OFFPRINTS FROM THE LEAFHOPPERS AND PLANTHOPPERS
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Acoustic Behavior of Leafhoppers and Planthoppers: Species Problems and Speciation

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5.1 INTRODUCTION

Some of the earliest classifications of the Homoptera divided the series of superfamilies that we now usually associate together as the Auchenorrhyncha, into two unequal groups dependent on whether or not they produced sounds. For example, Westwood (65) in 1840, largely following Latreille, gave the following divisions:

A. Chanteuses. Antennae six-jointed; ocelli three.
B. Muettes. Antennae only distinctly three-jointed; ocelli two.
  1. Fulgorelles. Antennae inserted beneath the eyes; forehead often rostrated.
  2. Cicadelles. Antennae inserted between the eyes.

The Chanteuses, or singers, clearly refer only to the modern Cicadoidea, and the Muettes, or dumb ones, to all remaining superfamilies, including the Cicadelloidea and Fulgoroidea. In 1889 Buckton (5) suggested a similar dichotomy with the group names, Stridulantia and Silentia, for the same two divisions. Thus, the notion that cicadas are clearly separated from other families, not only by morphological differences, but also by the behavior of sound production, was widely disseminated in the 19th century. Indeed this view was generally held until quite recently. For example, in 1951 the standard textbook of entomology by Imms (27) stated that the sound producing organs of cicadas are peculiar to them and that members of other families of Auchenorrhyncha do not seem to produce sounds. A few earlier publications suggested that at least some other species might stridulate by frictional mechanisms involving the wings (31, 32). However, it was not until the classic studies of Ossiannilsson (41, 42) in the 1940s that the false dichotomy between "singing" cicadas and "mute" leafhoppers and planthoppers was completely exposed. He studied the morphology of 79 species of Auchenorrhyncha from Sweden including Cicadellidae, Delphacidae, Cixiidae, Issidae, Cercopidae, and Membracidae. He identified structures in all adult males and in many females that appeared to be homologous with the well-known tymbal sound producing mechanism of male cicadas. Even more significantly, he gave verbal descriptions of the very quiet sounds that he heard produced by as many as 96 species of these insects. For some, he was able to obtain primitive oscillograph analyses of calls by enclosing living insects in a small insulated cage with a microphone connected to an amplifier and "radiograph" apparatus. Since 1949 other workers have followed up these pioneering studies, but no one has since attempted such a large scale, comparative work. The study of low intensity calls of small species has been made much easier in recent years with the development and general availability of simple magnetic tape recorders and electronic methods of sound analysis, especially oscilloscopes and sound spectrographs.

Chapter 5 discusses what is currently known of the mechanisms of sound production and reception, methods of recording and analysis and medium of transmission of the sounds, the nature of acoustic signals and their roles in behavior, especially in species recognition, and in the evolution and speciation of these insects.

5.2 SOUND PRODUCTION AND RECEPTION

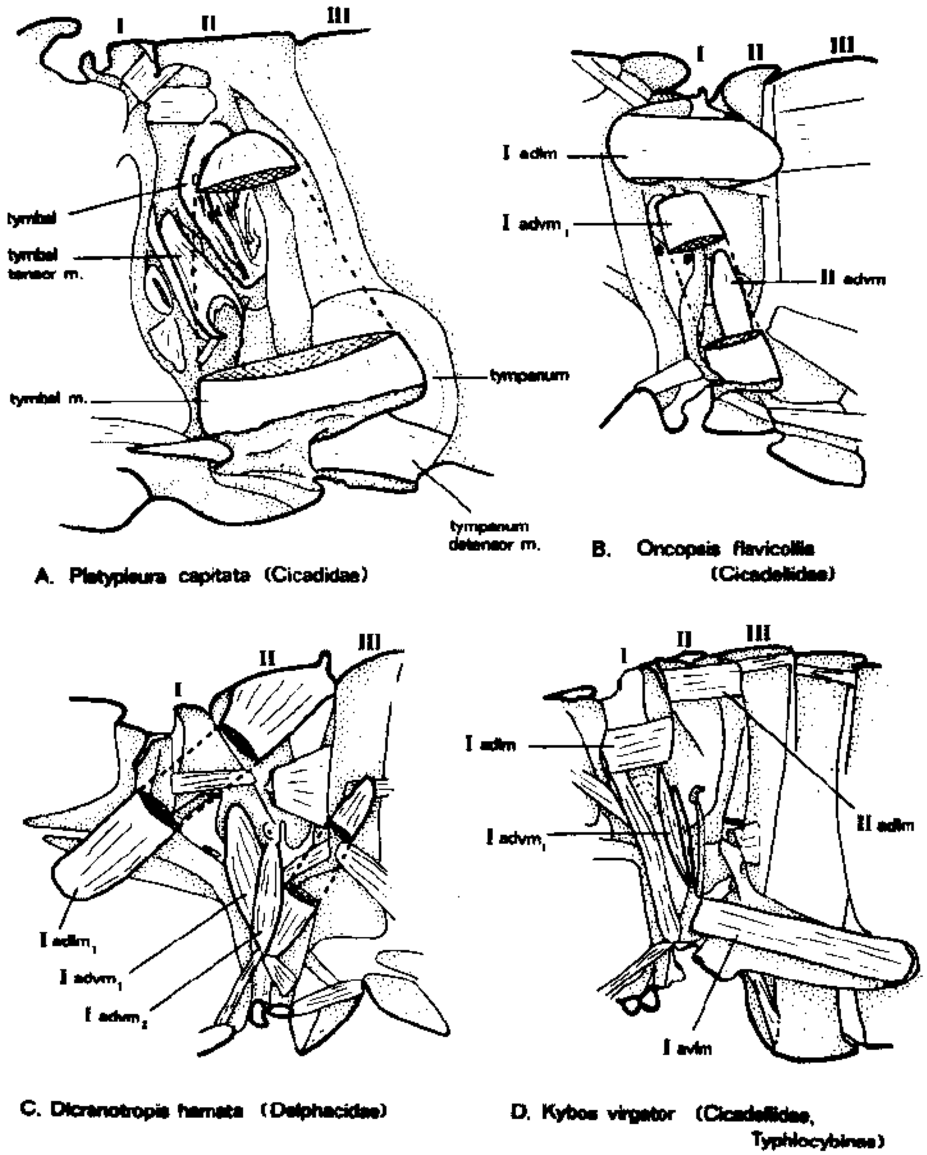
The mechanism of sound production in cicadas has been widely studied and recently reviewed (10). A specialized region of thin cuticle, usually traversed by a series of sclerotized ribs, the tymbal, is alternately distorted and relaxed by an underlying muscle, the tymbal muscle. This results in a series of clicks, or discrete sound pulses, which may be repeated at distinct pulse repetition frequencies and which often may be grouped into complex temporal sequences. In cicadas the males alone produce sounds and possess a pair of tymbals dorsolaterally on each side of the first abdominal segment. Internally the large tymbal muscles attach dorsally to the tymbal membranes and midventrally to sternal apodemes. Additional accessory muscles, including particularly the tymbal tensor muscles, may modify the call by changing the tension in the tymbal. Also in male cicadas a pair of large air sacs are associated with the tymbals and are tuned to resonate at the natural frequency of vibration of the tymbal. It is these air sacs that are primarily responsible for the very loud and penetrating calls that some cicadas produce. A diagrammatic representation of the mechanism in a typical cicada is given in Fig. 5.1A.

Descriptions of the sound producing mechanisms in Auchenorrhyncha other than cicadas are found particularly in the studies of Ossiannilsson (42). The only more recent works are the detailed investigations of Smith and Georghiou (54) on the beet leafhopper, *Circulifer tenellus* (Baker), and of Shaw and Carlson (53) on the potato leafhopper, *Empoasca fabae* Harris. Here only a general account of the variety of mechanisms can be given. No fully convincing physiological account of the sound producing mechanism in a leafhopper or planthopper has yet been published.

Ossiannilsson found dorsolateral striated "tymbals" to be present on the first abdominal segment in only a few species, but many others had specialized areas of thin cuticle in the same positions. No doubt it is the lack of an obvious external homologue to the cicada tymbal in most species that misled early workers into believing that no similar mechanism was present. Internally, both dorsally and ventrally, specialized and enlarged apodemes or phragmata are commonly found associated with the metathoracic and first and second abdominal segments. The development of different apodemes, associated with large dorsal and/or ventral longitudinal muscles, is characteristic of particular families and genera (Figs. 5.1B, C, and D). Often closely related species may differ in the degree of development and shape of particular apodemes. Recent monographs on leafhoppers and planthoppers have used these structures widely in diagnosing species (e.g., Ossiannilsson, 43).

In addition to the enlarged longitudinal muscles, certain dorsoventral muscles are also well-developed in the region of the first and second abdominal segments. In particular, in the first abdominal segment of species studied, a pair of muscles arise ventrally and insert dorsolaterally in the region of specialized cuticle that resembles a tymbal. This muscle Ossiannilsson termed *Ia* dvm_1. In many species other such pairs of muscles are present both in the first (Ia dvm_2, etc.) and the second segment (IIa dvm). Ossiannilsson suggested that Ia dvm_1 was probably homologous with the tymbal muscle of cicadas (Fig. 5.1). More importantly he suggested that the mechanism functioned in much the same manner as that of a cicada. Muscle Ia dvm in most species might, by alternate contraction and relaxation, produce the basic series of clicks or pulses characteristic of all calls. The nature of these pulses and their rates of repetition and patterning might be affected by other dorsoventral and longitudinal muscles, in a manner analogous to the functioning of the tymbal tensor muscles of cicadas. No leafhoppers are known to possess enlarged air sacs associated with the tymbal apparatus, so characteristic of cicadas (47).

Unlike cicadas, females of many species of planthoppers and leafhoppers possess tymbal sound producing mechanisms similar to their males, though usually they are less specialized. However, some females, including the brown planthopper, *Nilaparvata lugens* (Stål), lack a tymbal apparatus and in these



A. **Platypleura capitata** (Cicadidae)

B. **Oncopsis flavicollis** (Cicadellidae)

C. **Dicranotropis hamata** (Delphacidae)

D. **Kybos virgator** (Cicadellidae, Typhlocybinae)

Fig. 5.1 Diagrammatic lateral views, as seen from midline, to show musculature and internal skeletal structures associated with the sound producing mechanism of males of four species of Auchenorrhyncha (not to same scale). See text for explanation of terminology. [(A) after Pringle (47); (B), (C), and (D), after Ossiannilsson (42).]

sound production is usually accompanied by obvious dorsoventral vibrations of the abdomen (22, 25, 26). Normally this does not result in contact with, or percussion of, the substrate. The vibrations are apparently transferred to the plant through the legs and perhaps sometimes also through the feeding stylets, which may be inserted during calling. It must be assumed that the substrate transmitted elements of the signals of forms with a tymbal mechanism must also be transferred to the plant in a similar manner.

Both males and females of cicadas have large tympanic organs situated ventrally in the first abdominal segment, which function as sound receptors for the loud airborne signals produced only by males (Fig. 5.1A). Pringle (47) showed originally that in male cicadas a muscle, the tympanum detensor, associated with the tympanal membrane, functions to deactivate the organ while the insect itself is singing. It thus serves to avoid self-inflicted damage caused by the high intensity tymbal sounds. In the primitive cicada, *Tettigarcta tomentosa* White, no such tympanal organs are present (48). Similarly, no obvious auditory organs have been reported in any other families of Auchenorrhyncha. Assuming that sound signals are transmitted through the air by these insects, a variety of different potential receptors have been suggested (21), but no conclusive evidence has been presented. Alternatively, if the sounds of these smaller species are transmitted via the substrate, then any of a variety of internal chordotonal sensilla in different parts of the body might serve as vibration receptors.

5.3 MEDIUM OF SOUND TRANSMISSION AND METHODS OF RECORDING

In recent years some of the most exciting discoveries in the field of insect behavior have concerned the nature of acoustic signaling in small insects (3). For purely physical reasons of size, small insects would have to use very high frequency sounds in order to communicate through the air over distances of more than a few times the length of their own bodies (36, 37). However, in structurally diverse environments, high frequency sounds are not suitable for long-range communication because of scatter, reflection, and interference. Thus, for insects such as leafhoppers and planthoppers, which live in complex habitats dominated by plants, these antagonistic factors operate against efficient acoustic communication through the medium of air. However, such problems may be overcome by making use of the totally different properties of sound transmission in other media. Leafhoppers and planthoppers spend most of their lives on their food plants, which thus provide not only food, but also the substrate on which they live. Many different groups of insects are now known to use signals transmitted via a plant substrate in order to communicate, sometimes over distances of more than a meter (2, 35, 37, 63). Though Ossiannilsson (42) suggested that substrate transmitted signals might be involved, Ichikawa and colleagues were the first conclusively to demonstrate the importance of such signals for intraspecific communication in planthoppers and leafhoppers (22–26). They worked with pests of rice, including the brown planthopper, *Nilaparvata lugens*, the small brown planthopper, *Laodelphax striatellus* (Fall.), the white-backed planthopper, *Sogatella furcifera* (Horv.), and the green leafhopper, *Nephotettix cincticeps* (Uhler). In studies on *N. lugens*, these workers were able to demonstrate the all important nature of substrate transmission by studying communication between insects on separate potted plants. When the foliage of such plants was in physical contact, communication took place. However, as soon as the pots were moved so that the plants were just not in physical contact, communication ceased, though insects were observed to continue signaling. Other studies have since confirmed the importance of substrate transmitted signals in these families (4, 10, 12–15, 58–61, 63, 64). No unequivocal demonstration of the significance of airborne sounds in the communication of leafhoppers and planthoppers is known. However, so few species have been adequately studied that it is probably premature to generalize, but the problems involved with aerial transmission are theoretically so great (36, 37, 63) that the plant substrate must be regarded as the dominant medium of transmission for leafhopper and planthopper calls.

In his pioneering studies on the sounds of leafhoppers and planthoppers, Ossiannilsson (42) enclosed insects in a small cage with a microphone, the whole insulated against outside sounds, and was able to detect low intensity emissions as airborne sounds. Subsequent workers developed similar techniques, often going to great lengths to enclose the recording chamber in sound proofing material and to increase amplification. Notable among these workers was Strübing and colleagues (55). She was the first to produce good quality tape recordings and to analyze them with an oscilloscope. Other workers used these techniques on a variety of different species (16, 17, 39, 49, 52).

With the realization that the acoustic signals produced by leafhoppers and planthoppers were largely transmitted via a plant substrate, new and simpler techniques of recording were developed. Ichikawa and co-workers (22–26) first used a crystal gramophone cartridge as a transducer to pick up sounds of the brown planthopper in rice stems. This simple technique has now been used by others (4, 13–15, 28, 29, 58–61). In practice the stylus of a gramophone cartridge is brought lightly but firmly into contact with the plant on which the insects under study are calling. The output from the cartridge is then fed into a simple preamplifier, monitored by headphones, and recorded, preferably at a tape speed of 38 cm/sec. This technique has the advantage of being inexpensive and of reducing the need for elaborate sound proof enclosures.

An even better method of detecting substrate vibrations in plants is by the use of an accelerometer, such as the Brujel and Kjaer 8307 (Fig. 5.2). This is even less sensitive to airborne sound than the gramophone pickup and has a more linear response. Unfortunately, the accelerometer and required charge amplifier are both more expensive. Satisfactory results from a behavioral viewpoint may be obtained with either technique.

Most recently, techniques of laser vibrometry have been used to record vibrational sounds of various Hemiptera living on plants (37). Such techniques greatly reduce the load placed on the plant by the recording apparatus and make refined analyses possible but may be too expensive and impractical for most workers.

In order to play back recorded calls into a plant, Claridge and co-workers (12, 14) modified a small loudspeaker from a transistor radio by removing the paper cone and attaching a fine needle to the moving coil. The loudspeaker was then enclosed in a perspex casing, which allowed the needle to vibrate freely. The needle may be brought into contact with a plant on which an experimental insect is placed and the call can be played back from a tape recorder. The playback and any acoustic responses from the living insect may be monitored by headphones (Fig. 5.2). Such a simple apparatus produces very low levels of airborne sounds.

5.4 ACOUSTIC SIGNALS AND THE BEHAVIOR OF LEAFHOPPERS AND PLANTHOPPERS

The known calls of leafhoppers and planthoppers consist of trains of damped pulses repeated at characteristic rates and in distinctive temporal patterns, in which they often resemble the much louder calls of cicadas. Thus the most useful method of analysis for such signals is with an oscilloscope or other oscillographic apparatus. A disadvantage of the cathode ray oscilloscope is that it needs to be used in conjunction with a cumbersome and specialized camera. A direct printing apparatus is preferable. We have found an ink-jet oscillograph, such as the Siemens Mingograph, is particularly useful. The Kay Electric Co. sound spectrograph also may be used as a direct printing device (16, 39), but it does not give as much or as precise information as an oscillograph (Fig. 5.3). Since there is no indication that frequency modulation plays

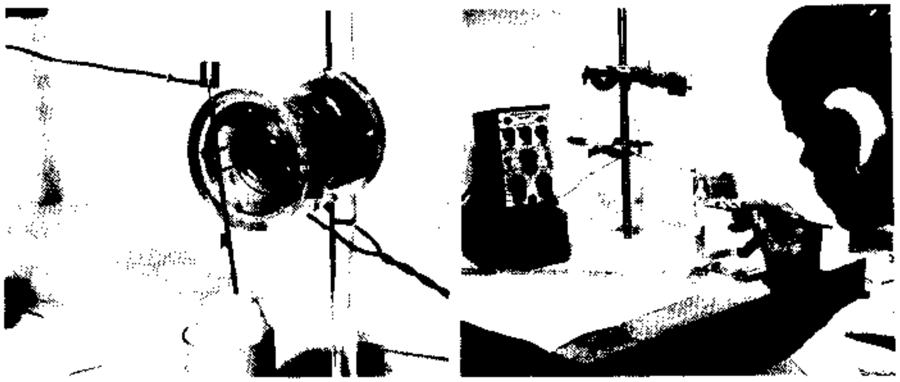


Fig. 5.2 Apparatus used to detect and play back substrate transmitted signals of *Nilaparvata lugens* on a small rice plant (detail at left). The accelerometer is attached to the top of the plant. A modified loudspeaker used for playback of calls makes light contact with the stem. See text for details.

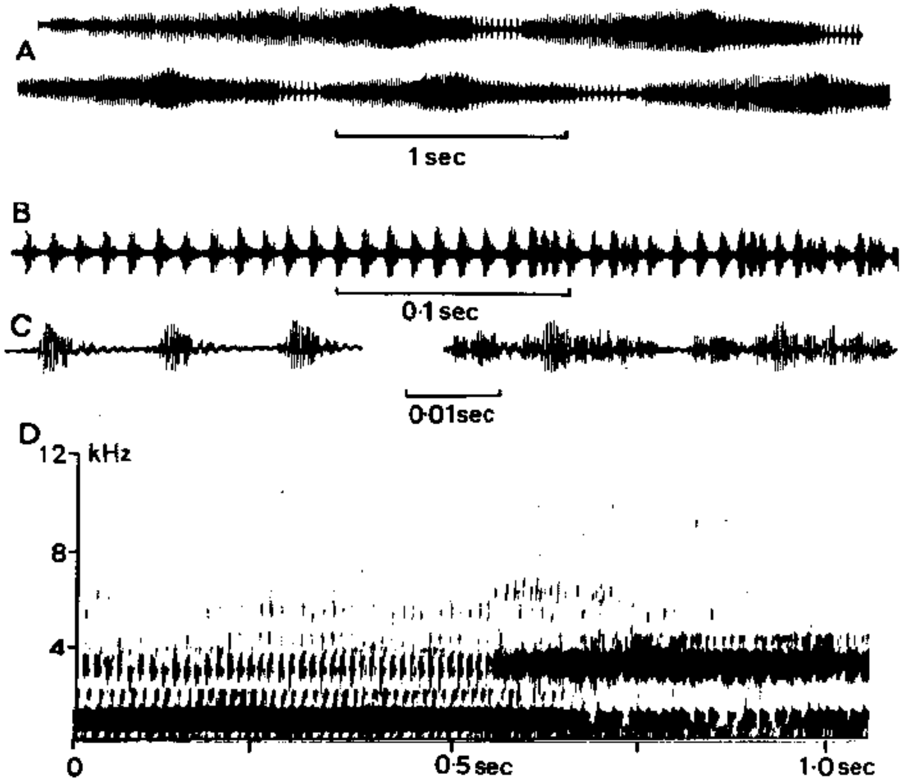


Fig. 5.3 Comparisons of (A) slow oscillogram, (B) and (C) fast oscillograms, and (D) spectrogram of part of same male call of the leafhopper, *Oncopsis flavicollis*. [After Claridge and Howse (16).]

any role in communication between these insects (10), there is no advantage to using a spectrograph.

Ossiannilsson (42) first suggested that particular species might produce different acoustic signals in different behavioral contexts. Very few complete studies on the roles of acoustic signals in the behavior of any leafhopper or planthopper have been made, but several have shown that some species have a wide repertoire of calls (4, 16, 24, 51, 52). It is generally agreed that the most distinctive signals are usually produced in the behavioral context of pair formation and most studies have concentrated on these (10). Such signals are often termed *calling songs* since they usually result in movements of individuals of one sex towards the other.

In *N. lugens* both sexes produce characteristic signals (12, 13, 15, 22–26). Sexually mature males and often also females call spontaneously on their food plants. Responsive insects reply by emitting their own signals and acoustic exchanges ensue during which males move about actively (Fig. 5.4). Such exchanges usually end with a male making contact with a female. There is presently no evidence that the male obtains any directional information from the call and orients in response to the female. Rather it seems that female calling releases spontaneous and random searching movements by males. However, Saxena and Kumar (51) suggested recently that males of the leafhopper *Amrasca devastans* (Dist.) may obtain some directional information from the calls of females. Similar exchanges of calls between males and females have been reported for many species (4, 23, 28, 42, 52). The patterns of amplitude modulated calls of leafhoppers and planthoppers may be complex and species specific. Groups of closely related species usually have distinctly different calls. This is shown by male calls of European species of the planthopper genus *Javesella* (64) (Fig. 5.5). Other examples include, among leafhoppers, species of *Oncopsis* (16, 17), *Euscelis* (56, 57, 59–61, 63), and *Nephotettix* (9, 28, 29, 66), and among planthoppers, species of *Muellerianella* (4) and *Nilaparvata* (14).

Fig. 5.4 Oscillogram of exchange of calling signals between male and female of *Nilaparvata lugens*. [After Claridge and co-workers (12).]

In addition to the distinctive grouping of pulses that characterize all species which have been adequately studied, different parts of calls may show consistent differences in rates of pulse repetition, or pulse repetition frequency (PRF). Some workers have measured PRF and other temporal variables of

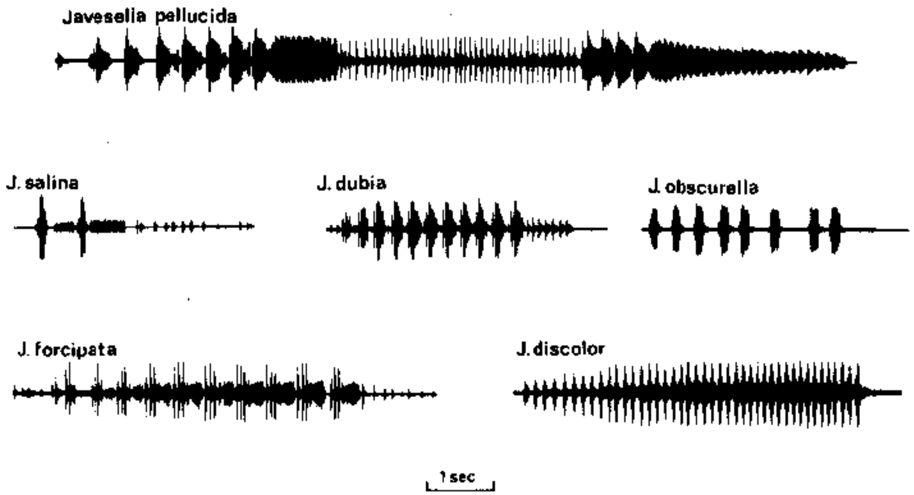


Fig. 5.5 Oscillograms of male calls of six species of *Javesella* (Delphacidae). [After de Vrijer (64).]

calling songs. Species of *Oncopsis* in Britain have characteristic PRF for male calls, even when the basic patterns of the calls are similar (17) (e.g. *O. carpini* and *O. avellanae* in Fig. 5.6). Booij (4) made a detailed study of the calls of three species of *Muellerianella* and showed some significant differences in PRF.

Female calls are generally much simpler than those of males of the same species and often consist of regularly repeated pulses, with little or no elaborate superimposed temporal patterning. Thus, the female call of *N. lugens* from rice consists of sequences of regularly repeated pulses. A closely related species associated with the weed grass, *Leersia hexandra* Swartz, produces a similar call, but at less than a third of the PRF of the rice species (14) (Figs. 5.9 and 5.10). Similar, less complicated, but species-specific female calls have been described for species of *Muellerianella* (4) and *Nephotettix* (28, 29, 66) (Fig. 5.8).

It has been suggested that patterning of amplitude modulated pulses embodies meaningful information to which conspecifics may respond. Until recently there was little experimental evidence for this. In a study of geographical variation in the male calls of *N. lugens*, Claridge and co-workers (13) showed that a population from the Solomon Islands differed significantly in mean PRF from another population from Queensland, Australia. Furthermore, it was suggested that the difference was responsible for behavioral incompatibilities observed during hybridization experiments between the same populations. A series of crosses were made between the two populations, and, for those crosses that were successful, male calls were recorded. Calls of successful males were then compared with those of a random sample of males from their own population. Successful Australian males in crosses with Solomon Islands females were found to be significantly lower in PRF than the mean for their own population, that is, significantly nearer to males of the Solomon Islands population. On the other hand, successful Solomon Islands males, in crosses with Australian females, were found to be significantly higher in PRF than the mean for their own population, that is, they more closely resembled Australian males in this feature (Fig. 5.7). This clearly indicates the importance of PRF in the communicative function of planthopper calls.

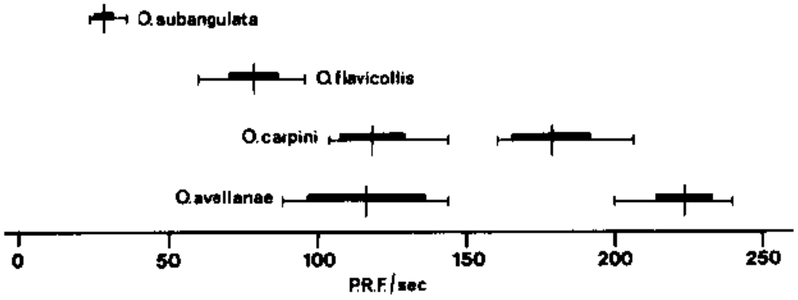


Fig. 5.6 Pulse repetition frequencies (PRF) of male calls of four British species of *Oncopsis*. Main phases only shown for *O. subangulata* and *O. flavicollis*, phases 1 and 2 for *O. carpini* and *O. avellanae*. Vertical lines represent population means, solid black horizontal lines one standard deviation on each side of the mean, and thin horizontal line total range of individual means. [After Claridge and Reynolds (17).]

Additional evidence for the role of PRF in the communication of these planthoppers was obtained by playback of recorded signals of two closely related species, presently both called *N. lugens*, and associated respectively with rice and *L. hexandra* (14). Both males and females were shown to respond to the recorded calls of the opposite sex of their own species very significantly more than they did to those of the other. Thus, there can be little doubt that PRF is an important factor giving specificity to the signals of planthoppers and leafhoppers.

Booij (4) and de Vrijer (personal communication) have shown that a number of variables in the calls of both *Muellerianella* and *Javesella* are subject to temperature effects. Thus PRFs may vary, depending on temperature. No experiments have been conducted to test the effect of this on communicative functions. However, it is probable that receptors sensitive to such sound patterns may show similar temperature responses and thus call specificity may be maintained. In tropical populations of *N. lugens* we have been unable to demonstrate much effect of temperature on calls. The insects generally call over a relatively narrow temperature range. At low temperatures, no calling is produced and at high temperatures the insects become very active and similarly do not call or show any obvious response to other individuals.

5.5 SPECIES AND SPECIES RECOGNITION SIGNALS

All leafhoppers and planthoppers feed on green plants and many show extreme host specificity. Their taxonomy is often difficult and species identification usually relies on small differences in the male genitalia. Many species are important crop pests and it is thus often especially important to have a real understanding of the status of different populations and of the genetic inter-

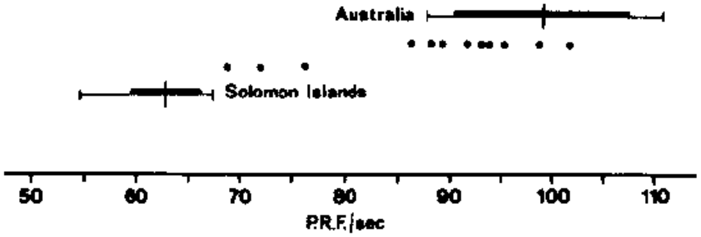


Fig. 5.7 Pulse repetition frequencies of male calls of samples from populations of *Nilaparvata lugens* on rice from Australia and the Solomon Islands. Solid dots represent PRF of individual males that were successful in crosses with females of the other population. Other conventions as in Fig. 5.6. See text for details. [After Claridge and co-workers (13).]

relationships between them (11). In this context the biological species concept, as first clearly elaborated by Mayr (34), is vital. Here different biological species are seen as representing distinct and separate gene pools, which do not exchange genes, or do so so rarely as not to affect the integrity of each other. Species of bisexually reproducing organisms are characterized by distinctive behavior patterns that serve to bring conspecific males and females together for mating. The signals involved in these behavioral exchanges may be termed *species recognition signals* (44–46). Not only do these signals serve the function of mate recognition, but also they may prevent or reduce the likelihood of interspecific matings and thus function in species isolation. They are what Mayr termed *premating isolating mechanisms*.

In order to recognize the true limits of biological species, it is important to study species recognition signals (1, 8, 9, 17). That is, we should attempt to identify the signals that the insects themselves use. These are the only characters that ultimately will enable us to differentiate groups of closely related species with certainty. In the Auchenorrhyncha, such species recognition signals are dominantly acoustic (10). Thus, the study of such signals may be critical in determining the specific status of different populations.

In a long series of studies, Strübing (56, 57, 59–61) and colleagues pioneered the use of acoustic signals to clarify the status of difficult groups, with particular emphasis on the genus *Euscelis*. In this genus genitalic structures are highly variable and their final form is influenced by environmental factors such as day length and temperature (40). On the other hand, acoustic signals show little or no such variation.

In the genus *Oncopsis*, two forms of doubtful status, *O. flavicollis* (L) and *O. subangulata* (Sahl.) both occur in Britain, often in mixed populations, on the same *Betula* host plants. The two differ in variable and rather slight characteristics of the male genital apparatus. Acoustic studies revealed them to be distinct species (17) (Fig. 5.6). In addition, recent work has demonstrated that what was previously thought to be a polymorphism in *O. flavicollis*, really represents three separate biological species (Claridge and Nixon, in preparation). Similar studies on the genera *Empoasca* (52) and *Macrosteles* (49) have also made possible the recognition of sibling species.

The leafhoppers, *Nephotettix virescens* (Dist.) and *N. nigropictus* (Stål), illustrate another type of problem. They are both widely distributed in Asia and Australasia where they may be important vectors of rice tungro virus. The two species are usually clearly separable on the basis of color patterns. In field samples small numbers of morphologically intermediate individuals are sometimes found, and it has been suggested that they might be naturally occurring, interspecific hybrids (50). Both male and female calls show clear differences between the two species (Fig. 5.8). Yusof (66) obtained true hybrids by laboratory crossing experiments and showed that the calls of F_1 hybrids were very variable and different from either parent (Fig. 5.8). Most individual hybrids showed some recognizable elements from the calls of both parental species. When field caught "intermediate" individuals were recorded, in all examples the songs were found to be either of *N. virescens* or *N. nigropictus* type, but not hybrids. Thus, acoustic techniques can be used to test the validity of morphological taxonomy. In the *Nephotettix* example it is clear that the use of color pattern to discriminate between the two related tropical species is not always adequate.

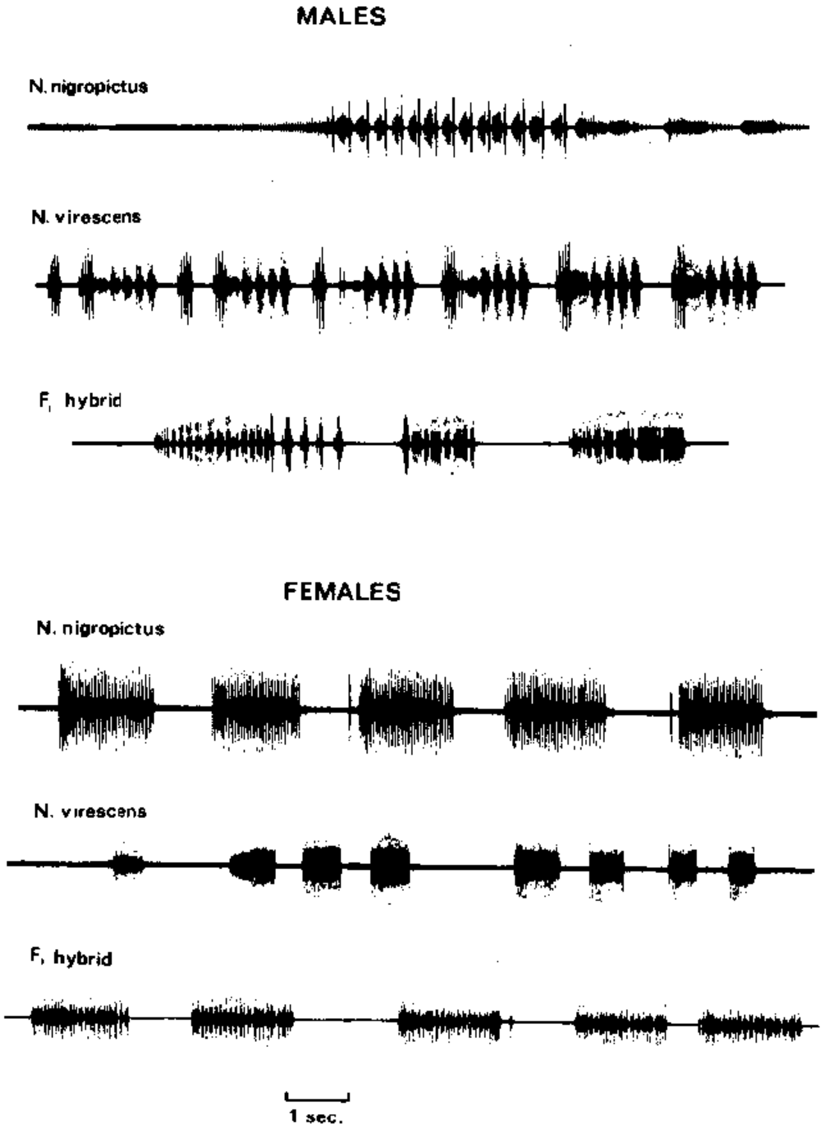


Fig. 5.8 Oscillograms of male and female calls of the leafhoppers, *Nephotettix virescens* and *N. nigropictus*, and of F_1 hybrids between them.

The Delphacidae have been studied similarly. Booij (4) made a thorough analysis of the acoustic behavior of *Muellerianella* species in Europe. He established beyond doubt the existence of three distinct biological species, *M. fairmairei* (Perr.), *M. extrusa* (Scott), and *M. brevipennis* (Boh.), where previously only one or two were recognized. The three differ clearly in male calling songs. Subsequently, small morphological differences in the male genitalia were found to differentiate the three biological species.

The calls and acoustic behavior of three rather distantly related planthopper pests of rice in Japan, *N. lugens*, *L. striatellus*, and *S. furcifera*, have been described by Ichikawa and colleagues (23, 26). These differ quite distinctly from each other in pulse patterns. Within the species *N. lugens*, populations have recently been identified in the Philippines that live and breed on a common weed grass of irrigation and drainage channels, *L. hexandra*. Otherwise, *N. lugens* is regarded as specific to wild rices (*Oryza* species) and their cultivars (38). Mate choice experiments with the two sympatric host associated populations show total preference for homogametic matings (14), though hybrids may be obtained in no choice experiments. The calling signals of males and females of both populations are similar in pulse patterning, but differ significantly in PRFs (Figs. 5.9 and 5.10). Thus, we have concluded that the two host plant associated populations are distinct, but very closely related sibling species. We have not yet been able to find any consistent morphological differences between them.

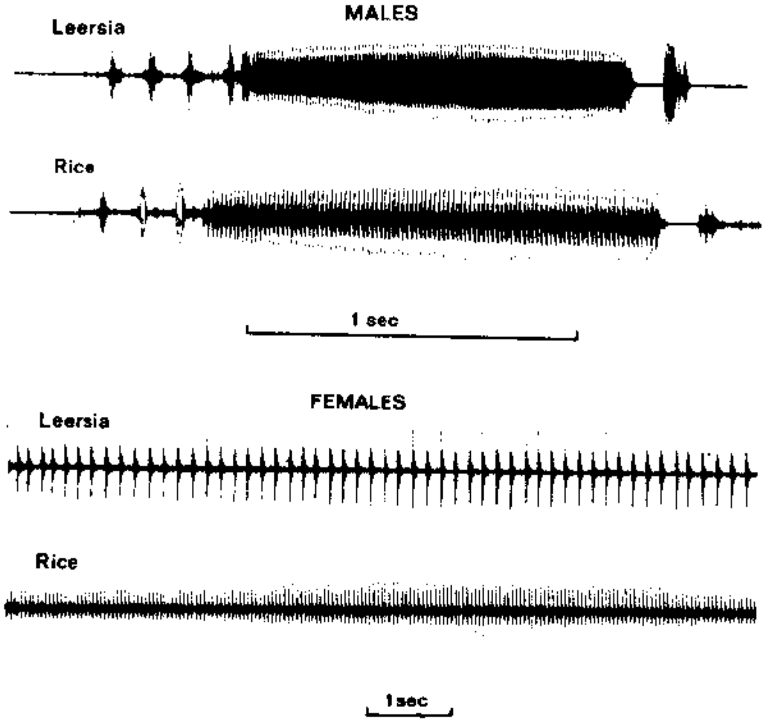


Fig. 5.9 Oscillograms of parts of male and female calls of *Nilaparvata lugens* from rice and from the weed, *Leersia hexandra*. [After Claridge and co-workers (14).]

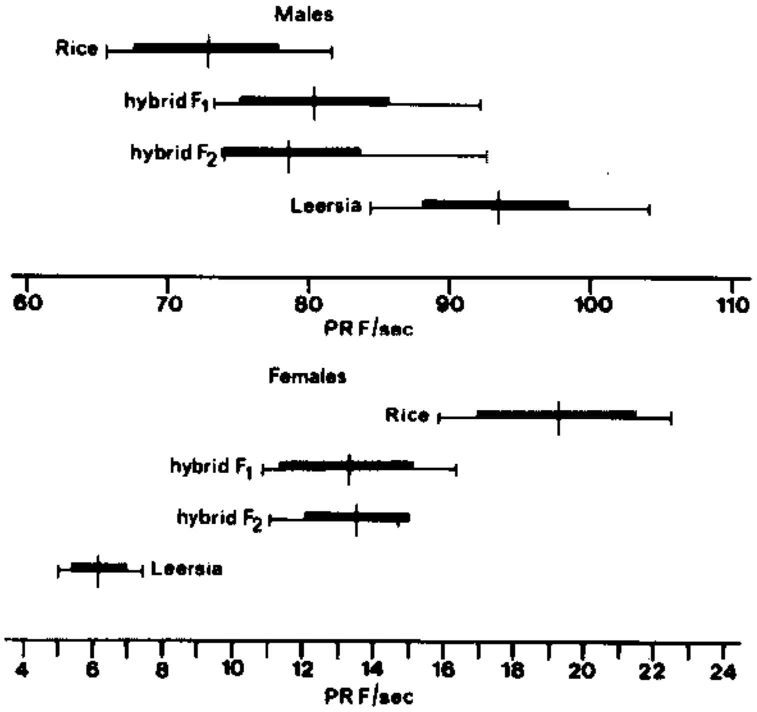


Fig. 5.10 Pulse repetition frequencies of male (above) and female (below) calls of rice feeding and *Leersia* feeding species of brown planthopper and F_1 and F_2 hybrids between them. Conventions as in Fig. 5.6. [After Claridge and co-workers' (14).]

It is clear that the study of acoustic signals has enormous potential for understanding variation in natural populations of leafhoppers and planthoppers.

5.6 VARIATION IN ACOUSTIC SIGNALS AND SPECIATION

Currently there is considerable controversy about processes by which insects, and especially parasitic and plant feeding species, may have evolved and diversified. The theories that embrace what is usually called *geographical speciation*, as advocated by Cain (7), Dobzhansky (19), Mayr (34), and others, all require some period during which an ancestral population is divided into at least two allopatric isolates. At least some degree of geographic, or what is better termed spatial, isolation is a prerequisite for initial divergence. This may occur by adaptation to local environments and possible chance effects within isolated subpopulations. Authors disagree as to how much genetic divergence in such populations may be necessary for subsequent speciation to be completed. Paterson (44–46) takes the view that complete speciation must be achieved in allopatry. On the other hand, Dobzhansky (19) and other recent authors such as Littlejohn (33) suggest that complete divergence may be achieved after the initially isolated populations have again become sympatric through the reinforcement of isolating mechanisms by natural selection.

A different mechanism has currently found favor with many biologists, following Bush (6, 18). Here a process of true sympatric speciation is postulated. That is, one panmictic population is seen as diverging by a slow process of adaptation to two or more separate habitats. This hypothesis has been supported especially by entomologists who work on insects with specialized host requirements, where different hosts may represent the different habitats of Bush's hypothesis. Often groups of related and morphologically very similar species are found to occur together in nature and to differ most obviously in distinct patterns of host utilization. It is tempting to conclude that host plant differentiation was a major factor in the initial origin of such groups of species. However, precise data are lacking for most groups and there are many problems associated with such hypotheses (20, 30).

It is not appropriate to discuss further the arguments about these theories here. However, in most discussions the role of isolating mechanisms in speciation has not been given sufficient emphasis. Indeed few studies are available that confront the issue of the evolution of species isolating mechanisms in plant feeding insects. This, despite the fact that, as Dobzhansky has put it, speciation consists of the evolution of species isolating mechanisms.

It is well-established that acoustic signals play a dominant role in species recognition, and therefore in premating isolation, in most groups of Auchenorrhyncha (10). Because of the ease with which it is possible both to rear many leafhoppers and planthoppers in the laboratory and also to record their calls, they are ideal animals for studying the evolution of species isolation. Unfortunately, to date few studies have been published on variation within and between populations of these insects.

Booij (4) described geographical variation in different parts of Europe for some variables of call structure in the planthoppers, *Muellerianella fairmairei* and *M. brevipennis*. Some allopatric populations of these species differ significantly in call characters, but no studies on hybrids between any of the populations have been published. Similarly, in the leafhoppers, *N. virescens* and *N. nigropictus*, there is evidence of geographical variation in calls in populations from different parts of Asia (66).

Perhaps the best studied example is that of *N. lugens*. This insect is widely distributed in south and southeast Asia, northern Australasia, and western Oceania. We have studied samples from 19 widely scattered localities over this range (12, 15) (Fig. 5.11). PRF of the main phase of male calls was measured under standard conditions for samples of each of these populations. Different populations were found to be characterized by particular ranges of variation (Fig. 5.12). Some differed significantly from others. Populations from the northern parts of mainland Australia were especially distinct in this characteristic. Laboratory experiments showed that the greatest problems in hybridization occurred between populations that differed most in male PRF. Remarkably, when hybrids were obtained between some divergent populations, they seemed to be completely fertile with no problems in producing apparently normal F_1 and F_2 generations and with no obvious sex ratio anomalies. It thus appears that the populations are genetically very closely related and that they differ mainly in call characteristics. Most importantly, recordings of F_1 and F_2 hybrid males were intermediate in PRF between the parental populations (Fig. 5.13), demonstrating a strong element of heritability to these characters. Thus, it is clear that divergence of species recognition calls in this species may take place in geographically isolated populations in advance of other major genetic differentiation. This is contrary to the ideas advocated by Paterson (44–46), who suggests that specific mate recognition signals will be strongly buffered against change by stabilizing selection and may only diverge very slowly following other genetic differentiation.

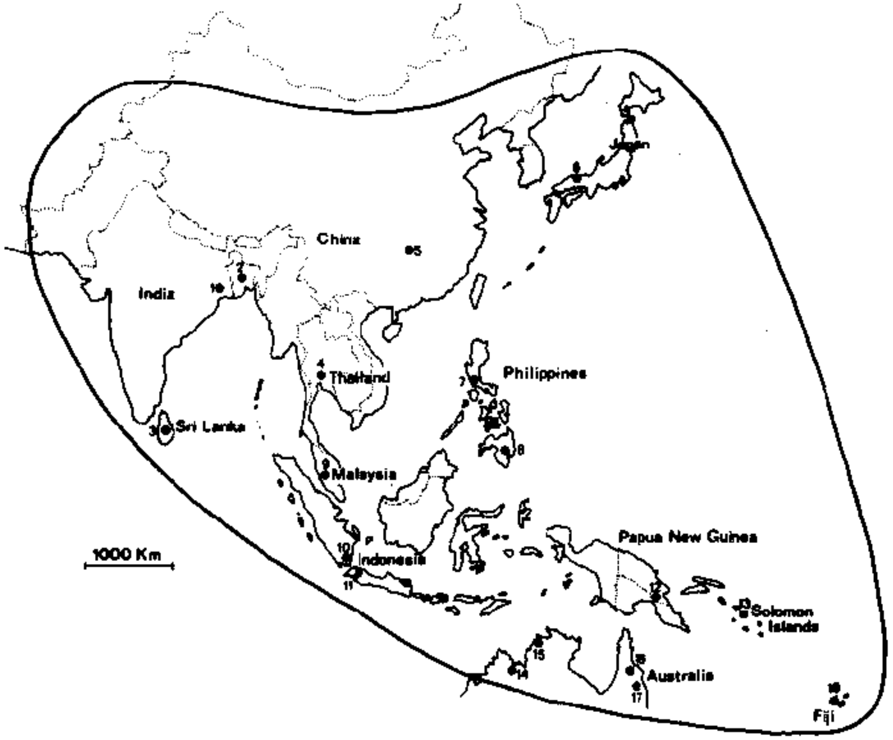


Fig. 5.11 Map of Asia and Australia to show area of distribution of *Nilaparvata lugens*, outlined by solid line. Localities from which sample populations were studied by Claridge and co-workers (12) are numbered.

N. lugens is well-known for its ability to adapt to different cultivars of rice

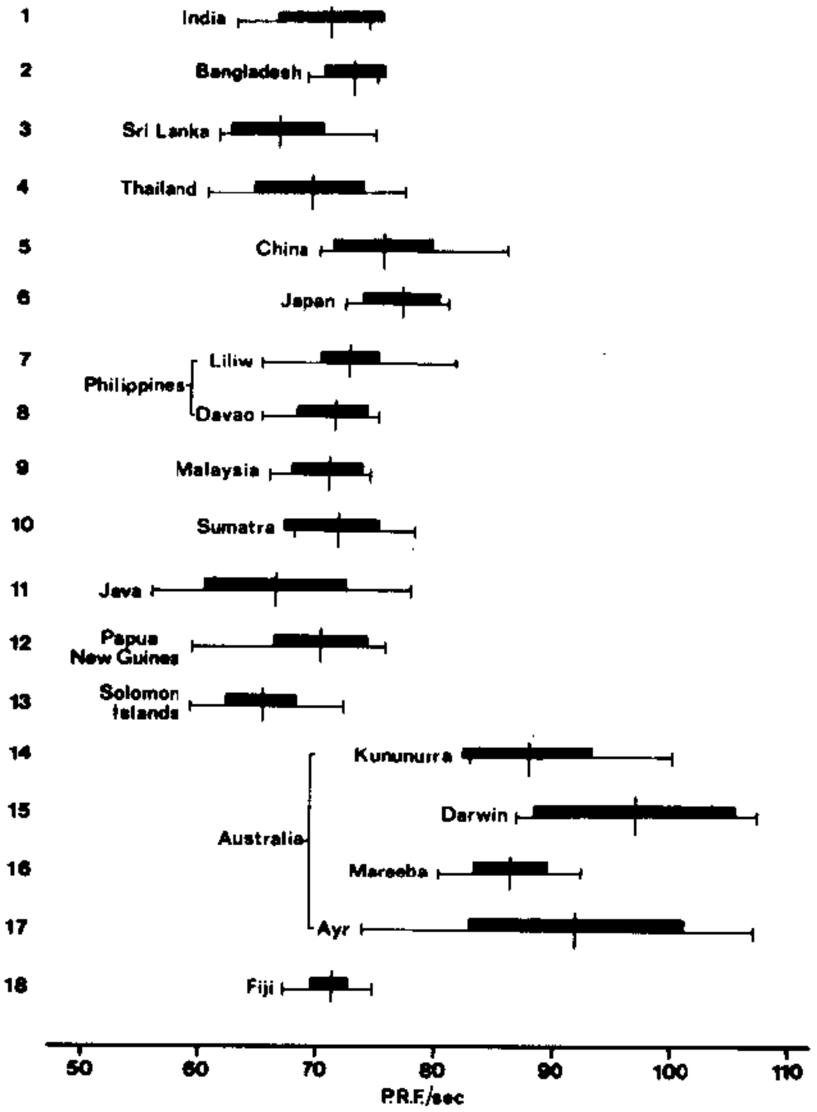


Fig. 5.12 Pulse repetition frequencies of populations of *Nilaparvata lugens* from 18 localities numbered as in Fig. 5.11. Conventions as in Fig. 5.6. [After Claridge and co-workers (12).]

and such adapted populations are often termed *biotypes* (11). It has been suggested that such sympatric biotypes may represent host races at an early stage in the process of sympatric speciation (Wilson and Claridge, chapter 16). We have found no evidence for any major genetic differences between such biotypes or for the differentiation of species recognition signals and mating barriers between them (12).

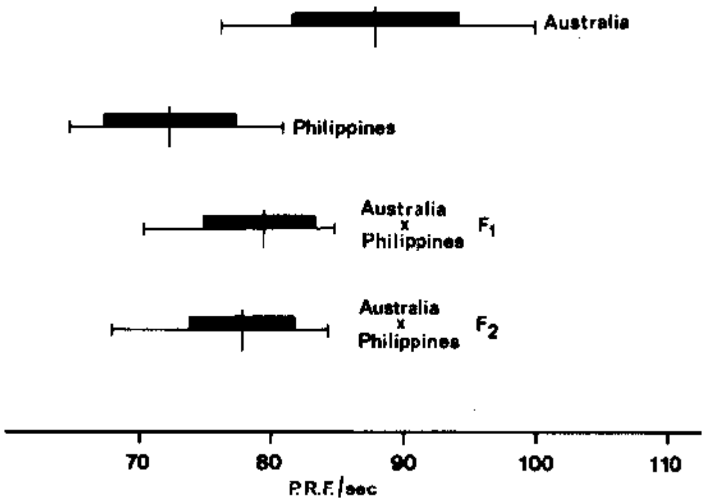


Fig. 5.13 Pulse repetition frequencies of male calls of rice feeding *Nilaparvata lugens* from Autralia and the Philippines, and of F_1 and F_2 hybrids between them. Conventions as in Fig. 5.6. [After Claridge and co-workers (12).]

The recently discovered populations of *N. lugens* in the Philippines associated with *L. hexandra* are also regarded by some workers as a new biotype or host race. However, as described above, Claridge and co-workers (14) have shown them to be a sibling species, distinct from the rice-feeding species. Undoubtedly, the acoustic differences between these two very closely related species are inherited and represent a major difference between them. It would be wrong to emphasize only the host plant differences between the two.

Thus, present evidence suggests that acoustic species recognition signals may vary between allopatric populations. Also, published studies have so far failed to identify any sympatric host races or biotypes that might represent intermediate stages in a process of sympatric speciation. The available and very limited evidence is consistent with some form of allopatric speciation. More evidence of this kind is urgently needed and leafhoppers and planthoppers are ideal animals for such studies.

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