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## Mutual Communication by Substrate Vibrations in the Mating Behavior of Planthoppers (Homoptera : Delphacidae)

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The mating behavior of three species of delphacid insects, *Nilaparvata lugens*, *Laodelphax striatellus* and *Sogatella furcifera*, was studied under laboratory conditions. It was demonstrated that both sexes of these species emitted species-specific vibratory signals perceived by the opposite sex as substrate vibrations. Most males of the three species emitted signals within five minutes after placed on a rice plant regardless of the presence or absence of other individuals. Stationary virgin females responded to male signals of the same species by performing abdominal vibration (FAV) by which signals were emitted. Males responded to female signals by moving toward females on rice plants. Males stopped moving and emitted signals immediately after female signals ceased. Thus, alternate signal emission by both sexes was continued until males came in close proximity to females. Males always emitted postcopulatory signals to which mated female partners showed no behavioral response. Normal mating behavior was performed both under fluorescent light and under darkness. In *N. lugens*, the entire process of mating behavior was observed on a sheet of thin paper without rice plants. Sexually mature virgin females responded to the playback of recorded male signals of the same species only when the signals were transmitted as substrate vibrations. Mated females and females of other species never responded to the signals. Although females emitted signals by monotonous vibration of whole abdomen (FAV), males emitted signals by vibration of specialized tymbal organs on the 1st and 2nd abdominal terga.

### INTRODUCTION

OSSIANNILSSON (1949) described for the first time about sound production in many small auchenorrhynchous Homoptera other than Cicadidae (males of 96 species out of 15 families and females of 6 species out of 5 families). He presumed males had means of finding females other than call or females had taken over the searching role in many species having mute females. He also inferred that emitted sounds were transmitted to other individuals mainly by solid substrate and to a lesser degree by the air. MOOR (1961) detected faint sounds produced by 13 species of Homoptera other than Cicadidae along with those produced by Heteroptera. It was inferred from low intensities of these sounds that primary sense stimuli in congregation, species recognition or courtship were olfactory or visual ones, and acoustic ones were secondary close-range signaling devices.

In some auchenorrhynchous Homoptera such as *Doratura stylata* (OSSIANNILSSON, 1949, 1953), *Calligypona lugubrina* (STRÜBING, 1958, 1962) and *Circulifer tenellus* (SMITH, Jr., 1971), it is known that both sexes emit faint sounds alternately at precopulation, and males approach stationary females. Sounds produced by both sexes were also detected in the leafhopper, *Euscelis ononidis* (MEBES, 1974). In the leafhopper, *Oncopsis*, undif-

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ferentiated sounds were emitted by both sexes when they were disturbed. On the other hand, only males were confirmed to produce very faint sounds just before copulation in their mating behavior (CLARIDGE and HOWSE, 1968; CLARIDGE and REYNOLDS, 1973).

Males of three species of planthopper, *Nilaparvata lugens*, *Laodelphax striatellus* and *Sogatella furcifera*, responded not to air-borne sound but to species-specific substrate vibrations (female signals) transmitted to rice plants by female abdominal vibration (FAV) of the same species (ICHIKAWA and ISHII, 1974; ICHIKAWA et al., 1975). Males placed on the stem of a rice plant exhibited a response to signals emitted by sexually mature virgin females when located on an adjacent rice plant as long as leaf blades of the two rice plants were in contact. The effective distance of signals for the three species were at least 60–80 cm.

The main purpose of this study was to clarify the mode by which females perceive males of the same species during mating behavior in *N. lugens*, *L. striatellus* and *S. furcifera*.

#### MATERIALS AND METHODS

The three species of delphacid insects used in this study have been reared with rice seedlings under laboratory conditions of  $25 \pm 1^\circ\text{C}$  and 14 hrs illumination per day. Newly emerged adults were sexed within one day after the last ecdysis prior to sexual maturation. Sexually mature adults were used in all experiments. Experiments were conducted under fluorescent light or darkness at  $25 \pm 1^\circ\text{C}$ .

Mating behavior on rice plants was observed after a male and female of the same species were respectively placed on each of two adjacent rice plants. Observations were made when leaf blades of adjacent rice plants were either detached or in contact.

Signals emitted by a single male were detected as substrate vibrations with the same methods described in a previous paper (ICHIKAWA et al., 1975). The method for the detection of signals emitted by both sexes at pre- and postcopulation is shown in Fig. 1. A male and female of *N. lugens* were released on tightly stretched thin paper disk (ca. 7 cm in diameter) in order to examine whether they perform normal mating behavior

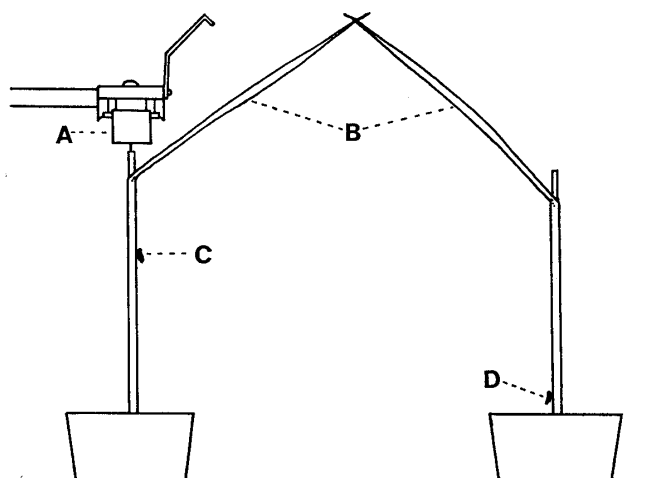


Fig. 1. Method for the detection of signals emitted by both sexes of three species of planthoppers. A, cartridge; B, rice plant; C, female; D, male.

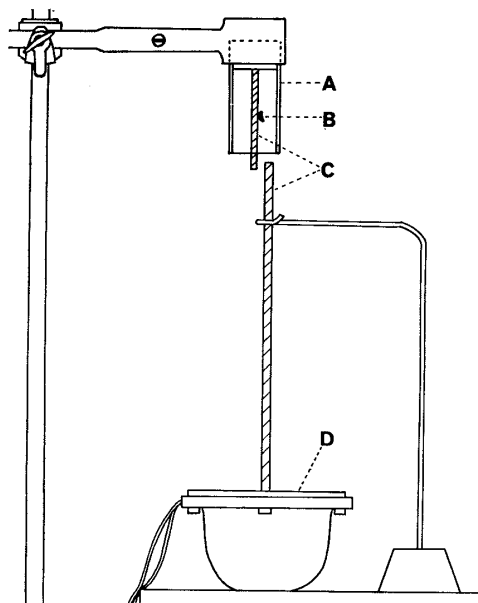


Fig. 2. Method for the examination of behavioral response of the female to the playback of recorded male signal on the rice plant. A, glass cylinder; B, female; C, stem of rice plant; D, sound speaker.

without rice plants. In all cases, detected signals were amplified electrically and monitored with a headphone (E-55, Coral Audio Corp., range of reproduced frequency, 20–20000 Hz), and the relation between the signals and behavior was examined. Wings of some of males anesthetized under  $\text{CO}_2$  were amputated at the base in order to observe body movement during signal emission. For analysis, signals emitted by both sexes of the three species were fed to an oscilloscope after recording on a sound tape as previously reported (ICHIKAWA et al., 1975).

Behavioral response of females to the playback of recorded male signals was observed on a piece of rice plant stem (Fig. 2) and on a sheet of thin paper. In these experiments, signals recorded on a sound tape were played back from a sound speaker (PC-399, Toa Electric Corp., range of reproduced frequency, 80–15000 Hz). The response of females was examined under three different conditions: 1, male signals were not played back and the two pieces of stem in Fig. 2 were detached. 2, male signals were played back at a certain level of volume (intensity was not measured) and the two pieces of stem were detached. 3, male signals were played back at the same level of volume as 2 and the two pieces of stem were in contact with each other. The response of females on the thin paper was observed under the condition that the paper was placed directly on the sound speaker throughout experiment.

## RESULTS

### *Mating behavior on rice plants*

When a male and female of the same species were respectively placed on adjacent rice plants, the female performed abdominal vibration (FAV) occasionally. The male did not show any response to FAV and remained in place when leaf blades of the two



Fig. 3. The duration of FAV (hollow rectangles) and that of male movement (solid rectangles) on two rice plants both when leaves were detached (A) and when in contact (B). 1. *N. lugens*; 2, *L. striatellus*; 3, *S. furcifer*.

plants were detached. On the contrary, when leaf blades of the two plants were brought into contact, the male responded to FAV by moving toward the female on the plant during the duration of FAV. Behavior of both sexes mentioned above was the same as previously reported (ICHIKAWA and ISHII, 1974; ICHIKAWA et al., 1975). In addition to these results, it was observed that the frequency of FAV in the three species increased conspicuously after leaf blades of the two plants were in contact with each other (Fig. 3). These results indicated that males of the three species also emitted some signals being transmitted through substrate.

After coming in close proximity to females, all macropterous males of *L. striatellus* and some macropterous males of *N. lugens* and *S. furcifer* rapidly raised their wings at times just before copulation. Except for males of *S. furcifer* which lack a brachypterous form, brachypterous males of the other two species also raised fore wings at times just before copulation.

The duration of copulation in the three species is shown in Table 1. The duration in *N. lugens* and *S. furcifer* did not exceed 3 minutes, and that in *L. striatellus* was shorter than 15 seconds. Although a few males approached females again after copulation, these females did not accept males but rejected them by violent bodily movement.

Table 1. DURATION OF COPULATION IN THREE SPECIES OF PLANTHOPPERS

Species	Combination	No. of couples	Duration of copulation (sec)
<i>N. lugens</i>	♀ B <sup>a</sup> × ♂ M <sup>b</sup>	11	90.6 ± 23.4 <sup>c</sup>
	♀ M × ♂ M	10	97.5 ± 20.4
<i>L. striatellus</i>	♀ B × ♂ M	9	6.7 ± 3.1
	♀ M × ♂ M	10	5.0 ± 1.0
<i>S. furcifer</i>	♀ M × ♂ M	10	67.4 ± 18.1

<sup>a</sup> Brachypterous form.

<sup>b</sup> Macropterous form.

<sup>c</sup> Mean ± 95% confidence limit.

*Signal emission by a single male*

Vibrations having species-specific patterns were always detected from a rice plant on which a single male was placed. Such vibrations emitted by males will be called "male signal" in contrast to "female signal" transmitted to substrate by FAV. Most males of the three species at six or seven days after the last ecdysis emitted the signals within five minutes after placement on a rice plant. Once they began emitting signals, many repeated intermittent emission of the same signal at least several times. Oscillograms of male signals of the three species are shown in Figs. 4 and 5. It was apparent from Fig. 4 that patterns of these signals were markedly different among the three species. Subunits of one complete unit of signal were indicated with a, b and c in *N. lugens* and *S. furcifera* or with a and b in *L. striatellus*. As shown in Fig. 5, wave forms of the subunits of the signals were also markedly different among the three species. Occasionally subunit c in *N. lugens* and subunit a in *L. striatellus* were not emitted. Function of these signals will be analyzed in this study.

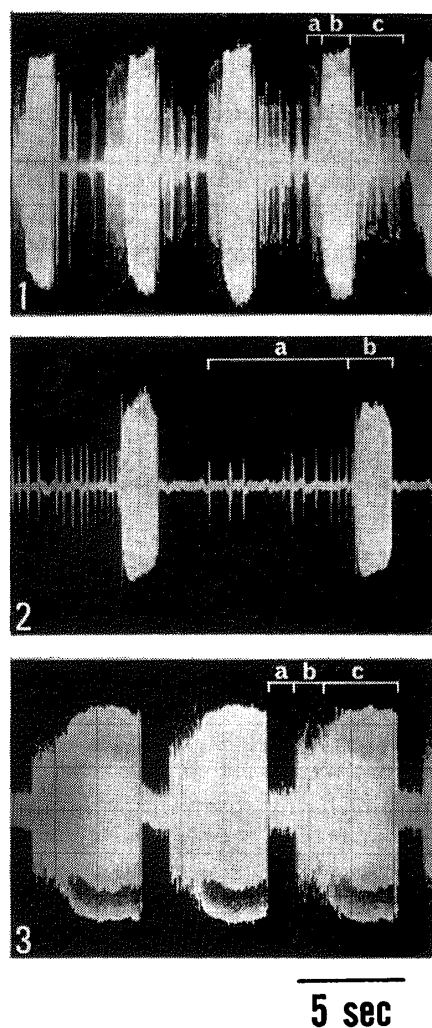


Fig. 4. Oscillograms of male signals emitted by a single male on a rice plant. Each subunit of one complete unit of the pulse pattern is indicated with a, b or c. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

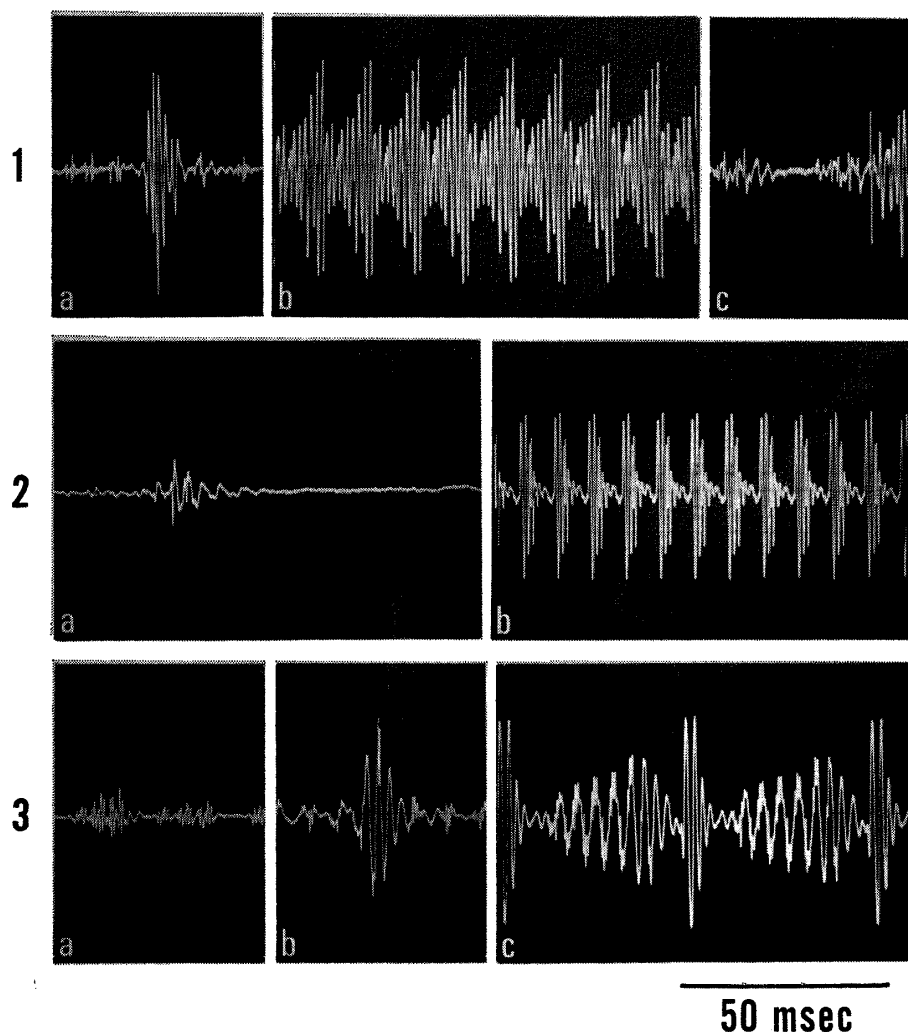


Fig. 5. Oscillograms of each subunit of the male signal emitted by a single male on a rice plant. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*. See Fig. 4 for description of a, b and c.

#### *Pre- and postcopulatory signal emission*

Signals were detected from the stem of a rice plant on which one female was placed. One male of the same species was placed on an adjacent rice plant. Leaf blades of the two plants were in contact throughout the experiment (See Fig. 1).

Males of the three species emitted signals within six minutes after placement on the rice plant. Female signals were transmitted to the plant by performing FAV just before or just after the cessation of the male signals. Movement of males toward females was observed during female signal emission. Males emitted signals without moving just after female signals ceased. Unless females responded by performing FAV, males continued to emit signals until females responded. Such alternate emission of signals by both sexes were continued until males came in close proximity to females (Fig. 6, A). Then, males emitted signals a few or several times just before copulation (Fig. 6, B).

In *N. lugens* and *S. furcifera*, wing raising just before copulation was observed simultaneously with the emission of certain parts of signals, namely, subunit c in *N. lugens*

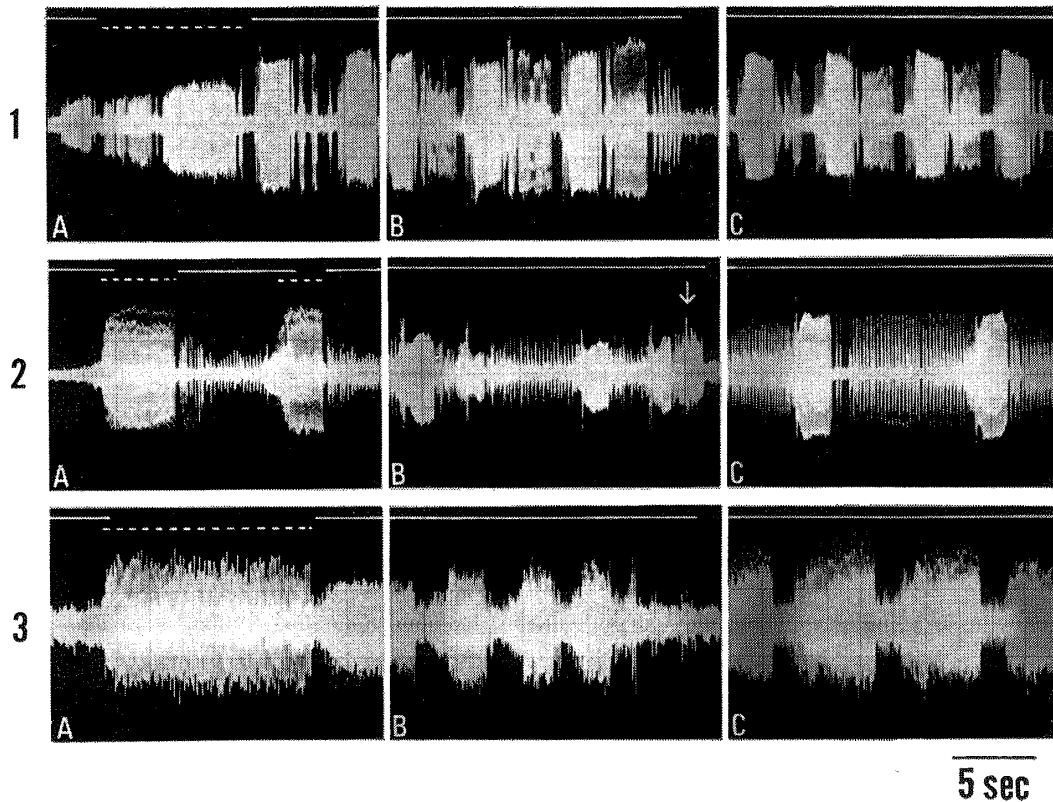


Fig. 6. Oscillograms of signals emitted by both sexes during mating behavior. The white solid line traced on the upper part of each oscillogram indicates the duration of the male signal, and the white dotted one indicates that of the female signal. A, signal emission by both sexes when a male was approaching a female on rice plants. B, signal emission by a male just before copulation. C, male postcopulatory signal. Arrow in 2-B indicates the vibrations detected during one wing-raising. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

and subunit a in *S. furcifera* (See Figs. 4 and 5). In *L. striatellus*, vibrations different from the signal shown in Fig. 4 were emitted at each wing raising as shown in Fig. 6 by the white arrow. Such vibrations were also detected in five wingless males. It was concluded from these results that no special signals were emitted by the motion of wing raising.

No signal was detected during copulation. All males of the three species under examination began to emit postcopulatory signals within a few minutes after copulation, and sometimes repeated this emission continually for more than 20 minutes (Fig. 6, C). Pulse patterns of male signals at pre- and postcopulation were similar to those emitted by a single male in each species. Female partners neither emitted postcopulatory signals, nor did they respond behaviorally to male postcopulatory signals of the same species.

The above mentioned results depicted the general features of the relationship between detected signals and behavior of both sexes during pre- and postcopulation in the three species under fluorescent light. Under darkness, the same process of signal emission by both sexes was detected in the three species, and they succeeded in copulation.

*Signal emission and mating behavior on the thin paper*

In a quiet room, faint sounds were heard even from a distance of about 1 meter when males of the three species were confined in a glass bottle (13 cm in height, 480 cm<sup>3</sup> in volume) and some of them were clinging on the inner surface of tightly-stretched paper lid (6 cm in diameter). The patterns of the faint sounds were similar to male signals detected from the rice plant. It was apparent that signals transmitted to the paper lid were amplified with the resonance of the paper.

When the male *N. lugens* were placed in sequence upon a piece of tightly-stretched thin paper which covered the open end (ca. 7 cm in diameter) of a plastic cup, all emitted signals within five minutes in a manner similar to the case when placed on a rice plant. A male and female were then placed on the paper to examine whether the pair would copulate without the presence of host plants. As shown in Fig. 7, they succeeded in copulation after alternate signal emission by both sexes. Males emitted postcopulatory signals. In this case, sounds were heard directly with the resonance of the paper while signals of both sexes were being emitted.

*Method of signal emission by male*

In females of the three species, signals were emitted by whole abdominal movement in a dorso-ventral direction which was apparent with the naked eye and was described as FAV. On the other hand, vibration in males could not be discerned by visual inspection. The 1st and 2nd abdominal terga of the planthopper, *Dicranotropis hamata*, have been described as a part of the sound producing organ (OSIANNILSSON, 1949). Thus, wings were amputated from males and movement of terga during signal emission was observed under a binocular microscope ( $\times 60$ ). All males placed on a sheet of thin paper moved about on the paper when female signals of the same species were played back from a sound speaker which was in contact with the paper. Movement ceased just after the playback was terminated. Males then continued emitting signals without movement. The 1st and 2nd abdominal terga vibrated rapidly during signal emission in all examined

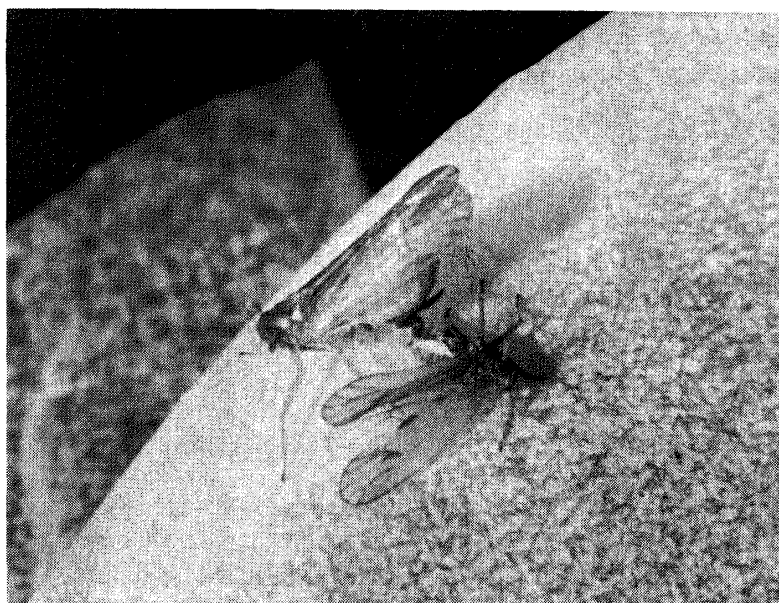


Fig. 7. *N. lugens* in copulation on a tightly stretched thin paper. Left, female; Right, male.



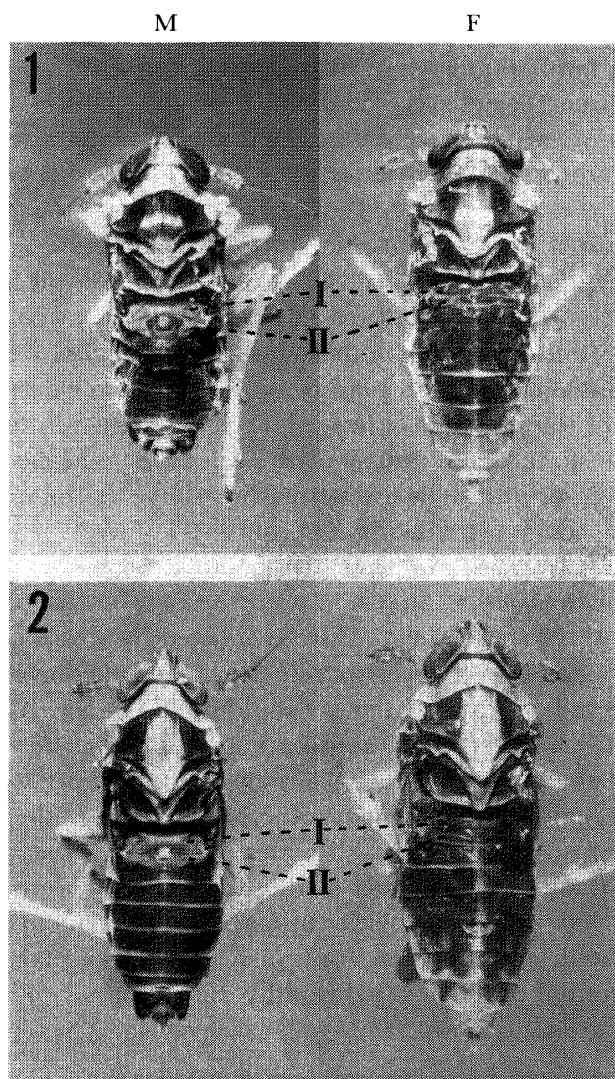


Fig. 8. Dorsal view of macropterous adults of *L. striatellus*(1) and *S. furcifera*(2). Wings were amputated. I, 1st abdominal tergum; II, 2nd abdominal tergum. M, male; F, female.

males. It was apparent that these abdominal terga specialized as tymbal organ in males of the three species as shown in *L. striatellus* and *S. furcifera* (Fig. 8). In the two species, the 1st abdominal tergum consists of a yellowish membrane, and the 2nd abdominal tergum consists of a central black part and a yellowish membrane. On the other hand, other abdominal terga of males and all abdominal ones of females consist of uniform black cuticles. A similar characteristic feature in the abdominal terga of males was also observed in *N. lugens* (ISHII and ICHIKAWA, 1975).

#### *Response of female to the playback of recorded male signal*

##### *1. Signal emitted by a single male*

When two pieces of stem of rice plant were detached (See Fig. 2), sexually mature virgin females of the three species did not show any behavioral response to the playback of recorded male signals of the same species. Though the females of the three species performed FAV sporadically under such conditions (Fig. 9, B), FAV was also observed

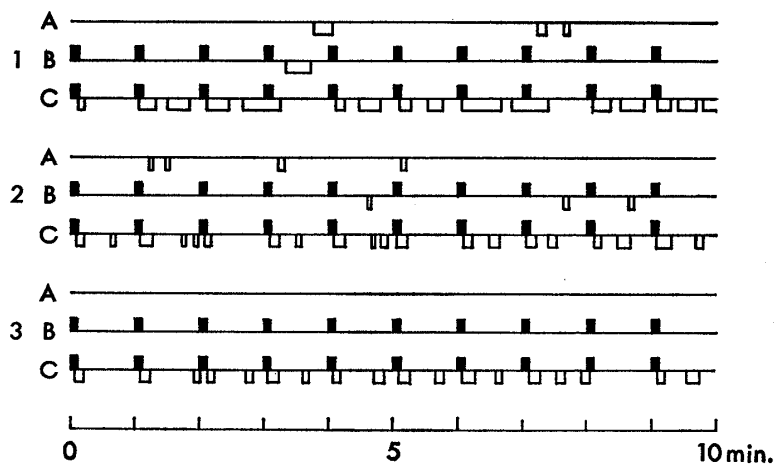


Fig. 9. Behavioral response of females (hollow rectangles) to the playback of recorded male signals (solid rectangles). A, male signals were not transmitted, and the two pieces of the stem were detached. B, male signals were transmitted, and the two pieces of the stem were detached. C, male signals were transmitted, and the two pieces of the stem were in contact. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*. See Fig. 2.

Table 2. SPECIES SPECIFICITY OF THE FEMALE RESPONSE TO THE PLAYBACK OF RECORDED MALE SIGNAL IN THREE SPECIES OF PLANTHOPPERS

Species	Female <sup>a</sup> No. used	Repetitions per female	Playback of recorded male signal <sup>b</sup>		
			<i>N. lugens</i>	<i>L. striatellus</i>	<i>S. furcifera</i>
<i>N. lugens</i>	5	10	49 <sup>c</sup>	1	0
<i>L. striatellus</i>	5	10	0	48	0
<i>S. furcifera</i>	5	10	1	1	47

<sup>a</sup> Sexually matured virgin females were used.

<sup>b</sup> Signals emitted by a single male were recorded on a sound tape, and the record was reproduced from a sound speaker, and transmitted to the stem of a rice plant on which one female was placed. See Fig. 2.

<sup>c</sup> Each female response was judged from performance of FAV just before or after the end of one complete unit of the male signal. See Figs. 4 and 5.

sporadically in these females even in the absence of the playback (Fig. 9, A). On the contrary, when two pieces of the stem were in contact, these females usually performed FAV just before or just after the end of each unit of the playback (Fig. 9, C). The same behavioral response of these females to the playback was also observed on a sheet of thin paper. These results indicated that signals emitted by a single male were significant for sexual excitation of females of the same species, and were not perceived as air-borne sound but as substrate vibrations.

Mated females of the three species (ca. 1 day after copulation), however, did not show any behavioral response to the playback. Females of each species showed no behavioral response to the playback of recorded male signals of the other two species either on a piece of the stem of rice plant (Table 2) or on a sheet of thin paper regardless of the intensity of the playback.

Table 3. INFLUENCE OF MATING ON THE FEMALE RESPONSE TO THE PLAYBACK OF RECORDED MALE POSTCOPULATORY SIGNAL IN THREE SPECIES OF PLANTHOPPERS

Female		Playback of recorded male signal <sup>a</sup>			
Species	No. used	Repetitions per female	<i>N. lugens</i>	<i>L. striatellus</i>	<i>S. furcifera</i>
<i>N. lugens</i>	Virgin 5	5	24	—	—
	Mated 5	5	0	—	—
<i>L. striatellus</i>	Virgin 5	5	—	23	—
	Mated 5	5	—	0	—
<i>S. furcifera</i>	Virgin 5	5	—	—	24
	Mated 5	5	—	—	0

<sup>a</sup> Postcopulatory signals were recorded on a sound tape, reproduced from a sound speaker, and transmitted to a sheet of thin paper on which a single female was placed.

<sup>b</sup> Each female response was judged from performance of FAV just before or after the end of one complete unit of the male signal.

## 2. Postcopulatory signal

As shown in previous experiments, mated females of the three species were indifferent to postcopulatory signals of males of the same species. These results suggested that the postcopulatory signals were different in some respect from signals emitted during precopulation or copulation triggered some sudden physiological change in females. To answer the question, the behavioral response of sexually mature virgin females and mated females of the same age (ca. 1 day after copulation) to the playback of recorded postcopulatory signals of the same species were examined on a sheet of thin paper. Virgin females of the three species performed FAV just before or just after the cessation of the playback. Mated females, however, showed no behavioral response to the playback (Table 3). These results indicated that some physiological change occurred in females after copulation made them indifferent to postcopulatory signals.

## DISCUSSION

It was revealed that both sexes of the three species of delphacid insects, *Nilaparvata lugens*, *Laodelphax striatellus* and *Sogatella furcifera*, communicated with species-specific vibratory signals emitted by both sexes alternately at precopulation, and perceived as substrate vibrations. Although males emitted signals by vibrations of well-developed tymbal organs on the 1st and 2nd abdominal terga, females emitted signals by whole abdominal vibrations in a dorso-ventral direction (FAV). Males of these species never perceived female signals as air-borne sounds (ICHIKAWA and ISHII, 1974; ICHIKAWA et al., 1975). It is obvious from Figs. 3 and 9 that females of these species also never perceive male signals as air-borne sounds. Alternate sound emission by both sexes in mating behavior has been reported in other auchenorrhynchous Homoptera (OSSIANILSSON, 1949, 1953; STRÜBING, 1958, 1962; SMITH, Jr., 1971) and Heteroptera, *Nezara viridula* (Čokl et al., 1972). Experimental evidence concerning communication via substrate vibration was not given by these authors. On the other hand, *Tritomegas bicolor* and *Canthophorus dubius* (Cydnidae, Heteroptera) are known to communicate by species-specific substrate-borne signals (GOGALA et al., 1974).

Many Orthoptera and Cicadidae having well-developed auditory organs emit loud sounds. On the contrary, small auchenorrhynchous Homoptera and Heteroptera emit very faint sounds hardly audible to the human ear, and the existence of auditory organs in these insects does not seem well founded (OSSIANNILSSON, 1949; LESTON and PRINGLE, 1963). In addition to these facts, three species of delphacid insects studied in this paper and above mentioned Cydnidae perceive species-specific substrate vibrations in intraspecific communication. Thus, it is reasonable to consider that small auchenorrhynchous Homoptera and low-voiced Heteroptera transmit vibratory signals directly to solid substrates on which they live, and perceive also as substrate vibrations.

Most males of the three species emitted signals within five minutes after placement on a rice plant regardless of the presence or absence of other individuals. Such male signals might be equivalent to common song of other Auchenorrhyncha (OSSIANNILSSON, 1949). Females responded to the playback of recorded signals emitted by a single male of the same species. Therefore, it is certain that signals emitted by a single male are directed at mating partners, and these signals act as an initiating cue for mutual communication in their mating behavior. Males of *N. lugens*, which exclusively live on rice plant, emitted signals even on a sheet of thin paper just like on a rice plant. Normal mating behavior was also observed on the paper. They seem not to discriminate between rice plant and the paper for at least several minutes after placement on these substrates. Males of the three species approached stationary females of the same species during the course of mutual communication via vibratory signals. All males emitted signals a few or several times in close vicinity of females just before they showed copulatory behavior. These results support the view that male signals just before copulation are the final essential sign stimuli for females to perceive and receive appropriate male partners. Wing raising of males just before copulation was shown not to be an essential sign stimulus for females. Wing raising might be an expression of extreme excitation of males. Postcopulatory signals were emitted by all males of the three species within a few minutes after copulation. Mated female partners were indifferent to the signals. At present, the biological significance of postcopulatory signals is unknown. Postcopulatory signals have also been reported in some species of Orthoptera (ALEXANDER, 1962) and in *Rhagadotarsas* (Gerridae, Heteroptera) (WILCOX, 1972). In *Rhagadotarsas*, it was demonstrated that communication in mating behavior was performed by surface waves produced by leg movement. This method of communication is essentially the same as that of delphacid insects from the standpoint of signal transmission via the substrate on which such insects live.

Females of the three species did not respond to the playback of recorded male signals of other two species. Such interspecific relation was also observed in the behavioral response of males to female signals (ICHIKAWA et al., 1975). It is considered from these results that these sympatric species which have similar methods of communication, are not confused with each other in perceiving respective mating partners in paddy fields. SUENAGA (1963) described that copulation of *N. lugens* was observed frequently from 6 to 8 o'clock in the evening under semi-field conditions in September. Although signal emission and mating behavior were demonstrated both diurnally and nocturnally in the three species of delphacid insects under laboratory conditions, circadian rhythm of signal emission and mating activity was not examined in the present study. The initial population density of *N. lugens* which immigrate into paddy fields in June or July is less than 5 per 100 rice plant hills (KISIMOTO, 1965, 1975; KUNO, 1968). Females of *N.*

*lugens* during the time of dispersal flight in September and October were sexually immature virgins, and those of *N. lugens* and *S. furcifera* migrating in June were also virgins (OHKUBO and KISIMOTO, 1971; KISIMOTO, 1975). In *N. lugens*, *L. striatellus* and *S. furcifera*, the number of males captured in yellow pan traps was more than that of females when the traps were set at the crop level in paddy fields (KISIMOTO, 1968, 1975; OTAKE, 1970). Results in the present study and the above-mentioned field surveys suggest that following dispersal flight, macropterous males of these delphacid insects perform random searching flight for mating from one rice plant hill to another and emit signals after landing on each hill.

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## REFERENCES

- ALEXANDER, R. D. (1962) Evolutionary change in cricket acoustical communication. *Evolution* **16**: 443-467.
- CLARIDGE, M. F. and P. E. HOWSE (1968) Songs of some British *Oncopsis* species (Hemiptera: Cicadellidae). *Proc. R. ent. Soc. Lond. (A)* **43**: 57-61.
- CLARIDGE, M. F. and W. J. REYNOLDS (1973) Male courtship songs and sibling species in the *Oncopsis flavicollis* species group (Hemiptera: Cicadellidae). *J. Ent. (B)* **42**: 29-39.
- ČOKL, A., M. GOGALA and M. JEŽ (1972) Analiza zvočnih signalov stenice *Nezara viridula* (L.). *Biološki Vestnik* **20**: 47-53.
- GOGALA, M., A. ČOKL, K. DRAŠLAR and A. BLAŽEVIČ (1974) Substrate-borne sound communication in Cydnidae (Heteroptera). *J. comp. Physiol.* **94**: 25-31.
- ICHIKAWA, T. and S. ISHII (1974) Mating signal of the brown planthopper, *Nilaparvata lugens* STÅL (Homoptera: Delphacidae): Vibration of the substrate. *Appl. Ent. Zool.* **9**: 196-198.
- ICHIKAWA, T., M. SAKUMA and S. ISHII (1975) Substrate vibrations: Mating signal of three species of planthoppers which attack the rice plant (Homoptera: Delphacidae). *Appl. Ent. Zool.* **10**: 162-169.
- ISHII, S. and T. ICHIKAWA (1975) The tymbal organ of the male brown planthopper, *Nilaparvata lugens* STÅL and a simple method for listening to the sound. *Jap. J. appl. Ent. Zool.* **19**: 295-296. (In Japanese).
- KISIMOTO, R. (1965) Studies on the polymorphism and its role playing in the population growth of the brown planthopper, *Nilaparvata lugens* STÅL. *Bull. Shikoku Agr. exp. Stn* **13**: 1-106. (In Japanese with English summary).
- KISIMOTO, R. (1968) Yellow pan water trap for sampling the small brown planthopper *Labdelphax striatellus* (FALLÉN), a vector of the rice stripe virus. *Appl. Ent. Zool.* **3**: 37-48.
- KISIMOTO, R. (1975) *Transoceanic Migration of Planthoppers*. Chûô-Kôron, Tokyo, Japan, pp. 233. (In Japanese).
- KUNO, E. (1968) Studies on the population dynamics of rice leafhoppers in a paddy field. *Bull. Kyushu Agr. exp. Stn* **14**: 131-246. (In Japanese with English summary).
- LESTON, D. and J. W. S. PRINGLE (1963) Acoustic behaviour of Hemiptera. In "Acoustic Behaviour of Animals" (BUSNEL, R. G. ed), p. 391-411. Elsevier.
- MEBES, H. D. (1974) Zur Biophysik der Schallerzeugung bei Kleinzikaden. *Forma et functio* **7**: 95-118.

- MOOR, T. E. (1961) Audiospectrographic analysis of sounds of Hemiptera and Homoptera. *Ann. ent. Soc. Am.* **54**: 273-291.
- OHKUBO, N. and R. KISIMOTO (1971) Diurnal periodicity of flight behaviour of the brown planthopper, *Nilaparvata lugens* STÅL, in the 4th and 5th emergence periods. *Jap. J. appl. Ent. Zool.* **15**: 8-16. (In Japanese with English summary).
- OSSIANNILSSON, F. (1949) Insect drummers. *Opuscula Entomol. Suppl.* **10**: 1-145.
- OSSIANNILSSON, F. (1953) On the music of some European leafhoppers and its relation to courtship. *Trans. IXth Int. Congr. Entomol.* **2**: 139-141.
- ÔTAKE, A. (1970) Catching at yellow pan water traps and the spacial distribution of the smaller brown planthopper, *Laodelphax striatellus* (FALLÉN), on rice plots. *Jap. J. appl. Ent. Zool.* **14**: 195-203. (In Japanese with English summary).
- SMITH, Jr., J. W. (1971) Studies on the acoustics of the beet leafhopper, *Circulifer tenellus* (BAKER) (Homoptera: Cicadellidae). *Diss. Abstr. (B)* **31**, 408, 4755 B.
- STRÜBING, H. (1958) Lautausserung der entscheidende Faktor für das Zusammenfinden der Geschlechter bei Kleinzikaden (Homoptera-Auchenorrhyncha). *Zool Beitr. N. F.* **4**: 15-21.
- STRÜBING, H. (1962) Paarungsverhalten und Lautausserung von Kleinzikaden demonstriert an Beispielen aus der Familie der Delphacidae (Homoptera-Auchenorrhyncha). *Verhandl. Intern. Entomol. Kongr. XI Viena* **3**: 12-14.
- SUENAGA, H. (1963) Analytical studies on the ecology of two species of planthoppers, the white back planthopper (*Sogata furcifera* HORVATH) and the brown planthopper (*Nilaparvata lugens* STÅL), with special reference to their outbreaks. *Bull. Kyushu agr. exp. Stn* **8**: 1-152. (In Japanese with English summary).
- WILCOX, R. S. (1972) Communication by surface waves-mating behavior of a water strider (Gerridae). *J. comp. Physiol.* **80**: 255-266.