

THE ROLE OF ACOUSTIC SIGNALS IN THE REPRODUCTIVE ISOLATION AND SPECIATION OF PLANTHOPPERS (HOMOPTERA, DELPHACIDAE)

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Summary

Although in general the plant-borne vibration signals of planthoppers show high species specificity, it is concluded that their contribution to the reproductive isolation of species is probably low compared to the effects of differences in specific hostplant relations. Acoustic interactions are likely to be more significant in species feeding on the same hostplant. Attention is therefore now being focussed on *Chloriona* species, which all live on one hostplant species.

INTRODUCTION

The study of acoustic communication in planthoppers (Homoptera, Delphacidae) has developed over the past 15 years into a fundamental research program on insect speciation (Claridge, 1985a and b). In planthoppers acoustic communication between sexes takes place by means of low-intensity vibration signals that are transmitted through the hostplants on which the insects feed. The main function of this system of communication is found in its relationship with reproductive behaviour, such as mate recognition, mate location and courtship. A recent overview of acoustic and reproductive behaviour in planthoppers is given by Claridge & de Vrijer (1991).

The general pattern that emerges from most acoustic studies on planthoppers is that both males and females produce species-specific acoustic signals. This specificity, especially of the male signals, which are far more elaborate than the simple female calls, has been a major reason for starting comparative acoustic studies in taxonomically problematic groups in order to delimit closely related species that morphologically are difficult to separate (e.g. Booij, 1982 ; den Bieman 1986; Claridge et al, 1985b; de Vrijer, 1986). The rationale for this follows from the definition of the Biological Species Concept, which defines species in terms of interbreeding populations that are reproductively isolated from other species (Mayr 1963), and the notion that populations which differ in their acoustic signalling might

be assumed to be non-interbreeding. The study of acoustic signals in planthoppers thus seemed to be aimed at a possible key factor of their reproductive isolation.

Although acoustic studies on planthopper populations proved successful in solving various taxonomic problems, they also gave rise to a number of new and fundamental questions. It was observed that distinct species, despite their clear differences in acoustic signals, sometimes could easily be induced to crossmate under laboratory conditions (e.g. den Bieman, 1988). How then is their reproductive isolation in the field maintained, and what is the role of their acoustic behaviour in connection with this? Also, for an adequate interpretation of various patterns of acoustic differentiation between closely related populations a better understanding is required of the processes which lead to this differentiation. In other words, what is the relation between acoustic differentiation and speciation?

ACOUSTIC SIGNALS AND REPRODUCTIVE ISOLATION

The observation of successful crossmating between distinct biological species seemed to conflict with the initial expectation that their differences in acoustic signalling would form a reliable basis for their reproductive isolation. For a good understanding of a possible role of acoustic communication in the reproductive isolation of planthopper species it is necessary to first consider a few elementary aspects of their mating behaviour.

Mating behaviour

Males and females usually become sexually active within a few days after their adult ecdysis. In order to find potential mates a sexually mature male actively starts to explore his direct environment by emitting calling signals. The acoustic range of these calling signals usually is limited to a few plant parts that are in physical contact and which allow the transmission of substrate vibrations. Therefore a calling male can only be detected by a female when she finds herself within his acoustic range. As soon as a mature and still unmated female perceives a calling signal of a conspecific male, she immediately will respond by emitting her own female signal. This female response signal in turn will induce the male to start an agitated searching behaviour during which an intensive exchange of calling signals with the female can be observed. Once the male has made physical contact with the female, which all the time remains at the same spot, close range courtship behaviour begins, which eventually leads to copulation. After successful copulation females no longer are receptive to further male calling signals, and will refuse new copulation attempts. Males are capable of mating with several females in succession.

Mate selection

A male planthopper can thus only detect mature females when they respond acoustically to his calling. A male that does not receive female response calls will move on to a new site. A simple way of ensuring reproductive isolation between different species then would be achieved if females of one species do not respond to male calling signals of other species. This can be tested in playback experiments by

feeding back prerecorded male calls of one species to females of another species. Contrary to expectations, it appeared that females often respond readily to heterospecific male calls, and certainly are not as specific in their response behaviour as would be necessary to achieve reproductive isolation (e.g. de Winter & Rollenhagen, 1990)

In mate choice tests, where females are confined with both a conspecific and a heterospecific male, usually significant levels of assortative mating are observed (e.g. Drosopoulos, 1985; den Bieman, 1988). However, in such tests it is impossible to assign the observed preference for mating with a conspecific male to the effect of a particular acoustic factor in the male call. Such tests inevitably involve the use of live males, of which the acoustic activity cannot be controlled during the experiment. Apart from male-female interactions, also female-male and even male-male interactions might play a role.

Unexpected positive results were obtained in playback experiments where males were tested for their response to different female calls. Although females of all species produce calls that basically are similarly structured as regularly repeated pulse trains ('drumming'), there are usually differences between species in the duration and rate of these drumming sequences. De Winter & Rollenhagen (1990) found that males of *Ribautodelphax* responded acoustically both to conspecific and heterospecific calls, but displayed searching behaviour only after stimulation with a conspecific female call.

These results were not only unexpected because the far more complex structure of the male song seemed to offer the better possibilities for effective species discrimination, they were also in contrast with the theory that the sex with the greater parental investment, i.e. the female, may be expected to be more discriminative in mate selection. As a consequence of these results a new question presents itself concerning the explanation of why male signals in planthoppers are so much more differentiated than female signals?

ACOUSTIC BEHAVIOUR AND EVOLUTION

When discussing the evolutionary differentiation of acoustic signals in planthoppers, we have to make a clear distinction between patterns and processes. Most of what has been said about processes appears to be largely based on speculative interpretations of patterns. The various patterns of acoustic differentiation that have been described include intraspecific variation among individuals of the same population, geographical variation between isolated populations, and interspecific differences between species of various levels of evolutionary divergence.

A well studied example of geographic variation in acoustic signals of planthoppers is found in the rice Brown Planthopper, *Nilaparvata lugens*, where acoustic differentiation seems to have occurred without any further indication of major evolutionary change (Claridge *et al.*, 1985a). All populations appeared to be

interfertile, but showed various degrees of assortative mating in mate choice tests. In a recent study on a related species, *Nilaparvata bakeri*, Claridge & Morgan (*in prep.*) also found considerable geographical variation in acoustic characters, but this time without any demonstrable signs of assortative mating. It thus seems that in the absence of geneflow isolated populations may differentiate acoustically, which possibly, but not necessarily, could be seen as a first step towards the formation of new species. Yet, these patterns do not give any clue as to which processes are responsible for changing the acoustic characters of a population.

If acoustic communication in planthoppers has a function in the specific mate recognition system of a population, then, according to Paterson (1985), it will be subject to strong stabilizing selection. Paterson expects the limits of variation in acoustic signals to be narrow because of a supposedly intimate coadaptation of the sender and the receiver. The main cause for evolutionary change in acoustic signals then primarily would come from changes in environmental conditions (e.g. a shift to a new hostplant, or predation by a vibration orientated spider) to which the specific mate recognition system has to be adapted for optimal functioning and survival. Even then, however, evolutionary change can only take place through very small steps, because each adaptive change in one partner requires a corresponding change in the other partner in order to maintain the coadaptation of both. Does this mean that the various patterns of acoustic differentiation among different planthopper groups should be considered primarily the result of environmental adaptation? In any case, the geographic variation in *Nilaparvata lugens* seems to have evolved without any obvious change in environmental conditions.

An interesting alternative explanation for evolutionary change of mate recognition signals might be found in the operation of sexual selection, i.e. intraspecific social competition for mates (West-Eberhardt, 1983). The adaptability of acoustic characters, either to environmental changes or sexual selection will primarily depend on the amount of genetic variation that exists for such characters in a population. From the studies of de Winter (this issue) it became clear that genetic variation for acoustic characters in planthoppers is much larger than expected, and provides large potentials for rapid divergence.

A further theoretical explanation for the acoustic divergence of planthopper populations is based on the operation of reproductive character displacement, which brings selective advantage to aberrant songtypes that have higher chances of assortative mating. The main driving force for this process has to be provided by a reduced fitness of any hybrids formed, which implies that at least some degree of postmating isolation already must exist before reproductive character displacement can be expected to take place. This seems to be in contrast with the finding that in various planthopper groups interspecific hybrids can be obtained without any sign of reduced viability or fertility. The theory predicts further that, at least initially, interspecific differences will be larger in areas of sympatry. Such data are not available at present for planthoppers, and seem to be documented for very few acoustic insects anyhow (Walker, 1974; Ome, 1989).

ACOUSTIC BEHAVIOUR AND HOSTPLANT RELATIONS

A major factor which so far has not been considered in connection with the acoustic behaviour and reproductive isolation of planthoppers are the often very specific hostplant relations of most species. In planthoppers the hostplant does not only perform the function of food resource, but also that of communication channel. Differences in hostplant specificity of species, i.e. each species feeds only on one or a few closely related hostplant species, provide an effective way of acoustic isolation on the level of their communication channel, even if their acoustic signals were identical. Indeed, the evolution of hostplant shifts should be considered a key factor in planthopper speciation.

It thus seems that the best objects for studying a possible role of acoustic differentiation in the reproductive isolation and speciation of planthoppers are to be found in groups where speciation has occurred in the absence of hostplant shifts. A very suitable group which represents such a case is the planthopper genus *Chloriona* of which all species are exclusively feeding on the common reed *Phragmites australis*, and which currently is being studied (see also Gillham *et al.*, this issue).

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