Density-Related Changes in Male-Male Competitive Behavior in the Rice Brown Planthopper, *Nilaparvata lugens* (Stål) (Homoptera : Delphacidae)[1]

Toshihide Ichikawa

Laboratory of Applied Entomology, Faculty of Agriculture, Kagawa University, Ikenobe, Miki-tyo, Kita-gun, Kagawa 761–07, Japan

Male-male competition in *Nilaparvata lugens* (Stål) was experimentally investigated under laboratory conditions. The males were reared at three different unisexual densities (D1, D2 and D5) for 5 days after emergence before being used in the experiments. Three types of vibration signals (VS) named the calling signal (CS), the pre-aggressive signal (Pre-AS) and the aggressive signal (AS) were detected in the communication between a pair of males in D5. A barrier to visual and tactile stimuli between a pair had no marked influence on the communication through VS. Most single males emitted only CS, irrespective of the adult density. All of the D1 pairs communicated only through CS. The D5 pairs emitted AS more frequently than the D2 pairs. Rejection behavior (RB) by body shake was never observed in the D1 pairs. Distinct aggressive behavior, direct body attack (DBA), was observed only in the D5 pairs. Receptive conspecific females responded to the playback of CS by emitting the invitation signal (IS), but they did not so respond to the playback of Pre-AS and AS.

INTRODUCTION

Auchenorrhynchous Homoptera other than Cicadidae had been generally thought to be silent until the publication of "Insect drummers" by Ossiannilson (1949). His work proved that they have sound-producing organs homologous to Cicadidae and that they produce extremely faint species-specific sounds. However, the question about the reception of air-borne sounds by auchenorrhynchous Homoptera has been controversial except in the case of Cicadidae (Ossiannilsson, 1949; Leston and Pringle, 1963; Claridge and Howse, 1968).

Experimental analyses on the perception of opposite sexes in the mating behavior of several species of Delphacidae, Deltocephalidae and Dictyopharidae revealed that opposite sexes of each species communicate with each other through vibration signals transmitted to their host plants, not through air-borne signals (Ichikawa and Ishii, 1974; Ichikawa et al., 1975; Ichikawa, 1976, 1979; Arai, 1977; Strübing, 1977). In these species, stationary females respond to the signals of conspecific males by the emission of invitation signals. Thus, the vibration signals of these auchenorrhynchous Homoptera have been clarified as being used as mating signals in sexual

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communication. On the other hand, male-male communication in auchenorrhynchous Homoptera seems to have been largely ignored, except for the suggestion of the presence of calls of rivalry in a species of Delphacidae, *Achorotile albosignata* (OSSIANNILSSON, 1949).

This paper deals with male-male competition mainly mediated by vibration signals in the rice brown planthopper, *Nilaparvata lugens*, which is one of the most serious insect pests attacking the rice plant in Asian countries. The relationship between male aggressiveness and population density is especially stressed and discussed.

MATERIALS AND METHODS

Insects used. A colony of the rice brown planthopper, *Nilaparvata lugens*, collected from a paddy field in Kagawa Prefecture in 1978 was maintained at $25 \pm 1°C$ and a photoperiod of 16 hr with fluorescent light. The insects were reared in a glass bottle (7.5 cm in diameter, 17.5 cm in height) containing rice seedlings throughout the developmental period. The number of adults emerging from each bottle was more than 300, and the ratio of macropterous form was 86% in males and 70% in females, on the average. All insects used for the present study were obtained from the stock culture.

Detection, analysis and playback of vibration signals. Vibration signals (VS) were detected by a crystal cartridge (Urasawa, PCL-17) touching the cut end of the leaf sheath of a rice plant on which a single male, a pair of males or a single female was placed. Detected VS were amplified by an electric amplifier (Pioneer, SA-8900), and monitored by a headphone (Pioneer, SE-405). A portion of the detected VS was recorded by a cassette tape recorder (Sony, TC-3000SD) on a cassette sound tape (Tokyo Denki Kagaku, AD-C60). A part of the recordings was fed to an oscilloscope (Hewlett-Packard, Model 1223A) and stored for measurement and photographing. Stored oscillograms were photographed with an oscilloscope camera (Hewlett-Packard, Model 197B) and a black and white film (Polaroid, Type 667). Playback of VS and/or
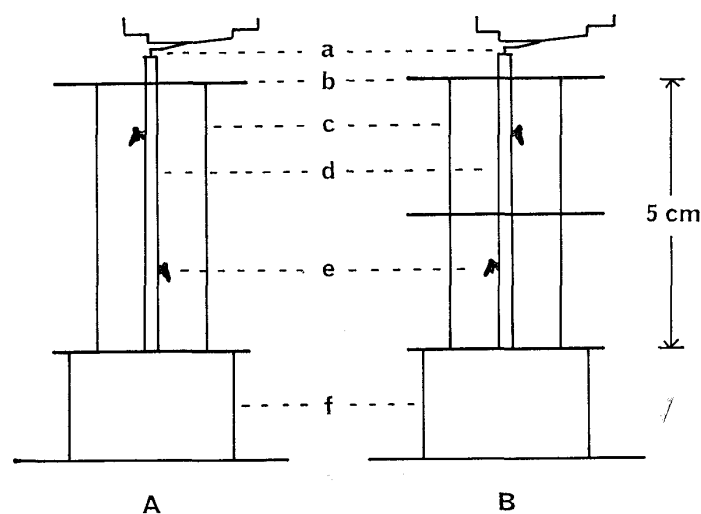

Fig. 1. Apparatus for the detection of VS and for the observation of behavior. a, Stylus of crystal cartridge; b, Kent paper; c, Cylindrical cell made of a sheet of cellophane paper; d, Stem of the rice plant; e, Insect; f, Polyurethane mat.

background noises (BGN) was transmitted from a cassette tape recorder (Sony, TC 1000B) to a rice plant via a stainless needle attached to the receptor site of a crystal earphone (Chorus Electric) to examine female response to male VS.

Experiment 1. Brachypterous and macropterous males were used. Five males having the same wing-form within a day after emergence were reared together in a glass tube (3 cm in diameter, 20 cm in length) with one rice seedling of ca. 3 cm in shoot length supported by a piece of moistened polyurethane mat for 5 days. This corresponds to D5 in Experiment 2. Then a pair of males with the same wing-form were placed on a rice plant after being confined in a paper cell as shown in Fig. 1A. VS emitted by the pair were monitored with the headphone, and their behavior was visually observed under fluorescent light. The duration of the experiment for each pair was 30 min.

Experiment 2. Macropterous males were reared at D5 for 5 days after emergence before being used in the experiment. In the unbarriered group, a pair of males were placed on a rice plant after being confined in a paper cell as shown in Fig. 1A, just as in Experiment 1. In the barriered group, a pair of males were placed on a rice plant after being confined separately in two paper cells as shown in Fig. 1B. The males in the barriered group could not see or make direct contact with each other. A piece of cotton tightly stuffed in a hole (ca. 2 mm in diameter) from which the stem of the rice plant was projected ensured that the barrier was complete. Other methods were the same as in Experiment 1.

Experiment 3. Macropterous males within a day after emergence were reared at three unisexual densities, one male (D1), two males (D2) and five males per glass tube (D5). A rice seedling for each tube was offered as food for 5 days before they were used in the experiment. In each density group, a single male or a pair of males were placed on a rice plant as shown in Fig. 1A. Other methods were the same as in Experiment 1.

Experiment 4. Virgin macropterous females on the 7th day of emergence were used. BGN detected from the rice plant, CS, Pre-As and AS were used as the playback source. Five repeats of BGN or AS of 5 sec each, five units of CS or five units of Pre-AS were intermittently played back to each female to examine whether she responded by emitting the invitation signal (IS). Refer to the results section for CS, Pre-AS and AS.

RESULTS

Experiment 1

Three types of vibration signals (VS) were emitted by the pairs of males which had been reared in D5 for 5 days after emergence. The time of the first emission of each type of VS by each pair is shown in Table 1 for the brachypterous form and in Table 2 for the macropterous form. In the two wing-forms, either member of a pair began emitting a type of VS quite similar to those emitted in the solo condition and in the mating behavior described by Ichikawa (1976, 1979) within 5 min after being set on a rice plant. This VS was named the calling signal (CS). Thereafter, CS was intermittently repeated by either member of a pair or alternately emitted by both of them (Fig. 2). A pair of each wing-form group emitted only CS for 30 min. In other pairs, either member of a pair began emitting VS utterly different

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Table 1. Time (sec) of the first occurrence of each activity after being set on the rice plant for each pair of brachypterous males

Activity	Pair No.									
	1	2	3	4	5	6	7	8	9	10
CS	30	5	15	8	80	112	141	103	30	83
Pre-AS	930	536	—[a]	691	—	658	298	624	620	165
AS	453	775	425	703	—	728	302	202	858	180
RB	—	—	—	—	—	308	—	—	112[b]	—
DBA	—	—	566	1200	—	320	—	—	—	—

[a] No activity was observed during a 30 min period.
[b] Copulatory attempt was observed.
CS, Calling signal ; Pre-AS, Pre-aggressive signal ; AS, Aggressive signal ;
RB, Rejection behavior ; DBA, Direct body attack.

Table 2. Time (sec) of the first occurrence of each activity after being set on the rice plant for each pair of macropterous males

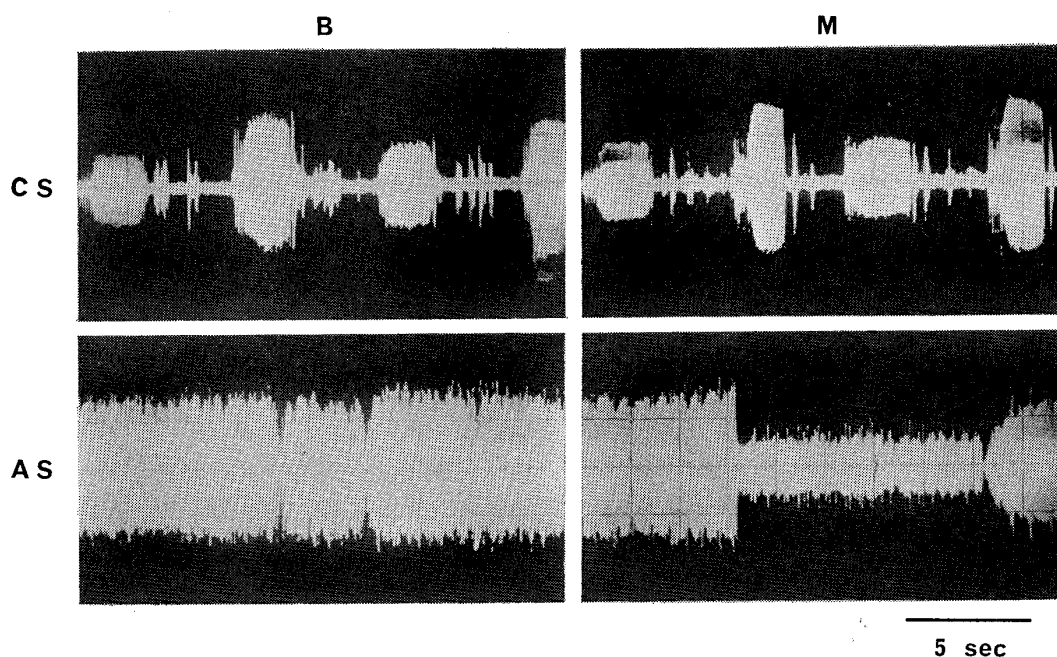| Activity	Pair No.									
	1	2	3	4	5	6	7	8	9	10
CS	13	280	160	32	109	36	43	108	148	60
Pre-AS	—	518	—	—	—	—	905	238	1600	1255
AS	404	670	520	773	—	317	204	393	1046	1425
RB	—	617	430	256	—	—	986	158	—	622
DBA	—	—	295	472	—	—	900	1294	—	384

See Table 1 for abbreviations.

5 sec

Fig. 2. Oscillograms showing alternate emission of CS and AS by a pair of brachypterous males (B) and by a pair of macropterous ones (M).

from CS after they had emitted CS for a while. This VS having a threatening tone was named the aggressive signal (AS). The emission of a simple vibration named the pre-aggressive signal (Pre-AS) sometimes preceded AS emission. Pre-AS was usually soon replaced by AS. AS emission often continued for an extended period without interval. The longest duration of one continuous AS emission by a brachypterous male was 542 sec, and that by a macropterous male 485 sec. Only one member of a pair emitted AS in 6 brachypterous pairs and in 7 macropterous pairs. Both members of a pair alternately emitted or duetted AS in 3 brachypterous pairs and in 2 macropterous pairs (Fig. 2).

Once two males were set on a rice plant, they always kept clinging to the plant without moving at least until the beginning of CS emission. It was often observed that one without emitting any type of VS approached the other which was emitting CS. One without emitting AS sometimes left the plant after the other began emitting AS. On the other hand, the males emitting AS for a long period never left the plant. Two types of characteristic behavior, reject behavior (RB) and direct body attack
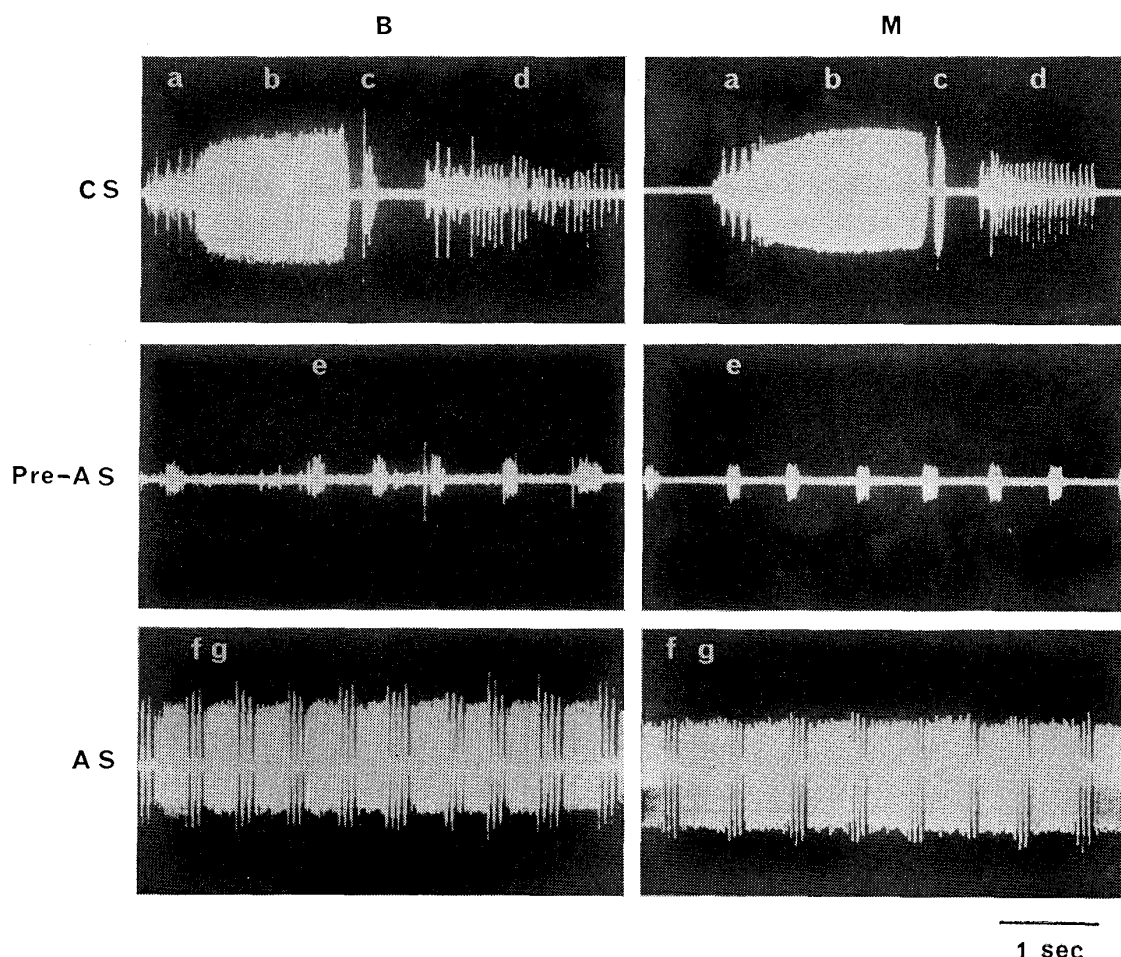

Fig. 3. Oscillograms of CS, Pre-AS and AS emitted by one of a pair of brachypterous males (B) and by one of a pair of macropterous ones (M). One complete unit of CS was composed of four subunits, *a*, *b*, *c* and *d*. Subunit *d* or subunits *c* and *d* were sometimes omitted. One unit of Pre-AS was composed of one simple pulse train, *e*. AS was composed of two subunits, *f* and *g*.

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(DBA), were observed after the beginning of CS or AS emission in several pairs of the two wing-forms (Table 1, Table 2). RB was observed in the following situation. One of a pair sometimes approached the other from behind and repeatedly emitted CS in close proximity like a courting male approaching a conspecific female. The latter did not emit any type of VS but performed RB by body shake at the time of CS emission by the former. The former usually retreated a short distance after repeated performance of RB by the latter. The male emitting CS in this situation seemed not to be intent on expelling the other male, but to have mistaken it for a conspecific female. The confusion was clearly confirmed in one brachypterous male which repeatedly attempted to copulate with the rejecting male. DBA was distinct aggressive behavior. The attacker rushed at and pushed the other. Such conflicts ended quickly when the attacked male retreated in response to a single attack. They, however, continued for a while when the attacked male held his position against the attack or retaliated with a similar attack upon the attacker. The most violent conflicts were observed in a brachypterous pair in which DBA was performed six times before one of them retreated.

Fig. 3 shows the oscillograms of each of the three types of VS emitted by the males of the two wing-forms. One complete unit of CS was composed of four different pulse trains, i.e., subunits a, b, c and d. Subunit d or subunits c and d were sometimes omitted. ICHIKAWA (1976, 1979) regarded subunits c and d as a single subunit c. The duration of one unit of CS was 4.68 ± 0.15 sec (mean$\pm$S.E., n=100) in brachypterous males and 4.77 ± 0.16 sec (n=100) in macropterous males. One unit of Pre-AS shown as e was composed of one pulse train having a duration of ca. 0.15 sec. AS was composed of a succession of three or, rarely, two or four common pulse trains, subunit f, and one longer pulse train, subunit g, and the two subunits were alternately emitted continuously. Each pulse train of subunit f had a duration of ca. 0.03 sec, and one of subunit g ca. 0.2–0.5 sec.

Table 3 shows the frequencies of CS and AS emitted by the two wing-forms. The frequency of CS emission is expressed as the total times of each unit. On the other hand, the frequency of AS emission is expressed as the total duration because each unit of this signal was successively emitted without cessation. A macropterous pair tended to emit CS more frequently than a brachypterous pair. On the contrary, a brachypterous pair emitted AS slightly more frequently than a macropterous pair.

Table 3. Frequencies of CS and AS emitted by both members of a pair of males in the two wing-forms

Wing-form	Frequency of VS emission[a]	
	CS[b]	AS[c]
Brachypterous	96.9 ± 23.9^x	676.7 ± 165.1^x
Macropterous	146.1 ± 23.3^x	627.2 ± 163.1^x

[a] Each value is the mean $\pm$S.E. for 10 pairs.
[b] Total times of the emission of each unit of CS during a 30 min period.
[c] Total duration (sec) of AS emission during a 30 min period.
Values followed by the same letter do not differ significantly at the 5% level.

Table 4. Influences of the paper barrier between members of a pair of macropterous males[a] on the performance of each activity

Barrier	N	No. of pairs in which each activity occurred				
		CS	Pre-AS	AS	RB	DBA
−	10	10	7	9	8	5
+	10	10	3	9	0	0[b]

[a] Males on the 5th day of emergence which had been reared in D5 after emergence.

[b] Direct body attack (DBA) was impossible because the pair of males could not come into contact with each other with the presence of the barrier.

N, Number of pairs used.

Experiment 2

Table 4 shows the number of pairs in which each type of VS or RB or DBA occurred in the unbarriered and barriered groups. CS emission was the first event occurring in all pairs of the two groups. The time of the first emission of CS after being set on the rice plant was 100.5 ± 30.6 sec (mean$\pm$S.E., n$=$10) in the unbarriered group and 134.0 ± 64.3 sec (n$=$10) in the barriered group. The males in the barriered group often walked rapidly on the rice plant or, sometimes, on the inner wall of the paper cell after the beginning of CS emission. Such movement was less often observed in the unbarriered group. Therefore, it seemed that the males of the barriered group were repeatedly attempting to locate the source of CS emission. Pre-AS emission sometimes preceded AS emission in 7 pairs of the unbarriered group and in 3 pairs of the barriered group. AS was detected in 9 pairs of each group. The time of the first emission of AS after being set was 458.2 ± 102.7 sec (n$=$9) in the unbarriered group and 607.1 ± 141.1 sec (n$=$9) in the barriered group. Only one member of a pair emitted AS in 7 pairs of each group. In these pairs, one which exhibited no AS emission sometimes left the rice plant after the other began emitting AS. Both members of a pair alternately emitted or duetted AS in 2 pairs of each group. The duration of the duet was always less than 10 sec. RB was observed in 8 pairs of the unbarriered group under the situation described in the results of Experiment 1. The absence of RB in the barriered group and the situations in which RB occurred indicated that CS emission by one during the close approach of the two males elicited RB from the other. DBA was observed in 5 pairs of the unbarriered group. The performance of DBA was naturally impossible in the barriered group because

Table 5. Influences of the paper barrier on the frequencies of CS and AS emitted by both members of a pair of macropterous males

Barrier	Frequency of VS emission[a]	
	CS[b]	AS[c]
−	160.9 ± 24.3^x	379.2 ± 111.0^x
+	110.4 ± 24.6^x	685.3 ± 168.9^x

[a] Each value is the mean $\pm$S.E. for 10 pairs.

[b] Total times of the emission of each unit of CS during a 30 min.

[c] Total duration (sec) of AS emission during a 30 min period.

Values followed by the same letter do not differ significantly at the 5% level.

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of the presence of the paper barrier between the pairs.

Table 5 shows the frequencies of CS and AS emitted by the pairs of the two groups. The pairs in the unbarriered group tended to emit CS more frequently than those in the barriered group. On the contrary, the pairs in the barriered group tended to emit AS more frequently than those in the unbarriered group.

Experiment 3

Table 6 shows the relationship between adult density before use in the experiment and the emission of each type of VS in single macropterous males. Most males began emitting CS within 5 min after being set on the rice plant, irrespective of the density for 5 days after emergence. No male of the three density groups emitted AS, though a few D2 and D5 males sporadically emitted Pre-AS.

As shown in Table 7, adult density influenced on VS emission and the performance of RB and DBA in male-male competition. In all macropterous pairs of the three density groups, one member of a pair began emitting CS within 5 min after being set on the rice plant. No D1 pair, however, emitted Pre-AS and AS. Each D1 pair usually kept away from each other, and they often left the rice plant after the beginning of CS emission. As a result, RB and DBA were never observed in the pairs of this density group. On the other hand, members of the D2 and D5 pairs tended to approach the other emitting CS. This activity led to occasional performance of RB. However, the aggressive behavior, DBA, was observed in only 3 D5 pairs. AS emission was detected in 7 D2 pairs and 9 D5 pairs. The D5 pairs usually began emitting AS earlier than the D2 pairs. The time of the first emission for the D2 pairs was 753.6 ± 193.3 sec (mean$\pm$S.E., n$=$7), and that for the D5 pairs 262.3 ± 72.3 sec (n$=$9). Only one of the two in a pair emitted AS in 5 pairs of D2 and 8 pairs

Table 6.   Influences of adult density on the emission of each type
of VS in single macropterous males

Adult density[a]	N	No. of males which emitted each type of VS		
		CS	Pre-AS	AS
1	10	10	0	0
2	10	10	2	0
5	10	10	1	0

[a] Unisexual density for 5 days after emergence before being used in the experiment.
N, Number of males used.

Table 7.   Influences of adult density on the performance of each activity
in the pairs of macropterous males

Adult density[a]	N	No. of pairs in which each activity occurred				
		CS	Pre-AS	AS	RB	DBA
1	10	10	0	0	0	0
2	10	10	4	7	7	0
5	10	10	1	9	3	3

[a] Unisexual density for 5 days after emergence before being used in the experiments.
N, Number of pairs used.

Table 8. Influences of adult density on the frequencies of CS and AS emitted by single macropterous males and by pairs of macropterous males

Adult density	Single male Frequency of VS emission[a]		Pair of males Frequency of VS emission[b]	
	CS[c]	AS[d]	CS	AS
1	10.8 ± 2.6^x	0	85.7 ± 10.7^x	0
2	45.5 ± 9.8^y	0	138.3 ± 13.9^y	275.6 ± 106.5^x
5	77.4 ± 16.4^z	0	139.3 ± 18.8^y	759.1 ± 149.6^y

[a] Each value is the mean $\pm$ S.E. for 10 single males.
[b] Each value is the mean $\pm$ S.E. for 10 pairs of males.
[c] Total times of the emission of each unit of CS during a 30 min period.
[d] Total duration (sec) of AS emission during a 30 min period.
Values followed by the same letter do not differ significantly at the 5% level.

of D5.

Table 8 shows the frequencies of CS and AS emitted by the single males and the pairs of males in the three density groups. The results supported male-male communication through VS and density-related changes in the quantitative aspects of the communication. The frequency of CS emission in the single males increased significantly with the increase of adult density, though they began emitting CS early in the experimental period, irrespective of adult density, as mentioned above. The average frequencies of CS emission in D2 and in D5 were ca. 4 times and ca. 7 times as many as that in D1, respectively. In D1, the frequency of CS emitted by a pair was ca. 8 times that emitted by a single male, on the average. It was apparent that the pairs of this density group communicated through CS because the frequency of CS emitted by a pair would be at most twice that emitted by a single male if both members of a pair were indifferent to each other. The frequency of CS emission in the D2 pairs and in the D5 pairs was significantly higher than that in the D1 pairs, though the differences were not so remarkable as those among the single males of the three density groups. Remarkable differences among the pairs of the three density groups consisted in the frequencies of AS emission. No D1 pair emitted AS, as mentioned above. The frequency of AS emission in the D5 pairs was ca. 2.7 times as many as that in the D2 pairs, on the average.

Experiment 4

Table 9 shows the female response by the emission of the invitation signal (IS) to the playback of the three types of VS. IS is the female signal emitted by abdominal vibration in the mating behavior. No female responded to the playback of BGN. They also showed little response to the playback of Pre-AS and AS. On the contrary, all females responded by IS emission to the playback of CS during the playback or immediately after the end of the playback of each unit, as if they were communicating with conspecific males in the mating behavior. It is noteworthy that there were no remarkable differences in the female response to CS emitted by the single males of the three density groups and CS emitted in the male-male competition of D5.

Table 9. Female response by IS emission to the playback of the three types of male VS*

Playback	Female No.									
	1	2	3	4	5	6	7	8	9	10
BGN	0 **	0	0	0	0	0	0	0	0	0
BGN+CS[a]	5	4	5	5	5	5	5	5	5	5
BGN+CS[b]	5	4	5	4	5	5	5	5	4	5
BGN+CS[c]	5	5	5	5	5	5	5	5	5	5
BGN+CS[d]	4	5	5	4	5	5	5	3	5	4
BGN+Per-AS[e]	0	0	0	1	0	0	0	0	0	0
BGN+As[f]	0	0	0	0	0	0	0	0	0	1

* Each female was discarded after her response to five repeats of playback had been examined.
** Times of female response by IS emission to five repeats of playback.
[a] CS emitted by a single male of D1.
[b] CS emitted by a single male of D2.
[c] CS emitted by a single male of D5.
[d] CS emitted by a pair of males of D5.
[e] Pre-AS emitted by a pair of males of D5.
[f] AS emitted by a pair of males of D5.
IS, Invitation signal of the female by abdominal vibration ; BGN, Background noises.

DISCUSSION

The results of the present study indicate that male-male competition in *N. lugens* is mainly mediated by vibration signals (VS) transmitted to the rice plant and sometimes by characteristic behavior. In addition, the manner of the competition was seen to change drastically with density at the adult stage.

According to DUMORTIER (1963), ALEXANDER (1967) and HASKELL (1974), acoustic signals having the function of attracting the opposite sex of conspecific members have been defined as calling signals (calling songs), and those emitted only in male-male rivalry behavior as aggressive signals or rivalry songs (rival's songs). Although the males of *N. lugens* are attracted to the signal emitted by stationary conspecific females, the male signal is usually the initiator of male-female communication in the mating behavior (ICHIKAWA, 1976, 1979). In the present study, the male signal commonly emitted in solo condition, in the mating behavior and in male-male competition was named the calling signal. The female signal emitted in the mating behavior was named the invitation signal (IS) after OSSIANNILSSON (1949) to discriminate it from the calling signal.

VS emitted in the male-male competition of *N. lugens* could be classified into three types, i.e., the calling signal (CS), the pre-aggressive signal (Pre-AS) and the aggressive signal (AS). Both brachypterous and macropterous males emitted these three types of VS (Fig. 3). CS was always emitted first, irrespective of the presence or absence of other conspecific males, and the time of the first emission of CS was usually within 5 min after being set on the rice plant. Communication through CS by the males is supported from the alternate emission of CS by a pair (Fig. 2), their active movement after the beginning of CS emission, and the marked difference in the frequency of CS emission between the pairs and the single males (Table 8). Pre-AS is considered to be merely the prelude to AS emission because this simple signal

was usually soon replaced by AS. It is apparent that AS is aimed at other conspecific males because no single male emitted this signal. The playback of CS emitted in male-male competition elicited the emission of IS from receptive conspecific females, as did the playback of CS emitted in the solo condition. On the contrary, the playback of Pre-AS and AS elicited no substantial response from the females (Table 9). Therefore, it is apparent that only CS is perceived by conspecific females as the mating signal, irrespective of the situation of the male emitting CS. In fact, I have never detected Pre-AS and AS in the mating behavior of *N. lugens*. Active movement by the males in pairs was always observed after the beginning of CS emission throughout the present study. This suggests that CS is the releaser of male-male communication, like male-female communication in the mating behavior. The results of Experiment 2, especially, indicate that male-male communication is initiated not by visual or tactile perception of other males, but by the perception of CS emitted by other males.

Density-related changes in male-male competitive behavior are apparent from the results of Experiment 3. Avoidance between a pair of males in D1 after the beginning of CS emission indicates that CS has practically aggressive effect in male-male competition for this density group. On the other hand, CS emission seemed to stimulate members to approach each other in the D2 and D5 pairs. Such approaches resulted in the occasional performance of rejection behavior (RB) or direct body attack (DBA). RB was always performed by the upper male clinging to the rice plant without its emitting VS of any type toward the lower one which emitted CS after approaching to a close proximity. As described in the results of Experiment 1, the lower male seemed to have mistaken the upper one for a conspecific female. This suggests that VS emission is essential for the discrimination of sex. RB was similar to the mate refusal behavior performed by sexually immature females or those which had successfully copulated (ICHIKAWA, 1979). So RB is considered to be a common pattern of behavior among males and unreceptive females to expel males emitting CS in close proximity. It must be noted that distinct aggressive behavior, DBA, was observed only in the D5 pairs. The D1 pairs never emitted AS, and the D5 pairs emitted AS significantly more frequently than the D2 pairs. Only one member of a pair was observed to emit AS in 28 out of 36 pairs in which AS was detected, and CS emission by one member of a pair was rarely observed when the other was emitting AS. Therefore, AS emitted by one seems to suppress the emission of CS and AS by the other. In addition, one which did not emit AS was sometimes observed to escape from the other which emitted AS. These facts indicate that dominant males emit AS more frequently than subordinate ones in D2 and D5.

In orthopterous crickets, the calling songs of the males are known to be used not only for the attraction of conspecific females but also for male-male communication as a mild aggressive signal. And hyper-aggressive males of these insects emit aggressive sounds in male-male communication (ALEXANDER, 1961, 1962). The present study indicates that CS corresponds to the calling sounds and AS to the aggressive sounds. However, it must be noted that aggressive effects in the male-male competition of *N. lugens* were fully exerted only by CS emission in D1, by CS emission and AS emission in D2 and by CS emission, AS emission and DBA in D5. Therefore, the intensity of the aggressive effects of CS is considered to be inversely correlated with their adult density. As the males come to emit CS within two days after emer-

gence at 25°C, irrespective of their nymphal density (ICHIKAWA, 1979), they might gradually come to be aggressive through competitive communication during the early period of adult life. The qualitative changes in male-male competition with the increase of their adult density must have evolved in connection with their characteristic mode of life, i.e., explosive population growth on one hill of the rice plant and the density-related changes in their wing-forms.

In Japan, a population of *N. lugens* in a given paddy field starts with macropterous adults of both sexes which have been shown to immigrate by flight in the pre-mating period over the East China Sea (KISIMOTO, 1976). Although their density is extremely low, ranging from one female per 100 hills to one per 7 hills, it increases almost exponentially for the ensuing three generations until it reaches an extremely high density, cousing hopper-burn (KISIMOTO, 1977). The discriminate changes in their wing-forms occur in the course of this population growth (KISIMOTO, 1965). In the first generation, the next generation to the macropterous immigrants, most females are brachypterous and males macropterous. Thereafter, the ratio of macropterous females increases with the increase in their population density. Brachypterous males appear in the second generation when their density is in a middle range. Most adults of both sexes are macropterous form in the third generation. Population density at their birth place can be divided into three levels, i.e., low, middle and high, for convenience' sake. All adults of both sexes emerged from the rearing of only ten nymphs per rice seedling were of the macropterous form (ICHIKAWA, 1979). So these three levels must not be determined by the number of individuals, but by the ratio of those of each wing form emerged from their birth place.

Dominant males in male-male competition are known to have the advantage in acquiring conspecific females in the winter cherry bug, *Acanthocoris sordidus* (FUJISAKI, 1980, 1981). Resident males in female galleries are dominant in competition with intruder males in two species of scolytid beetles, *Dendroctonus pseudotsugae* (RUDINSKY and RYKER, 1976) and *Pseudohylesinus nebulosus* (OESTER et al., 1981). Such a dominant-subordinate relationship in males regarding reproductive performance might be applicable to *N. lugens*. However, the meanings of male-male competition in *N. lugens* must be considered in connection with their population density. In the low population density, the males are macropterous and the females brachypterous. On one hill of the rice plant, the earlier emerged males might expel those emerged later by frequent CS emission. CS emission by the former is simultaneously available for successful copulation with brachypterous females at the birth place, as is apparent from the results of Experiment 4. In the middle population density, the two wing-forms are present in both sexes. The nymphal period of brachypterous males is somewhat shorter than that of macropterous ones (KISIMOTO, 1956), and the former can copulate within two days after emergence (TAKEDA, 1974). In addition to these characteristics, brachypterous males, which are unable to fly, might come to be more aggressive than macropterous ones due to continuous communication with other males which emerged from the same hill of the rice plant. On the other hand, brachypterous females come to respond to CS by IS emission within a few days after emergence, irrespective of their adult density (ICHIKAWA, 1979). Therefore, brachypterous males might have a greater chance than macropterous ones for copulation with brachypterous females at the birth place. The fate of macropterous females seems to be complicated. Some of them collected at the birth place were mated and had

mature eggs in their ovaries, while those just after dispersal by flight were virgin and had no mature eggs without exception (OHKUBO, 1981). It seems that behaviorally different types are present in macropterous females as with the three types, non-flier, flier and migrant, in alate alienicolae of *Aphis fabae* (SHAW, 1970a, b, c). If so, some of the macropterous females might behave like brachypterous ones as the source of reproduction at the birth place. Other macropterous females might fly out from the birth place with macropterous males before sexual maturation, and these will mate at the place to which they immigrate. In the high population density, a huge number of macropterous adults of both sexes usually emerge successively on one hill of the rice plant. The clamor caused by VS emission might make the males aggressive. On the other hand, sexual maturation of virgin macropterous females, which can be judged from the ability to emit IS, the presence of mature eggs in their ovaries and the period of successful copulation, is significantly delayed with high density at the adult stage (OHKUBO, 1967; ICHIKAWA, 1979). Besides, the ratio of virgin macropterous females having no mature eggs at the birth place increased at the period of high population density in paddy fields (OHKUBO, 1981). These findings indicate that dominant males in male-male competition in the high population density have little chance of mating with macropterous females at the birth place. What, then, is the outcome of the competition? First, it is probable that dominant males can reserve sound feeding spots on the rice plant which is destined to wilt as a result of an attack by a huge number. Secondly, the competition might contribute to the promotion of long-distance migration of both sexes in the premating stage. In this connection, I obtained results suggesting that sexually immature virgin females take part in the competition (ICHIKAWA, unpublished).

Although the above-mentioned possible implications of male-male competition in *N. lugens* in paddy fields are not yet proved, more detailed researches on the competition might throw light upon the mating system defined by EMLEN and ORING (1977) and the promotive factors of their migration.

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