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Studies on the Mating Behavior of the Four Species
of Auchenorrhynchous Homoptera which Attack the
Rice Plant

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Preface

The three species of planthoppers, *Nilaparvata lugens* (STÅL), *Laodelphax striatellus* (FALLÉN) and *Sogatella furcifera* (HORVÁTH), and the green rice leafhopper, *Nephotettix cincticeps* UHLER, are serious insect pests on the rice plant not only in Japan but also in other areas of Southeast Asia. In addition, the distribution of the brown planthopper, *N. lugens*, and the white backed planthopper, *S. furcifera*, covers India, Australia and Oceanic islands, and that of the smaller brown planthopper, *L. striatellus*, covers Europe (HINKLY, 1963; KISIMOTO, 1975; OKADA, 1977). *N. lugens*, *L. striatellus* and *S. furcifera* belong to Delphacidae, and *N. cincticeps* to Deltocephalidae.

In Japan, these four species propagate in paddy fields continuously for three to four generations a year (KISIMOTO, 1965; KUNO, 1968; KIRITANI *et al.*, 1970; HOKYO, 1972). *L. striatellus* and *N. cincticeps* are known to hibernate in Japan. Most of the macropterous migrants of *N. lugens* and *S. furcifera* are known to invade in paddy fields in June and July, and these migrants propagate in paddy fields thereafter. However, hibernation of these two species in Japan has not been proved for over 40 years' efforts. The discovery of the huge number of the migrants of these two species on a weather observation boat on the Pacific Ocean, 500 km southern point from the main land of Japan, in 1967 consolidated the possibility of the immigration from other countries year by year (ASAHINA and TURUOKA, 1968; KISIMOTO, 1975, 1977). The four species damage the rice plant by sucking the plant juice from the vascular bundles (SÔGAWA, 1973). Most conspicuous damage caused by sucking by *N. lugens* has been called as "Tsubogare" (hopperburn). Besides such direct damage by sucking, *L. striatellus* and *N. cincticeps* are known to transmit the virus diseases of the rice plant in Japan. *N. lugens* is also known as a vector of the grassy stunt disease in more southern areas of Southeast Asia (LING, 1977).

Serious damage on the rice plant caused by the outbreak of these insect pests has been recorded in many literatures. Their outbreaks in 1940 triggered the establishment of National project for the forecasting of occurrence. Nowadays, the damage of the rice plant is not so serious as old time by the benefit of the National project, the chemical control and other technological progresses, but difficulty in control has arisen owing to their high reproductive potential, the decrease of natural enemy by the application of insecticides, the development of insecticidal resistant strains in *N. cincticeps* and *L. striatellus*, and the annual recruit from other countries (KOJIMA *et al.*, 1963; OZAKI, 1966; OZAKI and KASSAI, 1970; KIRITANI, 1972; KISIMOTO, 1975).

Studies on these insect pests have been progressed by many entomologists, and many valuable knowledges have been accumulated. However, few studies have been made on their mating behavior so far (ESAKI and HASHIMOTO, 1937; OYAMA, 1972; TAKEDA, 1974). The mating behavior is one of the most important biological phenomena as a starting point of the reproduction and the propagation. Therefore, if the control of their mating behavior is possible,

the damage on the rice plant might be reduced. First of all, it is important to clarify the mechanisms by which the encounter of appropriate mating partners is realized. The mechanisms in their mating behavior have not yet been clarified.

This paper deals with the mating behavior of above mentioned three species of planthoppers and the leafhopper with special reference to the sign stimuli playing indispensable role in finding appropriate mating partners. In Chapter 1, the process of the mating behavior is described. Chapter 2 deals with the results of the analyses of the sign stimuli involved in the mating behavior. Chapter 3 deals with the physical properties of the sign stimuli, and the relation between the stimuli and the process of the mating behavior. Chapter 4 deals with some factors influencing upon the sexual behavior and the sexual maturation.

Chapter 1. The process of the mating behavior

I Introduction

It seems that the mating behavior of auchenorrhynchous Homoptera other than Cicadidae was first observed in *Laodelphax striatellus* by ESAKI and HASHIMOTO (1937), and characteristic behavior performed by both sexes was described. Thereafter, the process of the mating behavior has been studied in *Doratura stylata* (OSSIANNILSSON, 1953), *Callygypona lugubrina* (STRÜBING, 1958), *Sogatodes orizicola* (MCMILLIAN, 1963), *Circulifer tenellus* (SMITH, JR., 1971), *L. striatellus* and *Nephotettix cincticeps* (OYAMA, 1972), *Nilaparvata lugens* (TAKEDA, 1974), *Macrostelus fascifrons* (PURCELL and LOHER, 1976), *Hishimonus sellatus* (ARAI, 1977) and *Hishimonus* sp. (ARAI, 1978). The author and coworkers also studied the process of the mating behavior of *N. lugens*, *L. striatellus*, and *S. furcifera* (ICHIKAWA and ISHII, 1974; ICHIKAWA *et al.*, 1975; ICHIKAWA, 1976a, 1977) and *N. cincticeps* (ICHIKAWA, 1976b).

Characteristic behavior performed by *N. lugens*, *L. striatellus*, *S. furcifera* and *N. cincticeps* in the process of the mating behavior and the behavior performed by a single individual of *N. cincticeps* is described in this Chapter.

II Materials and Methods

L. striatellus and *S. furcifera* were collected in paddy fields in Chikugo city in 1969. *N. lugens* and *N. cincticeps* were collected in paddy fields in Kyoto city in 1973. These insects have been reared in glass bottles (7 cm in diameter and 13 cm in height) each containing rice seedlings as food and oviposition site at $25 \pm 1^\circ\text{C}$ under the photoperiod of 14 hr with fluorescent lighting. The source of insects was the same in all experiments in this paper.

Adult insects used for the observation of the mating behavior were sexed within one day after emergence (0 day) when at least all females of the four species were sexually immature virgin ones. Then each female was reared in a glass tube (2 cm in diameter and 17 cm in

height, or 3 cm in diameter and 20 cm in height) containing a rice seedling fixed to a piece of moistened polyurethane mat. The upper end of the glass tube was covered with a piece of gauze. Males were also reared in the glass tubes, but two to five individuals were confined together in each glass tube. The same rearing methods at the adult stage were applied for all experiments in this paper.

Behavior performed by both sexes of the three species of planthoppers was observed after a couple of both sexes of the same species were confined in the glass tube with a rice seedling of 5 cm in length or so, while each couple of *N. cincticeps* were confined in the tube with a larger rice seedling (ca 15 cm in the vegetative part) to facilitate the observation because of the very rapid movements of the males. All females were placed on the rice seedlings at the start of the observation, and all males were released into the tubes without restriction of the first place where they settled. The adults at the age of more than 4 days after emergence were used for above mentioned observation.

In *N. lugens*, following another method of observation was also used. A couple of both sexes were confined in a transparent plastics cup (11.5 cm in top diameter, 8.5 cm in bottom diameter and 8.5 cm in height). One female was placed on a rice seedling fixed to a piece of moistened polyurethane mat which was placed on the bottom of the cup. Then one male was released on the bottom of the cup. Behavior performed by both sexes was observed continuously for 6 hr in this case. Females used were the virgin ones at the 2nd day of adult emergence, the virgin ones at the 5th day and the mated ones at the 5th day.

The observation was made at $25\pm 1^{\circ}\text{C}$ or room temperature ($23-27^{\circ}\text{C}$) under fluorescent lighting.

III Results

1. Precopulatory behavior

Sexually mature virgin females of *N. lugens*, *L. striatellus* and *S. furcifera* began to vibrate their whole abdomens in a dorso-ventral direction after the settlement on the seedling. Although the amplitude of the abdominal vibration (AV) was less than 0.2 mm, this characteristic behavior could be observed by naked eye. As shown in Fig. 1, the females performing the AV never tapped the plant by their abdomens and usually kept inserting their stylets in the leaf sheath. Thus they never shifted during the period performing this behavior.

Males of the three species having settled on the seedlings began rapid walking immediately after the beginning of the AV. Most males moved directly toward the females by rapid walking and went to the close vicinity of the females. Some of them walked beyond the females and turned back toward the females, or once moved to the polyurethane mat and turned back toward the females. Males having settled on the polyurethane mat also performed the same rapid walking immediately after the beginning of the AV. On the contrary, males clinging to or walking on the inside wall of the glass tubes never responded to the AV even when the distance between both sexes was only about 1 or 2 cm. These males, however, immediately responded to the AV as mentioned above after they had settled on the seedlings.

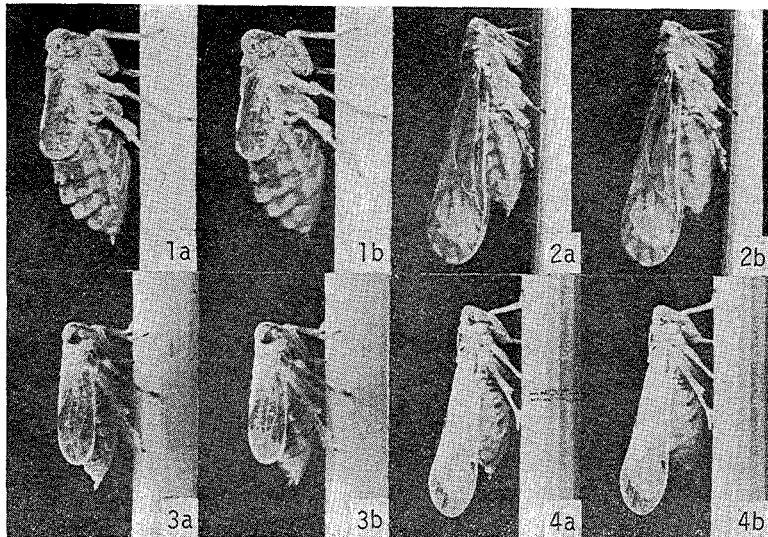


Fig. 1. Abdominal vibration (AV) performed by the females of the three species of planthoppers. 1, Brachypterous form of *N. lugens*; 2, Macropterous form of *N. lugens*; 3, Brachypterous form of *L. striatellus*; 4, Macropterous form of *S. furcifera*. a, Not vibrating; b, Vibrating. All photographs were taken at 1 sec exposure.

When a couple of *N. lugens* were confined in the plastics cup, behavior performed by both sexes was as follows. The time required for the males to come up to the side of the virgin females at the 2nd day of adult emergence (Group 1), the virgin ones at the 5th day (Group 2) and the mated ones at the 5th day (Group 3) was 146.4 ± 48.3 min (Mean \pm 95% f. l., $N=24$), 42.5 ± 14.6 min ($N=24$) and 162.0 ± 47.5 min ($N=23$), respectively. The difference of male behavior toward these female groups was clearly observed when the males came up to the lateral side of the polyurethane mat by walking. The males clinging to the mat never showed rapid walking toward the females of Group 1 and 3, and long time was needed for them to climb up to the seedlings on which the females were settling. On the contrary, the males began rapid walking immediately after the females of Group 2 began the AV, and they soon arrived at the side of the females. Only the females of Group 2 received courting males to copulate. The females of other two groups escaped from courting males or showed mate refusal response (body rolling).

Behavior performed by the males of the three species of planthoppers which arrived at the side of the conspecific females were as follows. The males flapped their wings a few times after stopping at the close vicinity of the females. The moment of one wing flap by the male *N. lugens* is shown in Fig. 2-a. Male copulatory attempt was observed after such wing flaps. Males once failed to copulate flapped their wings over again before the next copulatory attempt. Besides, such wing flaps by the males of the three species toward other conspecific males happened to be observed when the males were confined together in the glass tubes.

In addition to above mentioned behavior, a bout of wing beat (less than 1 sec in duration) was sporadically observed in both sexes of *N. lugens* having settled on the seedlings. But no

behavioral change was ever elicited from opposite sex by the behavior.

Precopulatory behavior of *N. cincticeps* was somewhat different from that of the three species of planthoppers. Both sexes of this species began peculiar behavior after the settlement on the rice plant. They usually began with rubbing on the head apex by the fore legs and rubbing on the edge of the fore wings by the hind legs, and wing beats and rubbing legs together were also observed. However, both sexes of most couples performed the mating behavior without performing the latter two types of the behavior. Females performing above mentioned behavior never attracted the males settling on the same rice seedling. Male rapid walking toward the female was observed shortly after the cessation of above mentioned behavior. Sometimes such

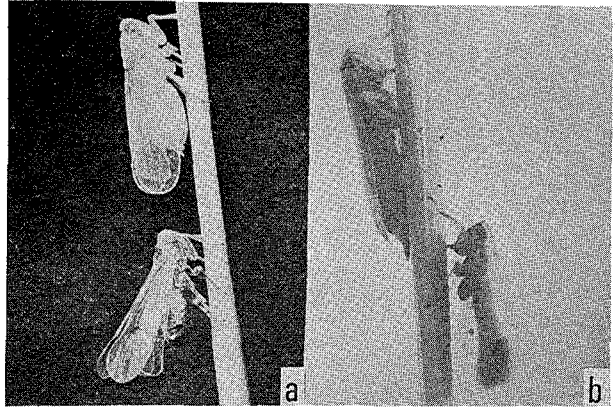


Fig. 2. Male wing flap immediately before copulation in *N. lugens* (a) and *N. cincticeps* (b). upper, Female; lower, Male.

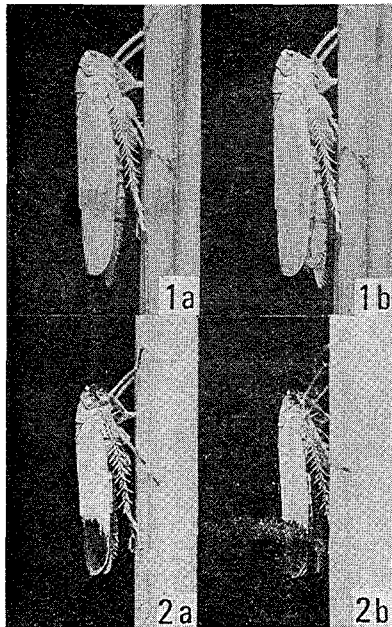


Fig. 3. Typical precopulatory behavior performed by both sexes of *N. cincticeps*. 1, Abdominal protrusion (AP) performed by the female. a, Not protruding; b, Protruding. 2, Abdominal vibration (AV) performed by the male. a, Not vibrating; b, A moment of the vibration.

male approach toward the females was observed shortly after the settlement on the seedlings without performing above mentioned behavior. It was found that the male approach toward the female was accompanied with the female abdominal protrusion (AP) (Fig. 3-1). Subtle vibration of the whole abdomen during the performance of this characteristic female behavior was observed by using a magnifying glass ($\times 20$). Thus the males having settled on the seedlings approached to the females. On the contrary, the males clinging to or walking on the inside wall of the glass tubes were indifferent to the females which were performing above mentioned four types of behavior on the seedling for a long time. However, the males approached toward the females by rapid walking shortly after they moved to the seedling from the inside wall.

Male *N. cincticeps* occasionally vibrated their abdomens in a dorso-ventral direction shortly after stopping their movements toward the females (Fig. 3-2). This male abdominal vibration (AV) had larger amplitude and slower tempo than those of the female planthoppers. Sometimes rapid wing flaps of the males were also observed simultaneously with the AV. The males flapped their wings rapidly one or a few times after stopping at the close vicinity of the females (Fig. 2-b). The AV was also

observed simultaneously with the wing flaps at this time. They attempted to copulate after such wing flaps. The males once failed to copulate flapped their wings over again before the next copulatory attempt. Such wing flaps and copulatory attempts by the males were also performed toward another conspecific males when two males were confined in the glass tube with the seedling.

2. Copulation

Most virgin females at the age of more than 4 days after emergence received the male copulatory attempt without any mate refusal response in the four species. The males of the four species approached to the conspecific females from behind to the side of them, and linked genital organs by bending their abdomens. Then the males turned backward and kept copulatory position. Macropterous males of the three species of planthoppers kept their wings opening and slanting backward during the duration of copulation as shown in *N. lugens* (Fig. 4-a). On the other hand, male *N. cincticeps* kept wings closing and completely end-to-end position (Fig. 4-b). The duration of copulation in the four species was at most within 3 min (Table 1). The duration in *L. striatellus*, 7 sec on the average,

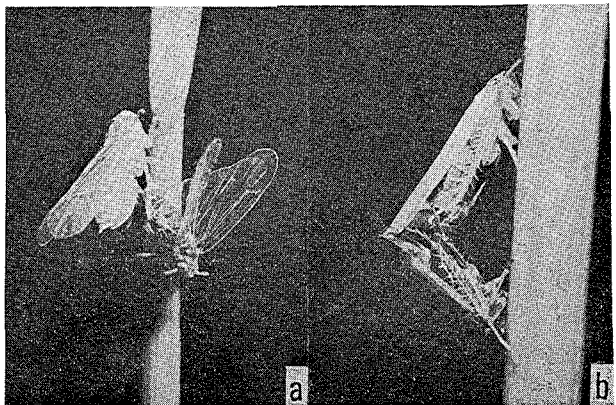


Fig. 4. Copulatory position in *N. lugens* (a) and *N. cincticeps* (b) a: left, Female; right, Male. b: upper, Female; lower, Male.

Table 1. Duration of copulation in the four species of Auchenorrhyncha

| Species | Combination | No. of couples | Duration of copulation (sec) |
|-----------------------|-------------|----------------|------------------------------|
| <i>N. lugens</i> | ♀ B × ♂ M | 11 | 90.6 ± 23.4* |
| | ♀ M × ♂ M | 10 | 97.5 ± 20.4 |
| <i>L. striatellus</i> | ♀ B × ♂ M | 9 | 6.7 ± 3.1 |
| | ♀ M × ♂ M | 10 | 5.0 ± 1.1 |
| <i>S. furcifera</i> | ♀ M × ♂ M | 10 | 67.4 ± 18.1 |
| <i>N. cincticeps</i> | | 10 | 121.0 ± 37.0 |

B, Brachypterous form.

M, Macropterous form.

* Mean ± 95% f. l.

was extremely short among these species. Adequate insemination in these species was ascertained from the hatch of the 1st instar nymphs from the eggs laid by the females. The females of the four species always took the initiative by walking or by kicking in parting at the end of the copulation.

3. Postcopulatory behavior

Both sexes of the three species of planthoppers performed no marked behavior after the

finish of the copulation. Oviposition by some of these females shortly after the finish of the copulation was the only one behavior observed.

On the contrary, both sexes of *N. cincticeps* began following peculiar behavior shortly after the finish of the copulation. Each of both sexes exuded a droplet from anus, and the droplet was grasped by the hind legs. Then the male transferred the droplet to the tip of his abdomen, and put in on the part (Fig. 5-1). And the female transferred the droplet to the vulva, and put it on the part (Fig. 5-2). After a while, both sexes grasped the droplets

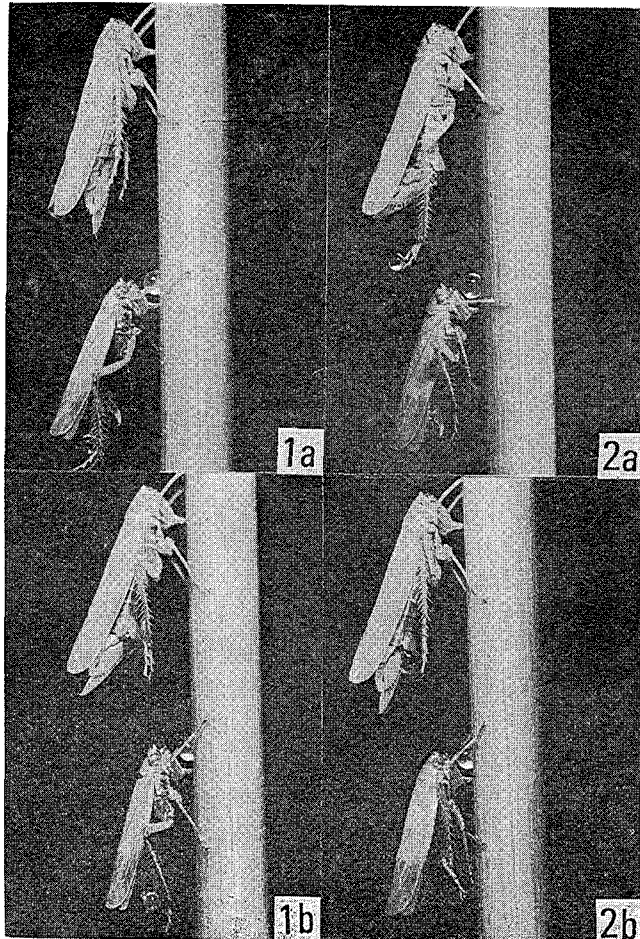


Fig. 5. Postcopulatory behavior performed by both sexes of *N. cincticeps*. upper, Female; lower, Male. 1: a, The male is going to grasp a droplet exuded from anus by his hind legs. b, The droplet was put on the tip of his abdomen. 2: a, The female is going to transfer a droplet to her vulva. b, The droplet was put on her vagina.

having put on above mentioned parts again by the hind legs, and immediately kicked out. In addition to these types of behavior, the female sometimes absorbed the droplet in vagina

without the help of the legs, and exuded it out from the vagina after a while. Then the droplet was grasped and kicked out by the hind legs. A series of above mentioned behavior was repeated 3—9 times by the males and 5—12 times by the females. Table 2 shows the time of the onset of the postcopulatory behavior, the number of the repetition of a series of

Table 2. Time of onset, repetition and duration of postcopulatory behavior in *N. cincticeps*

| Couple No. | Sex | Postcopulatory behavior | | |
|------------|-----|----------------------------------|-------------------------|-----------------------------|
| | | Time of onset ^a (sec) | Repetition ^b | Duration ^c (sec) |
| 1 | M | 86 | 6 | 305 |
| | F | 241 | 5 | 575 |
| 2 | M | 90 | 6 | 330 |
| | F | 130 | 7 | 334 |
| 3 | M | 160 | 4 | 181 |
| | F | 77 | 10 | 555 |
| 4 | M | 196 | 6 | 290 |
| | F | 176 | 12 | 850 |
| 5 | M | 108 | 9 | 720 |
| | F | 82 | 9 | 438 |

M, Male; F, Female.

a Time from the finish of copulation to the onset of the postcopulatory behavior.

b Number of the repetition of a series of the postcopulatory behavior.

c Duration of the repeated postcopulatory behavior.

the behavior and the duration of the repeated behavior on 5 couples of both sexes. Both sexes sometimes performed the rubbing on the edge of the fore wings by the hind legs or the rubbing legs together after the cessation of above mentioned postcopulatory behavior. The AV performed by the males was also observed around this time.

4. Behavior performed by a single individual of *N. cincticeps*

When a single male or a single female was placed on the rice seedling, they performed the rubbing on the head apex by the fore legs and the rubbing on the edge of the fore wings by the hind legs, the wing beats and the rubbing legs together just as mentioned in the precopulatory behavior of this species. Sometimes the male performed the AV. In addition to the behavior of these types, they sometimes began the behavior similar to their postcopulatory behavior. The behavior was as follows. The male or the female grasped the exuded droplet from the anus by the hind legs, and the droplet was transferred onto the seedling. Then the droplet was trampled by all legs for a while.

Similar behavior was also performed by the final (5th) instar nymphs of this species when they were individually placed on the seedling. These nymphs began the rubbing on the head apex by the fore legs and the rubbing on the abdomen by the hind legs at the time shortly after the placement. Then they performed the rubbing legs together. In addition to these types of behavior, they grasped the exuded droplets from the anus by the hind legs, and the droplets transferred onto the seedlings were trampled by all legs. The last behavior was observed at about 16 or 18 min after the placement.

IV Discussion

Marked precopulatory behavior of the three species of planthoppers was the monotonous abdominal vibration (AV) of the females. The males of these species rapidly approached to the conspecific females during the duration of the AV. The AV of the females was also described in other planthoppers, *Callygypona lugubrina*, *C. adela*, *Euidella speciosa* (STRÜBING, 1958, 1962) and *Sogatodes orizicola* (MCMILLIAN, 1963). Such AV of the females having been recorded in 6 genera (*Nilaparvata*, *Laodelphax*, *Callygypona*, *Euidella*, *Sogatodes* and *Sogatella*) seems to be the common behavior to attract conspecific males in Delphacidae. In *N. cincticeps* the females never performed such AV observable by naked eye. But the faint vibrations of whole abdomens during the abdominal protrusion (AP) could be observed by using a magnifying glass. It is obvious that the AP is the behavior to attract the conspecific males because male rapid walking toward the females was observed during the AP. Similar faint vibration of the abdomen was also described in the female leafhopper, *H. sellatus* (ARAI, 1977).

In the three species of planthoppers studied in this paper, above mentioned precopulatory behavior was never observed when the males were clinging to or walking on the inside wall of the glass tube irrespective of the distance between both sexes. In *N. lugens*, the males responded to the AV of the females from the lateral side of the polyurethane mat where the mat was the visual barrier between both sexes. These circumstances in *N. lugens* are schematically shown in Fig. 6. These results suggest that visual, olfactory or auditory factors

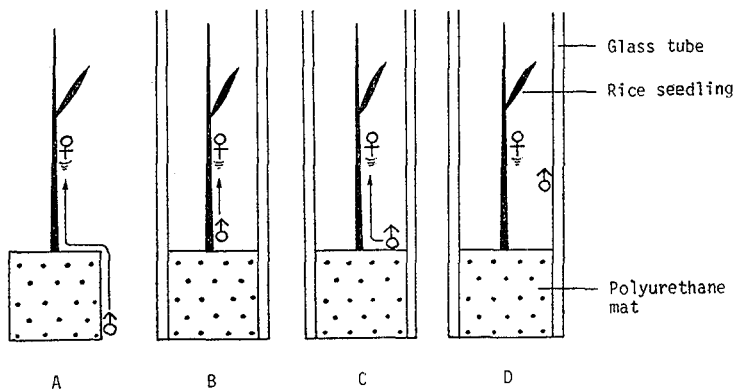


Fig. 6. Schematic representation of the manner of male response to the AV performed by female planthoppers. Arrows show the trace of male movements by rapid walking.

are not perceived by the males when the females are performing the AV. Vibration factors are the only remaining possibility to convey stimuli to the males which are some distance away. If vibration factors are really emitted by the AV of the females, the indifference of the males having clinging to the inside wall of the glass tube to the AV must be due to the

sudden weakening of the vibrations transmitted from the rice seedling to the glass via the polyurethane mat. It seems that the same discussion is possible for *N. cincticeps* as the precopulatory behavior was seen only when both sexes were settling on the same rice seedling though the relation between the AP and the male movement was not ascertained when the males were clinging to the inside wall of the glass tube.

The rubbing on the body parts by legs and the wing beat performed by both sexes of *N. cincticeps* can not relate with the mating behavior because no behavioral change occurred in both sexes during the duration of the behavior even when a couple of both sexes were placed on the same rice seedling. And the behavior performed by the 5th instar nymphs indicates that the behavior is not peculiar to the adults. The behavior resembles the cleaning behavior described in *Drosophila* (CONNOLLY, 1968; SZEBENYI, 1969), but exact meaning of the behavior has not been clarified so far.

The duration of copulation in the four species (within 3 min) was very short compared with that of other Auchenorrhyncha, *Magiccada septendecim* (more than 3 hr) (WHITE, 1973), *M. fascifrons* (15—95 min) (PURCELL and LOHER, 1976) and *H. sellatus* (2.5—3.0 hr) (ARAI, 1977).

Although many kinds of elaborate precopulatory behavior are known in wide range of insects (OBARA, 1968), it seems rather few knowledges about postcopulatory behavior excepting Orthoptera (ALEXANDER, 1962, 1967). Distinct postcopulatory behavior was observed in both sexes of the two species of leafhoppers, *N. cincticeps* (OYAMA, 1972) and *H. sellatus* (ARAI, 1977). Similar postcopulatory behavior of *N. cincticeps* was also observed by the author (see Fig. 5 and Table 2). Besides, a single male or female and a single 5th instar nymph of this species performed similar behavior. A common feature of the behavior is the grasp and transfer of the droplets exuded from the anus by the hind legs. As the nymphs and the adults did not always grasped the excreted droplets of their own, there may be some biological meaning in the behavior and the grasped droplets. Exclusive performance of the transfer of the droplets to the genital organs by the adults just mated suggests the further presence of some mate related factor.

Both sexes of the four species studied in this paper performed the mating behavior irrespective of the time of the day when a couple of both sexes was introduced on the same rice seedling under laboratory conditions. SUENAGA (1963), however, observed the copulation of *N. lugens* frequently at 18—20 o'clock in early October in a green house. ARAI (1977) also observed the copulation of *H. sellatus* from the evening to night in field. On the other hand, the flight behavior of *N. lugens*, *L. striatellus* and *N. cincticeps* seems to be active in the morning and from evening to night (KISIMOTO, 1968; OHKUBO and KISIMOT, 1971; MACQUILLAN, 1975). Although the exact meaning of such periodic flight activity has not yet been clarified, it is probable that the four species perform the mating behavior frequently during such times in paddy fields.

Chapter 2. Sign stimuli which release the mating behavior

I Introduction

Excepting the genus *Tettigarcta*, the male adults of Cicadidae are well known to emit loud sounds by tymbal organs (OSSIANNILSSON, 1949; NAKAO, 1952; PRINGLE, 1953, 1954; HAGIWARA, 1956; AIDLEY, 1969; REID, 1971; YOUNG, 1972, WHITE, 1973; HAYASHI, 1974; SOPER *et al.*, 1976). On the other hand, remaining smaller auchenorrhynchous Homoptera have been regarded as being silent though KIRKALDY stated in 1907 that several leafhoppers possessed the power of stridulation (OSSIANNILSSON, 1949).

General attention on the sound production of smaller Auchenorrhyncha other than Cicadidae was aroused by OSSIANNILSSON (1949). He described sound producing organs similar to those of Cicadidae, and faint sounds produced by 96 Swedish species. Today, it is widely known that the adults of the smaller Auchenorrhyncha emit faint sounds (OSSIANNILSSON, 1953; STRUBING, 1958, 1962, 1970, 1977, 1978; STRUBING and HASSE, 1975; CLARIDGE and HOWSE, 1968; CLARIDGE and REYNOLDS, 1973; SMITH, Jr., 1971; MEBES, 1974; PURCELL and LOHER, 1976; TRAUER, 1978).

Intraspecific communication by sounds in these smaller Auchenorrhyncha was considered to be restricted in close range owing to their low intensities (MOOR, 1961). Tympanal organs of Cicadidae are known to be the receptors of airborne sounds produced by other individuals of conspecific species (PRINGLE, 1953, 1954). Receptors of airborne sounds like those of Cicadidae, however, have failed to be found in these smaller Auchenorrhyncha up to now (OSSIANNILSSON, 1949; LESTON and PRINGLE, 1963; SMITH and GEORGHIOU, 1972). Possibility of Johnston's organs on antennae as the receptor of airborne sounds was discussed by MOOR (1961) and CLARIDGE and HOWSE (1968). On the other hand, substrate vibrations were considered to be the main factor in their communication, and airborne sounds to be a minor factor to function only over a short distance (OSSIANNILSSON, 1949; PRINGLE, 1957). Communication through substrate vibrations was revealed in the mating behavior of the beet leafhopper, *Circulifer tenellus* (PERKES, 1969), the three species of planthoppers, *N. lugens*, *L. striatellus* and *S. furcifera* (ICHIKAWA and ISHII, 1974; ICHIKAWA *et al.*, 1975; ICHIKAWA, 1976a, 1977), the green rice leafhopper, *N. cincticeps* (ICHIKAWA, 1976b), the rhombic-marked leafhopper, *Hishimonus sellatus* (ARAI, 1977) and *Hishimonus* sp. (ARAI, 1978).

In this Chapter the sign stimuli and the effective distance of the communication in the mating behavior of *N. lugens*, *L. striatellus*, *S. furcifera* and *N. cincticeps* are described.

II Materials and Methods

Unmated adults at the age of more than 4 days after emergence were used for all experiments. All experiments were done at $25 \pm 1^\circ\text{C}$ under fluorescent lighting.

Experiment 1

N. lugens, *L. striatellus* and *S. furcifera* were used for the experiment. A disk (8 cm in diameter) with a small hole (ca. 4 mm in diameter) in the center was made of a sheet of paraffin paper. One rice seedling, on which one female was placed, was projected through the hole, and one conspecific male was released upon the disk (Fig. 7). Behavior of the couple was observed both when the disk was kept 1–2 mm apart from the stem of the seedling (A) and when the disk was kept in direct contact with the stem (B). Then, three combinations each including two species, *N. lugens* and *L. striatellus*, *N. lugens* and *S. furcifera*, and *L. striatellus* and *S. furcifera*, were made, and the species-specificity in the male response to the AV of the females was examined by applying the same methods as mentioned above. In this case the disk was kept in direct contact with the stem throughout the experimental period.

Experiment 2

N. lugens, *L. striatellus* and *S. furcifera* were used for the experiment. Each of the three rice seedlings of 15–20 cm in length at the vegetative parts was fixed to a piece of moistened polyurethane mat, and these were arranged in a row on a wooden desk. The plant-b was brought to the close vicinity of the plant-a, but these two plants were kept apart in every parts throughout the experimental period. The distance between the plant-b and plant-c was ca. 10 cm at the foot, but these two plants were kept in direct contact with each other on the tips of the leaf blades. Two males (male-1 and male-2) were individually placed on the plant-a and the plant-c, and one conspecific female was placed on the plant-b (Fig. 8). The distance between the male placed on the plant-a and the female was 3–5 mm, and that between the male placed on the plant-c and the female

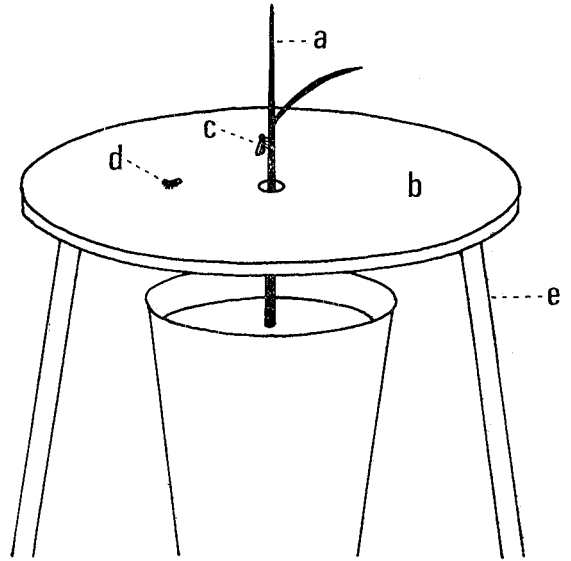


Fig. 7. An apparatus for the analysis of the manner of male response to the AV performed by female planthoppers. a, Rice plant; b, Paraffin paper disk; c, a virgin female; d, a male; e, Tripod.

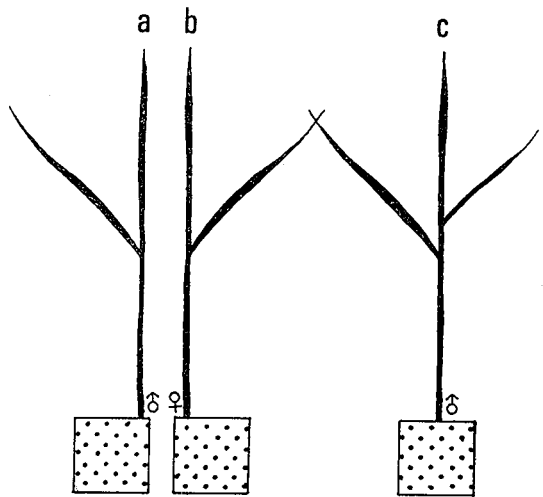
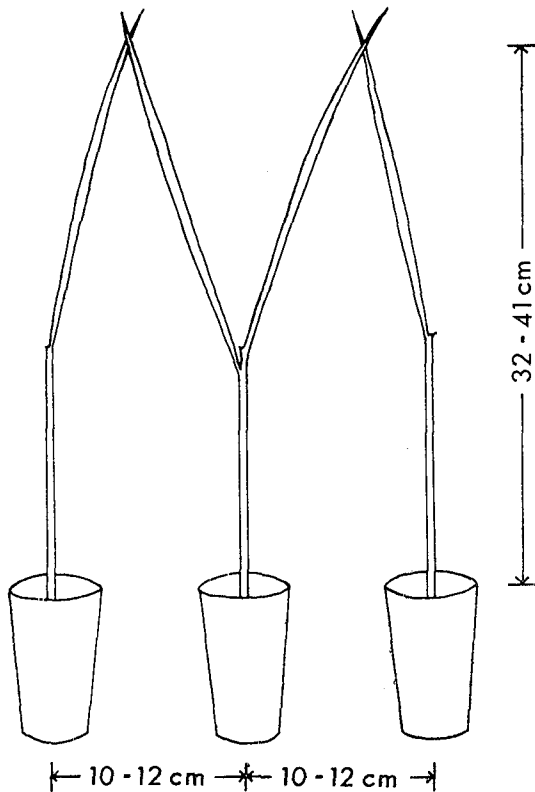


Fig. 8. A method to examine the possibility of the communication through airborne sounds. a, b and c indicate the three rice plants. Refer to the text.

was ca. 10 cm.

Experiment 3

N. lugens, *L. striatellus* and *S. furcifera* were used for the experiment. Among the three



Left Center Right

Fig. 9. A method to examine the manner of male response to the AV performed by female planthoppers. Refer to text.

rice plants having been cultured individually in pots, two leaf blades were left on one plant and one leaf blade on each of the other two plants, and other leaf blades were removed. The plant with two leaf blades was placed in the center of the three plants arranged in a row. The leaf blades of two adjacent plants were kept within the distance of direct contact (Fig 9). One male was placed on the leaf sheath of the plant set in the center, and one conspecific female on the leaf sheath of either of the outer two plants. Thereafter the behavior performed by the couple was observed. Then, species-specificity in the male response to the AV of the females was examined by placing the insects as follows. Three males each belonging to different species were placed on the plant set in the center, and one female of each species was placed on the plant set at the right side.

Experiment 4

N. lugens, *L. striatellus* and *S. furcifera* were used for the experiment. Four rice plants having been cultured individually in pots were arranged in a row. Two leaf blades were left in each rice plant, and other leaf blades were removed. Adjacent rice plants

were brought into contact with each other at the tip of the leaf blades (Fig. 10). One female was placed on the plant-b or the plant-c, and two conspecific males were placed on the plant-a and the plant-d. Thereafter the behavior performed by the three individuals was observed.

Experiment 5

N. cincticeps were used for the experiment. Two rice plants of ca 30 cm in length at the vegetative part were set side by side. One male was placed on the leaf sheath of the plant set at the left side, and one female on that set at the right side (Fig. 11). The behavior performed by the two individuals was observed while the two plants were being manipulated as follows. The leaf blade-a and the leaf blade-c were kept in contact with each other for a while. Then the leaf blade-a and the leaf blade-c were detached a few mm apart. After a while, the leaf blade-b and the leaf blade-c were brought into contact with each other, and the condition was kept for a while. Then the leaf blade-b and the leaf blade-c were detached

a few mm apart. Such manipulations were repeated in turn.

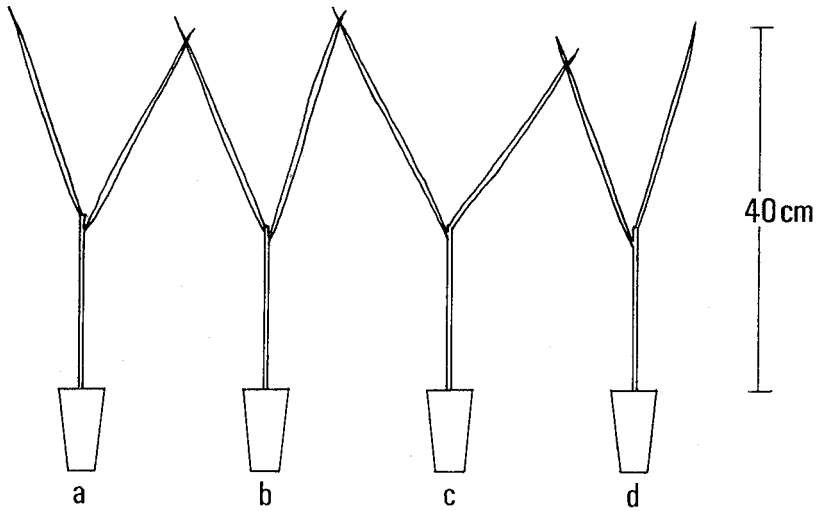


Fig. 10. A method to clarify the effective distance of the communication through vibration signals in the mating behavior of the planthoppers. Refer to text.

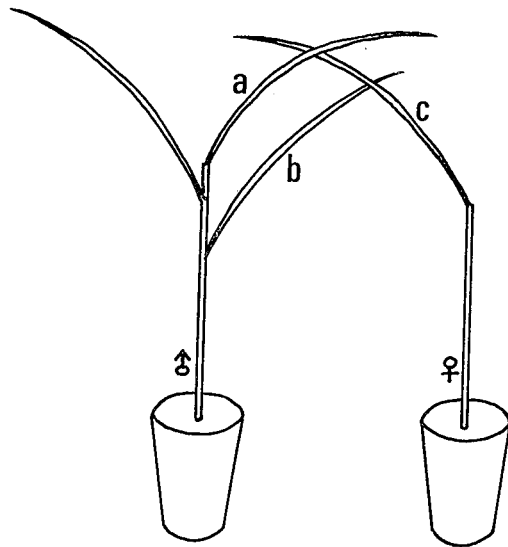


Fig. 11. A method to clarify the nature of the sign stimuli in the mating behavior of *N. cincticeps*. Refer to text.

III Results

Experiment 1

The males of the three species showed no behavioral response to the AV of the conspecific

females when the disk and the stem of the rice seedling were kept a few mm apart even when the distance between both sexes was less than 2 cm (Fig. 12-A). The same males began rapid

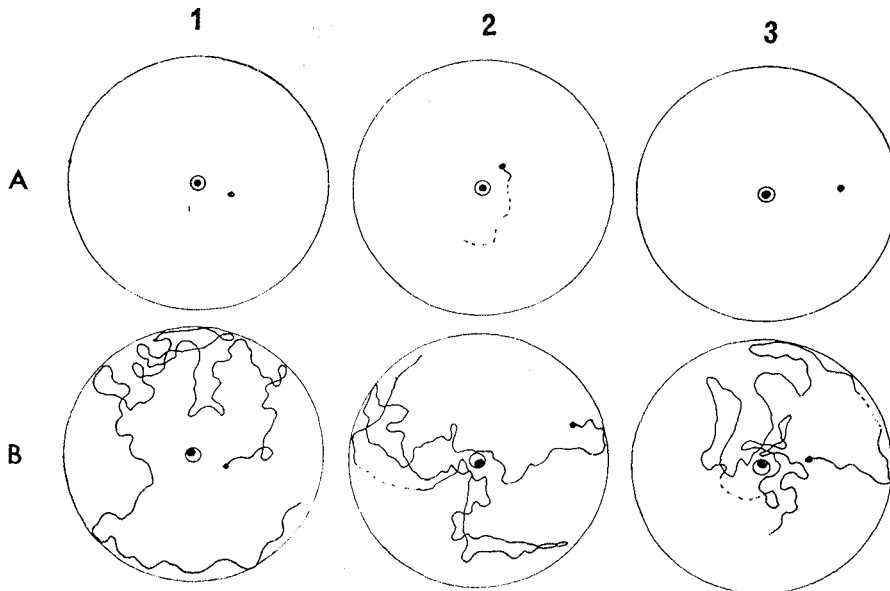


Fig. 12. Male response to the AV of the conspecific females in the three species of planthoppers. Each large circle indicates a paraffin paper disk. A small circle and a small solid circle in the center of each large circle indicate a small hole of the disk and the stem of a rice plant, respectively. The stem was detached from the disk (A) or both were kept in contact with each other (B). Male movements accompanied with the AV was traced with solid lines, and those not accompanied with AV with dotted lines. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*. Refer to Fig. 7.

walking immediately after the females began the AV when the disk was brought into contact with the stem of the seedling. This rapid walking of the males was almost synchronized with the duration of the AV (Fig. 12-B). The results obtained from the three combinations are shown in Fig. 13. The AV of the females of the three species elicited a distinct response from the conspecific males just as mentioned above. However, the AV of a given species did not elicit behavioral response from the males of other species.

The results of this experiment indicate that the males of the three species respond to some species-specific vibration signals produced by the AV of the conspecific females. It is evident that these males tried to locate the conspecific females only by following the vibration signals, but they did not moved directly toward the females. It is obvious that the manner of the transmission of the vibrations differ according to the size, the form and the physical properties of the substrates. It seemed that the effectiveness of the vibration signals and the male ability to locate the source of these signals were best investigated on grown rice plant on which these insects usually live and propagate. In addition, airborne sounds were still possible for the sign stimuli in their mating behavior when the distance of both sexes was in more close

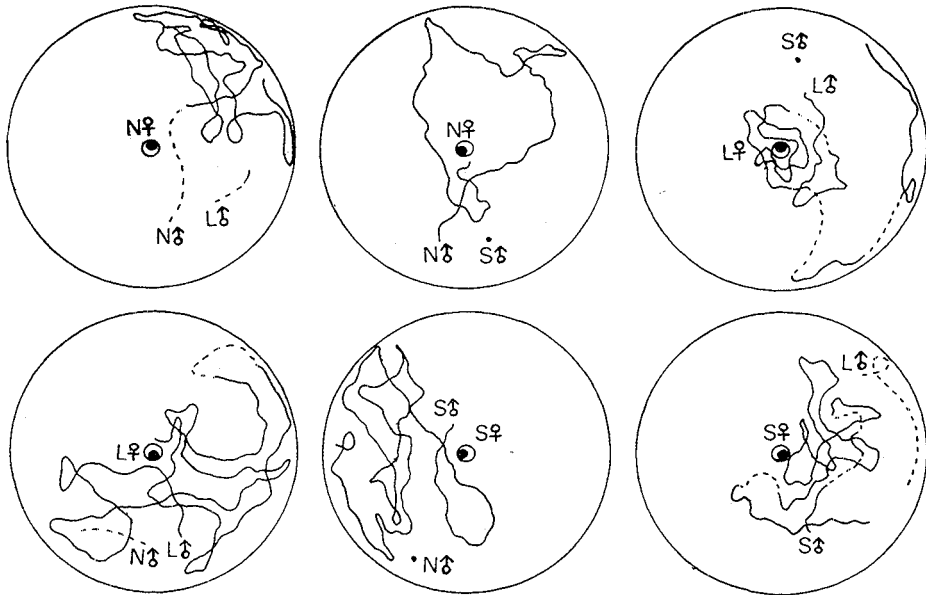


Fig. 13. Species specificity in the response of the males to the AV performed by the females in the three species of planthoppers. One female of each species was placed on the rice plant with which the disk placing two males was kept in contact throughout the experiment. N, *N. lugens*; L, *L. striatellus*; S, *S. furcifera*. Refer to Fig. 7 and Fig. 12.

proximity.

Experiment 2

The male (Male-2) placed on the plant-c began rapid walking immediately after the beginning of the AV of the females, and his rapid walking on the rice plant was almost synchronized with the duration of the AV. Having crossed the tips of the two leaf blades, this male came down to the vicinity of the female after she repeated a series of the AV. On the contrary, the male (Male-1) placed on the plant-a did not show any response to the AV even though the distance between him and the female performing the AV was 3—5 mm. Then Male-1 was moved to the plant-c and Male-2 to the plant-a. This time, only Male-1 responded to the AV, and he approached to the female by rapid walking. Above mentioned results were the same among the three species of planthoppers (Table 3).

It is apparent from this experiment that airborne sounds possibly emitted during the AV of the females are not perceived by the conspecific males even from the close proximity.

Experiment 3

Results obtained from a couple of both sexes of the same species were as follows. When the tips of the leaf blades of the adjacent rice plants were kept a few mm apart, the females of the three species of planthoppers performed the AV sporadically, and the males kept clinging to the leaf sheath of the plant set in the center without movement. On the contrary, most males began rapid walking immediately after the females began the AV when the tips of the leaf blades were kept in direct contact with each other. The duration of the movements of these males was well synchronized with the duration of the AV. The manner

Table 3. Feature of male response to the AV performed by the conspecific females* in the three species of planthoppers

| Species | Male No. | Male placement on the rice plant | No. of a series of the AV | | | | | | | | | | | | | |
|-----------------------|----------|----------------------------------|---------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
| <i>N. lugens</i> | 1 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | 2 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 1 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 2 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| <i>L. striatellus</i> | 1 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | 2 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 1 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 2 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| <i>S. furcifera</i> | 1 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| | 2 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 1 | c | + | + | + | + | + | + | + | + | + | + | + | + | + | |
| | 2 | a | - | - | - | - | - | - | - | - | - | - | - | - | - | |

* One female was placed on the rice plant-b.

+, Male rapid walking during the duration of the AV; -, Male indifference to the AV. Refer to Fig. 8 for a, b and c.

of male movements on the plants was as follows. The males soon climbed up to the vicinity of the two leaf blades of the plant set in the center. They chose the left leaf blade of the two, and proceeded rapidly when the females were placed on the plant set at the left side. Some of them chose the right leaf blade at first, but they turned back mid way, and went to the left. Having moved to the plant set at the left side by crossing the tips of two leaf blades, they walked down to the side of the females, and displayed courting behavior. On the other hand, they chose the right leaf blade of the plant set in the center when the females were placed on the plant set at the right side, and they found the females in the same manner as mentioned above. The number of males having approached to the females is

Table 4. Orientation of the males^a to the conspecific females performing the AV

| Species | Relative placement of a female on the rice plant ^b | Direction of male movement | | |
|-----------------------|---|----------------------------|-------|------------|
| | | Left | Right | Stationary |
| <i>N. lugens</i> | Left | 9 | 0 | 1 |
| | Right | 0 | 10 | 0 |
| <i>L. striatellus</i> | Left | 9 | 0 | 1 |
| | Right | 0 | 8 | 2 |
| <i>S. furcifera</i> | Left | 7 | 0 | 1 |
| | Right | 0 | 8 | 0 |

a Ten (*N. lugens* and *L. striatellus*) or eight (*S. furcifera*) males were used. Each male was placed on the rice plant set in the center.

b Refer to Fig. 9 and text for the arrangement of the plants.

shown in Table 4. The average time required from the onset of the AV to the male arrival at the vicinity of the females was 5.87 min for *N. lugens*, 4.94 min for *L. striatellus* and 7.60 min for *S. furcifera*. The males of each species showed no behavioral response to the AV of the other two species as the results obtained by using the paraffin paper disk (Table 5).

Table 5. Species-specific response and orientation of the males^a to the AV performed by the females in the three species of planthoppers

| Species | Female | | Direction of male movement | | | | | |
|-----------------------|---|------------------|----------------------------|-----------------------|------------|---------------------|------------|--|
| | Relative placement on the rice plant ^b | <i>N. lugens</i> | | <i>L. striatellus</i> | | <i>S. furcifera</i> | | |
| | | Right | Stationary | Right | Stationary | Right | Stationary | |
| <i>N. lugens</i> | Right | 5 | 0 | 0 | 5 | 0 | 5 | |
| <i>L. striatellus</i> | Right | 0 | 5 | 5 | 0 | 0 | 5 | |
| <i>S. furcifera</i> | Right | 0 | 5 | 0 | 5 | 5 | 0 | |

- a Three males each belonging to different species were simultaneously placed on the rice plant set in the center. Five males were used for each species.
- b Refer to Fig. 9 and text for the arrangement of the plants.

In addition to above mentioned results, it was observed that the frequency of a series of the AV increased conspicuously after the tips of the leaf blades were brought into contact with each other (Fig. 14). These results indicate that the males of the three species also emit some vibration signals to which the conspecific females excite and respond by performing the AV.



Fig. 14. The duration of the AV of the females (hollow rectangles) and that of the male movements (solid rectangles) in the three species of planthoppers. The behavior of both sexes was observed both when the leaves of the two plants were detached (A) and when those were kept in contact with each other (B). 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

Experiment 4

At first each female of the three species of planthoppers was placed on the plant-b. Most males of the three species placed on the plant-a responded to the AV of the females by rapid walking and approached to the females as was stated in previous experiments. On the other hand, the males placed on the plant-d showed no behavioral response to the AV, and all of them kept clinging to the leaf sheath without movement. Then the females were removed from the plant-b, and they were placed on the plant-c. All males, which showed no behavioral response to the AV under the former condition, responded to the AV by rapid walking and approached to the females. On the contrary, all of the males placed on the plant-a showed no behavioral response to the AV at this time. Above mentioned results were the same among the three species (Table 6).

Table 6. Effective range of the communication between both sexes on the rice plants^a in the three species of planthoppers

| Species | The rice plant placed one female | No. of males moved toward the female from the rice plant | |
|-----------------------|----------------------------------|--|------|
| | | a | d |
| <i>N. lugens</i> | b | 5(5) ^b | 0(5) |
| | c | 0(5) | 5(0) |
| <i>L. striatellus</i> | b | 5(5) | 0(5) |
| | c | 0(5) | 5(5) |
| <i>S. furcifera</i> | b | 4(5) | 5(5) |
| | c | 0(5) | 5(5) |

a Refer to Fig. 10 for the arrangement of the four rice plants (a, b, c and d).

b Figures in parentheses indicate the total number of the males used.

The results of this experiment and the last experiment indicate that the effective range of the communication through the vibration signals is restricted within two hills of the rice plant.

Experiment 5

When all of the tips of the leaf blades of the adjacent two rice plants were kept a few mm apart, a couple of both sexes of *N. cincticeps* kept staying on the leaf sheathes. After a while, the leaf blade-a was brought into contact with the leaf blade-c. The male having settled on the leaf sheath stopped the rubbing (R) on the head apex by the fore legs and/or R on the edge of the fore wing by the hind legs, and he began rapid walking immediately after the female began the abdominal protrusion (AP). The leaf blade-a was detached from the leaf blade-c when the male went up to the leaf blade-a. The male stopped walking immediately after this manipulation. The male began the AV in a short time at the place where he stopped. After a while, the female stopped the AP and began the R. The male continued the AV. The leaf blade-b was brought into contact with the leaf blade-c at this time. The female stopped the R immediately after this manipulation and began the AP. On the other hand, the male began rapid walking immediately after the change of the

female behavior and moved to the leaf blade-b. The leaf blade-b was detached from the leaf blade-c at this time. The male began the AV in a short time. The female stopped the AP afterwards and began the R. The leaf blade-a was brought into contact with the leaf blade-c when the male was performing the AV. The female stopped the R immediately after this manipulation and began the AP. The male began rapid walking immediately after the change of the female behavior and moved to the leaf blade-a. The leaf blade-a was detached from the leaf blade-c at this time. The male began the AV in a short time. The AV at this time was accompanied with rapid wing flaps (WF). After this time the WF was observed every time when they performed the AV. The same manipulation as mentioned above was repeated more than ten times, and the results were also the same as mentioned above. At last the leaf blade-a was kept in contact with the leaf blade-c. The male moved to the plant set at the right side by crossing the tips of the leaf blades of the two plants, and he went down to the female performing the AP. A part of above mentioned results are schematically shown in Fig. 15.

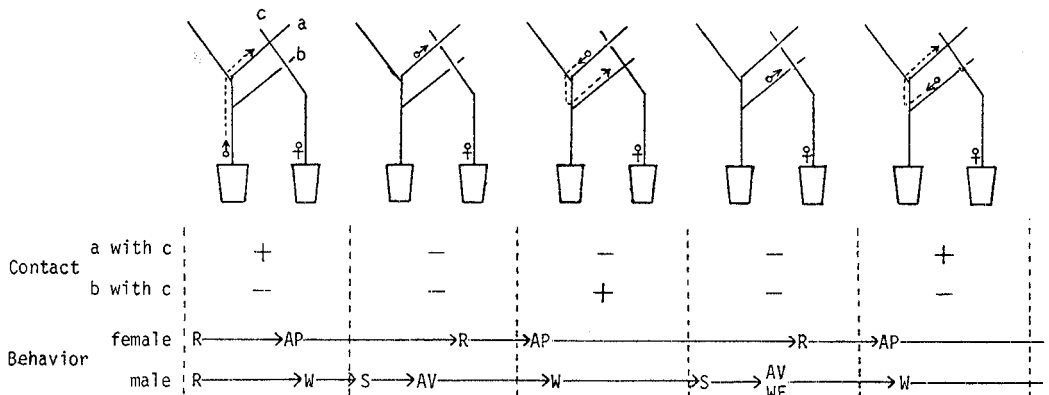


Fig. 15. Schematic representation of the communication between both sexes through substrate vibrations in the mating behavior of *N. cincticeps*. AP, Abdominal protrusion; AV, Abdominal vibration; R, Rubbing on the head apex by the fore legs and/or rubbing on the edge of the fore wings by the hind legs; WF, Wing flap, S, Stop; W, Walking. Refer to Fig. 11.

These results indicate that the sign stimuli involved in the mating behavior of *N. cincticeps* are some vibration signals transmitted to the rice plant by the AP of the female and the AV of the male.

IV Discussion

It is apparent that both sexes of the four species of Auchenorrhyncha studied in this paper communicate through some species-specific vibration signals transmitted to the rice plant in their mating behavior. Effective range of communication through the vibration signals attained to at least 60–80 cm on the rice plant. Such communication was possible between

two adjacent rice plants when these plants were only kept lightly in contact with each other. No experimental results, however, support the possibility of the communication through airborne sounds. In the species of Dictyopharidae, *Dictyophara europaea* (STRÜBING, 1977), and the species of Jassidae, *Euscelis insisus* (TRAUE, 1978), it was concluded that intraspecific communication through vibration signals transmitted to the host plants was valid. Many species of Heteroptera are known to emit faint sounds like auchenorrhynchous Homoptera (LESTON, 1957; HASKELL, 1958; MOOR, 1991; GOGALA, 1969, 1970; COKL *et al.*, 1972). However, the perception of airborne sounds in their intraspecific communication has not been ascertained so far. Among these Heteroptera, two species of Cydnidae, *Tritomegas bicolar* and *Canthopharus dubias*, were revealed to communicate with the conspecific individuals through substrate vibrations (GOGALA *et al.*, 1974). On the other hand, an Australian species of *Rhagadotarsus* (Heteroptera, Gerridae) were revealed to communicate through specific surface waves produced by the leg movements of both sexes (WILCOX, 1972). In the light of above mentioned results, it is assumed that auchenorrhynchous Homoptera other than Cicadidae and Heteroptera utilize substrate vibrations as the sign stimuli in their intraspecific communication.

According to MARKL (1969), intraspecific communication through substrate vibrations in insects was known in Plecoptera, Orthoptera, Isoptera, Psocoptera, Coleoptera, Diptera and Hymenoptera. In addition to these orders, Mecoptera (RUPPRECHT, 1974), Neuroptera (RUPPRECHT, 1975) and above mentioned Hemiptera including the four species of Auchenorrhyncha studied in this paper were also revealed to communicate through substrate vibrations. Since AUTRUM (1941) discovered that the subgenual organ of tettigoniid species (Orthoptera) responded to substrate vibrations, studies on vibration receptors have been progressed (AUTRUM, 1963), and trichoid sensilla and chordotonal sensilla were also considered to be the receptors (DETHIER, 1963). In the cricket, *Teleogryllus emma*, the sensory hairs on the tibial spur of the hind legs, which responded to the vibration stimuli by the distinct afferent impulses, were considered to be the vibration receptor (AI and MINAMIMURA, 1976). Vibration receptors of Hemiptera, however, seem not to have been detected so far.

Visual and olfactory factors were excluded from the possible sign stimuli involved in the mating behavior of the four species studied in this paper. Following results of the preliminary experiments done by using *N. lugens* also eliminated the possibility of olfactory stimuli; male indifference to the odor of the females confined in a simple olfactometer, male indifference to the female substances extracted with organic solvents (n-hexane, methylene chloride and methanol) and successful copulation by five males whose antennae were amputated at the base. Although olfactory stimuli (sex pheromones) are known to function in the mating behavior of sternorrhynchous Homoptera such as *Matsucoccus resinosae* (DOANE, 1966), *Aonidiella aurantii* (TASHIRO and CHAMBERS, 1967) and *Megoura viciae* (MARSH, 1975), and Heteroptera such as *Oncopeltus fasciatus* (LENER, 1967), *Nezara viridula* (MITCHELL and MAU, 1971; BRENNAN *et al.*, 1977) and *Rhodnius prolixus* (BALDWIN *et al.*, 1971), the author is not acquainted with studies dealing with olfactory factors as the sign stimuli in the mating behavior of Auchenorrhyncha.

Chapter 3. Properties and the roles of the vibration signals

I Introduction

OSSIANNILSSON (1949) devised the following methods for listening to faint sounds produced by Auchenorrhyncha other than Cicadidae. He listened to the sounds directly by ear from the distance of close proximity to the insects, or amplified the sounds with the aid of the belly of the violin as a resonant box, with the stethoscope or with the combination of microphones and an amplifier. LESTON (1957) used the stethoscope to detect faint sounds produced by Heteroptera. Thereafter other researchers used microphones and amplifiers to detect faint sounds produced by these groups of the insects (STRÜBING, 1958; HASKELL, 1958; MOOR, 1961; CLARIDGE and HOWSE, 1968; GOGALA, 1969; ČOKL *et al.*, 1972; MEBES, 1974; PURCELL and LOHER, 1976). On the other hand, the author and coworkers detected the vibration signals transmitted to the rice plant by the four species of Auchenorrhyncha with the phonograph cartridge put on the plant (ICHIKAWA and ISHII, 1974; ICHIKAWA *et al.*, 1975; ICHIKAWA, 1976a, b). ARAI (1977, 1978) used the crystal earphone to detect the vibration signals transmitted to the host plant by *Hishimonus*.

In this chapter the results obtained from the oscillographic analyses of the vibration signals emitted by the four species of Auchenorrhyncha, and their precise roles in the mating behavior are described.

II Materials and Methods

N. lugens, *L. striatellus*, *S. furcifera* and *N. cincticeps* were used for the experiments. These insects were sexed within one day after emergence (0 day), and they were reared on rice seedlings. Unmated sexually mature adults were used for most of the experiments. Experiments were done at 25 ± 1 °C with the fluorescent lighting or in darkness. Vibration signals transmitted to the rice plant were detected with a phonograph cartridge sensitive over a frequency range of 0.02–20 KHz (M-2100/5, Micro sound Co. Ltd.) put on the leafsheath of the plant. Vibration signals transmitted to a sheet of paraffin paper were also detected by the cartridge. In all experiments detected vibrations were amplified with an amplifier (PMA-350z, Nippon Columbia Co. Ltd.) and recorded on sound tapes (SLH-1100-BL, Sony Corp.) with a tape deck (A-3300-2T, TEAC Co. Ltd.). The records were fed on an oscilloscope (Model 181 A, Hewlett Packard), and obtained oscillograms were analysed. On the other hand, amplified vibrations were monitored with a headphone sensitive over a frequency range of 0.02–20 KHz (E-55, Coral Audio Corp.), and the relation between the vibration signals and the behavior was examined. In other experiments the manner of the response of the insects to the playback of the records was examined as follows. The records were played back and were transmitted from a loud-speaker sensitive over a frequency range of 0.08–15

KHz (PC-399, Toa Electric Corp.) to a sheet of thin paper or a rice plant on which a single insect was placed. Behavior performed by the insect was visually observed, and the vibration signals emitted by the insect was detected with the same methods mentioned above. Other detailed methods in each experiment will be described in the results section.

III Results

1. Vibration signals emitted by a single insect

1) *N. lugens*, *L. striatellus* and *S. furcifera*

Female signals

It was ascertained that sexually mature virgin females of the three species of planthoppers sporadically performed the abdominal vibration (AV) when they were individually placed on the rice plant without the presence of any male. Female vibration signals emitted by the AV were composed of a train of monotonous pulses (Fig. 16-A). Pulse repetition frequency

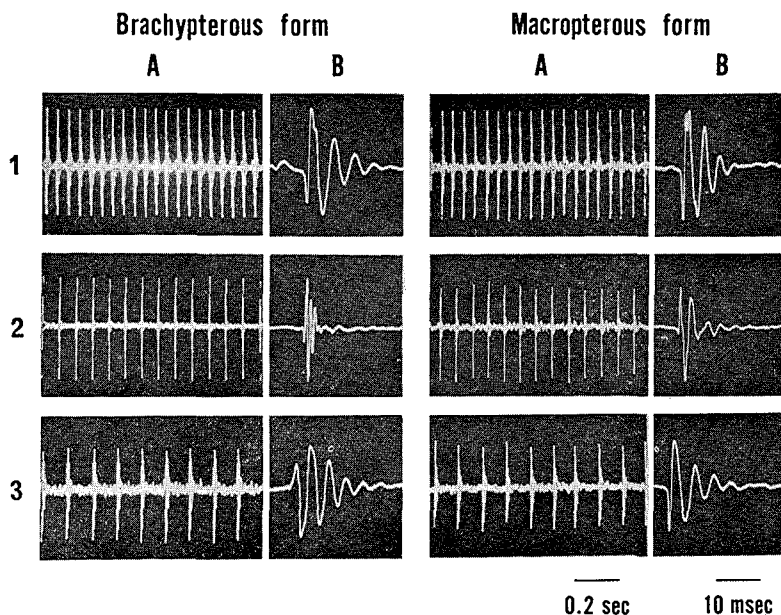


Fig. 16. Oscillograms of the female vibration signals transmitted to the rice plant by the AV in the three species of planthoppers. Signals were detected from the rice plant on which one female was placed. A, Features of pulse repetition frequency; B, Wave form of each pulse. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

of the signals was almost the same between the brachypterous form and the macropterous one in each species. The average pulse repetition frequency of the signals emitted by ten macropterous females of each species was 21.12/sec (18.89—23.44) for *N. lugens*, 13.23/sec (12.74—14.32) for *L. striatellus* and 9.68/sec (7.95—11.88) for *S. furcifera*. Thus the pulse repetition frequency differed among the three species though there were some intraspecific

variations as described in the parentheses. It was revealed from an analysis with a video tape recorder that one pulse of the signals was emitted during one going and returning movement of the abdomen in a dorso-ventral direction. The wave train in each pulse was also somewhat different among the three species, and the wave frequency was usually high in *L. striatellus* compared with that of the other two species (Fig. 16-B).

Male response to the playback of above mentioned female vibration signals was examined to know whether these signals were aimed at the conspecific males for mating. First experiment was done by using the males of *N. lugens* which were individually placed on the leaf sheath of the rice plant. The playback was transmitted from the loud-speaker to one of the three leaf blades of the plant. Five males responded clearly to the playback by rapid walking during each duration of the playback just as their response to the AV of the females. Thus they climbed up to the leaf blade on which the loud-speaker was put. At last they moved to the loud-speaker (Fig. 17). Next experiment was done by using the males of the

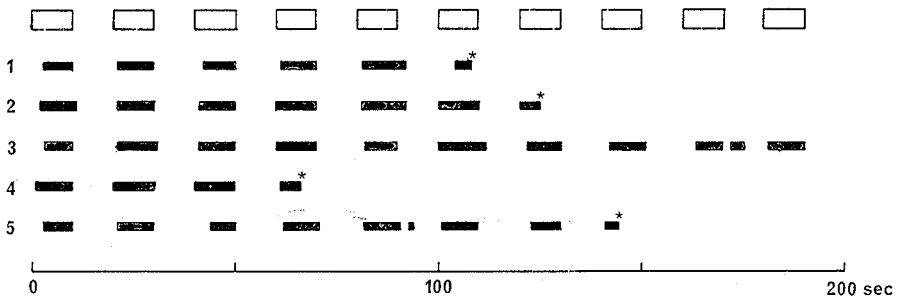


Fig. 17. Male response to the playback of the female vibration signals on a rice plant in *N. lugens*. Hollow rectangles indicate the duration of the playback, and solid rectangles the duration of the male movements on the rice plant. Asterisks indicate the time of male arrival at a loud-speaker. The playback was transmitted to one of the three leaf blades of the rice plant on which one male was placed. Five males were used.

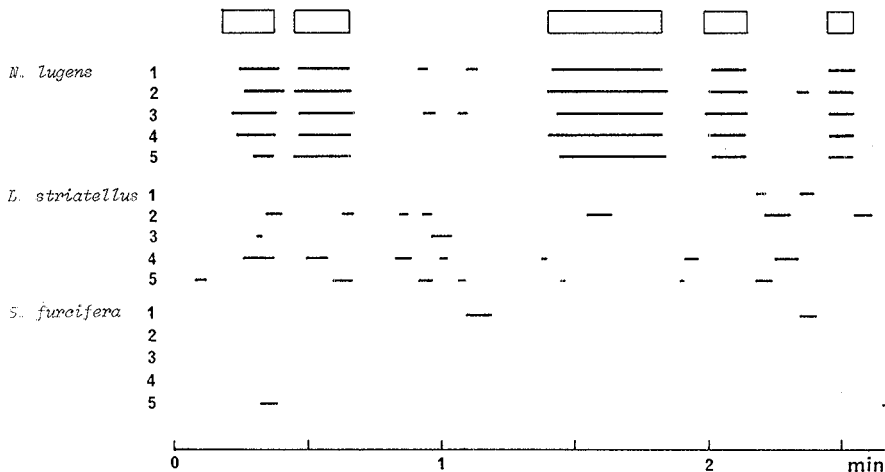


Fig. 18. Species-specificity in the male response to the playback in the female vibration signals of *N. lugens*. Hollow rectangles indicate the duration of the playback transmitted to a sheet of thin paper, and solid lines the duration of the male movements on the thin paper. Five males were used for each species.

three species to examine the species-specificity of the signals. The playback of the signals of each species was transmitted to a sheet of thin paper on which the males of the three species were individually placed. The responses of the males to the playback of the female signals of *N. lugens* by rapid walking are shown in Fig. 18. It is apparent that only the males of *N. lugens* respond to the playback. Similar species-specific male responses to the playback of the signals of the other two species are shown in Fig. 19 and Fig. 20.

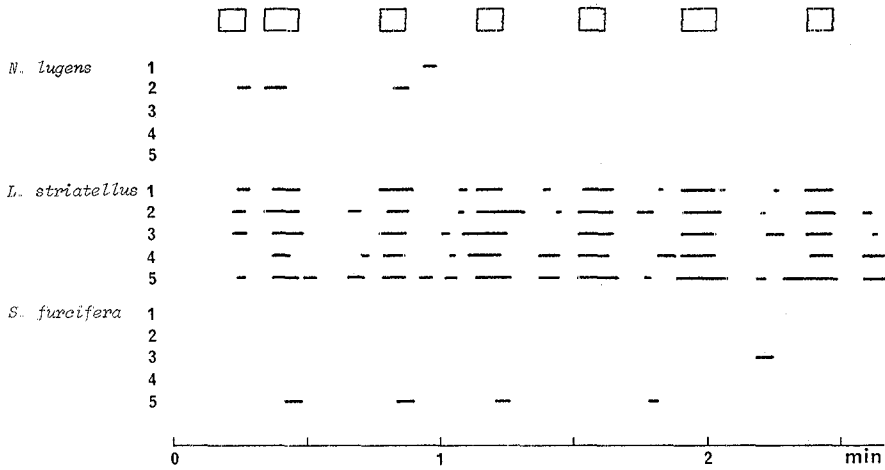


Fig. 19. Species-specificity in the male response to the playback of the female vibration signals of *L. striatellus*. Hollow rectangles indicate the duration of the playback transmitted to a sheet of thin paper, and solid lines the duration of the male movements on the thin paper. Five males were used for each species.

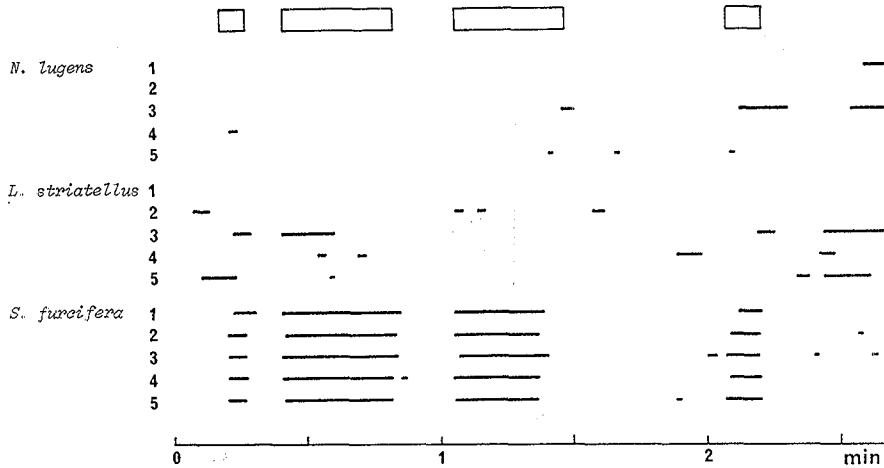


Fig. 20. Species-specificity in the male response to the playback of the female vibration signals of *S. furcifera*. Hollow rectangles indicate the duration of the playback transmitted to a sheet of thin paper, and solid lines the duration of the male movements on the thin paper. Five males were used for each species.

Male signals

The males of the three species of planthoppers performed no noticeable behavior when they

were individually placed on the rice plant. Most of them, however, began to emit species-specific vibration signals within 5 min after the settlement on the rice plants (Table 7).

Table 7. Time (sec) of the first emission of the vibration signals by a single male placed on the rice plant in the three species of planthoppers

| Species | Male* No. | | | | | | | | | | Mean |
|-----------------------|-----------|----|-----|-----|-----|----|-----|-----|----|-----|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| <i>N. lugens</i> | 362 | 90 | 108 | 75 | 250 | 62 | 160 | 205 | 30 | 45 | 158.7 |
| <i>L. striatellus</i> | 30 | 34 | 56 | 73 | 131 | 38 | 60 | 139 | 19 | 16 | 59.6 |
| <i>S. furcifera</i> | 160 | 22 | 31 | 102 | 84 | 64 | 68 | 342 | 81 | 179 | 113.3 |

* All males used were the 6th day of adult emergence.

Once they began to emit the signals, many of them repeated intermittent emission of the same signals at least several times. The oscillograms of the signals of the three species are shown in Fig. 21 and Fig. 22. It is apparent from Fig. 21 that the patterns of these signals are markedly different among the three species.

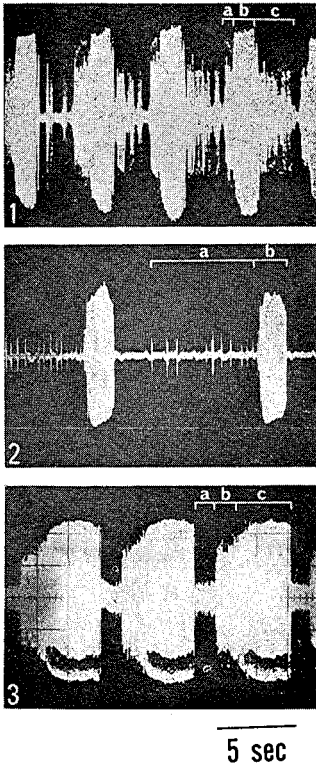


Fig. 21. Oscillograms of the male vibration signals transmitted to the rice plant in the three species of planthoppers. Signals were detected from the rice plant on which one male was placed. Each unit of one complete signal is indicated with a, b or c. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

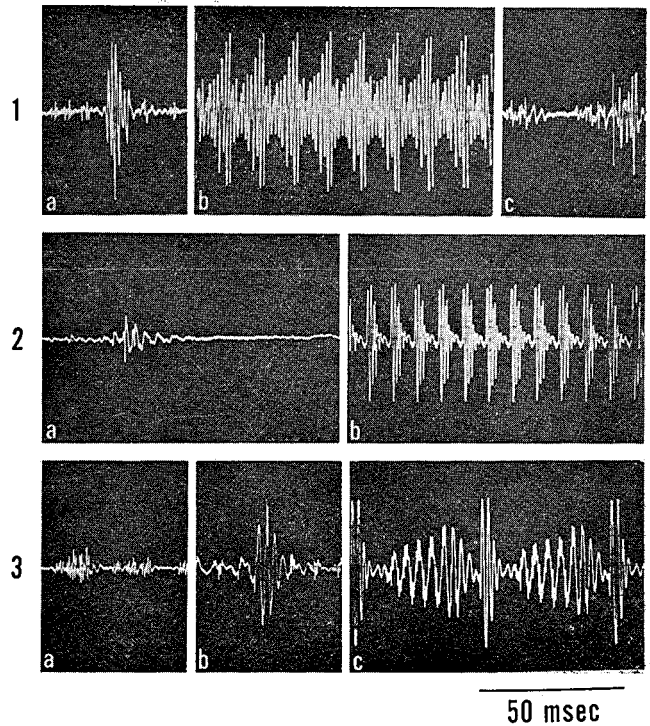


Fig. 22. Oscillograms of each unit of the male vibration signals in the three species of planthoppers. Refer to Fig 21 for a, b and c. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

The units of each complete signal were indicated with a, b and c for *N. lugens* and *S. furcifera* or with a and b for *L. striatellus*. As shown in Fig. 22, wave forms of the units were also markedly different among the three species. When ten males of *N. lugens* were individually placed on the rice plant or a sheet of paraffin paper, they emitted vibration signals within 5 min after the placement on each of the substrates (Table 8). These results indicate that sexually mature males emit vibration signals irrespective of the nature of the substrates on which they landed.

Table 8. Time (sec) of the first emission of the vibration signals by male *N. lugens* after settling on different substrates

| Substrate | Male No. | | | | | | | | | | Mean \pm 95% f. 1. |
|----------------|------------------|-----|-----|----|-----|-----|-----|-----|-----|-----|----------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Rice plant | 205 ^b | 40 | 55 | 57 | 210 | 38 | 90 | 110 | 275 | 60 | 114.0 \pm 60.7 |
| Paraffin paper | 95 | 205 | 167 | 19 | 67 | 108 | 245 | 56 | 169 | 158 | 128.0 \pm 51.1 |

a Each male was placed on either substrate on which a cartridge was attached to detect the vibration signals.

b Observation for each insect was discontinued immediately after the first signal emission.

Female response to the playback of above mentioned male vibration signals was examined to know whether these signals were aimed at the conspecific females for mating. The results are shown in Table 9. The females of the three species individually placed on the rice plant

Table 9. Species-specific response of the females to the playback of the male vibration signals in the three species of planthoppers

| Species | Female ^a No. used | Repetitions per female | Playback of male vibration signals ^b | | |
|-----------------------|---------------------------------|---------------------------|---|-----------------------|---------------------|
| | | | <i>N. lugens</i> | <i>L. striatellus</i> | <i>S. furcifera</i> |
| <i>N. lugens</i> | 5 | 10 | 49 ^c | 1 | 0 |
| <i>L. striatellus</i> | 5 | 10 | 0 | 48 | 0 |
| <i>S. furcifera</i> | 5 | 10 | 1 | 1 | 47 |

a Sexually mature virgin females were used.

b Playback was transmitted to the rice plant on which one female was placed.

c Response of each female was judged from the performance of the AV just before or after the end of one complete unit of the male signal.

responded clearly to the playback of the conspecific males by the performance of the AV. These females showed no behavioral response to the playback of the other two species.

External male organs to produce the vibration signals were scrutinized under a binocular microscope ($\times 60$) by making use of the distinct male response to the playback of the female signals. The males whose wings had been amputated at the base were individually released on the arena made of tightly stretched paraffin paper sheet on which the cartridge was

placed to detect the male signals. These males began rapid walking immediately after the playback was transmitted to the arena. They stopped the motion and began to emit the signals shortly after the playback was interrupted. The first and second abdominal terga of these males were vibrating during the signal emission. It was apparent that these male abdominal terga were specialized as a tymbal organ. In the males of the three species, the first abdominal tergum was consisted of a uniform yellowish membrane, and the second was consisted of a central black part and surrounding yellowish membrane. All other abdominal terga were consisted of uniform blackish cuticle. On the other hand, the abdominal terga of these females were consisted of uniform blackish cuticle. Above mentioned features of the abdominal terga are shown in Fig. 23.

2) *N. cincticeps*

Female signal

The females individually placed on the rice plant began the rubbing behavior and the wing beat described in Chapter 1. Irregular miscellaneous vibrations were detected during the performance of these types of behavior. The females emitted the vibration signals sporadically at intervals of above mentioned behavior. The signal was composed of a regular repetition of two different pulses (Fig. 24-A). One of the pulses was more faint in the intensity and preceded the other by 12—13 msec (Fig. 24-B). The average pulse repetition frequency of the signal emitted by ten females was 13.77/sec (12.66—14.79).

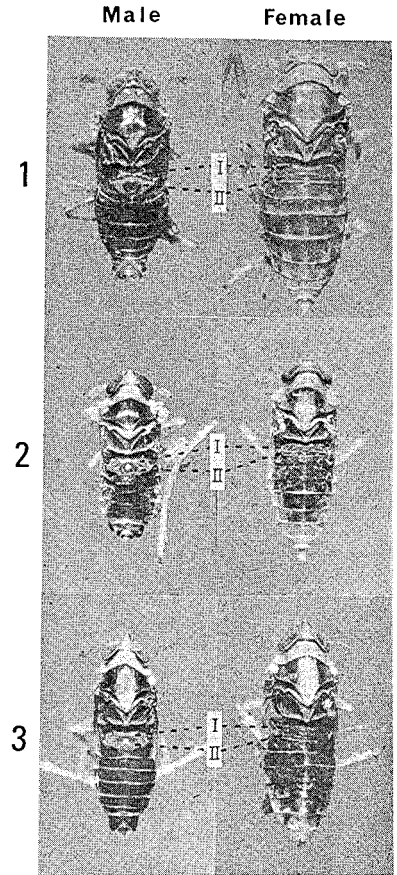


Fig. 23. Dorsal view of the macropterous adults of the three species of planthoppers. I, 1st abdominal tergum; II, 2nd abdominal tergum. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*.

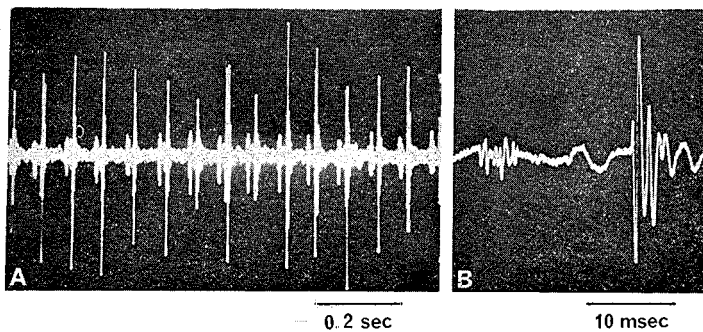


Fig. 24. Oscillograms of the female vibration signal transmitted to the rice plant by the AP in *N. cincticeps*. Signals were detected from the rice plant on which one female was placed. A, Features of pulse repetition frequency; B, Wave forms of two different pulses.

Male response to the playback of the signal was examined to know whether the signal was aimed at the conspecific males for mating. The playback was transmitted from the loud-speaker to the rice plant on which one male was placed. Five males clearly responded to the playback both by the emission of the vibration signals immediately after the transmission of the playback, and by the rapid walking during each duration of the playback. When the playback was transmitted to one of the three leaf blades of the rice plant, the males placed on the leaf sheath of the plant began rapid walking immediately after the beginning of the transmission, and climbed up to the leaf blade on which the loud-speaker was put. At last they moved to the loud-speaker. These males showed no response to the playback of the miscellaneous vibrations transmitted to the rice plant during the rubbing behavior and the wing beat of the females.

Male signal

The males individually placed on the rice plant began the rubbing behavior and the wing beat described in Chapter 1 just as the conspecific females. Irregular miscellaneous vibrations were detected during the performance of these types of behavior. On the other hand, the males emitted distinct vibration signals immediately after they settled on the rice plant and/or at intervals of above mentioned behavior. Average time from the settlement to the first emission of the signal by ten males was 72.2 sec. (8-207 sec). The author happened to hear the male vibration signal directly by ear at the distance of ca. 20 cm from the male which had just landed on an empty thin paper bag left on the floor of the author's house at around 21 o'clock on August 4 in 1977. Since no airborne sound could be heard when the male was emitting the signal on the rice plant, it was apparent that the signal was amplified with the resonance of the paper. These observations indicate that males of this species usually emit the vibration signals shortly after they landed on something irrespective of the quality just like the males of the three species of planthoppers. The oscillograms of the male vibration signal are shown in Fig. 25 and Fig.

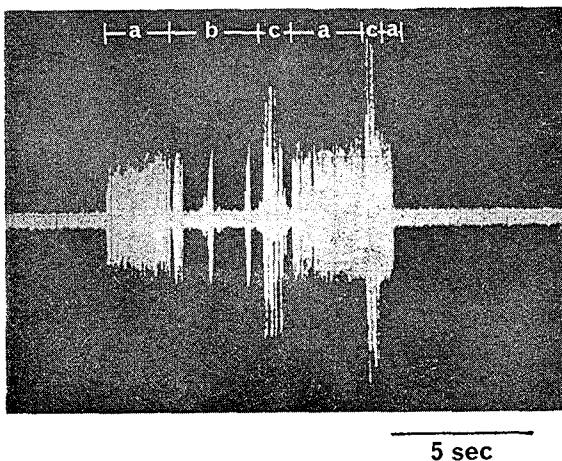


Fig. 25. Oscillogram of the male vibration signal transmitted to the rice plant in *N. cincticeps*. The signal was detected from the rice plant on which one male was placed. Each unit of one complete signal was indicated with a, b or c.

26. The signal was composed of the complex combination of the three different units of pulse trains indicated with a, b and c. As shown in Fig. 25, a, b and c were different each other both in wave form and in wave frequency.

Female response to the playback of the signal was examined to know whether the signal was aimed at the conspecific females for mating. The playback was transmitted 5 times per female. Five females clearly responded to the playback by the emission of the vibration signal immediately after the transmission of the playback. Female vibration signal at this time had the same pulse pattern with the signal emitted by a single female, and it was observed that the female

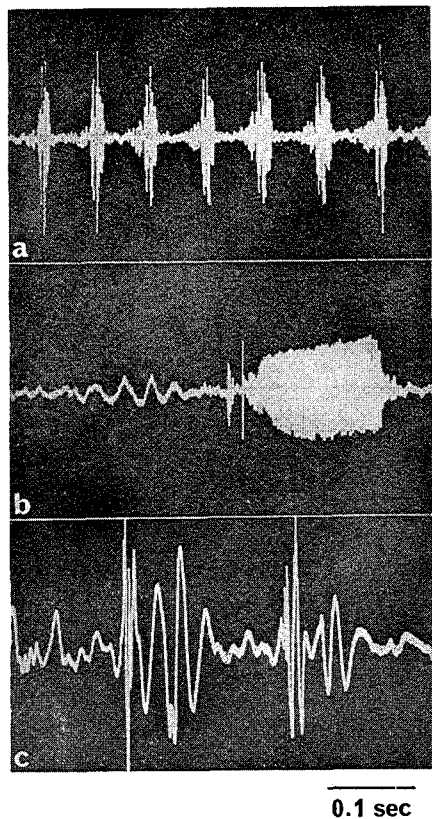


Fig. 26. Oscillogram of each unit of the male vibration signal in *N. cincliceps*. Refer to Fig. 25. for a, b and c.

emitting the signal was performing the abdominal protrusion (AP). These females showed no response to the playback of the miscellaneous vibrations transmitted to the rice plant during the rubbing behavior and the wing beat of the males.

2. Vibration signals emitted by both sexes in the mating behavior

1) *N. lugens*, *L. striatellus* and *S. furcifera*

The method for the detection of the vibration

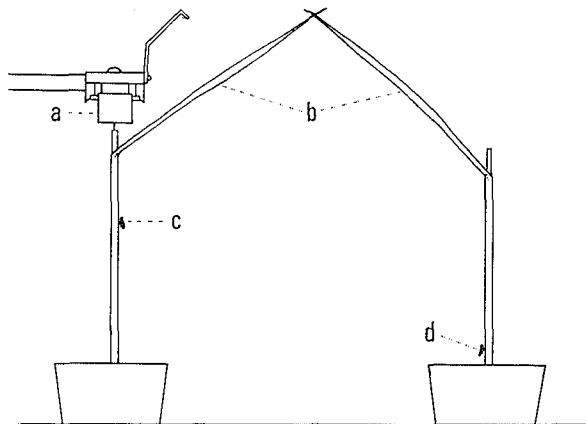


Fig. 27. A method for the detection of the vibration signals transmitted to the rice plant in the mating behavior of the four species of Auchenorrhyncha. a, Phonograph cartridge; b, Rice plant; c, One female; d, One male.

signals emitted during the mating behavior is shown in Fig. 27. One male was placed on the leaf sheath of a rice plant which was kept in direct contact with the rice plant having placed one conspecific female at the tips of the leaf blades. Vibration signals were detected from the plant on which the female had been placed.

Most males of the three species of planthoppers began to emit the vibration signals having species-specific pattern (see Fig. 21 and Fig. 22) within 5 min after the placement on the plant just as when they were individually placed on the plant. The females of the three species immediately responded to the signals of the conspecific males by the AV. Male rapid walking toward the females was well synchronized with the duration of the female vibration signals produced by the AV (see Fig. 16). The males stopped rapid walking and emitted the signals immediately after the females interrupted the AV. Unless the females responded to the signals by the emission of the signals by the AV, the males continued to emit the signals until the females responded. Such mutual communication through the vibration signals alternately emitted by both sexes was continued until the males came in close proximity to the females (Fig. 28-A). Thereafter the males emitted the signals a few or several times before copulatory

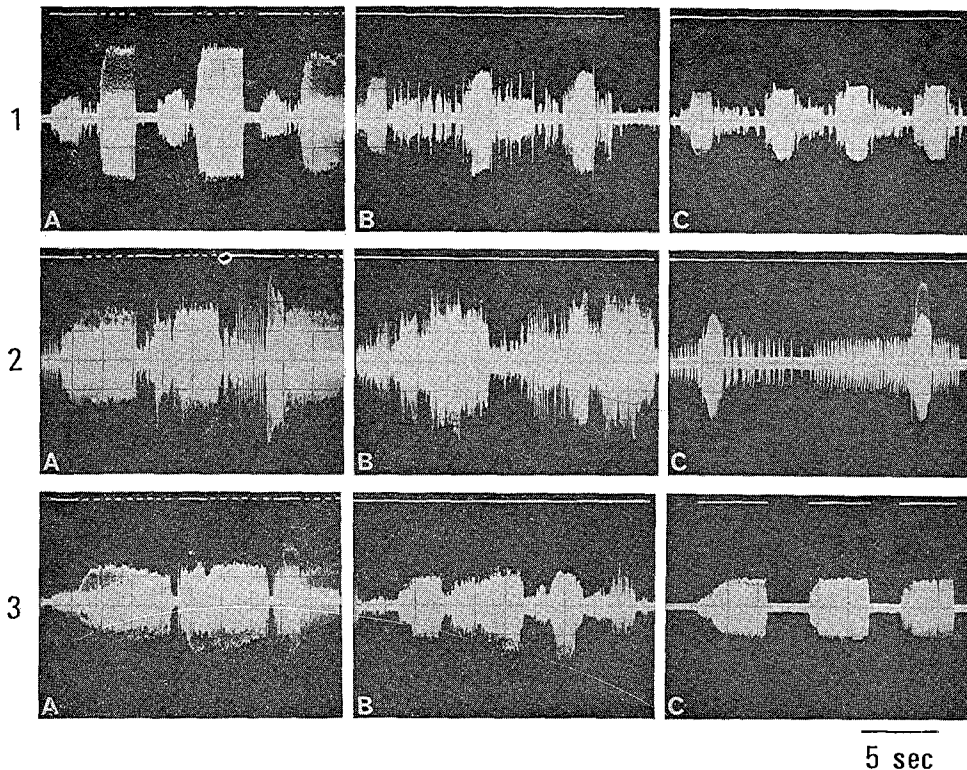


Fig. 28. Oscillograms of the vibration signals transmitted to the rice plant by both sexes in the mating behavior of the three species of planthoppers. White solid lines traced on the upper parts of the oscillograms indicate the duration of the male signals, and white dotted ones the duration of the female signals. A, Alternate signal emission by both sexes at the time of male approach toward the female; B, Signal emission by the male immediately before copulation; C, Male postcopulatory signals. 1, *N. lugens*; 2, *L. striatellus*; 3, *S. furcifera*. Refer to Fig. 27.

attempt (Fig. 28-B). Some males which once failed to copulate always emitted the signals before again performing copulatory attempt. In *N. lugens* and *S. furcifera*, male signals emitted at this time were similar to earlier signals. The wing flaps were frequently observed simultaneously with the signal emission at this time. In *L. striatellus*, male signals accompanied with the wing flaps were somewhat different from the earlier signals. Five males of each species whose wings had been amputated at the base also emitted normal vibration signals and succeeded in copulation. It is concluded from these observations that the wing flaps performed by the males shortly before copulation might be the expression of their extreme excitement. No signal was detected during the copulation.

All males of the three species began to emit postcopulatory signals within a few minutes after the copulation had finished (Fig. 28-C). The pulse patterns of the postcopulatory signals were similar to those emitted during the precopulatory period. On the other hand, mated females neither emitted postcopulatory signal, nor did they respond to the male postcopulatory signals. Above mentioned results depict the common feature of the relation between the emission of the vibration signals and the behavior under the fluorescent lighting. The same process of the

signal emission by both sexes of the three species was detected in darkness. And it was ascertained from the hatch of the 1st instar nymphs from the eggs laid by the females that all couples were succeeded in copulation (Table 10).

Table 10. Mating behavior under darkness^a in the three species of planthoppers

| Species | No. of couples | Signal emission | | No. of couples succeeded in copulation ^b |
|-----------------------|----------------|-----------------|--------|---|
| | | Male | Female | |
| <i>N. lugens</i> | 5 | 5 | 5 | 5 |
| <i>L. striatellus</i> | 5 | 5 | 5 | 5 |
| <i>S. furcifer</i> | 5 | 5 | 5 | 5 |

a Fluorescent light, sole light source, was put out after placing insects on the rice plants.

b Success in copulation was judged from the hatch of the 1st instar nymphs from eggs laid by the females.

Male postcopulatory signals in the three species seemed to play important role under some circumstance. Female response to the playback of the signals was compared between virgin ones and mated ones. The playback was transmitted to a sheet of thin paper on which one female had been placed. As a result, mated females (1 day after copulation) of the three species never responded to the playback. On the other hand, all sexually mature virgin females of the three species responded to the playback by the AV. These results are shown in Table 11. The results indicate that the postcopulatory signals are also aimed at the mating partners just like the signals emitted by a single male.

Table 11. Influence of the mating upon the female response to the playback of the male postcopulatory signals in the three species of planthoppers

| Female | | Repetitions per female | Playback ^a | | |
|-----------------------|----------|------------------------|-----------------------|-----------------------|--------------------|
| Species | No. used | | <i>N. lugens</i> | <i>L. striatellus</i> | <i>S. furcifer</i> |
| <i>N. lugens</i> | Virgin 5 | 5 | 24 ^b | — | — |
| | Mated 5 | 5 | 0 | — | — |
| <i>L. striatellus</i> | Virgin 5 | 5 | — | 23 | — |
| | Mated 5 | 5 | — | 0 | — |
| <i>S. furcifer</i> | Virgin 5 | 5 | — | — | 24 |
| | Mated 5 | 5 | — | — | 0 |

a Playback was transmitted to a sheet of thin paper on which one female was placed

b Response of each female was judged from the performance of the AV just before or after the end of one complete unit of the male signal.

The mouth of the glass bottle (7 cm in diameter, 13 cm in height) used for the mass rearing

of the insects were usually covered with the wire gauze. A sheet of thin paper was also used as the cover for the rearing of the 1st instar nymphs of *L. striatellus*, which was the smallest in body size among the four species, to protect them from escape. Male vibration signals were felt on the author's ear at the distance of about 30 cm apart from the bottle when some adults of this species had been confined in the bottle with the 1st instar nymphs. The sounds, however, could not be heard when the males were cleared off from the paper or the cover was changed to the wire gauze. Above mentioned observations indicate that the vibration signals emitted by the males clinging to the paper are amplified with the resonance of the paper. Male vibration signals of *N. lugens* and *S. furcifera* were also heard directly by ear when the cover was changed to the paper and the males were placed on the inner surface of the paper cover. When a couple of both sexes of *N. lugens* was placed on a sheet of tightly stretched paraffin paper which covered the open end (ca. 7 cm in diameter) of a plastic cup, the communication through the vibration signals and the mating behavior were normally performed excepting some difficulty for the male to locate the female. It is apparent from above mentioned observations that these planthoppers emit the vibration signals irrespective of the presence or absence of the rice plant, and that the mating behavior is performed on condition that substrates are suitable for the transmission of the signals.

2) *N. cincticeps*

The method for the detection of the vibration signals emitted during the mating behavior was the same with that used for the three species of planthoppers (see Fig. 26). Most males emitted the vibration signals similar to those emitted by a single male (see Fig. 24 and Fig. 25) within a few minutes after the placement of the rice plant. The females immediately responded to the male signals by the emission of the vibration signals having monotonous pulse train (see Fig. 23). The males performed the abdominal vibration (AV) at the time of the signal emission, and the females continued the abdominal protrusion (AP) during the time of the signal emission. The males began rapid walking immediately after the beginning of the emission of the female signals. The males stopped and began to emit the signals immediately after the females interrupted the signal emission. The males sometimes performed the wing flaps simultaneously with the signal emission. Such communication through the vibration signals between both sexes at the time of male approach to the females is shown in Fig. 29-A. The males arrived at the vicinity of the females emitted the part of the signal, the unit b in Fig. 24, just before copulatory attempt. The wing flaps were always accompanied with the signals emitted at this time. Some of the males which once failed to copulate always emitted the signal a few times before again performing copulatory attempt. Above mentioned male signals just before copulation are shown in Fig. 29-B, but the vibrations caused by the rapid male walking masked the signals. The unit b of the male signal was detected a few times immediately after the beginning of the copulation.

Both sexes began the peculiar behavior described in Chapter 1 (see Fig. 5) shortly after the finish of the copulation. This behavior, however, accompanied with no special vibration signal. The males occasionally emitted distinct postcopulatory signals whose pulse pattern was similar to those emitted during the precopulation period and those emitted by a single male (Fig. 29-C). In addition to the male postcopulatory signal, both sexes having been staying on the same plant

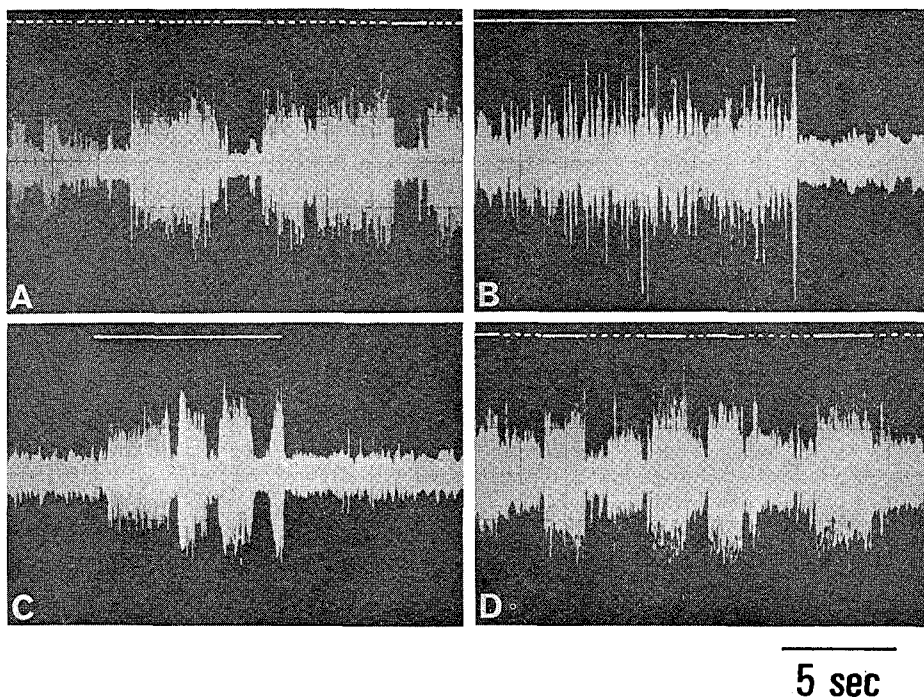


Fig. 29. Oscillograms of the vibration signals transmitted to the rice plant by both sexes in the mating behavior of *N. cincticeps*. White solid lines traced on the upper parts of the oscillograms indicate the duration of the male vibration signals, and white dotted ones the duration of the female vibration signals. A, Alternate signal emission by both sexes at the time of male approach toward the female; B, Signal emission by the male immediately before copulation; C, Male postcopulatory signal; D, Male another postcopulatory signal and female postcopulatory signal. Refer to Fig. 27.

began to emit two different postcopulatory signals which completely differed from those emitted by them by this time (Fig. 29-D). One of the vibration signals was completely synchronized with the slow movement of the female abdomen in a dorso-ventral direction. In the case of one couple, only a series of this signal was detected after the female kicked out the male from the plant at the end of the copulation. It is apparent that above mentioned signal is emitted by the female and another signal by the male. Both sexes were staying on the same plant during the emission of these postcopulatory signals, and no other behavioral change was observed.

Female response to the playback of the male postcopulatory signal shown in Fig. 29-C was compared between virgin ones and mated ones. The playback was transmitted to the rice plant on which one female had been placed. All sexually mature virgin females responded to the playback by the emission of the vibration signals. On the other hand, mated ones (1 day after copulation) showed no response to the playback. These results suggest that the male postcopulatory signal has the same function with those emitted by the males of the three species of planthoppers.

IV Discussion

OSSIANNILSSON (1949) detected the male calls of all examined species and the female calls of only 6 species out of 96 species of auchenorrhynchous Homoptera, and the females of many other species were presumed to have lost the capacity of answering by a call. However, in later studies female calls were detected in most species examined. They belong to Cercopidae (MOOR, 1961), Jassidae (STRÜBING, 1970, 1976, 1978; MEBES, 1974), Cicadellidae (SMITH, Jr., 1971; PURCELL and LOHER, 1976), Delphacidae (STRÜBING, 1958, 1962, 1975) and Dytio-phalidae (STRÜBING, 1977). Only one exception is the several species of *Oncopsis* in which the female call was not detected in their mating behavior (CLARIDGE and HOWSE, 1968; CLARIDGE and REYNOLDS, 1973).

According to the results of this paper, most receptive females were restricted to the sexually mature virgin ones, and only receptive ones emitted the vibration signals. On the contrary, the males of the four species emitted the vibration signals at any time from the time shortly after emergence (refer to Chapter 4). The insects studied by OSSIANNILSSON (1949) were collected at their natural habitats where adults of wide range of age and unmated ones might exist. Therefore, it is uncertain whether all of the females examined in his study were in receptive condition. Above mentioned things suggest that females must be carefully studied to clarify their ability to emit signals.

Both sexes of the four species studied in this paper emitted the vibration signals without the presence of other individuals. When the playback of these signals was transmitted to the substrates on which the conspecific adults of opposite sex have been individually placed, they showed distinct response to the playback just as observed in their mating behavior. These results indicate that the vibration signals emitted by a single adult are always aimed at the mating partners. At the same time, it is stressed that the playback transmitted to the substrates is sufficient to elicit normal response from the insects even when they were placed on a sheet of thin paper.

Female vibration signals were composed of monotonous pulse train in contrast with the male vibration signals with complex patterns. Such a difference between both sexes might be due to the difference of the elaborateness of the tymbal organs (ISHII and ICHIKAWA, 1975). Such differences of the tymbal organs between both sexes are also known in other Auchenorrhyncha other than Cicadidae (OSSIANNILSSON, 1949; SMITH, Jr. and GEORGHIOU, 1972).

In the four species studied in this paper, both sexes alternately emitted the vibration signals at the time of the male approach to the females. Such alternate emission of the calls is also known in other Auchenorrhyncha other than Cicadidae (OSSIANNILSSON, 1953; STRÜBING, 1962, 1970; SMITH, Jr., 1971). In all these Auchenorrhyncha, searching behavior during signal emission was the role of the males. In the four species studied in this paper, male vibration signals just before copulation were considered to be the essential stimuli for the female to receive the appropriate mating partners. However, wing flaps performed simultaneously with the emission of the vibration signals at this time was not essential for mating.

Male courtship behavior and copulatory attempt toward the insects other than the appropriate mating partners are known in wide range of Auchenorrhyncha. CLARIDGE and REYNOLDS (1973) observed that the males of the leafhopper, *Oncopsis flavicollis*, sometimes courted other conspecific males. Such homosexual activities are also known in the three species of periodical cicadas, *Magicicada septendecim*, *M. cassini* and *M. septendecula*, (WHITE, 1973), in the brown planthopper, *N. lugens* (TAKEDA, 1974) and in the leafhopper, *Macrosteles fascifrons* (PURCELL and LOHER, 1976). The author also observed such homosexual activities of the males of the four species studied in this paper when they were confined in small glass tubes as described in Chapter 1. Besides, the males of *N. lugens* attempted to copulate with the females of *L. striatellus* (TAKEDA, 1974) and the males of *M. fascifrons* with unreceptive mated females and even with the nymphs (PURCELL and LOHER, 1976). Above mentioned common behavioral characteristic in wrong copulatory attempt by the males suggests that the males of Auchenorrhyncha can not discriminate between appropriate mating partners and other insects when other insects are in close proximity.

Interspecific crosses in Heteroptera are known to be common between the two species of the bugs, *Nezara viridula* and *N. antennata*, in the areas of overlapping distribution (KIRITANI, *et al.*, 1963). However, interspecific crosses in Homoptera under natural conditions seems not to have been discovered so far. Successful interspecific crosses in Auchenorrhyncha under artificial conditions were obtained among the three species of periodical cicadas, *Magicicada septendecim*, *M. cassini* and *M. septendecula* (WHITE, 1973), between the leafhoppers, *Nephotettig impicticeps* and *N. apicalis* (LING, 1968), *Euscelis alsius* and *E. plebejus* (STRÜBING, 1970), and long winged form of *Macrosteles fascifrons* species complex and short winged form of the species complex (PURCELL and LOHER, 1976), and between the planthoppers, *Javesella azorica* and *J. pellucida* (STRÜBING, 1975). It seems that such interspecific crosses between closely related species might be ensued from above mentioned, wrong copulatory attempt by the males. Interspecific crosses might be very few, if any, under natural conditions because closely related species might have the different signals as clarified in *Oncopsis* species complex (CLARIDGE and HOWSE, 1968; CLARIDGE and REYNOLDS, 1973), in *Euscelis* (STRÜBING, 1970), and *Javesella* (STRÜBING, 1975), and because they live on different host plants as the two species of *Hishimonus* (ARAI, 1978). In the four species studied in this paper, appropriate mating partners always encounter after the alternate emission of the vibration signals by both sexes. It is apparent that these signals emitted by both sexes are functioning as double safety valves in protecting from the selection of wrong partners.

Postcopulatory signals were always emitted by the males of the four species studied in this paper. Excepting other postcopulatory signals emitted by both sexes of *N. cincticeps* (see Fig. 29-D), the patterns of the male postcopulatory signals were similar to those emitted by a single male and those emitted at precopulation period. Distinct responses of sexually mature virgin females of the same species to the playback of the postcopulatory signals indicate that the signals are aimed at the mating partners for some purpose. The roles of the postcopulatory signals in the three species of planthoppers will be again analyzed in Chapter 4.

Chapter 4. Factors influencing upon the sexual behavior and the sexual maturation

I Introduction

In many insects male sexual behavior is known to be evoked by suitable stimuli even at the time shortly after emergence, and this behavioral state is known to persist until death. On the other hand, it is known that female behavior is usually more complex than that of males, and their behavior change in accordance with the activity of corpora allata, the development of the ovaries, the completion of the copulation and so on (MANNING, 1966; TRUMAN and RIDDIFORD, 1974).

Such behavioral differences between both sexes are known in the sexual behavior of the planthopper, *Sogatodes orizicola*. The males of this species showed no behavioral change after the copulation, and they could successively copulate. On the contrary, the mated females showed no sexual behavior characteristic to the virgin ones (MCMILLIAN, 1963). Similar results were obtained in the sexual behavior of *L. striatellus*, *N. cincticeps* (OYAMA, 1972) and *N. lugens* (TAKEDA, 1974). The males of *N. lugens* within one or two days after emergence are known to be capable of insemination to the females (TAKEDA, 1974). In the females of the planthoppers, *N. lugens*, *L. striatellus* and *S. furcifera*, it is known that the preoviposition period in the macropterous ones is longer than that in the brachypterous ones (SUENAGA, 1963, KISIMOTO, 1957, 1965; MOCHIDA, 1970). However, the sexual behavior throughout their adult stages and the process of sexual maturation from the viewpoint of the acquisition of the ability to emit the vibration signals have not yet been clarified.

In this Chapter female sexual behavior throughout adult stage and the process of sexual maturation in the four species of Auchenorrhyncha are described.

II Materials and Methods

Experiment 1

N. lugens and *N. cincticeps* were used for the experiment. Each female of the two species within one day after emergence (0 day) was confined in a glass tube (3 cm in diameter and 20 cm in height) containing a rice seedling fixed to a piece of moistened polyurethane mat.

All females were reared in the glass tubes throughout the experimental period at $25 \pm 1^\circ\text{C}$. In each species half of the females were made to copulate with the conspecific males after they were ascertained to attain sexual maturation. All males were removed from the glass tubes within 1 hr after the finish of the copulation. Behavior performed by the females of *N. lugens* was observed for 1 hr a day, and their performance of the abdominal vibration (AV) by which their vibration signals were emitted was recorded. In the females of *N. cincticeps*, following another methods were adopted to ascertain their performance of the signal emission because of the difficulty of the direct observation on their behavior to emit the vibration signals. The responses of the females to the playback of male vibration signals by the emission of the

vibration signals were examined with the apparatus shown in Fig. 30. Each female was confined in a case made of a sheet of paraffin paper (1×1×5 cm), and the playback was

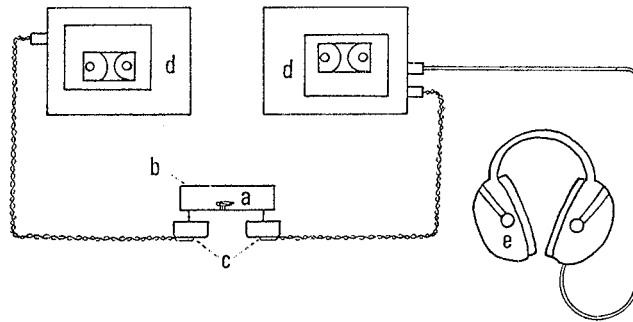


Fig. 30. An apparatus for the detection of the vibration signals emitted by an insect at the time of the response to the playback of the vibration signals of opposite sex. a, An insect; b, Case made of paraffin paper; c, Crystal earphone; d, Tape recorder; e, Headphone.

transmitted to the case via the tip of a stainless needle attached to a crystal earphone. The playback was transmitted five times per female in each experimental period. Their responses to the playback by the emission of the vibration signals were detected with another crystal earphone kept in contact with the case at the tip of the needle.

Experiment 2

N. lugens and *N. cincticeps* were used for the experiment. Each female of the two species within one day after emergence was confined in the glass tube, and they were reared until death with the same methods as Experiment 1. Female behavior toward the conspecific males were observed as follows. Virgin males more than 4 days after emergence were individually confined in the glass tubes in which the females were being reared. Thus the pairs of both sexes were made, and behavior performed by them was observed every other day at room temperature under fluorescent lighting. Observation was started after each male was placed on the rice seedling on which one female was settling. The distance between both sexes at the start of the observation was less than 5 cm. All males were removed from the glass tubes immediately after the end of each observation period.

Experiment 3

Virgin adults of *N. lugens*, *L. striatellus* and *S. furcifera* more than 5 days after emergence were used for the experiment. Virgin males were made to mate successively with the conspecific virgin females as follows. One male and one female were placed individually on two rice plants, and the vibration signals transmitted to the plants were detected with the phonograph cartridge. The tip of the leaf blade of another plant having placed another female was brought into contact with the plant on which above mentioned couple has just finished the copulation. Virgin females were recruited with the same way as mentioned above until the male did not approach to recruited female. Thus the manner of female response to male post-copulatory signals and the male ability of successive matings were examined.

In *N. lugens* all females successively mated by one male were individually reared in the glass tubes afterward. The fertilization of the eggs laid by these females was judged from the hatch of the 1st instar nymphs and the embryonic formation in the eggs. The responses of these females to the playback of the male vibration signals were also examined with the same methods as those in Experiment 1 (see Fig. 30).

Experiment 4

The virgin females of *N. lugens*, *L. striatellus* and *S. furcifera* were used for the experiment. Each female was confined in the glass tube with a rice seedling within one day after emergence. Behavior performed by these females was observed for 1 hr a day to ascertain the time of the onset of the AV. In *N. lugens* other females of both wing forms (brachypterous one and macropterous one) were grouped into three different densities within one day after emergence, one individual per glass tube (density 1), two individuals per glass tube (density 2) and five individuals per glass tube (density 5). The methods of rearing and observation were the same as those mentioned above. Two rice seedlings were confined in each of the glass tubes of the density 5 during the observation period to place all of them on the rice seedling. In the density 2 and the density 5, the females having performed the AV for the first time in their adult lives were marked with a paint at the tip of the fore wing in order to discriminate them from those not having performed the AV.

Experiment 5

Both sexes of *N. lugens*, and the males of *L. striatellus*, *S. furcifera* and *N. cincticeps* were used for the experiment. The females of *N. lugens* within one day after emergence were grouped into two different densities, one individual per glass tube (density 1) and five individuals per glass tube (density 5). The males of *N. lugens* were reared under the density 1 or the density 10 throughout the nymphal and the adult stages. All other insects were individually reared at adult stage. The sexual maturation of these insects was judged from the response to the playback of the vibration signals of the opposite sex of the same species by the emission of the vibration signals. The methods of the experiment were the same with those in Experiment 1 (see Fig. 30). In the two density groups of the female *N. lugens*, all individuals were dissected immediately after examining the response to the playback to know the degree of ovarian development. In the density 10 of the male *N. lugens*, the adults having responded to the playback for the first time in their adult lives were marked with a paint at the tip of the fore wing in order to discriminate them from those not having responded to the playback.

III Results

1. Factors influencing upon the sexual behavior

Experiment 1

Fig. 31 shows the daily change of the number of a series of the AV performed by two virgin females of *N. lugens*. They performed the AV only sporadically at the day when the AV was first observed, but they came to perform the AV frequently thereafter. The duration of a series

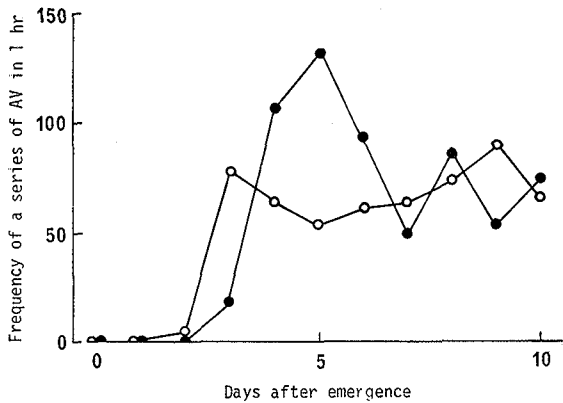


Fig. 31. Daily changes of the frequency of a series of the AV performed by a virgin brachypterous female (hollow circles) and a virgin macropterous one (solid circles) in *N. lugens*.

of the AV was from less than 1 sec to more than 3 min. The number often exceeded one per min since 3 or 4 days after emergence. Therefore, observation for 1 hr a day was considered to be enough to examine whether the females perform the AV.

The influence of age and mating upon the performance of the AV in the brachypterous and the macropterous females of *N. lugens* is shown in Fig. 32 and Fig. 33, respectively. Most of once mated females never performed the AV. Only a few of them resumed the AV at the 19th or the 21st day of the mating. On the contrary, all virgin females continued to perform the AV until death.

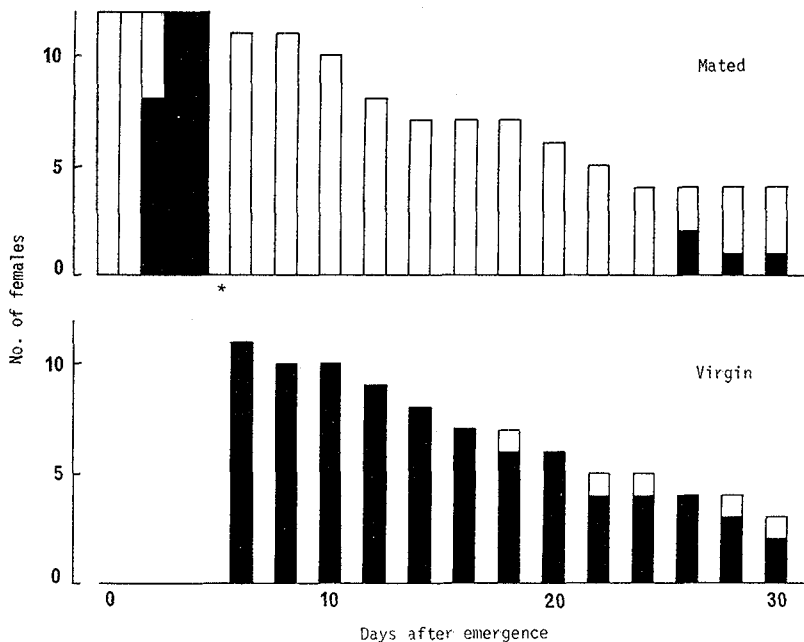


Fig. 32. Influence of age and mating upon the performance of the AV in the brachypterous females of *N. lugens*. Solid parts indicate the number of the females having performed the AV during the observation period (1 hr a day). Asterisk indicates the time of the mating.

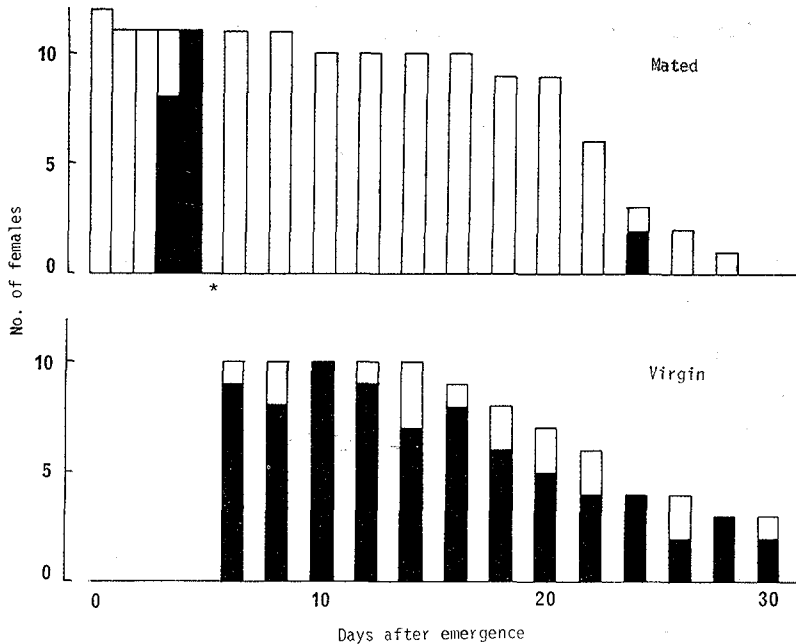


Fig. 33. Influence of age and mating upon the performance of the AV in the macropterous females of *N. lugens*. Solid parts indicate the number of the females having performed the AV during the observation period (1 hr a day). Asterisk indicates the time of the mating.

Fig. 34 shows the influence of age and mating upon the female response to the playback of male vibration signals by the vibration signals in *N. cincticeps*. Virgin females came to respond to the playback from the 2nd day of adult emergence. All of the virgin ones responded to the playback by the 4th day of adult emergence. These females, however, showed no response to the playback after the mating. On the other hand, virgin ones continued to respond to the playback as long as they live.

Experiment 2

Table 12 shows the typical female behavior toward the courting males in *N. lugens*. It is apparent that the females were in sexually immature stage until they performed the AV. Two types of mate refusal behavior, escape by walk-

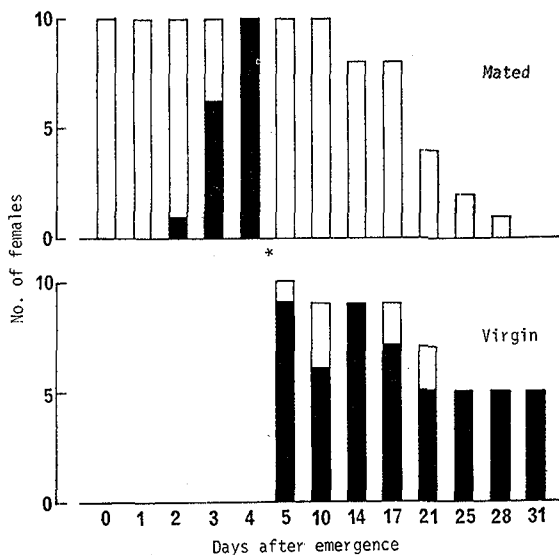


Fig. 34. Influence of age and mating upon the response to the playback of male vibration signals in *N. cincticeps*. Solid parts indicate the number of the females having responded to the playback. Asterisk indicates the time of the mating.

Table 12. Female behavior toward courting males in *N. lugens*

| Days after emergence | Female number | | | | | | | | | |
|----------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|------------------|------------------|----------------------|--------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 0 | E | E | E | E | E | E | E D ₁ | E | R | E |
| 2 | E R ₁ | E | E | E R ₁ | E R ₁ | R ₁ | E | E R ₁ | E R ₁ | E |
| 4 | E A V C | E R ₁ | E R ₁ | E R ₁ | A V C | A V C | E | E R ₁ | E R ₁ | C |
| 6 | E R _{1 2} | E A V C | A V C | A V C | E R ₁ | R _{1 2} | A V C | A V C | A V C | E R _{1 2} |
| 8 | E R _{1 2} | R _{1 2} | R _{1 2} | R _{1 2} | R ₁ | R _{1 2} | E R ₁ | R ₁ | E | R _{1 2} |
| 10 | R _{1 2} | R ₁ | R ₁ | E R _{1 2} | E R _{1 2} | E | E R ₁ | R _{1 2} | R _{1 2} | R _{1 2} |
| 12 | E R _{1 2} | E R _{1 2} | E R _{1 2} | R ₂ | | E R _{1 2} | R _{1 2} | R _{1 2} | R _{1 2} | R _{1 2} |
| 14 | E R _{1 2} | R _{1 2} | R _{1 2} | E R ₂ | | E R _{1 2} | R ₁ | R ₂ | R ₂ | |
| 16 | E R _{1 2} | R | E R ₂ | E R ₂ | | E R _{1 2} | R ₂ | | R ₂ | |
| 18 | A V C | R _{1 2} | R ₂ | R ₂ | | | R _{1 2} | | R _{1 2} A V | |
| 20 | E R _{1 2} | R _{1 2} | | R _{1 2} | | | R ₂ | | R ₂ A V C | |
| 22 | | R ₁ C | | R ₂ | | | E R ₂ | | R ₂ | |
| 24 | | E R _{1 2} | | R ₁ | | | | | | |
| 26 | | R ₂ | | | | | | | | |

E, Escape; R₁, Body rolling; R₂, Protrusion of ovipositor; AV, Abdominal vibration; C, Copulation.

ing (E) and body rolling (R₁), were observed at this immature stage. The males succeeded in copulation with the females having performed the AV. Receptive condition in the females terminated after the mating. Mate refusal behavior by once mated females was classified into three types, E, R₁ and the protrusion of the ovipositor (R₂). Seven of the ten females continued to perform the mate refusal behavior until death. On the other hand, three females mated again at the 14th or 16th day of the first mating, and two of the three females were ascertained to perform the AV immediately before the copulation. These three females continued to perform the mate refusal behavior again after the second mating until death. Male rapid approach toward the females was observed only when the females performed the AV during the whole observation period though the distance between both sexes at the start of each observation period was within 5 cm. However, male copulatory attempt was repeated many times for a long time after the males approached to unreceptive females.

Table 13 shows the typical female behavior toward the courting males in *N. cincticeps*. It is apparent that all females attained to sexual maturation by the 4th day of adult emergence. The abdominal protrusion (AP) of the females could not be ascertained owing to too rapid precopulatory behavior performed by the males in close range. The process of the sexual maturation and the termination of the receptive condition after mating in the female *N. cincticeps* were similar to those in the female *N. lugens*. Mate refusal behavior performed by the females was classified into three types, escape by walking (E), body rolling and kicking by the hind legs (R_a) and the spread of the hind legs (R_b). All types of the mate refusal behavior were performed by both sexually immature ones and once mated ones. Only one of the eight females mated again at the 10th day of the first mating. Male copulatory attempt toward unreceptive females was repeated just as observed in *N. lugens*.

Table 13. Female behavior toward courting males in *N. cincticeps*

| Days after emergence | Female number | | | | | | | |
|----------------------|------------------|------------------|--------------------|--------------------|------------------|------------------|----------------|------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| 0 | R _a | E | E | E | R _a | R _a | E | R _b |
| 2 | R _a | E | E R _a | E | R _a b | R _a | R _a | R _a b |
| 4 | C | R _a C | C | C | R _a C | C | C | C |
| 6 | E R _a | R _a | E R _a | E R _a | E R _a | E R _a | R _a | R _a |
| 8 | R _a b | E R _a | E R _a b | E R _a b | E R _b | R _a | R _a | R _a b |
| 10 | R _a b | E R _a | R _b | E R _a b | | E R _a | R _a | R _a b |
| 12 | E R _a | R _a | E | E R _a b | | R _a | | R _b |
| 14 | R _a b | | | R _a C | | | | R _b |
| 16 | E | | | E R _a | | | | |
| 18 | | | | E R _a | | | | |
| 20 | | | | R _b | | | | |

E, Escape; R_a, Body rolling and kicking by the hind legs; R_b, Spread of the hind legs; C, Copulation.

It is apparent from the results obtained from Experiment 1 and 2 that only one chance of insemination by virgin males is enough for a long-term maintainance of the female unreceptive condition.

Experiment 3

Table 14 shows the number of male successive matings and female response to the male post-

Table 14. Influence of male successive matings upon the female response to the male postcopulatory signals in the three species of planthoppers

| Species | Male No. | Female ^a No. in male successive matings | | | | | | | | | | Experimental period (min) | | | | | | | | | | | |
|-----------------------|----------|--|---|---|---|---|---|---|---|---|---|---------------------------|---|---|---|---|---|---|---|---|----|------------------|----|
| | | 1 | | 2 | | 3 | | 4 | | 5 | | | 6 | | 7 | | 8 | | 9 | | 10 | | |
| | | v | m | v | m | v | m | v | m | v | m | | v | m | v | m | v | m | v | m | v | m | |
| <i>N. lugens</i> | 1 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | 80 | |
| | 2 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | + ^b | 78 |
| | 3 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | | 60 |
| | 4 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | + ^b + | 90 |
| | 5 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | | 70 |
| <i>L. striatellus</i> | 1 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | 35 | |
| | 2 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | + ^b | 55 |
| | 3 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | | 40 |
| | 4 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | + ^b | 45 |
| | 5 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | | 45 |
| <i>S. furcifera</i> | 1 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | 25 | |
| | 2 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | 23 | |
| | 3 | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | - | + | + ^b | 40 |

v, Precopulation period; m, Postcopulation period.
 +, Female response to male postcopulatory signals by the emission of the vibration signals; -, Female indifference to male postcopulatory signals.
 a Sexually mature virgin females were used.
 b Female mated twice or more by the same male.

copulatory signals in the three species of planthoppers. Each of the recruited virgin females of the three species responded to the postcopulatory signals emitted by the conspecific male which had finished one of the copulations within a few minutes before. Then mutual communication through the vibration signals between the male and the recruited female was commenced, and the male moved to the plant on which the female was placed. Usually mated females never responded to the male postcopulatory signals. However, some of the females mated at the last two times of the male successive matings responded to the signals even in postcopulation period. These females were mated twice or four times by the same males. These females continued to respond to the male postcopulatory signals after such multiple matings. Thus the males of *N. lugens* (5♂♂), *L. striatellus* (5♂♂) and *S. furcifera* (3♂♂) mate 4-11 times within 90 min, 3-6 times within 55 min and 3-8 times within 40 min with the conspecific virgin females respectively. Besides, even the males, which could not move toward new virgin females after successive matings, communicated with the females through the vibration signals.

Table 15 shows the percentage of fertilized eggs laid by the mated females and the female response to the playback of the male vibration signals for all female *N. lugens* mated successively by the males. The females mated earlier in the male successive matings continued to lay fertilized eggs for a long time, and they continued to be indifferent to the playback. On the other hand, those mated later, especially those mated later than 5th or 6th time of male successive matings, laid few fertilized eggs, and they began to respond to the playback within 4 days after mating. Even in the females mated earlier, some of them began to respond to the playback shortly before the decline of the fertilized eggs.

Results of this experiment indicate the short-term unreceptive conditions of mated females can be induced by the copulation without insemination, and the long-term unreceptive conditions of them by the copulation with insemination.

2. Factors influencing upon the sexual maturation

Experiment 4

Time of the onset of the AV in isolated females of the three species of planthoppers is shown in Table 16. Brachypterous females began the AV earlier than macropterous ones in *N. lugens*

Table 16. Adult age (days after emergence) at the time of the onset of the AV in the females of the three species of planthoppers

| Species | Wing form | No. used | Onset of the AV |
|-----------------------|-----------|----------|-----------------|
| <i>N. lugens</i> | B | 12 | 2.3±0.30* |
| | M | 11 | 3.1±0.47 |
| <i>L. striatellus</i> | B | 12 | 2.4±0.33 |
| <i>S. furcifera</i> | M | 11 | 4.4±0.69 |

* Mean±95% f. 1.

B, Brachypterous form; M, Macropterous form.

Table 15. Influence of male successive matings upon the fertilization of eggs laid by mated females and the response of mated females to the playback of male vibration signals in *N. lugens*

| Male No. | Female No. | Duration of copulation (sec) | Days after mating | | | | | | | | | | | | | | | | | | | |
|----------|------------|------------------------------|-------------------|---|-----|---|-----|---|-----|---|------|---|-------|---|-------|---|-------|---|-------|---|-------|---|
| | | | 0-2 | | 2-4 | | 4-6 | | 6-8 | | 8-10 | | 10-12 | | 12-14 | | 14-16 | | 16-18 | | 18-20 | |
| | | | F | R | F | R | F | R | F | R | F | R | F | R | F | R | F | R | F | R | | |
| 1 | 1 | 132 | 100 | - | 90 | - | 100 | - | 94 | - | 100 | - | D | + | | | | | | | | |
| | 2 | 103 | 100 | - | 82 | - | 88 | - | 100 | - | 100 | + | 38 | | 64 | + | 33 | - | 40 | - | 100D | |
| | 3 | 136 | 100 | - | 50 | - | 100 | - | 89 | - | 92 | + | 93 | + | 100 | + | 100 | + | | - | D | |
| | 4 | 137 | 100 | - | 93 | + | 83 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0D | |
| 2 | 1 | 82 | 100 | - | 100 | - | 100 | - | 95 | - | 100 | - | 100 | - | 100D | | | | | | | |
| | 2 | 88 | 73 | - | 93 | - | 76 | - | 60 | - | 0 | + | 0D | | | | | | | | | |
| | 3 | 79 | 92 | - | 71 | - | 88 | - | 86 | - | 86 | + | 78 | + | 72 | + | 29 | + | 73 | + | 0D | |
| | 4 | 132 | 93 | + | 87 | + | 100 | + | 65 | + | 0 | + | 0D | | | | | | | | | |
| | 5 | 47 | 33 | + | 89 | + | 41 | - | 86D | | | | | | | | | | | | | |
| | 6 | 90 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0D | | | |
| | 7 | 49 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0D | | | | | |
| | 8 | 111 | 0 | + | 0 | + | 0 | + | 0D | | | | | | | | | | | | | |
| | 9 | 127 | 0 | + | 0 | + | D | | | | | | | | | | | | | | | |
| | 10* | 76,16 | | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0D | | | | | |
| 3 | 1 | 87 | 100 | - | 95 | - | 100 | - | 90 | - | 69 | - | 100 | - | 100 | - | D | | | | | |
| | 2 | 80 | 77 | - | 100 | - | 100 | - | 90 | - | 100 | - | 71 | - | D | | | | | | | |
| | 3 | 133 | 100 | - | 43 | - | 50 | - | 57 | - | 90 | - | 50D | | | | | | | | | |
| | 4 | 56 | 67 | - | 100 | + | 69 | + | 81 | + | 42 | + | D | | | | | | | | | |
| | 5 | 89 | 100 | + | 100 | + | 50 | + | 17 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + |
| 4 | 1 | 74 | 100 | - | 100 | - | 97 | - | 86 | - | 100 | - | 90 | - | 87 | + | 0 | + | 0 | + | 0 | + |
| | 2 | 73 | 100 | - | 89 | - | 100 | - | 100 | - | D | | | | | | | | | | | |
| | 3 | 85 | 100 | - | 83 | - | D | | | | | | | | | | | | | | | |
| | 4 | 52 | 100D | | | | | | | | | | | | | | | | | | | |
| | 5 | 96 | 73 | - | 92 | + | 90 | + | 63 | + | 92 | + | 75 | + | 36D | | | | | | | |
| | 6 | 90 | 0 | - | 0 | - | 0 | + | 0 | + | D | | | | | | | | | | | |
| | 7 | 34 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | - | 0D | | | | | | | | | |
| | 8 | 54 | 56 | - | 0 | - | D | | | | | | | | | | | | | | | |
| | 9* | 88,40 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | - | 0 | - |
| | 10* | 44 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + |
| 5 | 1 | 76 | 100 | - | 100 | - | 100 | - | 100 | - | 100D | | | | | | | | | | | |
| | 2 | 95 | 100 | - | 87 | - | 71 | - | 27 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + |
| | 3 | 97 | 100 | - | 100 | - | 78 | + | 69 | + | 46 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + |
| | 4 | 122 | 60 | - | 90 | - | 50 | - | 81 | - | 0 | + | 0 | + | 0 | + | 0 | + | D | | | |
| | 5 | 99 | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + | 0 | + |

F, % fertilized eggs; R, Response to the playback; D, Dead.

+, Female response to the playback by the emission of the vibration signals; -, Female indifference to the playback.

* Female having responded to the male postcopulatory signals in postcopulation period. Refer to Table 14.

and *L. striatellus*. Among the macropterous females of the three species, *S. furcifera* began the AV later than the other two species.

Table 17 shows the relation between the onset of the AV and the rearing density at adult stage in the two wing forms of *N. lugens*. Time of the onset in the brachypterous females was

Table 17. Influence of the rearing density at adult stage upon the onset of the AV in the female *N. lugens*

| wing form | Density* | Days after emergence | | | | | | | | | | | | Mean \pm 95% f. 1. | | |
|-----------|----------|----------------------|---|----|---|---|---|---|---|---|---|----|----|----------------------|----|-----------------|
| | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | 12 | |
| B | 1 | | | 11 | 4 | | | | | | | | | | | 2.27 \pm 0.25 |
| | 2 | | | 8 | 8 | | | | | | | | | | | 2.50 \pm 0.28 |
| | 5 | | | 3 | 9 | 3 | | | | | | | | | | 3.00 \pm 0.36 |
| M | 1 | | | | 7 | 6 | | | | | | | | | | 3.46 \pm 0.31 |
| | 2 | | | | 2 | 4 | 4 | 1 | 2 | | | | | | 1 | 5.29 \pm 1.39 |
| | 5 | | | | | 1 | 2 | 5 | 1 | 1 | 1 | 1 | | | | 6.50 \pm 1.10 |

B, Brachypterous form; M, Macropterous form.

* Number of the females per glass tube.

generally earlier than that in the macropterous ones as mentioned above. The time in the brachypterous ones changed only slightly when the density increased. On the contrary, the time in the macropterous ones became distinctly longer with increasing density. The average time in the density 5 almost doubled that in the density 1. It is also noted that the range of the variation of the time in the macropterous ones became larger with increasing density.

Experiment 5

Fig. 35 shows the relation between the female response to the playback of the male vibration signals and the females having mature eggs in *N. lugens*. In the brachypterous form the number of the females having responded to the playback increased rapidly from the 2nd day of adult emergence, and all of the females after the 4th day of adult emergence responded to the playback. On the other hand, the number increased slowly from the 3rd day in the macropterous form. The trends of the increase of the number were similar between the density 1 and the density 5 in the brachypterous form though the increase was somewhat slower in the density 5. On the contrary, the trends were considerably different between the density 1 and the density 5 in the macropterous form, namely the increase of the number was conspicuously slow in the density 5. Some of the females in the density 5 did not respond to the playback even at the 7th day of adult emergence. Most females of the two wing forms having responded to the playback had mature eggs in their ovaries irrespective of their wing forms and age. Although five macropterous females having responded to the playback had no mature egg in their ovaries, it was ascertained that these females had more than seven immature eggs.

Table 18 shows the day of the first response of the isolated males to the playback of the female vibration signals of the same species in the three species, *L. striatellus*, *S. furcifera* and *N. cincticeps*. It is apparent that the most males of the three species began to emit the vibration signals by one day after emergence in response to the playback. Most vibration signals

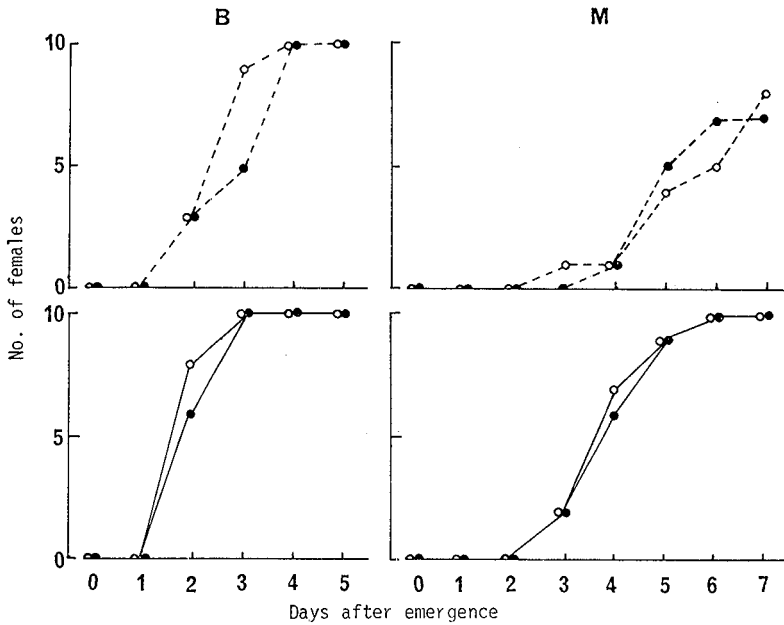


Fig. 35. Relation between the sexual maturation of the females and the development of eggs in their ovaries in *N. lugens*. Hollow circles indicate the females having mature eggs. Solid circles indicate the females having responded to the playback of male vibration signals by the emission of the vibration signals. Solid lines indicate the density 1, and dotted ones the density 5. B, Brachypterous form; M, Macropterous form.

Table 18. Adult age (days after emergence) at the time of male first response to the playback of the vibration signals of the conspecific females

| Species | No. used | Wing form | Male first response ^a (Days) |
|-----------------------|----------|-----------|---|
| <i>L. striatellus</i> | 10 | M | 0.70±0.48 ^b |
| <i>S. furcifera</i> | 10 | M | 0.90±0.23 |
| <i>N. cincticeps</i> | 10 | | 0.80±0.30 |

M, Macropterous form.

^a Male response to the playback by the emission of the vibration signals.

^b Mean±95% f. 1.

detected for the first time of their adult lives had low intensities and incomplete patterns, but the signals detected on the next day were revealed to be more complete ones. Table 19 shows the relation between the rearing density at the nymphal stage and the wing forms of emerged adults in *N. lugens*. Although the wing form of all males emerged from the density 1 and the density 10 was macropterous one, dominant wing form of the females changed from

Table 19. Relation between the rearing density at the nymphal stage and the wing forms of emerged adults in *N. lugens*

| Density | Nymphal mortality(%) | No. of males | | No. of females | |
|---------|----------------------|--------------|----|----------------|----|
| | | B | M | B | M |
| 1 | 10.20 | 0 | 24 | 19 | 1 |
| 10 | 31.43 | 0 | 27 | 2 | 19 |

B, Brachypterous form; M, Macropterous form.

brachypterous one (density 1) to macropterous one (density 10). In these macropterous males of *N. lugens*, the first day of the signal emission after emergence was almost same between the density 1 and density 10 (Table 20). The results obtained from the male *N. lugens* indicate that the process of the male sexual maturation is not affected by the rearing density at the nymphal and the adult stages.

Table 20. Adult age (days after emergence) at the time of male first response to the playback of the female vibration signals in *N. lugens*

| Density ^a | No. used | Wing form | Male first response ^b |
|----------------------|----------|-----------|----------------------------------|
| 1 | 10 | M | 0.70±0.68 ^c |
| 10 | 10 | M | 0.50±0.38 |

M, Macropterous form.

a Rearing density at the nymphal and the adult stages.

b Male response to the playback by the emission of the vibration signals.

c Mean±95%f. 1.

IV Discussion

In *N. lugens* and *N. cincticeps*, sexually immature virgin females and mated ones were revealed to be in unreceptive condition. They never emitted the vibration signals, and performed mate refusal behavior toward the courting males when the conspecific males were placed in the close vicinity of them. Only a few of the mated females resumed receptive condition after maintaining unreceptive condition for a long time (more than 10 days). Unreceptive condition of female insects is known to be mediated by the mechanical stimulus of the spermatophore in the cockroach, *Nauphoeta cinerea* (ROTH, 1962), by the mechanical stimulus of eggs developed in the ovaries of mated females in the grasshopper, *Chorthippus curtipennis* (HARTMAN and LOHER, 1974), by implanted sperm in the fly, *Drosophila melanogaster* (MANNING, 1962), or by proteins or polypeptides secreted from the male accessory glands in the mosquitoes, *Culex*, *Anopheles* and *Aedes* (CRAIG, Jr., 1967). Although the factors controlling the female behavioral

change after mating in Auchenorrhyncha are not known, the feature of the results obtained from the male successive matings gives some suggestions upon the problem (see Table 14 and Table 15). The males of the three species of planthoppers, *N. lugens*, *L. striatellus* and *S. furcifera*, could mate with three to ten conspecific virgin females successively in 23–90 min. Such rapid successive matings were possible because of the distinct response of the virgin females to the postcopulatory signals of the conspecific males by the emission of the vibration signals. Some of the females mated at the last two times of the male successive matings responded to the postcopulatory signals even at postcopulation period, and they received the same males twice or four times. The rest of the females responded to the postcopulatory signals only in pre-copulation period, and they received the males only once. In *N. lugens*, the females mated later than 5th or 6th of the male successive matings laid few fertilized eggs, and most of them began to respond to the playback of the male vibration signals within 4 days after mating though most of them were indifferent to the postcopulatory signals of the males in postcopulation period. Some of the females mated at 1st to 4th time of the male successive matings also began to respond to the playback shortly before the decline of the fertilized eggs laid by their own. These results suggest that the female behavioral change after mating in these planthoppers is mediated by some unknown substances in implanted sperm.

Although the adult longevity of the four species of Auchenorrhyncha under laboratory conditions was more than 20 days on the average (KISIMOTO, 1965; NAKASUJI and KIRITANI, 1970), their adult longevity in field is known to be within 10 days on the average (KISIMOTO, 1965; HOKYO and KUNO, 1970; KUNO and HOKYO, 1970). In the light of such a short longevity in field, it seems that the females of these species usually mate at most once throughout their adult lives. Multiple matings of these females in field might be possible only when inadequate copulation of the females occurs as seen in the male successive matings.

SUENAGA (1963) and YOSHIMEKI (1966) reported that most female migrants of the two species of planthoppers, *N. lugens* and *S. furcifera*, had no mature egg in their ovaries. In addition, all macropterous females of *N. lugens* having took flight from the hopperburn were unmated ones having immature ovaries (OHKUBO and KISIMOTO, 1971). In Japan, immigrants of the macropterous adults of these two species, which appear in most cases in June and July, are considered to migrate from more southern areas of Southeast Asia (KISIMOTO, 1975, 1977). The females of these immigrants were also found to be unmated ones having immature ovaries (KISIMOTO, 1975). It is known that the number of macropterous adults of *N. lugens* which immigrate into paddy fields in June or July were less than 5 per 100 rice plant hills (KISIMOTO, 1965, 1975; KUNO, 1968). Among these immigrants, more males than females were caught in the yellow pan water traps though visual counting indicated that there were more females than males in paddy fields (KISIMOTO, 1975, 1977). In *L. striatellus* caught in the pan traps in paddy fields, the number of the males were also usually more than that of the females (KISIMOTO, 1968; Otake, 1970). These findings suggest that the macropterous males of these planthoppers fly more actively than the macropterous females in paddy fields. The author found that the most females of *N. lugens* having responded to the playback of male vibration signals by the AV had mature eggs in their ovaries irrespective of their age, wing form and the rearing density at adult stage. On the other hand, KATAYAMA (1975) clarified that the females

of *N. lugens*, *S. striatellus* and *S. furcifera* mated around the time of the formation of mature eggs in their ovaries. The results of these experiments indicate that the sexual maturation of the virgin females of the three species accompanies with the full development of their ovaries.

The process of the mating behavior of the planthoppers in paddy fields might be as follows. Macropterous males perform random flight from one rice hill to another, and emit the vibration signals after landing on each hill. If the receptive females of the same species are clinging to the plant on which the males have landed, or to an adjacent plant whose leaves are in contact with the plant on which the males have landed, they begin mutual communication through the vibration signals, after which they copulate. The males overlook unreceptive females (sexually immature ones or mated ones) and the females of other species which are indifferent to the male signals. Take *N. lugens* for example, they have brachypterous males which lack the flight ability. Most of the brachypterous males are known to emerge from the middle range of density at nymphal stage from which the macropterous males and the females of both wing forms also emerge (KISIMOTO, 1965). According to TAKEDA (1964), the brachypterous males attain to sexual maturation shortly after emergence just as the macropterous males. The role of the two wing forms of the males in the mating behavior is presumed as follows. Sexual maturation of the macropterous females is delayed by the presence of other individuals as shown in Table 17 and Fig. 35, and they fly out from the habitat before sexual maturation. As a result, the mating partners of the brachypterous males are restricted to the brachypterous females. On the other hand, the macropterous males may mate with the females of both wing forms because of the rapid sexual maturation irrespective of the density as shown in Table 20.

In the females of *N. lugens*, time of the sexual maturation in the brachypterous ones was generally shorter than that in the macropterous ones. In addition to such a difference, the macropterous ones were sensitive to the crowded conditions. Even among the macropterous ones, very sensitive individuals and not so sensitive ones were observed (refer to Table 17). According to OHKUBO (1973) who examined the flight ability of the female *N. lugens* with the method of tethered flight, the macropterous females were grouped into three types, those not having performed wing beat, those having continued wing beat only for a short time and those having continued wing beat for a long time (more than 10 hr on the average). On the other hand, MORI and KIRITANI (1971) obtained the results that the relative length of male elytron to that of the tibia of the hind leg (E/T ratio) in *N. lugens* became larger with increasing rearing density at nymphal stage and with increasing cumulative crowded conditions. These findings suggest that different types are present in the macropterous adults of *N. lugens* like the three types (non-flyer, flyer and migrant) of the winged form of the alienicolae of *Aphis fabae* (Shaw, 1970a, b).

In *N. cincticeps* having no different wing forms, it is known that the females mate before the time of the formation of mature eggs in their ovaries when both sexes were confined in test tubes (KATAYAMA, 1975). And he suggested that the females of this species staying on the rice plants where they emerged mate before the egg maturation, and disperse after the egg maturation. It is known that the probing frequency and the movements in the adults of this species increase from 18 to 21 o'clock (NAITO, 1967) and most adults of this species disperse

after sunset (OHKUBO and KISIMOTO, 1971). HOKYO (1972) found that some of the females of this species having flown to the light trap in night had no mature eggs in their ovaries. In addition, the author and coworkers found that the unmated females of this species having no mature eggs in their ovaries were included among those having flown to the fluorescent light in night, and that the ratio of such females in the third generation was much higher than that in the second generation (ICHIKAWA *et al.*, unpublished). It is evident that the virgin females of this species are not always mated by the males before dispersal in field. According to KIRITANI *et al.* (1970), the number of the adults of this species emerged per hill in the third generation were about five fold of those in the second generation. NASU (1963) pointed out that the ovarian development of the females of this species in the hibernating generation was much more rapid than that in the first generation. In the light of above mentioned findings, it is concluded that the behavioral and physiological characteristics of the female *N. cincticeps* are not invariable but vary according to the change of external and internal factors.

Summary

Mating behavior of the four species of Homoptera Auchenorrhyncha, *Nilaparvata lugens*, *Laodelphax striatellus*, *Sogatella furcifera* and *Nephotettix cincticeps* was studied under laboratory conditions.

1. Searching behavior for the mating partners on the rice plant was always the role of the males. The abdominal vibration (AV) performed by the female planthoppers, *N. lugens*, *L. striatellus* and *S. furcifera*, and the abdominal protrusion (AP) performed by the female *N. cincticeps* were the behavior to attract the conspecific males. The duration of the copulation was less than 3 min in the four species. Both sexes of *N. cincticeps* performed the peculiar postcopulatory behavior.

2. It was revealed that the vibration signals transmitted to the rice plant was the sign stimuli involved in the mating behavior of the four species. Auditory, visual and olfactory factors were excluded from possible sign stimuli. Both sexes of the four species transmitted the vibration signals to the rice plant in the mating behavior. Communication through the vibration signals was possible between two rice plants on condition that these plants were kept in contact with each other. Thus the distance of the communication on the rice plants was attained to at least 60 cm. The vibration signals transmitted to the substrates other than the rice plant such as paraffin paper also elicited the normal response from the opposite sex of the same species.

3. The vibration signals of the four species detected from the rice plant were revealed to have species-specific pattern and wave form. The male vibration signals were more complex than the female vibration signals. In both sexes of the four species, a single adult emitted the vibration signals. Sexually mature males and sexually mature virgin females responded to the playback of the vibration signals of the opposite sex of the same species. A couple of both sexes encountered after the alternate emission of the vibration signals on the rice plants. The males of the four species always emitted the vibration signals immediately before copu-

latory attempt. The males of the four species always emitted the postcopulatory signals within a few minutes after the finish of the copulation. Once mated females were indifferent to the signals. Sexually mature virgin females responded to the playback of the postcopulatory signals of the conspecific males by the emission of the vibration signals.

4. In the females of *N. lugens* and *N. cincticeps*, receptive females, which were capable of the emission of the vibration signals, were usually restricted to sexually mature virgin ones. Their receptive condition maintained until death. The males of the three species of planthoppers mate successively 4-11 times with the conspecific virgin females. In *N. lugens*, the females mated earlier in the male successive matings continued to lay fertilized eggs for a long time, and they continued to be indifferent to the playback of the vibration signals of the conspecific males. On the other hand, most of the females mated later in the male successive matings laid few fertilized eggs, and they began to respond to the playback within 4 days after mating.

In the four species, time required for the sexual maturation after emergence was within one or two days in the males, or a few or several days in the females. In *N. lugens*, macropterous females were sensitive to the rearing density at adult stage, and the acquisition of the ability to emit the vibration signals and the ovarian development delayed conspicuously under crowded conditions. Time of the sexual maturation of male *N. lugens* was not affected by the rearing density at nymphal and adult stages.

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イネを加害する4種の同翅亜目頸吻群昆虫の 配偶行動に関する研究

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イネの重要害虫である4種の同翅亜目頸吻群昆虫、トビイロウンカ、*Nilaparvata lugens* (SIÁL) ヒメトビウソカ、*Laodelphax striatellus* (FALLÉN)、セジロウンカ、*Sogatella furcifera* (HORVÁTH)、およびツマグロヨコバイ、*Nephotettix cincticeps* UHLER の配偶行動に関する研究を行なった。

1. 4種の雄はイネ苗上において素早く歩行して性的に成熟した同種雌に接近した。雄の接近に際して、3種ウンカの雌は腹部振動(AV)を、ツマグロヨコバイの雌は腹部押し出し行動(AP)を行なった。同種雌の至近距離に到達した雄は多くの場合、交尾直前に数回はばたき行動をとり、この時点でツマグロヨコバイの雄はAVを行なった。以上の交尾前行動に引き続き、交尾が行なわれた。4種の交尾時間は3分以内であった。肉眼で観察する限り、3種ウンカは特別な交尾後行動をとらなかった。ツマグロヨコバイの雌雄は排泄液を後肢で取り、交尾器上に付着し、しばらく放置した後除去するという特異な交尾後行動をとった。本種の単独成虫および5令幼虫は排泄液を後肢で取り、肢で踏みつけるような行動をとった。

2. パラフィン紙上に雄を、イネ上に同種の雌を付着させた場合、パラフィン紙とイネが接触している場合のみ3種ウンカの雄は雌のAVに対して素早く歩行して反応した。雌雄をそれぞれ付着させた2本のイネを葉身の先端で接触させると、雌のAVは雄の接近行動を解発したが、葉身の先端を離すと、雌雄間の距離が3~5mmの至近距離でも雌のAVに対して雄は何ら行動の反応を示さなかった。以上の結果から雌のAVにより発せられ、雄の接近行動を解発する刺激は振動刺激であることが示された。生長したイネを用いた場合、この振動刺激は雌から60~80cm離れた隣接するイネ上の雄に対して有効であった。パラフィン紙およびイネ上で3種ウンカの雄が同種の雌のAVのみに反応したことはこれらの振動刺激が種特異性の高い信号であることを裏付けた。葉身の先端を離した場合に比べ、接した場合に雌のAVの頻度が顕著に高まることから、雄も振動信号をイネに伝達して雌のAVを誘発していることが示された。ツマグロヨコバイの場合、雌雄をそれぞれ付着させた2本のイネが接触している状態のみ雌のAPに対する雄の接近行動が解発された。更にこの状態のみ雄のAVは雌のAPを誘発した。この結果は本種の配偶行動もイネに伝達される振動信号により解発されることを示した。

3. イネから検知した4種の振動信号は種特異的なパターンと波形を示した。雌の振動信号が単調なパルス振動であるのに対して、雄の振動信号は一定のパターンを有する複雑な振動であった。4種の雌雄は単独状態でも振動信号を発した。同種異性はその録音再生信号に反応するため、これらの信号が配偶者探索のためのものと考えられた。配偶行動において同種の雌雄は振動信号を交互に伝達して交信を行なった。雄の素早い歩行による雌への接近行動は雌の振動信号とはほぼ同調していた。同種雌の至近距離に到達した雄は常に1~数回振動信号を発した後、交尾を行なった。同時に行なわれた雄の翅上げ行動は雌に対して意味を持つ行動ではなかった。4種の雄は交尾終了後、数分以内に常に振動信号を発したが、既交尾雌はこの信号に反応しなかった。しかし性的に成熟した未交尾雌は同種雄のその録音再生信号に反応して振動信号を発した。

4. トビイロウンカおよびツマグロヨコバイの性的に成熟した未交尾雌は成虫期を通じて振動信号を発し続けるが、既交尾雌の大半は振動信号を発しなかった。また性的未成熟雌および未交尾雄と交尾した雌は交尾拒否行動をとり、雄を受け入れなかった。性的に成熟した未交尾雌が同種雄の交尾後の振動信号に反応することを利用して、3種ウンカの未交尾雄を複数の未交尾雌と連続的に交尾させると、23~90分間に4~11回交尾可能であった。各雄が最後或いはその前に交尾した雌の中には交尾終了後も雄の交尾後の信号に反応し、同一雄と繰り返し交尾するものがみられた。トビイロウンカの場合、雄の5~6回目以降の交尾雌の大半は交尾後4日以内に同種雄の録音再生信号に反応し始め、産下卵の殆どは不受精卵であった。雄の1~4回目の交尾雌中にも数日或いは10日以上は無反

応期の後に録音再生信号に反応するものが現れたが、不受精卵産下率はその後上昇した。以上の結果から、既交尾雌の行動変化の原因は交尾時に注入される雄の精液中の何らかの物質であることが示唆された。

羽化後性的成熟に達するまでの期間は4種とも雄では48時間以内であったが、雌では雄より長かった。トビイロウンカの場合、長翅雌は短翅雌よりその期間が長いと同時に飼育密度に対して敏感で、成虫期の密度の増加につれてその期間が延長した。他方、同種の雄は幼虫期と成虫期を通じた高密度飼育の場合も単独飼育の場合とその期間に差は認められなかった。

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