THE BROWN PLANTHOPPER, NILAPARVATA LUGENS (STÅL), AND SOME RELATED SPECIES: A BIOTAXONOMIC APPROACH

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ABSTRACT

Sixteen named species from the major tropical regions of the world have been attributed to the genus Nilaparvata. Limited host data for some African and Asian species suggest a close relationship with rice (Oryza species and their cultivars) and related weed grasses, particularly species of Leersia. N.lugens (Stål) is a major pest of rice in Asia and Australasia. N.maeander Fennah has been recorded from cultivated rice in Nigeria. N.bakeri (Muir) and N.muiri China are associated with Leersia in Asia where they are widely sympatric with N.lugens. Behaviour and hybridisation studies are revealing a complex of sibling species and geographical races within the morphospecies N.lugens. The biological nature of these populations has been obscured by the use of the blanket term "biotype" without adequate genetic study. Courtship signals confirm the species status of N.bakeri, N.muiri and N.maeander.

INTRODUCTION

To the cynic the term biotaxonomy (or biosystematics) may mean nothing more than an attempt by taxonomists to achieve scientific respectability. More realistically the current popularity of the term indicates a growing awareness among biologists of the need to understand the nature of variation both within and between natural populations of living organisms. Nowhere is the need greater than in the study of insect pests of agriculture (see Claridge & Den Hollander 1983).

The genus Nilaparvata is known to applied entomologists almost entirely because of the one species, N.lugens (Stål) the rice brown planthopper, which, since the early 1970's, has become one of the most important pests of irrigated rice in Asia (IRRI 1979). At the first workshop in this series we reported on the then available information on variation in N.lugens and its so-called biotypes (Claridge et al. 1983). In the intervening years a major discovery has been that of populations morphologically apparently indistinguishable from N.lugens, but feeding and reproducing on the weed grass, Leersia hexandra Schwartz. These populations from the Philippines were designated by us as a separate biological species, distinct from the sympatric rice feeding form (Claridge et al. 1985), but others regard it as a biotype of N.lugens (Saxena et al. 1983). This problem has led us to attempt a wider biological treatment of these and related species. The present paper reports on the beginnings of such a biotaxonomic review.

METHODS OF BIOTAXONOMY

The main aim of biotaxonomic studies, as we understand them, is to determine the genetic status of groups of related organisms. It is therefore based on the biological species concept as elaborated by Mayr (1942), Cain (1954), and others. This concept emphasises genetic isolation in the field between different sympatric species. This isolation allows such species to maintain and develop their distinctive characteristics which would otherwise be swamped by

hybridization. Species are thus genetically isolated units which may also differ one from another in distinct morphological characteristics, but equally may not. Genetic isolation is the most important criterion for establishing species status.

In order to determine the genetic status of different populations, many different techniques may be used. We shall mention only some which are particularly applicable to the Auchenorrhyncha.

1. <u>Hybridization experiments</u> in the laboratory allow some estimate of genetic differentiation between populations to be made. If hybrids are sterile or of low viability, then it is unlikely that natural hybridization will be important in the field and therefore it is probable that the two populations represent different species. However, if apparently fertile hybrids can be produced in the laboratory, it is difficult to draw meaningful conclusions. In nature such hybridisation either may not occur or may be so rare as not to affect the separate gene pools of the two forms.

2. <u>Mate choice experiments</u> give some of the best experimental data on species status (see Claridge <u>et al</u>. 1984, 1985a, 1985b). Here a female of one population is given a choice between mating with a male of its own population or with one from the test population. Reciprocal tests may also be made giving males a choice of females. Such data are amenable to statistical analysis and may give very good indications of field behaviour.

3. <u>Premating ethological isolating mechanisms</u> are signals which are exchanged during courtship and by which conspecific males and females recognise each other. The term isolating mechanism was first used by Dobzhansky (1937) and has been widely used since by evolutionists for a variety of pre- and post-mating differences between related species. The term presupposes that such differences between species have evolved as responses to other species and have the function (in the sense of Williams, 1966) of species isolation. Though such premating "mechanisms" clearly do serve to prevent interspecific hybridisation, there is considerable controversy as to the role of natural selection in their evolution. Paterson (1985 for review) suggests that they function primarily as specific mate recognition signals and that species isolation is only an incidental property. This is not the place to pursue this controversial and important idea. However, in practise these characteristics of premating behaviour provide major species differences, and, when adequately investigated, give some of the most valuable information on the genetic status of populations. Thus for practical purposes we may regard premating behavioural isolating mechanisms as being effectively what Paterson terms "specific mate recognition signals".

Following the pioneering work of Ossiannilsson (1949), it is now clear that acoustic signals generally transmitted through the plant substrate are of great importance in the specific mate recognition systems of most, if not all, leafhoppers and planthoppers (Claridge 1983, 1985a, 1985b). Thus, the recording and analysis of such signals, which may be relatively simple, provides important biotaxonomic information. In the species <u>N.lugens</u> there is strong evidence that pulse repetition frequency of calls is an important factor giving specificity to the signals (Claridge <u>et al</u>. 1984).

4. <u>Host plant relations</u>. Unlike the preceding categories of information, differences between populations in host plant preference and utilisation are not necessarily concerned in the processes associated with mating and mate choice. Nevertheless, such characteristics may often be of major economic importance in the case of pests and are always of ecological significance in any example. Experimental manipulation of populations on different hosts and choice

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experiments thus also provide valuable biotaxonomic data.

Obtaining precise host records for leafhoppers and planthoppers in field habitats is a difficult problem. The relevance of data obtained simply from adult collections is difficult to assess. Grasses and herbaceous plants generally grow in complex and inter-mixed communities so that sweep net or suction sampling cannot give precise host records. In addition 'host plant' is a very vague term. It is important at least to differentiate between 1. plants on which adults will alight and possibly feed, 2. plants on which eggs may be laid, and 3. plants on which immatures will develop from 1st instar to reproductive adult. As Mochida & Okada (1971) stressed, it is the third of these possibilities which is generally most important. It is also necessary to emphasise that oviposition plants may not always be the same as suitable nymphal food plants, and that species may alternate hosts at different seasons (see Claridge & Wilson 1978). Thus, patterns of host plant utilisation may be very complex even in one species and can only be elucidated by careful field work and laboratory rearing.

5. Comparative studies of any kind provide potentially useful information and may come from a variety of disciplines. Techniques which certainly provide valuable data are electrophoresis, chromosome morphology, comparative behaviour studies, etc., in addition to traditional methods of comparative anatomy.

Only by a combination of all these types of study is it possible to be confident of the genetic relationships of allied forms.

THE GENUS NILAPARVATA

Sixteen described species, distributed primarily in the major tropical regions of the world are now attributed to Nilaparvata Distant (Table 1). Mochida & Okada (in IRRI 1979) listed 14 named and two undescribed species. Huang Chi-lin et al. (1979) described two further new species from China. Most of these forms are known only as morphospecies and are clearly separable on a basis of characters of the male, and sometimes also of the female, genitalia. Many are described and figured by Hasigawa (1955),Okada (1977) and Mochida & Okada (1979).

The host plant relations of most species are not known. N.lugens is generally agreed to be restricted to wild and cultivated rices of the genus Oryza in Asia and Australasia. Mochida & Okada (1971) give species of the related genus Leersia as major hosts in Japan for N.bakeri (Muir) and N.muiri (China). N.maeander Fennah has been recorded recently as a pest of rice seed beds in Nigeria (Alam et al. 1983).

Ichikawa and his colleagues (1974, 1975) were the first to record the acoustic signals of males and females of N.lugens and to show that they differed from the two other common Delphacid pests of rice in Japan, Sogatella furcifera (Horvath) and Laodelphax striatellus (Fallén). These workers suggested that the calls functioned as important premating isolating mechanisms.

Here we report studies on N.lugens and the status of its so-called "biotypes", and also some preliminary studies on N.bakeri, N.muiri and N.maeander.

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TABLE 1

Checklist of described species attributed to the genus <u>Nilaparvata</u> in alphabetical order according to major geographical regions.

Asian and Australian species

<u>N.albotristriata</u> (Kirkaldy, 1907)
<u>N.bakeri</u> (Muir, 1917)
<u>N.castanea</u> Huang & Ding, 1979
<u>N.chaeremon</u> Fennah, 1974
<u>N.lineolae</u> Huang & Ding, 1979
<u>N.lugens</u> (Stål, 1854)
<u>N.muiri</u> China, 1925
<u>N.myersi</u> Muir, 1923
<u>N.seminula</u> Melichar, 1914

African species

<u>N.angolensis</u> Synave, 1959
<u>N.camilla</u> Fennah, 1970
<u>N.diophantus</u> Fennah, 1958
<u>N.maeander</u> Fennah, 1958
<u>N.nigritarsis</u> Muir, 1926

American species

<u>N.caldwelli</u> Metcalf, 1955
<u>N.wolcotti</u> Muir & Gifford, 1924

N.LUGENS: BIOTYPES AND SIBLING SPECIES

Rice feeding populations

N.lugens has been recorded as a pest of cultivated rice widely in Asia and Australasia (IRRI 1979, Claridge et al. 1983). It has become particularly important since the early 1970's with the development and widespread cultivation of high yielding dwarf varieties and the greater use of nitrogen fertilisers and pesticides. A major strategy for control is that of breeding resistant cultivars: work which was pioneered and still continues at the International Rice Research Institute (IRRI), Philippines (see IRRI 1979, Heinrichs et al. 1985). The field release of varieties with known genes for resistance led to the evolution of virulent populations of the planthopper which were able to damage previously resistant cultivars. Such populations have been widely termed biotypes and categorised by a system of numbering. They differ from each other primarily in their distinctive patterns of virulence in mass screening tests (Table 2).

The nature of these biotypes is a subject of controversy. The term biotype is itself confusing, since it has been used to refer to various distinct biological phenomena, as different as sibling species, geographical variants, individual morphs in a polymorphic population, etc. (see Claridge & Den Hollander 1983). Perhaps it would be wise to follow the advice of Diehl & Bush (1984) who suggest "that future application of this term (biotype) be restricted to use as a temporary and provisional designation for cases where biological differences have been observed between organisms but where the genetic basis and evolutionary status of the differences have yet to be ascertained."

Our own studies on the three biotype populations from IRRI suggest that they

are genetically closely related populations which have adapted to rice varieties with particular genes for resistance (see Table 2) (Claridge & Den Hollander 1982). Selection experiments show that one biotype population may be converted to another under laboratory conditions after about 10 generations on an appropriate host plant (Claridge & Den Hollander 1982, Pathak & Heinrichs 1982).

TABLE 2

Possible biotypes of N.lugens, using the IRRI system of numbering, with some traditional and modern IRRI rice varieties susceptible to each, listed together with associated nomenclature and dominance status of resistance genes in the plants (after Claridge & Den Hollander 1982).

| Biotype | Rice cultivars | | Resistance gene |
	Traditional	Improved	
1	TN1	IR8	None identified
2	Mudgo	IR26	Bph 1 (dominant)
3	ASD7	IR36, IR42	bph 2 (recessive)
4	Rathuheenati	IR56	Bph 3 (dominant)
5	Babawee	–	bph 4 (recessive)

We thus suggested that the IRRI biotypes differ biologically only in their characteristic patterns of virulence and show little evidence of other genetic divergence. However, Saxena and co-workers at IRRI have consistently claimed greater genetic differentiation between these biotype populations, which they suggest represent stages in the speciation process. Most particularly they have studied morphometric differences, which they claim clearly identify each biotype (Saxena & Rueda 1982, Saxena & Barrion 1985). We recently confirmed that it is possible to separate the IRRI biotypes by multivariate techniques when reared on their normal host cultivars (Claridge, Den Hollander & Haslam 1984). However, when all three were reared on the same susceptible variety, TN1, after only one generation no significant difference was found between them (Figure 1). Thus we suggest that the differences reported by Saxena & Rueda are predominantly environmentally induced and do not represent major genetic differentiation. In their recent review, Saxena & Barrion (1985), though citing our paper, ignored our new data and made no attempt to counter this compelling evidence.

It has to be emphasised that most studies on N.lugens biotypes have been made on the IRRI cultures. These themselves were originally established from local field collections in Luzon and have been inbred for many generations since the early 1970's, since when they may have developed differences due to founder effects, drift, selection, or a combination of these processes, within the culture systems. It is thus extremely dangerous to generalise from work on these cultures to field populations, even in the Philippines. Nevertheless, the biotype numbering system has been extended not only to field populations in that country, but also to populations with similar virulence patterns elsewhere in Asia. Indeed, Saxena & Rueda (1982) suggested that the morphometric characters identified by them in the IRRI biotype cultures could be used to identify field populations in other regions with the same virulence characteristics. As yet they have published no data to validate this suggestion.

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Thus N.lugens is a very labile species in virulence characteristics and is, therefore, capable of rapid adaptation to new host cultivars. This is particularly well illustrated by our study on six populations collected from different rice varieties within a small geographical area of Sri Lanka, none separated from each other by more than 200 km (Claridge et al. 1982). Each population differed significantly from all others in virulence characteristics and was best adapted to the rice variety from which it was collected. It would not be very helpful to give each one of these populations a separate biotype designation.

Recently reported populations virulent to IR36 in Mindanao, southern Philippines, further illustrate the problems involved. Medrano & Heinrichs (1985) showed that these field populations, when tested at IRRI, were not biotype 3, as expected. In fact they combined virulence characteristics of both biotypes 2 and 3. Similar problems of field identification of biotypes were reported earlier in Taiwan (Cheng & Chang in IRRI 1979). Medrano & Heinrichs (loc.cit.) concluded that the Mindanao populations probably represent a new and different biotype! A better conclusion might be that the system of numbering biotypes is not helpful when studying field populations.

Thus though there certainly are some major differences in patterns of virulence in different parts of Asia (Seshu & Kaufman 1980, Claridge et al. 1983), a specific biotype terminology, whether by naming or numbering, is likely to be misleading and to cause unnecessary problems to field workers.
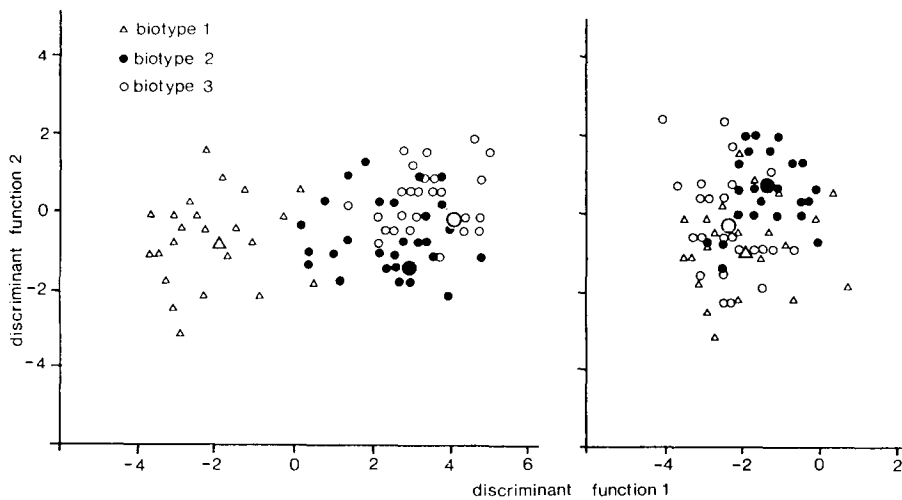

Figure 1.   Plots of discriminant function 1 against discriminant function 2 for canonical analysis of morpnometric characteristics of the IRRI biotypes of N.lugens.   Biotype 1 on iN1, biotype 2 on Mudgo and biotype 3 on ASD7 (left), and biotypes 1, 2 and 3 all on TN1 (right) (after Claridge, Den Hollander & naslam 1984).

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Irrespective of virulence characteristics we have demonstrated some genetic differentiation between geographically separate (allopatric) populations of N.lugens from rice in Asia and Australasia (Claridge et al. 1985a). Hybridisation studies and analyses of courtship signals both indicated some geographical differentiation. This was most marked when comparing Australian populations with Asian ones. Indeed it could be argued that these allopatric forms should be regarded as different biological species. However, since they are entirely allopatric it is not possible to be certain of their status.

Weed feeding populations

As noted above, populations indistinguishable from N.lugens have been collected and reared on the grass Leersia hexandra in the Philippines (Medrano & Heinrichs 1982, Domingo, Heinrichs & Saxena 1983, Heinrichs & Medrano 1984). When tested in mate choice experiments with sympatric rice feeding insects, we found that each population showed an absolute preference for mating with its own type (Claridge et al. 1985b). In addition, significant differences were found between male and, most obviously, female courtship signals (Figure 2). In the laboratory it was possible to obtain hybrids between the two forms. These were intermediate in song characters between the parental populations. For the females, there was little overlap in pulse repetition frequencies of the three songs (Figure 3). We have recorded numerous field samples of insects from the Philippines and have found no evidence of hybridisation. On a basis of these results we conclude that the two host associated forms of N.lugens in the Philippines must be regarded as separate biological species.

On the contrary, Saxena et al. (1983a) considered the Leersia -feeding populations as "a non virulent biotype of N.lugens". They regard the differences between these populations then as of no greater significance than those separating the IRRI biotype populations. Thus there is a major and worrying difference of opinion about the nature of these populations. Saxena & Barrion (1985) have most recently repeated their views on the nature of these host associated forms, without any reference to our findings. They presented no data on mate choice or courtship signals and thus, in our view, have not made adequate studies to substantiate their suggestion, based mainly on morphometric and host plant data.

Since the original discovery of Leersia-feeding populations in the Philippines, Sogawa et al. (1984a, 1984b) have noted them from Sumatra (Indonesia) and we have collected insects from Sri Lanka and Australia. Analyses of the acoustic signals of insects from Sri Lanka show them to be very similar in PRF to those from the Philippines (Figure 3). It thus seems that this sibling species is widely distributed in Asia.

Leersia associated insects from Queensland, Australia, are very interesting and also show significant differences from sympatric rice feeding insects. However, in addition they also differ clearly from the Philippine Leersia feeding insects. Further studies are currently in progress on this fascinating and complex story and will be published elsewhere.

Conclusions

We thus conclude from our studies on the morphospecies N.lugens in Asia that it consists of at least two widely sympatric biological species, one associated with Oryza species and cultivars and one with Leersia hexandra. The major distinguishing features of these two very similar species lie in their acoustic signals. Within the geographic range of the better known rice-feeding species some geographical divergence is detectable on a basis of acoustic signals and
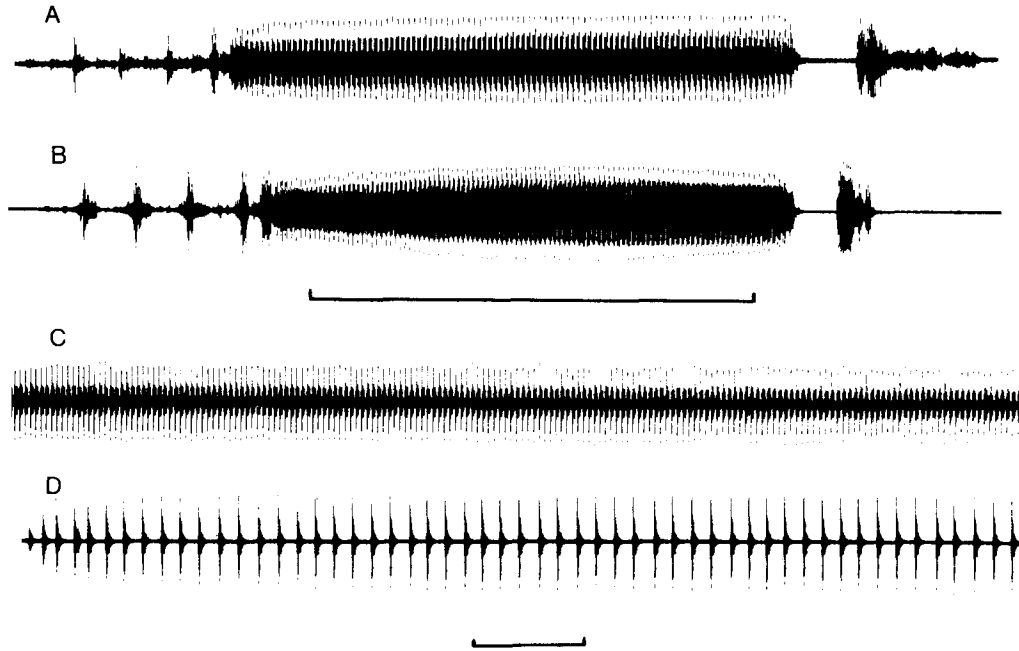
Figure 2.   Oscillograms of typical signals of males (A and B) and females
(C and D) of N.lugens from rice-feeding population (A and C) and Leersia-
feeding population (B and D) from the Philippines.   Time marks 1 second.
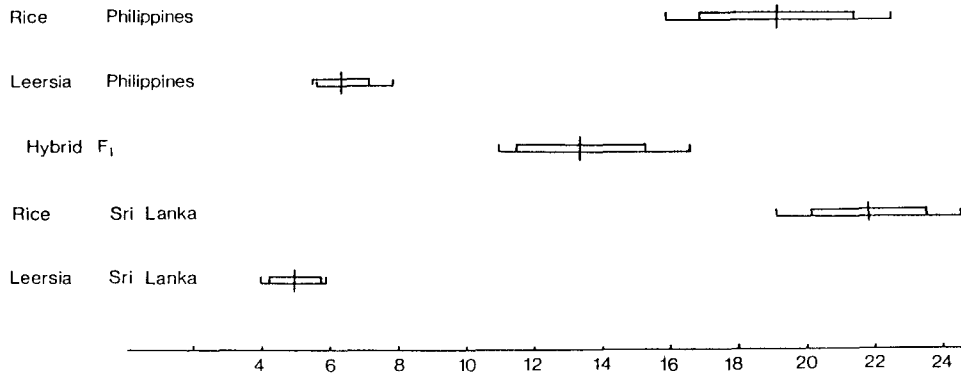(after Claridge, Den Hollander & Morgan 1985b).

Figure 3.   Pulse repetition frequencies per second (PRF) of female calls of
rice-feeding and Leersia-feeding populations of N.lugens from the Philippines
and Sri Lanka, and hybrids between the two from the Philippines.   Vertical
lines represent means for each sample, thick bars one standard deviation on
either side of mean, thin bars total ranges (after Claridge, Den Hollander &
Morgan 1985b).

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hybridisation experiments. However, virulence to rice cultivars is exceedingly variable and does not provide a good indicator of general genetic differentiation.

Thus the rice associated biotype populations from IRRI which have been so intensively studied are quite different in order of magnitude of differentiation and evolutionary status to the sympatric Leersia associated populations. It is extremely misleading to use the term biotype for all of these populations, as suggested by Saxena & Barrion (1985).

The status of the allopatric populations of N.lugens in Australia are more difficult to determine. The better known rice feeding populations are clearly differentiated from all others from Asia and even from such neighbouring areas as Papua/New Guinea, Fiji and the Solomon Islands (Claridge et al. 1985a). The acoustic differences between the Leersia feeding forms from Asia and Australia, so far as known, are also great and the relative status of these allopatric forms from the same hosts is not clear. Within Australia, the rice and Leersia feeding forms, though less clearly separated on acoustic grounds than the similar Asian ones, appear to be separate biological species with no indication of natural hybridisation (Claridge, Den Hollander & Morgan, in preparation).

It is thus clear that, even though much more work remains to be done, the morphospecies N.lugens consists of a complex of biologically differentiated populations distributed over a wide area of Asia and Australasia. However, it is certain that simply giving any population which can be differentiated in some way from others the status of a new biotype, does nothing to help in our understanding of the true biological nature of the diversity of these forms.

THE STATUS OF OTHER MORPHOSPECIES: N.BAKERI AND N.MUIRI

In Asia the species N.bakeri (Muir) and N.muiri (China) are relatively well known. N.muiri appears to be a more northern form, recorded from China, Japan and Korea. It has also been found in northern Luzon, Philippines. N.bakeri is more widely distributed, being known from much of tropical Asia in addition to more temperate regions in Japan and Korea, where both occur on species of Leersia (Mochida & Okada 1971). In the Philippines, N.bakeri is known to feed and breed on L.hexandra (Saxena et al. 1983b). These authors also recorded laboratory hybridisation between N.bakeri and Leersia feeding N.lugens. We have collected N.bakeri from L.hexandra in the Philippines, Indonesia and Sri Lanka and have populations from these three regions in culture in Cardiff where they thrive on L.hexandra. Similarly we have a population of N.muiri from Japan which also does well in culture on the same host.

Acoustic signals Like N.lugens, males and females of N.bakeri exchange acoustic signals during courtship. The female call consists of trains of simple, regularly repeated pulses. The male call is more complex and clearly differentiated from those of all populations of N.lugens so far studied (Figure 4). Similarly the calls of N.muiri are quite distinctive (Figure 4). Thus these signals confirm the genetic status of these three widely sympatric species, already well established on a basis of genitalial morphology.

Hybridisation We have attempted to hybridise Leersia feeding N.lugens and N.bakeri on many occasions, but always without success. We have also muted insects by applying a minute quantity of grease to the basal region of the abdomen of a living adult. Such insects were then confined with unmated individuals of the opposite sex of the other species whilst prerecorded signals, also of the other species, were played back into the plants (as described by Claridge et al. 1985a) in an attempt to deceive the insects into accepting

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A

B

C

1 s

D

E

F

1 s

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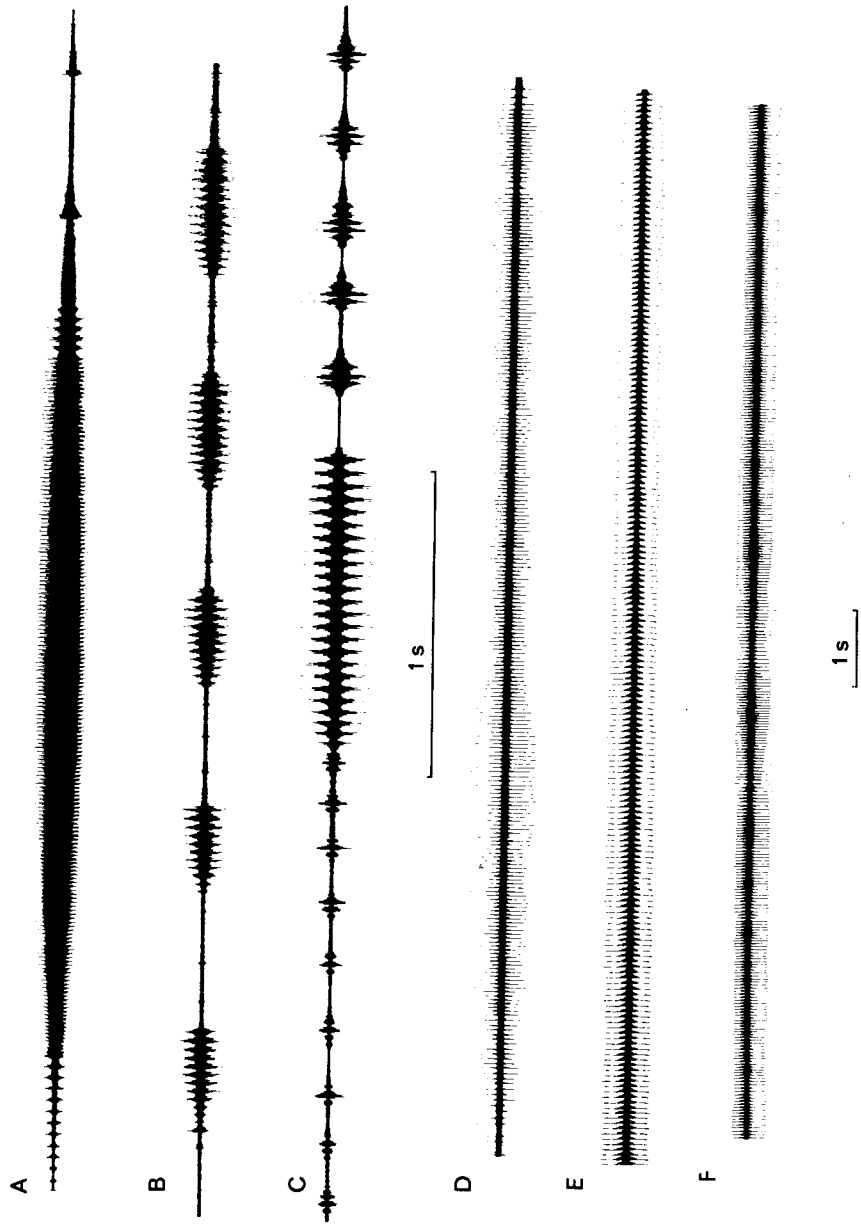
partners of the wrong species. All such experiments have so far been without success. We are therefore surprised that Saxena et al. (1983b) recorded successful hybridisation between the same species at IRRI. We are further puzzled that in all crosses these authors report that the "genitalia characters of F₁ progenies of the interspecific crosses resembled those of their respective immediate female parents." In our experience species hybrids usually produce individuals with variable and intermediate characters between the two parental species. This is well illustrated in the call characters of hybrids between the two N.lugens species feeding on rice and Leersia (Claridge et al. 1985b). Also F₁ hybrids between the green leafhoppers of rice, Nephotettix virescens and N.nigropictus, show intermediate morphological characters of the genitalia (Yusof 1978,Inoue 1986). Saxena et al. suggest a theoretical model to explain their unusual results. In view of our inability to obtain hybrids between these species after prolonged and repeated attempts, we suggest that their results might be explained by the accidental inclusion either of already mated females or of males of both species in the experimental cages. It is unfortunate that no acoustic studies were made on the supposed hybrids.

AN ALLOPATRIC SPECIES: N.MAEANDER

N.maeander has been recorded widely in West Africa (Soto & Sidiqui 1978). More recently it was noted as a pest in rice seed beds at the International Institute for Tropical Agriculture (IITA), Nigeria (Alam et al. 1983).

N.maeander has very characteristic genitalia. The distinct median pale longitudinal marking on adults of both sexes gives the insect a superficial similarity to the well known rice pest of Asia, Sogatella furcifera, the white-backed planthopper. We have reared N.maeander successfully in the laboratory on various rice cultivars and also on a wild rice Oryza rufipogon, which originated from Nigeria.

As with Asian species, so both sexes of N.maeander exchange acoustic signals during courtship (Figure 4). The male call is quite unlike any of the Asian species. Unfortunately as yet we have not been able to study any of the other African Nilaparvata.

GENERAL DISCUSSION

The view is widely held that most grass feeding insects are relatively polyphagous. Waloff (1980), in her review of studies on grassland Auchenorrhyncha in Britain, supported this idea. However, a growing number of studies are now revealing often high levels of specificity in some grassfeeding species (eg Whitcomb et al. 1986).

Undoubtedly the single best documented example is provided by the elegant studies of Nault and his co-workers (see Nault 1985) on species of Dalbulus and other closely related genera, all of which are restricted to hosts from the related genera Zea and Tripsacum in central America and the southern U.S.A. Most of these leafhoppers feed only on one or a few very closely related host species.

Figure 4 (page 28). Oscillograms of male (A-C) and female (D-F) calls of N.bakeri from Philippines (A and D), N.muiri from Japan (B and E) and N.maeander from Nigeria (C and F). Time marks 1 second.

The more limited data presently available for species of Nilaparvata, summarised above, suggest a relationship with species of Oryzeae. Indeed at present confirmed host records are only known from Oryza and Leersia and no species is known to feed on both genera. A similar pattern of host preference within the Oryzeae is shown by the Asian species of Nephotettix (Inoue 1986). This genus of course includes several important pests and vectors of virus diseases of rice in Asia.

The generally distinctive nature of the Auchenorrhyncha fauna of rice (see Wilson & Claridge 1985) is thus probably part of a more general phenomenon. Further studies on the faunas associated with wild species of Oryza, Leersia and other genera of Oryzeae are urgently needed, especially in tropical Africa and the Americas. With the ever increasing expansion of rice cultivation in tropical countries, such information may help us to understand and even to predict possible pest problems of the future.

ACKNOWLEDGMENTS

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