrata</i>								1n
<i>Rhytistylus proceps</i>							1n	
<i>Turrutus socialis</i>								
Unidentified nymphs							1	
Delphacidae:								
<i>Criomorplus albomarginatus</i>								1f + 1m