Techniques for sampling Auchenorrhyncha in grasslands

ALAN J.A. STEWART

Abstract

The relative merits of different techniques for sampling the Auchenorrhyncha community in grasslands are reviewed. As is the case when studying many other invertebrate groups, no single technique can be relied upon to reveal the full range of species at a site or provide unbiased estimates of population density for all species. Nevertheless, with moderate effort and inexpensive equipment and if due attention is paid to the importance of standardising sampling procedures to allow comparisons across both space and time, reliable estimates of both relative and absolute population density can be achieved. Sweep-netting is an inexpensive and simple method for providing relative estimates of population density but it is hard to standardise and it under-samples the epigeal species. The conventional D-Vac suction sampler has now been largely superseded by a variety of smaller and cheaper hand-held suction devices that have been developed by modifying devices that are sold for collecting garden refuse. They can be used to give estimates of absolute population density in grasslands and tend to sample the epigeal species better than sweep nets. However, a true picture of the species living in the lowest vegetation stratum or close to the soil surface can best be obtained by using pitfall traps. A comprehensive inventory of species would therefore need to combine pitfall trapping with either sweep netting or suction sampling. Brief discussions are also presented of techniques for sampling the aerial fauna and for estimating dispersal and movement between populations.

Key words: Auchenorrhyncha, sampling, grasslands, sweep-netting, suction samplers, pitfall traps, population estimates, standardization.

Denisia 04,
zugleich Kataloge des OÖ. Landesmuseums,
Neue Folge Nr. 176 (2002), 491-512

Introduction

The Auchenorrhyncha form an important component of the invertebrate fauna of most temperate grasslands. The group has a number of properties which make it very suitable for monitoring the biotic conditions and assessing the conservation status of a range of grassland types (HILDEBRANDT & NICKEL in press):

(i) Population densities in grasslands often exceed those of other key invertebrate taxonomic groups such as the Heteroptera and Coleoptera and can reach remarkably high levels (in excess of 1,000 individuals per m^2; WALOFF 1980). Potential species richness is high enough to be a useful ecological indicator, with individual grassland sites often supporting in excess of 40 species (MORRIS 1971).

(ii) The autecology of many grassland Auchenorrhyncha is well studied in terms of host plants, habitat associations and responses to management. It is therefore possible to provide a detailed ecological interpretation of the community from data on species occurrence or relative abundance.

(iii) The Auchenorrhyncha perform an important functional role in the grassland community as herbivores, by tapping into the phloem or xylem sap or extracting the contents of the mesophyll cells of their host plants. When population densities are high, this action induces a substantial photosynthetic drain on the plants and may influence the outcome of competition between plant species and hence the course of succession (BROWN et al. 1988). The transmission of plant pathogens by many Auchenorrhyncha may compound such effects. Removal of plant sap followed by excretion of soluble waste material by these insects will undoubtedly have significant effects on nutrient cycling within the grassland ecosystem, although this effect has received rather less attention than it deserves.

(iv) The structure and composition of grassland Auchenorrhyncha communities generally reflect a combination of the species composition and physical structure of the vegetation (BROWN et al. 1992). Auchenorrhynchan species richness tends to be much greater in undisturbed and lightly grazed grasslands where the vegetation is taller, compared to closely grazed or regularly mown grasslands where the vegetation remains generally short (MORRIS 2000). For this reason, the Auchenorrhyncha community is a good reflection of the intensity of grassland management, responding both rapidly and precisely to any changes in the management regime such as the imposition or cessation of grazing (MORRIS 1981a, 1981b; MORRIS & PLANT 1983).

(v) At a more practical level, there are well tested and widely accepted techniques for sampling the Auchenorrhyncha community in grasslands, although there is no technique that will suit all circumstances, nor one that is devoid of sampling bias. Nevertheless, reliable population estimates can be generated using simple, inexpensive and portable equipment. In general, at least in Europe, the taxonomy of the group is well documented, stable and supported by high quality identification keys.

When embarking upon a programme of research on the ecology of grassland Auchenorrhyncha, one of the first questions to be answered will be: what sampling technique should be used? This deceptively simple question turns out to be remarkably complex to answer, as the rest of this paper will show. Field entomologists have shown considerable ingenuity in developing a wide variety of collection and sampling methods, responding to the considerable range of habitat associations and behaviour patterns exhibited by this group of insects. Most field research programmes will initially be concerned with tackling two primary questions: what species occur in a habitat and at what densities? Faced with this challenge, selection of the most appropriate sampling technique is not always straightforward. There is no universally applicable sampling technique that will suit all purposes. Furthermore, all techniques are selective to some degree, the extent of the bias being dependent on a number of factors. Reliable estimation of population density may require employing several techniques in combination.

The researcher who is faced with deciding which sampling techniques to employ has to take a number of considerations into account. The most important of these is sampling efficiency: the effectiveness with which the technique reveals all the individuals in the target area. This will vary between species, habitats, seasons, environmental conditions and, to a lesser extent, between field workers. Cost is always a major consideration. It includes not just the cost of the materials and the time needed to sample, but also the time required to process any material collected. The latter includes separation of the insect specimens from plant material and other debris inadvertently collected during the sampling process, identification of specimens and curation of the samples or selected voucher material for future reference. The time required to do this post-sampling work is often under-estimated. For quantitative studies, it must be possible to standardise the technique, so that it can be replicated with confidence over both space and time. Not all techniques lend themselves to this. Other considerations such as the amount of training required and the extent to which sampling is weather-dependent may also have to be built into the selection process. Generally, the final choice is based on a balance of the appropriateness of the technique measured against time and cost.

Programmes for sampling Auchenorrhyncha in grassland must be guided by these general principles. Here, I review the techniques that have been developed or adapted to sample these insects in the grassland habitat and comment on their effectiveness. The review is concerned solely with the efficacy of the techniques themselves; issues relating to the statistical design of field sampling programmes (HURLBERT 1984; EBERHARDT & THOMAS 1991; DUTILLEUL 1993) and subsequent analysis of the data (see summary of key references in POTVIN & TRAVIS 1993) have been covered in general terms elsewhere. SOUTHWOOD (1978), DENT (1991) and KUNO (1991) consider the application of general principles specifically to sampling insect populations. Techniques for sampling the predators and parasitoids of Auchenorrhyncha (many of which are the same as for their hosts) are not dealt with here, but are covered fully by POWELL et al. (1996).

As is the case in other invertebrate groups, certain features of the ecology and behaviour of Auchenorrhyncha have an important bearing on which sampling techniques are most appropriate in different circumstances. These include:

i) Vertical stratification of species:

Many species select particular strata within the vertical structure of grassland vegetation (DENNO 1980; DENNO et al. 1980). This is demonstrated particularly clearly by the use of different techniques (e.g. pitfall trapping, suction sampling and sweep netting) that sample different subsets of the total fauna (ANDRZEJEWSKA 1965; PAYNE 1981; PETER 1981; TÖRMÄLÄ 1982; NOVOTNY 1992; CHERRILL & SANDERSON 1994). Furthermore, there is evidence that this stratification changes seasonally (ANDRZEJEWSKA 1965) and diurnally (ROMNEY 1945).

ii) Sexual differences in activity patterns:

These may result in biased sex ratios in the catches produced by particular techniques. For example, pitfall trap catches of certain species tend to be dominated by males (LEQUESNE & MORRIS 1971; PAYNE 1981; TÖRMÄLÄ 1982), possibly because the females are more sedentary.

iii) Differences in sampling efficiency between life history stages:

The same technique may not be appropriate for all life history stages, even within the same species. This may be because, for example, nymphs and adults inhabit different parts of the host plant (overwintering nymphs of certain species typically reside close to the soil surface) or have different susceptibilities to being caught. SIMONET et al. (1979) concluded that the D-Vac was the most appropriate technique for sampling adults of the potato leafhopper, *Empoasca fabae*; however, nymphs were more efficiently extracted by placing excised branches of the plant for 24 hr in containers with small Dichlorvos squares (SIMONET et al. 1978).

iv) Diurnal changes in behaviour:

Whilst diurnal periodicities in leafhopper flight activity have been known for some time (LEWIS & TAYLOR 1965), rather little is known about whether analogous changes occur in other behavioural traits. DONDALE et al. (1972) and SCHAEFER (1973) report diurnal changes in pitfall trap catches, whilst PAYNE (1981) has suggested that these changes differ between the sexes. ROMNEY (1945) reports diurnal changes in vertical positioning of *Eutettix tenellus* on beet plants, but this effect has not been widely investigated in other species. In the light of these possible effects, sampling programmes that involve any sort of evaluation of treatment effects (e.g. different grassland management regimes) should stipulate that samples are taken at similar times of day to ensure comparability of catches.

v) Spatial distribution patterns:

The number and location of replicate samples within a site or experimental plot need to be chosen bearing in mind the importance of spatial factors in determining abundance. In addition to the possibility of direct spatial autocorrelation (the phenomenon where the similarity between samples is related, positively or negatively, to their physical distance apart (LEGENDRE 1993)), insect species occurrence and/or abundance may be highly correlated with one or more key environmental factors (such as soil conditions, aspect or vegetation composition) which are themselves spatially correlated. Rather few studies on Auchenorrhyncha have tested for such autocorrelation (SANDERSON et al. 1995) or attempted to quantify spatial variation in general terms and how this changes temporally (GYÖRFFY & KARSAI 1991).

A comparison of the relative efficiencies of the different available sampling techniques should be done as part of the preparatory work for any field study. Failure to do this may result in erroneous conclusions based on inappropriate comparisons, for example by comparing results from the same technique in different habitats or in different environmental conditions. Such considerations are particularly relevant in community studies, where apparent differences in the relative abundance of species may simply reflect differences in sampling efficiency. Few community studies address this problem, despite TÖRMÄLÄ 's (1982) warning that different techniques for sampling grassland faunas produce very different results. Comparative studies should consider not just sampling efficiency (the number of insects extracted per unit area) but also the relative precision of each technique, measured as the variability amongst replicated samples (e.g. BUNTIN 1988). Where the use of more than one sampling technique is unavoidable, an attempt should be made to calibrate between the results (e.g. CHERRY et al. 1977; SIMONET et al. 1978, 1979; TÖRMÄLÄ 1982; BUNTIN 1988).

It is important to distinguish at the outset between different types of field work. 'Collecting', for species inventory work or to obtain material, perhaps for experimentation or a taxonomic investigation, is an essentially non-quantitative exercise; there is no particular interest in determining population size. On the other hand, true 'sampling' has the specific objective of providing an unbiased estimate of population density and is by definition quantitative. This paper is concerned primarily with techniques to achieve the latter objective. Of course, most of the techniques used for quantitative sampling can also be used for general collecting.

Absolute <u>versus</u> relative population size estimates

In quantitative sampling, there is an important distinction between estimates of <u>absolute</u> as opposed to <u>relative</u> population size or density (SOUTHWOOD 1978; DENT 1991). An estimate of absolute population density is a count of the numbers of individuals within a specified area. As it is an estimate of the actual density, it should be comparable both spatially and temporally (i.e. with estimates derived from other sites or on other dates). One should realise however that techniques designed to estimate absolute population density, whether by visual searching or some sort of extraction technique, rarely detect 100% of the insects actually present; in fact, extraction efficiencies are frequently much less than this. As the resultant count will therefore be an under-estimate of the true population density, caution should be exercised when extrapolating from small samples to produce population estimates for large areas, as the under-estimates then become greatly magnified.

If areal densities are either inappropriate or impracticable, the next best estimate of absolute density expresses the population count in units of habitat; for the Auchenorrhyncha, this is most appropriately some component of the host plant (e.g. a count of numbers per leaf, unit leaf area, stem length or whole plant). These 'habitat units' will change as the plant grows, so a measure of the number of habitat units per unit area is also needed before a true population density estimate can be derived.

When it is impossible to estimate absolute densities, the field researcher must resort to relative population estimates. Here, the estimate is no longer a true count of numbers in a given area, as the unit of measurement is usually unknown. Data from traps generate this type of relative estimate, as it is impossible to be certain about the absolute area or volume over which the trap is operating. If external conditions (weather, habitat structure etc.) are similar, estimates using the same sampling technique should be broadly comparable across space and time. Active sampling techniques such as sweep-netting can be standardised by expressing samples in numbers caught per unit of effort (usually sampling time or the number of sweeps), but can not readily be expressed directly in terms of densities.

The distinction between absolute and relative population sampling techniques is not always clear cut. Relative estimates can sometimes be converted to absolute densities, if a good correlation can be demonstrated between counts from the technique and those from another more accurate estimate of absolute density. However, the calibration is likely to be both species- and site-specific and assumes that various extraneous environmental factors are kept constant. Wherever possible, attempts should be made to quantify the efficiency of the technique being employed. This can be done by comparing the sample count with the number of insects added after a comprehensive search of the target area, perhaps by removal or fumigation of the whole plant or grassland turve and careful examination for any individuals missed by the initial sampling. Similarly, active sampling (such as direct counts or sweep netting) should be carried out wherever possible by the same person, to avoid introducing individual operator bias. If more than one worker is involved, their relative 'sampling efficiencies' should be compared, with total counts adjusted accordingly if they differ consistently.

Trapping techniques exploit the fact that most insects move through their habitat. A simple distinction can be made between 'interception traps' that collect insects moving through the habitat as part of their normal behaviour and 'attraction traps' that provide a stimulus which draws the insects towards the sampling point. Such techniques are usually highly cost-effective as they are generally less time-consuming and require less skill than active sampling techniques (LOTT & EYRE 1996). They also have the advantage of sampling continuously over an extended period, including night as well as daytime. Due to the length of operating time, often several days, the influence of short-term fluctuations in weather are evened out. 'Instantaneous' sampling techniques, by comparison, are always subject to the influence of time of day, weather conditions and other short-term factors. Measured against this, traps left untended are vulnerable to adverse weather, human vandalism and damage by other animals (e.g. grazing stock). The single greatest disadvantage, however, of most trapping techniques is that the resultant catch is strongly influenced by the activity of the insects themselves. Sedentary species will be caught less frequently than highly active ones, even if their actual population densities are similar. Consequently, data from attraction or interception traps should not be analysed quantitatively until the relationship between catch size and population density has been checked. This relationship will undoubtedly vary between species and, for any one species, between sexes, seasons or different habitats.

In summary, in order to generate the most accurate population estimate, a selection of different techniques should be tested simultaneously and the results compared. The final choice of technique(s) to adopt will be a trade-off between accuracy and cost. Similarly, before proceeding with detailed studies, researchers should have a clear appreciation of the absolute efficiency of their chosen sampling technique(s) for the species under investigation and within the context of the particular habitat.

Estimation of absolute population density

i) Direct counts

Counting individuals in situ is clearly the most direct method for estimating population density on plants, but is not always possible or practicable, particularly with very active species. This approach is best applied to large or conspicuous species, but may also be favoured when counting the earlier life-history stages or adults of the more sedentary species. WHITTAKER (1965) for example was able to measure the density of spittle masses of the cercopids *Neophilaenus lineatus* and *N. exclamationis* within wire quadrats in grassland, whilst vertical stratification in the community of planthoppers on the salt marsh grass *Spartina patens* was quantified by counting directly the number of individuals in five vertical strata up the stem (DENNO 1980).

Many continental European workers studying grassland communities have favoured a direct counting technique called the 'biocenometer' (KONTKANEN 1950; ANDRZEJEWSKA 1965; NOVOTNY 1992). In essence, this involves delimiting a unit area of ground (typically 0.25 m^2) by covering it with a cylinder or box that has an open base and gauze-covered top, from which all insects are extracted by hand-held aspirator. Other authors refer to this device as a 'box quadrat' (CHERRILL & BROWN 1990). It is designed to provide a standardized areal count, but its accuracy is reliant both on the box being positioned rapidly before any highly mobile individuals escape and on the observer detecting all the trapped insects. Although the equipment costs are negligible, sampling using this method is very time-consuming and has largely been superseded by the more automated methods dealt with below.

The egg stage within the life cycle presents special sampling problems. In most Auchenorrhyncha species, the eggs are too small to be detected easily and most are inserted directly into the plant tissue of either leaves or stems. Eggs laid within the leaf lamina are generally placed just beneath the surface and are therefore detectable under relatively low magnification as simple bulges in the leaf epidermis. Sometimes, detection can be improved by varying the angle of incidence of the light or by using transmitted light. A similar technique can be used for eggs laid into small leaf veins, but those placed in larger veins, petioles, buds or stems can usually be detected only by careful dissection of the plant. This is laborious but produces very detailed information on oviposition behaviour (CLARIDGE & REYNOLDS 1972; THOMPSON 1978; STILING 1980).

Attempts have been made to accelerate the process of detecting eggs laid within plant tissue using a variety of chemical techniques. These generally involve clearing the plant tissue in boiling lactophenol, which also serves to coagulate the egg proteins so that the outlines of the eggs become visible under magnification (CARLSON & HIBBS 1962). Other techniques use hydrogen peroxide or glacial acetic acid for clearing the leaf tissue, followed by staining with acid fuchsin (CHATTERJEE & RAM 1970). Such techniques, or modifications thereof (SIMMONS et al. 1984), have now been used to detect eggs in a wide variety of plant species (SIMONET & PIENKOWSKI 1977; SIMMONS et al. 1985; HEADY et al. 1985). Major disadvantages are that they are time-consuming to perform and involve the use of hazardous chemicals.

ii) Suction samplers

Various mechanical devices have been developed for the physical extraction of insects from vegetation, using a strong current of air generated by a motorised fan. The first device to achieve widespread use was the DIETRICK, or 'D-Vac', suction sampler (DIETRICK 1961) (Fig. 1). Typically, it comprises a fan unit powered by a 100 cm^3 two-stroke engine, connected via a flexible hose to a plastic or fibreglass cylindrical inlet tube housing a mesh collection bag. The inlet cylinder has gauze-covered apertures around the rim to allow air to enter near the soil when it is held over the vegetation. The result is a powerful updraught of air through the vegetation, which sucks the insects into the collection bag.

As the material does not pass through the fan, the insects are generally retained in near-perfect condition. This means that Auchenorrhyncha collected alive with this apparatus can be used for subsequent experimentation.

It should be noted however that smaller and more delicate species may receive some damage. Also, parasitised Auchenorrhyncha may suffer increased mortality and rearing parasitoids from surviving individuals may be less successful.

The whole unit is mounted on a backpack worn by the operator, whose hands are left free to place the nozzle over the vegetation and empty the bag at the end of sampling without the need to take off the equipment or stop the engine. The collection nozzle is placed vertically over the vegetation for a standard time period (at least 20 s.), after which any insects sucked into the collection bag can be emptied into a separate container, killed and stored. The greatest advantage of this technique is that it facilitates sampling of a standardized area of ground. As the cross-sectional area delimited by the inlet nozzle is generally c. 0.1 m^2, it is customary to take ten such 'sucks' to produce a sample from 1m^2 of ground.

D-Vac suction sampling is often the preferred method for sampling grassland and low crops when compared with other techniques such as sweep netting and various types of trap or beating tray (e.g. SIMONET et al. 1979; BUNTIN 1988). This is because it often produces the highest density estimates and the lowest variation between samples. When measured, D-Vac extraction efficiencies have been shown to vary for different insect groups (HENDERSON & WHITTAKER 1977) and to be sensitive to a number of extraneous factors (HAND 1986). Rather few of these studies provide data specifically for Auchenorrhyncha. DUFFEY (1980) reported Auchenorrhyncha extraction efficiencies in rough grassland that varied from 23% in May to 62% in August (presumably coinciding with the peak nymphal and adult stages respectively). Efficiency rose to 70% on grazed (i.e. short) grassland. HENDERSON & WHITTAKER (1977) also reported a sward-length effect, with extraction efficiency in-creasing from 32% in long grassland (20-30 cm height) to 76% in short grass (<5cm tall).

Efficiency is severely compromised if the vegetation is moist (although probably not as seriously as when using a sweep net) or 'lodged' (flattened by wind, rain or trampling). Theoretically, as this method provides an absolute estimate of population density, samples from contrasting grassland types should be directly comparable. However, there is a limit to the vegetation height beyond which the process of positioning the inlet tube will flatten or compress the plant material so that air is sucked over, rather than through, the vegetation.

The D-Vac, including various minor modifications of the original design (e.g.

Fig. 1.
D-Vac suction sampler. The engine and fan unit is mounted on a backpack frame (left) and connected via a long flexible hose (middle) to the inlet cylinder which contains the sample bag (right).

Fig. 2.
Two types of G-Vac suction sampler. Right: the simplest design has a net collection bag inserted into the inlet tube and secured around the nozzle. The inlet tube has a cross-sectional area of 0.01m^2. Left: alternative design where a custom-built inlet tube has a larger cross-sectional area (0.025m^2) and a flange with gauze-covered holes that is mounted beyond the collection bag to allow unimpeded entry of air into the inlet tube. Both samplers are powered by 30 cm^3 engines.

THORNHILL 1978), has remained the standard equipment for quantitative sampling from a variety of crops and grassland habitats for many years. It does, however, suffer from a number of severe disadvantages, not least of which are cost, weight and a poor reputation for mechanical reliability. In recent years, various workers have developed smaller hand-held suction samplers, by modifying 'suck-or-blow' machines sold for collecting garden refuse (SUMMERS et al. 1984; HOLTKAMP & THOMPSON 1985; DE BARRO 1991; WILSON et al. 1993; ARNOLD 1994; MCLEOD et al. 1994, 1995; SAMU & SÁROSPATAKI 1995; STEWART & WRIGHT 1995). BELL & WHEATER (2001) refer to these types of machine as 'G-Vacs'. The various models available are generally similar in design and operation, in that power is provided by a 30 cm^3 petrol-driven engine which sucks air through a smaller (usually c.12 cm. diameter) inlet tube. The only modification of the gardening equipment that is needed to convert it to an insect suction sampler is to attach a fine net bag to the inside of the inlet nozzle to retain the insect material collected (Fig. 2) (STEWART & WRIGHT (1995) provide more detailed instructions).

The inlet nozzle cross-sectional area of these more compact machines is rather too small (~ 0.01 m^2) for each 'suck' to be regarded as a single sample. However, sampling from a larger area can be standardized by delimiting a fixed area of ground with an open-ended cylinder (e.g. 36 cm diameter, to be comparable to the D-Vac collection nozzle) placed over the vegetation. The nozzle of the G-Vac suction sampler can then be inserted into the cylinder and passed repeatedly across the vegetation for a set time interval to collect any insects trapped inside.

In the only detailed study of the efficacy of this equipment for sampling Auchenorrhyncha, STEWART & WRIGHT (1995) showed that catches of most species using a G-Vac sampler were comparable with those taken from an equivalent area of ground by D-Vac. Some species known to inhabit the layer closest to the ground were sampled in greater numbers with the G-Vac, although this effect was better demonstrated in certain epigeal species of Coleoptera and Araneae. This observation reflects the considerably greater air velocity and suction power generated by these machines compared to the original D-Vac. The portability of these new machines make them ideal for more general collecting, especially of those species which reside close to the ground or in otherwise inaccessible places (WILSON et al. 1993). It is also a useful technique for collecting from very tall plants that are not easily swept (e.g. the reed *Phragmites australis*) or in damp or flooded situations where a sweep net bag would soon become saturated and unworkable.

The inlet nozzle of any suction sampler has to be placed quickly onto the ground in order to avoid invertebrates from outside the delineated area being sucked into the sample. SAMU et al. (1997) compared samples of spiders taken from an alfalfa crop by a hand-held suction apparatus from within enclosed areas (each approximately 0.5m^2) with samples representing the same area of ground but taken from a series of unenclosed sampling points. Although the species compositions and abundance rankings were similar for the two sampling methods, the catches based on unenclosed sampling points were substantially larger than those where the sampling area was enclosed. They therefore suggest that the action of placing the inlet tube nozzle onto the ground draws in extra individuals from outside the target area and that such an 'edge effect' may produce inflated estimates of population density.

The suction power of most conventional samplers is severely reduced when the air flow is impeded; this may happen when the inlet nozzle is placed over the ground surface or when a large amount of debris builds up in the collection bag. The *Vortis* sampler is designed to circumvent these problems, firstly by introducing air into the system from higher up the inlet tube, and secondly by dispensing with any sort of collection bag (ARNOLD 1994). Instead, insects are sucked up the inlet tube into an enlarged chamber designed to create a vortex of circulating air, from which centrifugal forces propel the insects into a detachable collection vessel mounted on one side (Fig. 3). Whilst the mechanical principles behind this device represent an improvement on the design of previous suction samplers, its use in practice is prone to a new set of problems. The insects have much further to travel before reaching the collection vessel, including passing through a set of fixed metal vanes that induce the vortex of air; risk of damage to specimens is therefore increased. Similarly, there is an enhanced danger of specimens adhering to the interior walls of the suction tube or chamber if either become coated in moisture. The only published data on sampling efficiency suggest that Homoptera are sampled substantially better by the conventional D-Vac (ARNOLD 1994). The absolute efficiency of the apparatus for this or any other insect group remains to be tested.

Any type of suction sampler will remove some quantities of dead plant material, soil particles and other debris (more powerful machines will collect more). Sorting dead insects from this waste material is probably the most time-consuming part of this sampling method. Consequently, several workers have attempted to develop techniques whereby, before being killed, the insects' phototactic responses are exploited to segregate them from the unwanted material. DIETRICK et al.'s (1959) original method was to transfer the material collected by D-Vac into a Berlese funnel to sort the animals into tubes of alcohol. WALOFF (1980) reported using a 'sorting frame' to separate Auchenorrhyncha from debris collected by D-Vac sampling. This comprised a wooden-framed muslin funnel with a clear plastic window at one end. The frame was placed in front of a light source and the whole sample was emptied into the funnel. Emergent insects were attracted to the light and moved towards the plastic window, from which they could be removed by hand-aspirator. MOORE et al. (1993) have attempted to take this principle a stage further towards automation, by developing a field-based method that can be employed immediately after collection of the sample. Using the principle employed in the traditional capture of lobsters (Crustacea: Nephropidae), they constructed a 'light-sorter' device from joined sections of plastic soft drink bottles that were painted matt black or left clear. The suction sample debris was placed in the dark section of the sorter and the insects were left to move of their own accord away from the debris and into the light section, where they could be easily removed and killed (see MOORE et al. (1993) for full details). Both adult and nymphal Auchenorrhyncha self-sorted very rapidly in this apparatus, nearly 100% of individuals separating within 4-8 hours. BUNTIN (1988) achieved 94% recovery of leafhoppers using a laboratory-based device that was similar in principle, funnelling the insects straight into an ethanol-filled vial.

Fig. 3.
Vortis suction sampler. Suction is provided by a 30 cm^3 engine (top). Air is sucked into the inlet tube through a gauze cone (bottom), drawn through a set of radiating internal vanes that generate a vortex and then into an expansion chamber (middle). Insects that are circulated by the vortex in the expansion chamber are propelled by centrifugal forces into an escape tube mounted on the side (middle left) and drop down into a detachable collection vessel below.

Fig. 4.
Sorting the catch from a suction sampler. Most suction samples contain substantial amounts of plant and soil debris. The debris (left) is examined carefully and all insects are removed with fine forceps (top). The catch can then be sorted into species (right).

Where such automatic sorting devices are not available or the insect sample has already been killed, catches have to be separated from the associated plant and soil debris by hand. Finding small insects in larger amounts of debris can be extremely time-consuming and the process is also subject to a number of biases connected with the skill of the sorter, the amount, nature and condition of the dead plant material and the relative crypsis of the insect species. The most efficient technique is to spread the entire sample evenly onto a clean light background, such as a white plastic tray. Individual specimens can then be picked out from the debris using fine forceps (Fig. 4). Sorting effort can be standardised by imposing a fixed time limit for processing each sample. Where either the number of insects or the amounts of debris are excessive, it may be pragmatic to process only a sub-set of the material in each sample. This can be done by evenly spreading each sample over the sorting tray and separating off a fixed fraction for detailed sorting.

iii) Emergence traps

Emergence traps make use of the positive phototactic response of many mobile insects. Individual trap designs vary but all consist of an open-ended opaque box or cylinder, with an aperture at the top providing the only source of light. Insects moving up the chamber towards the light are funnelled into a collection vessel. Samples are standardized because the trap base covers a fixed area of ground. The apparatus is placed rapidly over the vegetation and sealed at the soil surface to prevent insects escaping. CHERRY et al. (1977) suspended the trap from the end of a long pole which was used to lower the trap over the vegetation at a distance from the operator; this was intended to reduce disturbance of the resident Auchenorrhyncha by the operator. The alternative is to position the trap early in the morning when the insects are likely to be least active and then leave it in place for several hours (TÖRMÄLÄ 1982) or days (CLEMENTS 1979). CHERRY et al.(1977) found that this method recovered more than 80% of potato leafhoppers *E. fabae* from alfalfa (absolute densities being calculated after fumigation of the trap to retrieve any individuals remaining). They found that trap efficiency was generally unaffected by wind, temperature or crop height but was significantly reduced at lower sunlight levels. However, SIMONET et al. (1979) found that this method was considerably less efficient for sampling *E. fabae* adults than either suction or sweep net techniques. BUNTIN (1988) came to a similar conclusion for extracting cicadellid adults from bermudagrass, *Cynodon dactylon*, and found that the technique did not recover any nymphs. In the cooler climate of central Finland, TÖRMÄLÄ (1982) reported this method to be very inefficient for sampling the grassland Auchenorrhyncha community, comparing unfavourably with sweep netting, suction sampling and even pitfall trapping in terms of the numbers of individuals and species caught.

iv) Marking techniques

Mark-release-recapture techniques have been used to estimate population sizes of a wide variety of mobile animals including insects (SOUTHWOOD 1978). At their simplest, these involve catching, marking and releasing a number of individuals within a population, followed by re-sampling after a period to allow for re-mixing. The ratio of marked to unmarked individuals in the second sample should be the same as that in the population as a whole; this fact allows a simple estimation of the total population size. The technique makes a number of critically important assumptions, including (i) random selection of individuals for marking (e.g. across sexes, phenotypes and age classes), (ii) fully random mixing of marked individuals with unmarked ones after release, (iii) a marking technique that is persistent but does not affect survival or subsequent behaviour of individuals, and (iv) a population which is closed (i.e. no birth, immigration, death or emigration) within the period of study. These assumptions are rarely fully met and their violation can produce serious biases in the resultant population estimates. The comparative ease and accuracy of other methods of population estimation have meant that this technique has not been widely used by workers studying Auchenorrhyncha.

However, various marking techniques have been employed in studies of local dispersal by leafhoppers and planthoppers. The most popular technique has been the use of fluorescent powders or coloured dyes (PURCELL & SUSLOW 1982; LARSEN & WHALON 1988; WHITNEY & MEYER 1988; POWER 1992). A sample of insects is confined in a vessel containing a small amount of the marker. The vessel is gently agitated to ensure that all individuals are covered and then the insects are released at a single point. Insects recaptured after a period of time in traps that have been positioned at known distances and directions from the release point are then checked for traces of the marker. Re-captures may need to be examined under low-power magnification and (for fluorescent powders) ultra-violet light. Different colours can be used to denote different release dates and/or locations, although PURCELL & SUSLOW (1982) warn that colours that are too similar may be difficult to separate in the small quantities found on recaptured insects.

PADGHAM et al. (1984) and PERFECT et al. (1985) adopted a mass-marking technique, both to monitor flight activity in planthopper pests of rice and to help in the interpretation of catches from other trap types. They applied rubidium chloride as an aqueous foliar spray to the crop and then attempted to recover marked individuals using various types of trap (water, suction and light) situated in or adjacent to the treated plot. All planthoppers caught were checked for traces of rubidium using atomic absorption spectrometry. ALVERSON et al. (1980) used a similar technique to mark the black-faced leafhopper, *Graminella nigrifrons*, a virus vector on corn.

With all these techniques, the critically important assumption is that the marking does not significantly affect the insects' behaviour or viability. All of the aforementioned studies have therefore had to include a careful comparison of the behaviour and survival of marked individuals with controls.

Estimation of relative population density

Absolute population estimates often necessitate expensive equipment or are time-consuming to produce. Fortunately however, relative population estimates are perfectly adequate for many studies, where the primary interest is simply in comparing population levels and there is no specific requirement to know the absolute population density. This is generally the case where the focus is on monitoring how populations change across years or comparing between different experimental treatments. Relative population estimates can be derived by active sampling using nets or through passive sampling using various types of stationary trap.

i) Sweep netting

A sweep net is a particularly robust type of net used to dislodge and collect insects from vegetation. It must have a reinforced rim to withstand the impact of jarring against plants and the net bag should be constructed from a natural fibre or synthetic cloth material that is similarly durable. The most efficient mode of action is to pass the net repeatedly through the vegetation using alternate forehand and backhand strokes whilst walking forward at a constant speed. At the end of this sweeping, any insects caught can be extracted from the bag using a portable aspirator or the entire catch can be emptied straight into a collection bag or killing bottle. At the end of each sweeping episode, care should be taken to wrap the end of the net around the rim to prevent the more mobile species from escaping; for this reason, the bag length should be at least one and a half times the diameter of the net aperture.

The sweep net is almost certainly the most widely used method for collecting herbivorous insects from vegetation. Its principal advantages are that it is simple and inexpensive to construct, easy and quick to use, large numbers of insects can be caught and extensive areas of ground can be covered. For these reasons, it is widely used for non-quantitative survey work, for example the rapid production of faunal inventories. A significant drawback is that it can not be used if the vegetation is wet, flattened or very short. Also, the technique can seriously damage the vegetation if applied too vigorously (an important consideration when sampling crop plants) and it is not appropriate if plants are too large or robust (taller crop plants, bushes or trees).

Sweep nets are sold and can be made in a variety of forms (Fig. 5). The important variables are the size and shape of the aperture, the material used for the collection bag and its length. Larger diameter nets can be used to sample a greater volume of vegetation but become excessively heavy and cumbersome to control once the diameter of the aperture exceeds about 60 cm. Smaller nets collect less material but have a narrower aperture through which insects can escape. Nets made from soft natural fibre cloth or 'nylon' are generally favoured because the catch can be temporarily contained at the end of the sweeping by folding the bag over the frame. However, a variety of stiffer synthetic mesh materials (e.g. 'tygan') have also been used to produce nets that retain their open shape permanently. Although this increases the risk of insects escaping through the open aperture, this can be minimised by taking advantage of the insects' natural phototaxis. If the net is held with its apex pointing in the direction of the sun and with the aperture inclined slightly downwards, the insects will tend to move upwards and towards the light and therefore become trapped at the closed end of the net. The aperture of the net can be held close to the user's face for close inspection of the catch and selective removal of individual insects with an aspirator.

Fig. 5.
Sweep nets. A range of sweep nets, illustrating the potential variation in size, shape and net material. The net in the centre is made with semi-rigid gauze netting designed to maintain the open net shape permanently.

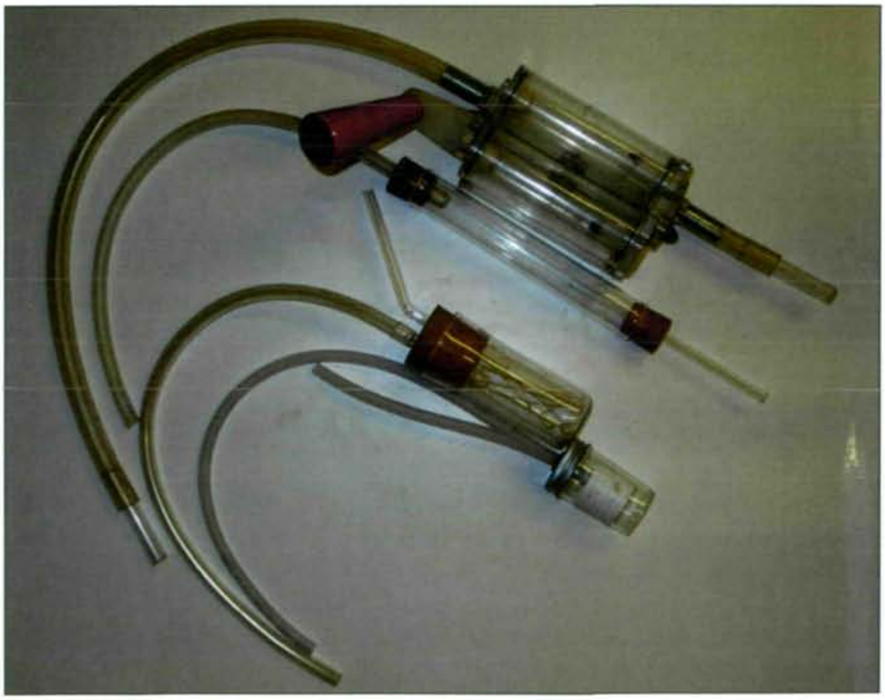

Fig. 6.
Selection of hand-held aspirators ('pooters'). The basic design of an aspirator can be modified to suit the particular purpose, but should have a collection barrel that is transparent to allow inspection of the catch. A multi-barrel aspirator (top) can be used to segregate samples, for example from different sites, habitats or experimental treatments.

Portable aspirators (sometimes referred to as 'pooters') are also produced in a variety of forms (Fig. 6). It is important that the barrel of the aspirator is made of transparent material so that the catch can be inspected during collecting. Glass tubing presents a safety risk under field conditions but will usually remain clear for longer, whilst plastic scratches easily and therefore reduces visibility for inspection of the catch. Multi-barrel aspirators can be used to keep catches from different sites or habitats separate.

Whilst sweep netting is widely used for general collecting, there are considerable problems in using it for quantitative sampling. This is because capture efficiency is affected by a number of factors, including vegetation type, weather conditions and the effect that both of these have on the behaviour of the insects. Other biases may be created by variation in the speed, height and angle of the net as it hits the vegetation and its orientation in relation to the wind. Recognition of these potential biases has prompted different responses: DELONG (1932) doubted whether relative population densities could be estimated with any accuracy using this technique, whilst ROMNEY (1945) concluded that it was justified if allowance was made for the effect of important environmental variables.

Sweep netting samples only the middle and upper layers of the vegetation, so that species occupying the layer nearest the ground will tend to be under-represented in catches, as shown repeatedly in comparisons of sweep net and pitfall trap catches (PAYNE 1981; TÖRMÄLÄ 1982; NOVOTNY 1992; CHERRILL & SANDERSON 1994). Reactions to disturbance of the vegetation will differ between species. Highly mobile species will fly away whilst more sedentary species may drop deeper into the vegetation, in both cases causing an under-representation in the sweep net catch. Conversely, some Delphacidae that dwell near to the ground respond to disturbance of the upper vegetation layers by climbing the plant stems (perhaps in preparation for flight). Differences in response may also be apparent between the sexes; DECKER et al. (1971) report that ovipositing female potato leafhoppers (*Empoasca fabae*) are less easily prompted to fly than males.

Recognizing these potential sources of bias, various attempts have been made to establish the relative efficiency of sweep netting in comparison with other techniques. Using emergence traps to determine absolute population densities, CHERRY et al. (1977) found that sweep net catches of the potato leafhopper, *Empoasca fabae*, were very strongly affected by weather conditions. They therefore developed a calibration for conversion of sweep-net catches to areal population estimates, that included an allowance for both wind speed and temperature. Although WALOFF & SOLOMON (1973) used a D-Vac for their detailed population studies, sweep net catches were occasionally substituted using a conversion factor, when suction sampling was not possible (WALOFF & THOMPSON 1980). Other workers have attempted to convert sweep net catches to absolute population densities (HEIKINHEIMO & RAATIKAINEN 1962; SIMONET et al. 1978, 1979; TÖRMÄLÄ 1982). In spite of these shortcomings, sweep netting often compares very favourably with other sampling techniques (SIMONET et al. 1979; BUNTIN 1988) and has the merits both of speed and of minimal cost.

If sweep net catches are to be used for relative estimates of population density, it is important to minimize as many potential sources of bias as possible by standardising the procedure. This should include the area covered, the total number of sweeps, the walking pace and the height at which the net is drawn through the vegetation. Additionally, it may be necessary to check for differences in capture efficiency between workers and adjust the resultant figures if necessary. In community studies, the relationship between sampling effort (in this case, the total number of sweeps) and number of species recorded will follow the familiar asymptotic species-area curve, whereby new species are initially added rapidly but the species accumulation rate levels off after a critical sample size has been exceeded. The speed with which this asymptote is reached will depend not only on the species richness of the community but also on the structure of the habitat. In early studies comparing a wide range of different grassland types, KONTKANEN (1950) determined that samples of 200 sweeps were needed to reflect the full spectrum of species present.

ii) Pitfall traps

Pitfall traps are glass, metal or plastic collection vessels, typically 8-10 cm in diameter and 10cm deep, set into the soil and part filled with a preserving fluid (Fig. 7). Invertebrates that are active on the soil surface or within the epigeal layer fall into the trap and are unable to escape (SOUTHWOOD 1978). The precise design of the trap is largely unimportant, as long as the rim of the collection vessel is set at or just below the soil surface. After setting, traps are typically left for one to two

Fig. 7.
Pitfall trap. A collection vessel (plastic, metal or glass, approximately 8-10cm. diameter) is embedded into the soil so that the rim is at or slightly below the soil surface. Epigeal invertebrates fall into the vessel which contains a small amount of preservation fluid. Rain-shields (in this case, an inverted plant pot saucer held in place by a metal wire frame) can be used to prevent the trap from flooding in wet weather.

weeks before the contents are removed for sieving and examination. Various fluid preservatives have been used (varying-strength solutions of alcohol, ethylene glycol or formaldehyde, with a few drops of detergent to reduce the surface tension), some of which may have an attractive effect although this has not been fully evaluated for Auchenorrhyncha. Some workers (e.g. NOVOTNY 1992) have chosen to shield the trap with a flat metal or plastic sheet (slightly larger than the aperture of the trap and suspended a few centimetres above its rim); this serves to protect the trap from rainfall, deter interference from mammals and define more precisely the vertical zone being sampled.

The merits of pitfall traps are that they are cheap, easy to set and can produce large catches containing a range of species. As with other fixed traps, they can be used to sample continuously over long periods of time, giving a more realistic picture than the 'snapshot' provided by other 'instantaneous' sampling methods. Despite these advantages, the use of pitfall traps has never been a mainstream technique for sampling grassland Auchenorrhyncha. However, recent evidence suggests that it has considerable potential for sampling certain species groups. A number of studies comparing this method with sweep netting or other types of sampling (CHERRILL & SANDERSON 1994; NOVOTNY 1992; PAYNE 1981; TÖRMÄLÄ 1982) have been instrumental in indicating that grassland Auchenorrhyncha are vertically stratified within the physical structure of the vegetation. European genera which are caught in disproportionate numbers in pitfall traps and are therefore assumed to dwell close to the soil surface include *Agallia*, *Aphrodes*, *Eurysa*, *Delphacodes*, *Macustus*, *Megamelodes*, *Megophthalmus*, *Streptanus*, *Stroggylocephalus* and *Ulopa*.

Pitfall traps have also been used successfully in compiling faunal inventories for certain habitat types where other techniques are not practicable. In Britain, large-scale surveys of both lowland and upland peat bogs using pitfall traps have revealed a number of delphacid species which were previously thought to be rare and restricted in their range (HOLMES et al. 1993). Another survey of open, sparsely-vegetated shingle habitats rediscovered considerable numbers of a species which had not been recorded for more than 50 years in Britain (MORRIS & PARSONS 1992). It is clear that some of these species may have been previously overlooked because they occupy the lowest layer within the vegetation which is poorly sampled by other methods.

A further characteristic of pitfall trap catches is that they tend to be dominated by male specimens. This feature has been noted by several workers (LE QUESNE & MORRIS 1971, PAYNE 1981, A.J.A. STEWART, unpublished data). The discrepancy may be very marked: NOVOTNY (1992) recorded a sex ratio of 17:1 in *Aphrodes bicinctus* (SCHR.) and LE QUESNE & MORRIS (1971) found a 26:1 ratio in *Aphrodes albifrons*. It is likely that this effect results from the males being more active rather than because they occupy a lower stratum within the vegetation. This highlights the problem of catch sizes being activity dependent, which has been recognised for some time in other invertebrate groups (ADIS 1979; DEN BOER 1986; TOPPING & SUNDERLAND 1992). Nevertheless, pitfall trapping remains a useful and considerably under-exploited technique for general collecting and for site inventory studies on Auchenorrhyncha. More research on how pitfall trap catches relate to actual population densities would be valuable.

iii) Attraction and interception traps for capturing flying insects

In addition to the simple pitfall trap, a variety of other trap types have been used for different purposes. All operate by either attracting insects to the trap, using visual or olfactory cues, or by intercepting their normal movement patterns. In both cases, as with pitfall traps, the resultant catches reflect a combination of abundance and activity; the relationship between catch size and true abundance will vary between species and possibly also spatially and temporally. Hence, it is unwise to use the size of such catches for quantitative studies, unless their accuracy in the particular situation has been verified by another method. However, information from such traps are useful in species inventory work and in indicating seasonal phenologies (e.g. the initiation of dispersal or migratory behaviour).

Although most often associated with sampling nocturnal Lepidoptera, light traps have also been used to sample Auchenorrhyncha. Trap efficiency varies markedly between different climatic regions. In temperate climates, Rothamsted light traps (Williams 1948) sporadically catch a limited range of species in modest numbers (A.J.A. Stewart, unpublished data). However, tropical environments induce substantially larger catches, enabling routine monitoring for pest management (Perfect et al. 1985), biodiversity inventory studies (Sutton 1983; Rees 1983) and long-term studies of seasonality (Wolda 1980). Taylor et al. (1982) developed an upwardly-directed light trap, incorporating a device for segregating the catch into time intervals, specifically for monitoring flight activity (especially landing and settling times) in the planthopper *N. lugens*. If behavioural differences exhibited by the Lepidoptera are representative, the attractiveness of light traps for Auchenorrhyncha is likely to vary considerably between species and sexes, but no work has yet been done on this aspect.

The attraction of flying insects to particular colour spectra can be turned to advantage by using water-filled coloured bowls as traps (Fig. 8). Colours differ in their attractiveness to different insect groups; yellow and to a lesser extent white are generally the most attractive, but may even be repellent to some groups (Disney et al. 1982). Kisimoto (1968) showed that yellow water traps were most effective for catching the common rice-feeding planthoppers. Colours that match the background vegetation more closely, such as green and brown, provoke the least marked responses (either attraction or repulsion) and therefore may be used to produce a less selective, although lower, catch. Water traps have the advantage of modest cost, which means that large numbers can be used to survey distribution patterns over substantial areas (eg. Györffy & Karsai 1991). It would be important to standardise on vertical positioning, as evidence from using water traps to catch other insect groups suggests that height (particularly height above the upper vegetation surface) has a pronounced effect on catch size (Usher 1990).

Sticky traps (small coloured plates covered with a proprietary banding grease or other adhesive that is resistant to water and remains sticky over long periods) are perhaps the entomologist's least favoured technique, as the specimens caught are difficult to extract from the adhesive and rarely remain in good condition. Nevertheless, they are widely used as an inexpensive technique for monitoring the distribution and spread of leafhopper populations in commercial crops; for example, they have been one of the principal methods for sampling leafhopper vectors of X-disease in Californian cherry orchards (Purcell & Elkington 1980). Comparison of sticky traps with sweep netting and suction sampling in such orchards showed that each technique produced a different numerical balance between the common species. Interestingly however, the sticky traps caught the most species, probably due to the continuous nature of the sampling over a long period compared to the near-instantaneous sampling of the other techniques.

Fig. 8.
Water trap. Made from a plastic plant pot saucer mounted on a short stake and part-filled with water. Light colours (white, yellow, orange) tend to be more attractive to insects than darker shades or colours (green, brown) that blend more with the background vegetation .

'Flight-interception' or 'window' traps operate by blocking the flight path of individuals moving laterally through the habitat. They comprise a vertical barrier of transparent material (glass, plastic or thin mesh) suspended above a fluid-filled collection trough which the insects drop into after colliding with the barrier (Fig. 9). Paired troughs either side of the vertical barrier allow segregation of the catch into individuals moving in each of the two opposite directions. It is customary to use this feature to measure movement of flying

Fig. 9.
Window trap. A perspex sheet (approximately 1x1m.) is mounted vertically on a metal frame. Flying insects are intercepted and fall down into fluid-filled collection troughs running along the base of the 'window'. Separate troughs on either side of the 'window' allow an assessment of numbers of insects moving in the two opposite directions.

insects across habitat boundaries (e.g. between a crop and adjacent semi-natural habitat). There are few examples in the Auchenorrhyncha literature, but Györffy & Szönyi (1989) report a remarkable 41,000 individuals across 118 species caught over two years with this method in a study of movement patterns between ungrazed grassland and adjacent pasture and forest. Schultz & Meijer (1978) employed these and 'strip traps' (pitfall traps placed in the middle of a length of gutter sunk into the soil) to monitor immigration into new polders, but found that neither caught large numbers of leafhoppers.

Fig. 10.
Malaise trap. Vertically positioned sheets of black netting arranged like an open-sided tent intercept the movement of insects through the habitat. Once intercepted, insects respond phototactically and move upwards towards the white roof. The inclined ridge of the 'tent' funnels the insects towards the top corner, where an aperture leads into a collection vessel (top left) filled with preservation fluid.

A further type of flight-interception trap, the Malaise trap, is constructed in the fashion of an open-sided tent (Malaise 1937). It is generally constructed with dark walls and a light roof to encourage insects to move upwards and be funnelled into a collection bottle (Fig. 10). It is very efficient at catching Diptera and Hymenoptera, but has not been widely used by collectors of Auchenorrhyncha. However, Owen (1991) reports captures of considerable numbers in Britain across thirty species, most of which were cicadellids.

Measurement of movement and dispersal

The measurement of dispersal rates and movement patterns in small animals such as invertebrates remains a major challenge for field biologists. The basic equation of population flux ($N_{t+1} = N_t$ + Birth + Immigration - Death - Emigration, where N_t = the population density at time t) recognises the effect on population dynamics of individuals moving into and out of the population. Because of the difficulties in tracking small and highly mobile organisms, many population studies (and the theoretical models underlying them) have ignored the processes of immigration and emigration and chosen instead to concentrate on measuring the birth and death rates. This approach makes one of two assumptions: either that exchange of individuals with other populations is negligible and can therefore be ignored (unlikely to be true for highly mobile species), or that immigration and emigration are equal and therefore cancel each other out. The latter assumption, even if numerically correct, is unlikely to hold for the secondary attributes of the population (e.g. sex ratio, age distribution, genetic structure). Population studies therefore should always attempt to quantify rates of movement into and out of the population.

This problem can be tackled in several ways, each method providing data of differing value and cost. Direct measures of dispersal using mark-release-recapture techniques have been dealt with already and have been useful in quantifying small-scale movement within and between adjacent habitats (e.g. Purcell & Elkington 1980). More technologically advanced methods, such as using allozyme variation (den Hollander 1989) and DNA techniques to measure genetic differentiation and thereby infer rates of gene flow between populations, have yet to be exploited widely in this group.

Raatikainen (1972) inferred rates of dispersal of leafhoppers into oatfields in Finland by collecting a series of samples at evenly-spaced distances into the crop from the margin with an adjacent ley. The results enabled him to distinguish between species that flew only trivial distances or not at all, which declined in density from the crop edge towards the middle, and species that he classed as migrants because their densities were more even. Raatikainen & Vasarainen (1973) developed a stand-mounted net apparatus that could rotate with the wind direction, to monitor movement of flying insects above cereal crops. Functioning of the trap was dependent on a certain minimum wind velocity to keep the net elevated. Also, the lack of a collection vessel meant that insects could crawl or fly out of the net unimpeded. Nevertheless, the apparatus sampled some 12,500 individuals across 57 species during seven 2-month field seasons.

The best studies have used more than one technique to measure different components of population flux. In an exemplary study, PERFECT et al. (1985) employed different types of trap to separate the different components of flight activity in delphacid pest populations in flooded rice. They suggested that the total aerial density (measured using suction traps) could be partitioned into immigrants (monitored with green water traps) and emigrants (using 'net canopy traps'). Insects over-flying the resident population (as well as immigrants into it) were sampled using upward-pointing light traps.

Long-distance mass migrations of certain important agricultural pest species have been monitored using radar (RILEY et al. 1991) and trapping from aircraft (TAYLOR & RELING 1986). Other authors working with wing-polymorphic delphacids have used the balance between macropters and brachypters to infer the migratory tendency of the population (reviewed in KISIMOTO & ROSENBERG 1994).

Choice of technique and minimum sample size

A number of studies comparing the sampling efficiency of different methods such as sweep netting, suction sampling and pitfall trapping (CHERRILL & SANDERSON 1994; NOVOTNY 1992; PAYNE 1981; TÖRMÄLÄ 1982) have shown that each technique samples a subtly different component of the total fauna. The conclusion usually drawn is that, if a complete inventory of a grassland fauna is sought, sweep netting or suction sampling has to be combined with pitfall trapping, since the latter technique is needed to reveal the species living in the lowest vegetation stratum or very close to the ground. However, in a study of the invertebrate fauna of a calcareous grassland in north-east England, STANDEN (2000) found that a combination of sweep net and suction sampling revealed nearly all the resident Auchenorrhyncha species. Her total sample of over 4100 individuals comprised 45 species, 40 of which were captured by the suction sampler and 21 by sweep netting; the pitfall traps collected 28 species, but only one of these was unique to this method. The difference in conclusion between this and previous studies illustrates the point that the relative efficiency of any sampling method should be tested in the context of the particular habitat being studied prior to detailed work on community composition and structure. Unfortunately, financial and time constraints often preclude this important preparatory work.

A further important consideration concerns the minimum sample size required to provide a reliable estimate of species richness. The number of species recorded will increase with increasing total sample size up to an upper asymptote, which, if reached, can be taken as a true reflection of the species richness of the community. The sample size required to reach this asymptotic species richness level will vary between taxonomic groups. STANDEN (2000) also showed that it will vary according to the sampling technique used. In her study, the combined sweep net and suction sampler technique produced a species accumulation curve that started to level off at around 400 individuals and approached its asymptote at around 1500 individuals. Conversely, the species accumulation curve for the pitfall trap technique was still rising steeply at the end of the study when approximately 600 individuals had been sampled.

Summary and future research

Techniques for sampling populations of Auchenorrhyncha (or indeed any other insects) that are completely objective and unbiased simply do not exist; all methods carry inherent biases. Table 1 summarises these and other attributes of the main sampling techniques described in this paper. The relative efficiency of any technique will depend upon a range of factors related to the physical environmental conditions, the structure of the habitat and the behaviour of the insects themselves. Consequently, all population or community studies should (but rarely do) start by evaluating the efficiency of the

Table 1:
Attributes of different techniques for sampling grassland Auchenorrhyncha.

Method	Cost of equipment *	Time efficiency *	Sampling interval: instantaneous (I) or extended (E)	Absolute (A) or relative (R) estimate of population density	Ability to standardize *	Skill required *	Activity dependence *	Weather dependence *	Range of habitats in which applicable *	Taxonomic bias*. Groups favoure (italics)	Advantages / Disadvantages (*italics*)
Direct counts	L	L	I	A	H	H	M	H	H	*Large spp., sessile* spp.	Non-destructive. Allows recording of microhabitat, host-plant association, feeding position.
D-Vac	H	M	I	A	H	M	L	H	L-M	L	*Weight. Poor reliability. Efficiency declines with increasing vegetation height and density*
G-Vac	M	M	I	A	H	M	L	H	L-M	L	*Time needed to sort sample from debris*
Emergence	L	H	E	A	H	L	M	M	L	?	*Small catches.*
Sweep net	L	M	I	R	M	M	M	H	H	*Spp in middle-upper layer of vegetation*	*Efficiency varies between operators*
Pitfall trap	L	H	I	R	M	L	H	L	L	*Epigeal spp.*	Low cost.
Light trap	M	H	E	R	M	L	H	H	M	?	*Mains electrical source required (some traps). Differential attractiveness to different spp.*
Water trap	L	H	E	R	M	L	H	M	H	?	*Requires regular checking & change of fluid*
Sticky trap	L	H	E	R	L	L	H	H	M	?	*Poor condition of specimens*
Flight interception ("window") trap	L	H	E	R	L	L	H	H	M	?	Can be used to Indicate direction of movement
Malaise trap	M	H	E	R	L	L	H	H	M	?	Large catches of certain groups
Mark-release-recapture	L	L	I	-	-	H	-	H	M	-	*Need high recapture rate.*

* H: high; M: medium; L: low.

sampling technique proposed. This is especially important when monitoring the dynamics of populations over time or when comparing spatially separated populations. It may be possible to do this in near-absolute terms, for example by expressing the catch from a standard sample as a percentage of the total numbers recovered after any extra individuals found by a thorough hand-search of the habitat are included. In other cases, comparison may be possible only with another relative estimate of population density. In either case, the investigator should be aware of how extrinsic factors such as weather conditions affect sampling efficiency and whether both sexes and both nymphal and adult stages are affected equally. Much more research is needed on the comparative efficiency of different techniques in sampling Auchenorrhyncha (c.f. TÖRMÄLÄ 1982).

This review also shows that, whilst a limited range of conventional sampling methods has been widely used, a number of other techniques more generally associated with collecting other insect groups may also be applicable to the Auchenorrhyncha. These techniques however would need to be tested rigorously for taxonomic bias before being adopted in community studies and for activity-dependence if used in population monitoring.

The distribution and behaviour of the species and the architecture of the habitat usually dictate which sampling technique is most appropriate. Standard equipment or techniques will often have to be modified to improve sampling efficiency under the particular conditions presented by the study. Whilst particular techniques have been developed to sample broad species-habitat combinations, new studies should not adopt these uncritically. In their understandable enthusiasm to progress to examining patterns and processes in Auchenorrhyncha populations, investigators should not fail to check that the techniques which they are using will provide results that are reliable both statistically and biologically.

Zusammenfassung

Die verschiedenen Methoden, um Zikaden-Zönosen in Grünland zu erfassen, werden vorgestellt und hinsichtlich ihrer Vor- und Nachteile diskutiert. Wie bei den meisten Wirbellosen, so gibt es auch für Zikaden keine einzelne Methode, um das vollständige Artenspektrum eines Lebensraums mit hinreichender Sicherheit zu erfassen oder Populationsgrößen und Individuendichten aller Arten eines Lebensraums korrekt zu ermitteln. Dennoch können mit vertretbarem Einsatz von Zeit und Ausrüstung gute Näherungswerte sowohl für relative als auch für absolute Populationsdichten ermittelt werden, wenn der Erfassungsmethodik (Standardisierung; Vergleichbarkeit in Raum und Zeit) entsprechende Beachtung zuteil wird. Streifnetzfänge (Kescherfänge) sind eine kostengünstige und einfache Methode, um relative Häufigkeiten zu ermitteln, haben aber den Nachteil, daß sie schwer standardisierbar sind und daß damit zudem die Häufigkeiten epigäischer Arten unterschätzt wird. Die herkömmlichen „D-Vac“-Sauger wurden in jüngerer Zeit durch verschiedene kleinere und billigere umgebaute „Laubsauger“ ersetzt. Sie können gut dazu eingesetzt werden, um absolute Häufigkeiten in Grünlandökosystemen zu ermitteln und erreichen insbesondere bei epigäischen Arten einen höheren Erfassungsgrad als Streifnetzfänge. Die effektivste Methode zur Erfassung der epigäischen Arten sind jedoch Bodenfallen (Barberfallen). Um ein möglichst vollständiges Zikadenartenspektrum eines Lebensraums zu erhalten, sollten daher Bodenfallen entweder mit Streifnetzfängen oder Saugproben kombiniert werden. Methoden zur Erfassung fliegender Insekten und zur Abschätzung von Ausbreitungs- und Wanderverhalten werden ebenfalls kurz diskutiert.

References

Adis J. (1979) Problems of interpreting arthropod sampling with pitfall traps. — Zoologischer Anzeiger Jena **202**: 177-184.

Alverson D.R., All J.N. & P.B. Bush (1980) Rubidium as a marker and simulated innoculum for the black-faced leafhopper, *Graminella nigrifrons*, the primary vector of maize chlorotic dwarf virus of corn. — Environmental Entomology **9**: 29-31.

Andrzejewska L. (1965) Stratification and its dynamics in meadow communities of Auchenorrhyncha (Homoptera). — Ekologia Polska Seria A **13**: 685-715.

Arnold A.J. (1994) Insect suction sampling without nets, bags or filters. — Crop Protection **13**: 73-76.

Bell J.R. & C.P. Wheater (2001) Analysis of the most popular techniques for sampling spiders in large-scale ecological experiments in grasslands. — Newsletter of the British Arachnological Society **91**: 10-12.

Brown V.K., Jepson M. & C.W.D. Gibson (1988) Insect herbivory: effects on early old field succession demonstrated by chemical exclusion methods. — Oikos **52**: 293-302.

Buntin G.D. (1988) Sampling techniques, population dispersion, and sampling plans for leafhoppers (Homoptera: Cicadellidae) in bermudagrass. — Environmental Entomology **17**: 872-877.

Carlson O.V. & E.T. Hibbs (1962) Direct counts of potato leafhopper, *Empoasca fabae*, eggs in Solanum leaves. — Annals of the Entomological Society of America **55**: 512-515.

Chatterjee S.N. & R.D. Ram (1970) A technique for staining and counting leaf-hopper eggs in leaf tissue. — Science & Culture **36**: 597-598.

Cherrill A.J. & V.K. Brown (1990) The life cycle and distribution of the Wart-biter (*Decticus verrucivorus* (L.) (Orthoptera: Tettigoniidae) in a chalk grassland in southern England. — Biological Conservation **53**: 125-143.

Cherrill A.J. & R.A. Sanderson (1994) Comparison of sweep-net and pitfall trap samples of moorland Hemiptera: evidence for vertical stratification within vegetation. — The Entomologist **113**: 70-81.

Cherry R.H., Wood K.A. & W.G. Ruesink (1977). Emergence trap and sweep net sampling for adults of the potato leafhopper from alfalfa. — Journal of Economic Entomology **70**: 279-82.

Claridge M.F. & W.J. Reynolds (1972) Host plant specificity, oviposition behaviour and egg parasitism in some woodland leafhoppers of the genus *Oncopsis* (Hemiptera Homoptera: Cicadellidae). — Transactions of the Royal Entomological Society of London **124**: 149-166.

Clements R.O. (1979) A collapsible emergence trap for grassland insects. — Entomologist's Monthly Magazine **115**: 219-224.

Decker G.C., Kouskolekas C.A. & R.J. Dysart (1971). Some observations on fecundity and sex ratios of the potato leafhopper. — Journal of Economic Entomology **68**: 563-564.

De Barro P.J. (1991) A cheap lightweight efficient vacuum sampler. — Journal of the Australian Entomological Society **30**: 207-208.

De Long D.M. (1932) Some problems encountered in the estimation of insect populations by the sweeping method. — Annals of the Entomological Society of America **25**: 13-17.

den Boer P.J. (1986) Carabids as objects of study. — In: Carabid beetles; their adaptations and dynamics (eds den Boer P.J., Luff M.L., Mossakowski D. & F. Weber) pp. 539-551. Stuttgart: Gustav Fischer Verlag.

den Hollander J. (1989) Electrophoretic studies on planthoppers and leafhoppers of agricultural importance. — In: Loxdale H.D. & J. den Hollander (eds), Electrophoretic studies on agricultural pests. Oxford: Clarendon Press.

Denno R.F. (1980) Ecotope differentiation in a guild of sap-feeding insects on the salt marsh grass, *Spartina patens*. — Ecology **61**: 702-714.

Denno R.F., Raupp M.J., Tallamy D.W. & C.F. Reichenderfer (1980) Migration in heterogeneous environments: differences in habitat selection between the wing-forms of the dimorphic planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). — Ecology **61**: 859-867.

Dent D. (1991) Insect Pest Management. — Wallingford: C.A.B. International.

Dietrick E.J. (1961) An improved backpack motor fan for suction sampling of insect populations. — Journal of Economic Entomology **53**: 394-395.

Dietrick E.J., Schlinger E.I. & R. van den Bosch (1959) A new method for sampling arthropods using a suction collecting mechine and modified Berlese funnel separator. — Journal of Economic Entomology **52**: 1085-1091.

Disney R.H.L., Erzinclioglu Y.Z., Henshaw D.J. de C., Unwin D.M., Withers P. & A. Woods (1982) Collectings methods and the adequacy of attempted faunal surveys, with reference to the Diptera. — Field Studies **5**: 607-621.

Dondale C.D., Redner J.H. & R.B. Semple (1972) Diel activity periodicities in meadow arthropods. — Canadian Journal of Zoology **50**: 1155-1163.

Duffey E. (1980) The efficiency of the Dietrick vacuum sampler (D-Vac) for invertebrate population studies on different types of grassland. — Bulletin of Ecology **11**: 421-431.

Dutilleul P. (1993) Spatial heterogeneity and the design of ecological field experiments. — Ecology **74**: 1646-1658.

Eberhardt L.L. & J.M. Thomas (1991) Designing environmental field studies. — Ecology **61**: 53-73.

Györffy G. & I. Karsai (1991) Estimation of spatiotemporal rearrangement in a patchy habitat and its application to some Auchenorrhyncha populations. — Journal of Animal Ecology **60**: 843-855.

Györffy G. & G. Szõnyi (1989) Movements of phytophagous insect populations between ungrazed sandy grassland and adjacent areas. — Acta Biologica Szegediensis **35**: 129-155.

Hand S.C. (1986) The capture efficiency of the Dietrick vacuum insect net for aphids on grasses and cereals. — Annals of Applied Biology **108**: 233-241.

Heady S.E., Madden L.V. & L.R. Nault (1985) Oviposition behaviour of *Dalbulus* leafhoppers (Homoptera: Cicadellidae). — Annals of the Entomological Society of America **78**: 723-727.

Heikinheimo O. & M. Raatikainen (1962) Comparison of suction and netting methods in population investigations concerning the fauna of grass leys and cereal fields, particularly in those concerning the leafhopper *Calligypona pellucida* (F.) — Publ. Finn. State Agirc. Res. Board **191**: 1-31.

Henderson I.F. & T.M. Whittaker (1977) The efficiency of an insect suction sampler in grassland. — Ecological Entomology **2**: 57-60.

Hildebrandt J. & H. Nickel [in press]: Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera) - a case study from the Elbe flood plains (Northern Germany). — Agriculture, Ecosystems and Environment.

Holmes P.R., Boyce D.C. & D.K. Reed (1991) The Welsh Peatland Invertebrate Survey - Preliminary Report: Methodology and study sites. — Chief Scientist's Directorate Report No. **1125**. Peterborough: Nature Conservancy Council.

Holtkamp R.H. & J.I. Thompson (1985) A lightweight, *self-contained insect suction sampler. — Journal* of the Australian Entomological Society 24: 301-302.

Hurlbert S.H. (1984) Pseudoreplication and the design of ecological field experiments. — Ecological Monographs **54**: 187-211.

Kisimoto R. (1968) Yellow pan water trap for sampling the small brown planthopper, *Laodelphax striatellus* (Fallén), a vector of the rice stripe virus. — Appl. Entomol. & Zool. **3**: 37-48.

Kisimoto R & L.J. Rosenberg (1994) Long-distance migration in delphacid planthoppers. — In: Denno R.F. & T.J. Perfect (eds), Planthoppers: their ecology and management. New York: Chapman & Hall.

Kontkanen P. (1950) Quantitative and seasonal studies on the leafhopper fauna of the field stratum on open areas in North Karelia. — Annls Zool. Soc. Zool.-Bot. Fenn. „Vanamo" **13**(8): 1-91.

Kuno E. (1991) Sampling and analysis of insect populations. — Annual Review of Entomology **36**: 285-304.

Larsen K.J. & M.E. Whalon (1988) Dispersal of *Paraphlepsius irroratus* (Say) (Homoptera: Cicadellidae) in peach and cherry orchards. — Environmental Entomology **17**: 842-851.

Legendre P. (1993) Spatial autocorrelation: trouble or new paradigm? — Ecology **74**: 1659-1673.

LeQuesne W.J. & M.G. Morris (1971) Auchenorrhyncha from pitfall traps at Weeting Heath National Nature Reserve, Norfolk. — Entomologist's Monthly Magazine **107**: 39-44.

Lewis T. & L.R. Taylor (1965) Diurnal periodicity of flight by insects. — Transactions of the Royal Entomological Society of London **116**: 393-479.

Lott D.A. & M.D. Eyre (1996) Invertebrate sampling methods. — In: Eyre M.D., Environmental monitoring, surveillance and conservation using invertebrates. EMS Publications: Newcastle-upon-Tyne.

Malaise R. (1937) A new insect-trap. — Ent. Tidskr. **58**: 148-160.

McLeod A., Wratten S.D. & R.W.J. Harwood (1994) The efficiency of a new lightweight suction sampler for sampling aphids and their predators in arable land. — Annals of Applied Biology, **124**: 11-17.

McLeod A., Sotherton N.W., Harwood R.W.J. & S.D. Wratten (1995) An improved suction sampling device to collect aphids and their predators in agroecosystems. — In: Toft S. & W. Riedel (eds), Arthropod Natural Enemies in Arable Land. I. Density, spatial heterogeneity and dispersal. Aarhus University Press.

Moore R., Clarke R.T. & S. Creer (1993) An insect sorting device to be used in conjunction with insect suction samplers. — Bulletin of Entomological Research **83**: 113-120.

Morris M.G. (1971) Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. IV. Abundance and diversity of Homoptera-Auchenorrhyncha. — Journal of Applied Ecology **8**: 37-52.

Morris M.G. (1981a) Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorrhyncha. — Journal of Applied Ecology **18**: 107-123.

Morris M.G. (1981b) Responses of grassland invertebrates to management by cutting. IV. Positive responses of Auchenorrhyncha. — Journal of Applied Ecology **18**: 763-771.

Morris M.G. (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. — Biological Conservation **95**: 129-142.

Morris M.G. & R. Plant (1983) Responses of grassland invertebrates to management by cutting. V. Changes in Hemiptera following cessation of management. — Journal of Applied Ecology **20**: 157-177.

Morris R.K. & M.S. Parsons (1992) A survey of invertebrate communities on the shingle of Dungeness, Rye Harbour and Orford Ness. — JNCC Report **77**. Peterborough: Joint Nature Conservation Committee.

Novotny V. (1992) Vertical distribution of leafhoppers (Hemiptera, Auchenorrhyncha) within a meadow community. — Acta Entomol. Bohemoslov. **89**: 13-20.

Owen J. (1991) The ecology of a garden: the first fifteen years. — Cambridge: Cambridge University Press.

Payne K. (1981) A comparison of the catches of Auchenorrhyncha (Homoptera) obtained from sweep netting and pitfall trapping. — Entomologist's Monthly Magazine **117**: 215-223.

Perfect T.J., Cook A.G., Padgham D.E. & J.M. Crisostomo (1985) Interpretation of the flight activity of *Nilaparvata lugens* (Stål) and *Sogatella furcifera* (Horváth) (Hemiptera: Delphacidae) based on comparative trap catches and field marking with rubidium. — Bulletin of Entomological Research **75**: 93-106.

Padgham D.E., Cook A.G. & D. Hutchison (1984) Rubidium marking of the rice pests *Nilaparvata lugens* (Stål) and *Sogatella furcifera* (Horváth) (Hemiptera: Delphacidae) for field dispersal studies. — Bulletin of Entomological Research **74**: 379-385.

Peter H.-U. (1981) Weitere untersuchungen zur einnischung der Zikaden in den Halbtrockenrasen des Leutratals bei Jena. — Zool. Jb. Syst. 108: 563-588.

Potvin C. & J. Travis (1993) Concluding remarks: a drop in the ocean ... — Ecology **74**: 1674-1676.

Powell W., Walton M.P. & M.A. Jervis (1996) Populations and communities. — In: M.A. Jervis & N.A.C. Kidd (eds.), Insect Natural Enemies: Practical Approaches to their Study and Evaluation. London: Chapman & Hall.

Power A.G. (1992) Host plant dispersion, leafhopper movement and disease transmission. — Ecological Entomology **17**: 63-68.

Purcell A.H. & J.S. Elkington (1980) A comparison of sampling methods for leafhopper vectors of X-disease in California cherry orchards. — Journal of Economic Entomology **73**: 854-860.

Purcell A.H. & K.G. Suslow (1982) Dispersal behaviour of *Colladonus montanus* (Homoptera: Cicadellidae) in cherry orchards. — Environmental Entomology **11**: 1178-1182.

Raatikainen M. (1972) Dispersal of leafhoppers and their enemies to oatfields. — Annales Agriculturae Fenniae **11**: 146-153.

Raatikainen M. & A. Vasarainen (1973) Early- and high-summer flight periods of leafhoppers. — Annales Agriculturae Fenniae **12**: 77-94.

Rees C.J.C. (1983) Microclimate and the flying Hemiptera fauna of a primary lowland rainforest in Sulwesi. — In: Sutton S.L. & T.C. Whitmore, Tropical Rainforest: ecology and management. pp. 121-136.

Riley J.R., Cheng X.N., Zhang X.X., Reynolds D.R., Xu G.M., Smith A.D., Cheng J.Y., Bao A.D. & B.P. Zhai (1991) The long-distance migration of *Nilaparvata lugnes* (Stål) (Delphacidae) in China: radar observations of mass return flight in the autumn. — Ecological Entomology **16**: 471-489.

Romney V.E. (1945) The effect of physical factors upon catch of the beet leafhopper (*Eutettix tenellus* (Bak.)) by a cylinder and two sweep net methods. — Ecology **26**: 135-147.

Samu F. & M. Sárospataki (1995) Design and use of a hand-hold suction sampler, and its comparison with sweep net and pitfall trap sampling. — Folia Entomologica Hungarica Rovartani Közlemények **56**: 195-203.

Samu F., Nemeth J. & B. Kiss (1997) Assessment of the efficiency of a hand-held suction device for sampling spiders: improved density estimation or oversampling? — Annals of Applied Biology **130**: 371-378.

Sanderson R.A., Rushton S.P., Cherrill A.J. & J.P. Byrne (1995) Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. — Journal of Applied Ecology **32**: 506-518.

Schaefer M. (1973) Untersuchungen über Habitatbindung und ökologische Isolation der Zikaden einer Küstenlandschaft (Homoptera: Auchenorhyncha). — Arch. Naturschutz u. Landschaftsforsch **13**: 329-352.

Schulz C.A. & J. Meijer (1978) Migration of leafhoppers (Homoptera: Auchenorrhyncha) into a new polder. — Holarctic Ecology **1**: 73-78.

Simmons A.M., Pass B.C. & K.V. Yeargan (1984) Influence of selected legumes on egg production, adult survival, and ovipositional preference by the potato leafhopper. — Journal of Agricultural Entomology **1**: 311-317.

Simmons A.M., Godfrey L.D. & K.V. Yeargan (1985) Ovipositional sites of the potato leafhopper (Homoptera: Cicadellidae) on vegetative stage soybean plants. — Environmental Entomology **14**: 165-169.

Simonet D.E. & R.L. Pienkowski (1977) Sampling and distribution of potato leafhopper eggs in alfalfa stems. — Annals of the Entomological Society of America **70**: 933-966.

Simonet D.E., Pienkowski R.L., Martinez D.G. & R.D. Blakeslee (1978) Laboratory and field evaluation of sampling techniques for the nymphal stages of the potato leafhopper on alfalfa. — Journal of Economic Entomology **71**: 840-842.

Simonet D.E., Pienkowski R.L., Martinez D.G. & R.D. Blakeslee (1979) Evaluation of sampling techniques and development of a sampling program for potato leafhopper adults on alfalfa. — Environmental Entomology **8**: 397-399.

Southwood T.R.E. (1978) Ecological Methods. 2nd edition. — London: Chapman & Hall.

Standen V. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. — Journal of Applied Ecology **37**: 884-893.

Stewart A.J.A. & A.F. Wright (1995) A new inexpensive suction apparatus for sampling arthropods in grassland. — Ecological Entomology **20**: 98-102.

Stiling P.D. (1980) Host plant specificity, oviposition behaviour and egg parasitism in some leafhoppers of the genus *Eupteryx* (Hemiptera: Cicadellidae). — Ecological Entomology **5**: 79-85.

Summers C.G., Garrett R.E. & F.G. Zalom (1984) New suction device for sampling arthropod populations. — Journal of Economic Entomology **77**: 817-823.

Southwood T.R.E. (1978) Ecological Methods. 2nd edn. — London: Chapman & Hall.

Sutton S.L. (1983) The spatial distribution of flying insects in tropical rainforest. — In: Sutton S.L. & T.C.Whitmore. Tropical Rainforest: ecology and management. pp. 77-91.

Taylor J., Padgham D.E. & T.J. Perfect (1982) A light-trap with upwardly directed illumination and temporal segregation of the catch. — Bulletin of Entomological Research **72**: 669-673.

Taylor R.A.J. & D. Reling (1986) Preferred wind direction of long-distance leafhopper (*Empoasca fabae*) migrants and its relevance to the return migration of small insects. — Journal of Animal Ecology **55**: 1103-1114.

Thompson P. (1978) The oviposition sites of five leafhopper species (Hom. Auchenorrhyncha) on *Holcus mollis* and *H. lanatus*. — Ecological Entomology **3**: 231-240.

Thornhill E.W. (1978) A motorised insect sampler. — Pest Articles and News Summaries **24**: 205-207.

Topping C.J. & K.D. Sunderland (1992) Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. — Journal of Applied Ecology **29**: 485-491.

Törmälä T. (1982) Evaluation of five methods of sampling field layer arthropods, particularly the leafhopper community, in grassland. — Annales Entomologici Fenniae **48**: 1-16.

Usher M.B. (1990) Assessment of conservation values: the use of water traps to assess the arthropod communities of heather moorland. — Biological Conservation **53**: 191-198.

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

Waloff N. & M.G. Solomon (1973) Leafhoppers (Auchenorrhyncha: Homoptera) of acidic grassland. — Journal of Applied Ecology **10**: 189-212.

Waloff N. & P. Thompson (1980) Census data and analyses of populations of some leafhoppers (Auchenorrhyncha, Homoptera) of acidic grassland. — Journal of Animal Ecology **49**: 395-416.

Whitney S.P. & J.R. Meyer (1988) Movement between wild and cultivated blueberry by two species of sharpnosed leafhoppers (Homoptera: Cicadellidae) in North Carolina. — Journal of Entomological Science **23**: 88-95.

Whittaker J.B. (1965) The biology of *Neophilaenus lineatus* (L.) and *N. exclamationis* (Thunberg) (Homoptera: Cercopidae) on Pennine moorland. — Proceedings of the Royal Entomological Society of London, Series A **40**: 51-60.

Williams C.B. (1948) The Rothamsted light trap. — Proceedings of the Royal Entomological Society of London **23**: 80-85.

Wilson S.W., Smith J.L. & A.H. Purcell (1993) An inexpensive vacuum collector for insect sampling. — Entomological News **104**: 203-208.

Wolda H. (1980) Seasonality of tropical insects. I. Leafhoppers (Homoptera) in Las Cumbres, Panama. — Journal of Animal Ecology **49**: 277-290.

Address of the author:

Dr. Alan J.A. Stewart
School of Biological Sciences,
University of Sussex, Falmer,
Brighton, Sussex, BN1 9QG, UK.
e-mail: a.j.a.stewart@sussex.ac.uk

Zeitschrift/Journal: Denisia

Jahr/Year: 2002

Band/Volume: 0004

Autor(en)/Author(s): Stewart Alan J.A.

Artikel/Article: Techniques for sampling Auchenorrhyncha in grasslands 491-512