ACOUSTIC SIGNALS AND SPECIES PROBLEMS IN THE AUCHENORRHYNCHA

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ABSTRACT

Acoustic signals are important in intraspecific interactions in most groups of Auchenorrhyncha. Males of the larger Cicadidae produce loud airborne signals which act, in part, as species recognition signals. Songs of sympatric species usually differ in features of amplitude modulation and patterning. Smaller Cicadellidae and Delphacidae produce similar vibrational sound patterns which are transmitted via the substrate. Males and females are usually involved in exchanges of signals whilst on their host plants. The pulse patterns of such calls may be complicated and, for sympatric species, are usually very distinct. Vibrational signals may be recorded and analysed by simple techniques. Relatively few species have been investigated, but it is already clear that such studies provide a powerful tool for precise species determination and for the recognition of complexes of sibling species. There is also the potential for studying geographical variation and the status of allopatric populations.

INTRODUCTION

The most important task for the taxonomist concerned with groups of economically important insects is to recognise and describe distinct biological species. This work is frequently made difficult by problems of variation both within and between populations. Also, groups of biological species are often found to exist which show little or no morphological differentiation recognisable by standard taxonomic procedures. Nevertheless the biological differences between such sibling species, such as for example, host preferences, may be very important and make the difference between a pest and a non-pest. Clearly, therefore, it is vital whenever possible to seek sources of information, other than purely morphological ones, which may help in the difficult problems of species taxonomy.

In nature, most insect species are bisexually reproducing and have specific behavioural mechanisms which serve to bring together the sexes for mating. Such behaviour patterns usually consist of an exchange of specific signals which function not only to bring together individuals of the same species (species recognition), but also to prevent, or greatly reduce, the possibility of interspecific matings (species isolation). The signals themselves usually are either visual, acoustic or chemical. Probably for most species a mixture of different types of signals is involved in complete courtship sequences.

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Various authors (e.g. Alexander, 1967; Claridge, 1965; Claridge & Reynolds, 1973) have stressed the importance of studying courtship signals for the practical recognition of biological species. Visual signals may involve the development of characteristic and species-specific colour patterns and structures. Thus insects which predominantly use visual signals, such as for example many butterflies and dragonflies, may often pose fewer problems to the taxonomist, since the patterns and distinctive structures used by the insects themselves may make for relatively easy species discrimination. However, most insects communicate mainly by chemical senses and pose great difficulty for taxonomists since chemical signals are only rarely accompanied by distinct morphological characteristics.

Insects which signal by acoustic means were until recently regarded as interesting, but relatively few in number and confined to a few isolated groups, including only the single family Cicadidae amongst the Auchenorrhyncha. However, in the last 30 years or so many studies have shown the importance of low-intensity sounds in a wide variety of insects including many Heteroptera, Diptera and Coleoptera. Most importantly here, Ossiannilsson (1949), in a classic study, demonstrated that most groups of Auchenorrhyncha produce low-intensity acoustic signals. Indeed, most if not all species of this group probably produce such signals and use them in communication. Studies of these signals then may be of great value to the taxonomist where species limits are difficult and the existence of sibling species is suspected.

Cicadas and loud airborne signals

The loud songs of male cicadas (Cicadidae) have been described many times since the ancient classical writings of Aristotle (Myers, 1929). Fabre (1897), the greatly underestimated French entomologist, was one of the first to give useful descriptions of the songs of different species and to note differences between them. The nature of the tymbal mechanism had been elucidated even earlier and was well described, for example, by Réaumur (1740). Myers (1929) brought together a wealth of information on this group of insects and summarised what was known up to the 1920s of their songs and behaviour. He said "Every cicada with which we are familiar may be recognised with certainty by its song" (page 217). Thus the potential importance of song in the taxonomy of these insects was early realised.

The tymbal mechanism of sound production in cicadas has been the subject of refined physiological analysis in recent years. Perhaps most notably Pringle (1954) first demonstrated the significance not only of the paired tymbals and their muscles, but also of the associated air-filled sacs in the base of the abdomen. These sacs, which are part of the insect's tracheal system, are tuned to resonate at the carrier frequencies of the sounds produced by the vibrating tymbals. They thus act as amplifiers and make possible the great intensities of sounds which are produced by many cicadas and enable them to communicate, often over very great distances.

Although many authors had speculated about the functions of the calls of male cicadas in attracting females, this was only conclusively shown in 1958 by Alexander and Moore for species of Magicicada in North America. These authors clearly demonstrated both the species recognition and isolation functions of calls in these species. No female cicadas are known to call or to possess a tymbal mechanism. The behaviour of individual species may be quite complex and contrast with that of related ones, but there can be little doubt of the general significance of songs in attracting females of the same species to the vicinity of singing males (Claridge, Wilson & Singhrao, 1979). They may thus be expected to have an important function in species isolation.

All known calls consist of trains of amplitude-modulated pulses with characteristic carrier frequencies. In many species, pulses are grouped in complex sequences giving great specificity to each species call. With the development of simple electronic techniques of recording by means of portable magnetic tape recorders, considerable advances have been made in the objective description of cicada songs. For example, sonagraph and oscillograph analyses have been used to describe songs of species from all over the world - for example from Australia (Young, 1972), Brazil (Aidley, 1969), Europe (Claridge, Wilson & Singhrao, 1979), Japan (Hagiwara and Ogura, 1960), North America (Alexander and Moore, 1958), New Zealand (Fleming, 1971, 1973), Sri Lanka (Pringle, 1954) and USSR (Popov, 1975).

The value of song studies in establishing the biological species status of populations has been most graphically demonstrated by the classic studies of Alexander & Moore (1958) in which they were able to establish the existence of six species of Magicicada on a basis of call differences where previously only one or two were suspected. It is unlikely that the Magicicada group is unique in this respect but few other studies have been made. Though few species of this family seem to be pests, the scope for further study in all parts of the world is immense.

Smaller Auchenorrhyncha and Substrate-Transmitted Signals

Until the studies of Ossiannilsson (1946, 1949), it was widely believed that the Cicadidae were unique amongst the Auchenorrhyncha in possessing tymbal organs and that most species did not produce acoustic signals. In his major paper, Ossiannilsson (1949) described in detail the morphology of structures resembling to varying degrees the tymbal organs of the Cicadidae from all other major families of Auchenorrhyncha represented in northern Europe. More remarkably, with only very simple and primitive apparatus he was able to hear and to record very quiet calls from many of the species which he studied and showed that in many species females also produced acoustic signals. He thus pioneered a totally new field of investigation which has been extended by many others with the advent of better methods of recording and analysis.

Like the calls of cicadas, those of other families of Auchenorrhyncha consist of trains of pulses or amplitude-modulated sounds which may be quite complex. They differ from cicada calls most obviously in being highly damped and thus of low intensity. The patterns produced may be species-specific as first demonstrated by Ossiannilsson (1949) and subsequently by many others since, including Moore (1961), Strubing (1962 and many since), Claridge & Howse (1968) and Claridge & Reynolds (1973). Most of these studies used sensitive microphones in heavily sound-proofed chambers to record the signals.

In 1974 Ichikawa & Ishii, working in Japan with the Brown Plant-hopper, Nilaparvata lugens, were the first to demonstrate conclusively that the calls were substrate-transmitted through the plant and picked up by other individuals on the same plant or on a surface acoustically continuous with it. They showed that it was possible to use a simple transducer attached to the host plant to detect and record such signals. This discovery revolutionised the technique of recording leafhopper and planthopper signals and has since been modified and used by others including Strubing (1977, 1978, 1980), Booij (1982), Claridge et al. (1982) and de Vrijer (1982).

Recording and analysis of signals

The simplest technique for recording the signals of leafhoppers is to use a crystal gramophone pick-up with the stylus lightly, but firmly, attached to the plant on which the insects under study are living. The signals can be passed through a simple preamplifier and recorded on magnetic tape. An open spool recorder is preferable with a tape speed of at least 7½ ips and preferably 15 ips. Such a recording system is relatively cheap and insensitive to airborne sounds, though a quiet room is needed. More recently techniques have been developed which use an accelerometer, such as the Brujel and Kjaer 8307 (see Booij, 1982). This is to be preferred to the crystal cartridge because of its almost total lack of sensitivity to background noise and its linear response. However, unfortunately, the accelerometer is much more expensive than the cartridge and also requires to be used with an expensive charge amplifier. Very satisfactory results for taxonomic purposes can be obtained with the cheap crystal technique.

Since the signals consist of trains of pulses repeated in characteristic patterns and at characteristic rates, the simplest means of analysis is by the production of oscillograms. The generally widely available cathode ray oscilloscope and camera are suitable for this, but some form of direct printing system is preferable. We have found the most useful to be an ink-jet oscillograph, such as the Siemens Mingograph.

From the oscillograms of calls it is possible to describe precisely the patterns of pulses and to calculate pulse repetition frequencies. These variables may then be compared both within and between individuals and populations by appropriate statistical tests.

Species problems and geographical variation

The analysis of male calls in many groups of Auchenorrhyncha has helped to establish the species status of different populations and to demonstrate the existence of sibling species in many groups. De Vrijer (1982) has recently presented oscillograms of the male calls of six species of the planthopper genus *Javesella* from the Netherlands. Each is quite distinct. Claridge and Howse (1968) and Claridge and Reynolds (1973) described the patterns of male calls in British species of the leafhopper genus *Oncopsis* and used estimates of pulse repetition frequencies (PRF) from oscillograms to establish significant differences and to establish species status of some populations previously considered the same. Strubing (1970) also used call differences as evidence for the specific status of *Euscelis alsius* Ribaut and *E. plebejus* Fallén. Booij (1982) has recently used similar analyses in a study of the *Muellerianella* complex of planthoppers in Europe. He was able to demonstrate the existence of three distinct biological species where previously only one or two were recognised.

Such methods of analysis have been concerned mostly with non-pest species, though Shaw *et al*. (1974) and Purcell & Loher (1976) have studied pests of the genera *Empoasca* and *Macrosteles* respectively in North America. Most of the work so far on pest species has concentrated on the planthoppers, *Nilaparvata lugens* (Stål), *Sogatella furcifera* (Horvath) and *Laodelphax striatellus* (Fallén), and leafhoppers of the genus *Nephotettix* - all associated with rice in Asia.

Ichikawa & Ishii (1974), Ichikawa, Sukawa & Ishii (1975) and Ichikawa (1976) demonstrated most beautifully the mutual exchange of substrate-transmitted signals between males and females of *N. lugens*, *S. furcifera* and *L. striatellus*. Both male and female signals are quite distinct and act as efficient premating barriers to hybridisation, though it must be said that the three species are not very closely related.

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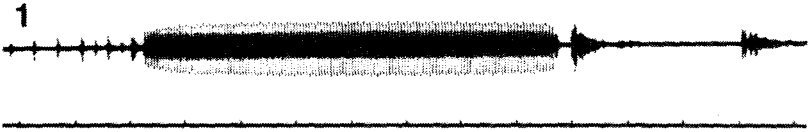
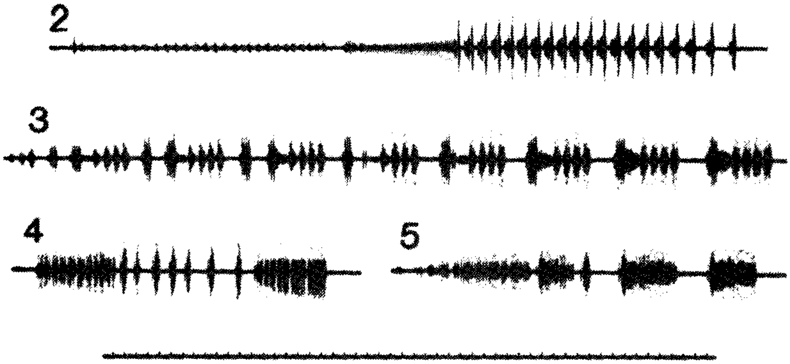


Figure 1. A single repeatable unit from the call of a male *Nilaparvata lugens*. Time marks at 0.25 second intervals.

Claridge et al. (1982) have briefly described studies on intraspecific variation in populations of N. lugens from different parts of Asia and Australia. The female calls of this species are simple trains of regularly repeated pulses, as described by Ichikawa & Ishii (1974). The corresponding male signal is relatively more complicated and consists of repeated units, each consisting of three recognisable phases (fig. 1). The first phase consists of a variable number of from 3-10 complex pulses, the second of a series of many regularly and rapidly repeated pulses and the third of further variable complex pulses. Many detailed features of this basic pattern are variable even within the calls of one individual, but the most consistent feature we have found is the pulse repetition frequency of the second phase. Measure of this frequency for many different populations gives a value of between 65 and 70 pulses/sec.. However, populations from Queensland, Australia, differ greatly from most others with a pulse repetition frequency of almost 90. These differences are significant and may account for the difficulty which we have experienced in obtaining hybrids from crosses between such populations. Booij (1982) has found some evidence of similar statistical variation in geographically isolated populations of Muellerianella in Europe.

The green leafhoppers of the genus Nephotettix are well known as important vectors of rice virus diseases in Asia (Nasu, 1969). Ichikawa (1979) described the acoustic signals and behaviour of N. cincticeps (Uhler) from Japan. The group has posed numerous taxonomic problems because of considerable colour variation and polymorphism, and relatively small differences in male genitalia (Ghauri, 1968; 1971). Several authors, notably Ramakrishnan & Ghauri (1979), have suggested that the presence of apparently intermediate individuals between N. virescens (Distant) and N. nigropictus (Stål) in field populations from tropical regions indicated frequent natural hybridisation between them. Both species are widely sympatric in Asia. The hybridisation hypothesis is strengthened by the work of Ling (1968) who described hybrids between the same species in the laboratory and showed them to be intermediate in many characters. However, Cruz (1975) was unable to obtain such hybrids despite extensive efforts. Yusof (1982) working in Cardiff has recently recorded the calls of both males and females of N. virescens and N. nigropictus and found them to be very distinct, each with very complex patterns of pulses in the males (fig. 2). With difficulty and many failures he obtained true hybrids in the laboratory. Male hybrids did indeed resemble some of the so-called intermediates from field samples in colour pattern characteristics. However, when hybrid males were recorded they were found to be very variable and to include obvious elements from both parental species. The simpler female calls were also intermediate between the parental species. Thus hybrids of both sexes can be distinguished from the parental species by their calls.



Figures 2 to 5. Parts of male calls of Nephotettix. 2, N. nigropictus. 3, N. virescens. 4 and 5, two different hybrid individuals from a cross between a ♂ N. nigropictus and a ♀ N. virescens. Time marks at 0.25 second intervals.

When the calls of "intermediate" male individuals from field samples in laboratory culture were recorded from both Malaysia and Sri Lanka, they were found to produce typical N. virescens calls and not hybrid ones. Detailed genitalia studies also show that N. virescens and N. nigropictus are distinct in field samples with no indication that natural hybridisation occurs. This is a good example of the practical utility of acoustic studies in taxonomy.

CONCLUSIONS

It is clear that the analysis of acoustic signals can provide a powerful tool for investigating the biological status of different populations of Auchenorrhyncha and for the elucidation of difficult groups of sibling species in which morphological differentiation is slight. The painstaking work of Booij (1982) is an excellent example of this. The work on Nephotettix also shows how acoustic information may be used to investigate possible hybridisation between populations or species both in the field and laboratory.

In addition to establishing the species status of sympatric populations, it is clear that such studies may help us to detect previously unknown geographical variation. Where such geographical differences are well established we may be able to contribute useful and novel information to the important arguments concerning the possibilities of large-scale migration in many pest species and groups of species. Thus, although the importance of long-distance migrations in peripheral populations of N. lugens is well established (Kisimoto, 1979), the existence of similar movements in tropical regions is less certain. Acoustic analyses, together with other techniques, may help to elucidate this important problem.

Very few studies have yet been made on the acoustic behaviour of Auchenorrhyncha but it is clear that the information which may be obtained with quite simple techniques may be of the greatest significance in pest problems.

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