Certain Environmental Factors Influencing the Acoustic Communication in the Sexual Behaviour of the Leafhopper *Amrasca devastans* (DISTANT) (Homoptera: Cicadellidae)

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The role of certain environmental factors in influencing the substrate-borne acoustic communication associated with the sexual behaviour of the leafhopper, *Amrasca devastans* (DISTANT) was studied under the laboratory conditions. The sound emission as well as the sexual behaviour was high at 28 ± 1°C and was inhibited by a low (18 ± 1°C) or a high temperature (38 ± 1°C). A high humidity (≥80% r.h.) was found to inhibit the sexual communication and behaviour of this leafhopper whereas a low humidity (30–40% r.h.) had no effect on these responses. Singing by the sexes in complete darkness was as high as in the presence of light. However, the copulatory responses were reduced in the dark. The leafhoppers kept under a short day-length (8L–16D) for 5 days after emergence sang and copulated as high percentages as those kept under a long day-length (13L–11D) for 5 days after emergence. The sexual communication leading to mating was not done by the two sexes being present on different leaves which had been in out of contact with each other; but was done by those being present on the same leaf. This fact imposes a severe limitation in the reproduction of these insects since no air-borne distance stimulus is involved in their communication.

INTRODUCTION

Sound emission among the auchenorrhynchous homopterans is widely known (Osiannilsson, 1949; Ichikawa, 1976, 1977; Inoue, 1982; Strübing, 1980; Saxena and Kumar, 1984; Claridge, 1985). However, little information is available on the factors governing the acoustic communication and the associated behaviour in this group of insects. We are therefore studying the role of various physiological and environmental factors in influencing the sonic communication in the sexual behaviour of the leafhopper *Amrasca devastans* (DISTANT). In our previous paper (Kumar and Saxena, 1985), we have described as to how certain physiological factors influence the sexual communication and behaviour of this leafhopper (see Ichikawa, 1979). In the present paper, we describe the role of certain environmental factors in influencing the acoustic communication in the sexual behaviour of the leafhopper, *A. devastans*.

MATERIALS AND METHODS

The nymphs of *Amrasca devastans*, collected from the fields of okra (*Abelmoschus...
esculentus), were reared on whole okra fruits (Saxena and Saxena, 1971). The emerging males and females were then reared singly on a piece of whole okra fruit inside a glass vial (5 cm long; 2 cm diam.). The insects were reared at 28±1°C under a 13L-11D cycle, unless otherwise stated. Five- to seven-day-old insects, when they show maximum sound emission and mating (Kumar and Saxena, 1978, 1985), were tested for their sexual communication and behaviour on a freshly excised cotton leaf (cv. PS-10). The methods to pick up, monitor and record the sounds emitted by the insects were the same as those described previously (Saxena and Kumar, 1984; Kumar and Saxena, 1985). Environmental conditions in the laboratory during the experiments varied according to the nature of each experiment.

For each experiment, 30 males and 30 females were tested, in three separate sets of 10 each (unless otherwise stated, the ns for all the means shown are therefore 30). The data were processed statistically through the usual procedure (Snedecor and Cochran, 1970).

For studying the effects of temperature on acoustic communication and sexual behaviour, single pairs of males and females were released on cotton leaf kept in a room maintaining low (18±1°C), optimum (28±1°C) or high (38±1°C) temperature, the humidity being 40–50% r.h. Prior to each test, the sexes were kept for 1 hr at the temperature whose effect was to be studied. This was done to allow the sexes to get adapted to the desired temperature.

The effects of different humidities were studied by releasing single pairs of males and females on a watered cotton leaf kept inside a rectangular chamber (40×20×20 cm), having low or high humidity. The front, back and side walls of the chamber had clear plexiglass. The top of the chamber had a detachable glass plate and the bottom was formed by a fixed nylon-net (40 mesh/cm) wall. The bottom of the chamber was supported on a glass tray (40×20×20 cm) such that the lower margins of the chamber rested on the upper rim of the glass tray. Thus, the cavity of the tray was separated from the inside of the chamber only by the nylon-net wall. The front wall of the chamber was provided with a hole (2 cm diam.) through which a phonograph cartridge was introduced into the chamber to monitor the sounds produced by the insects. The low humidity inside the chamber was the same as prevailing in the experimental room. The high humidity (≥80% r.h.) was generated inside the chamber by keeping a double-layered muslin cloth soaked in distilled water inside the tray. The water vapours from the wet muslin entered the chamber through its bottom to build up a high humidity around the leaf on which the insects were released.

In order to study the effects of light, single pairs of males and females were released on a watered cotton leaf kept inside a dark chamber (40×20×20 cm) for 30 min. Various sexual responses of the insects were monitored inside the dark chamber by listening to various sounds as described by us previously (Saxena and Kumar, 1984) and summarized below: After the onset of courtship sounds, the male approached the female termed as ‘dancing’ which was indicated in the headphones by loud ‘thundering’ sound caused by the friction of the moving male against the leaf; Arrest of the male by the side of the female was indicated by the ‘snoring’ sound; copulatory attempt by the ‘pattering’ sounds and copulation by the ‘drumming’ sounds. After the drumming sounds, the dark chamber was opened to confirm the copulation by the sexes. The sexual responses in the dark were then compared with the same responses of the insects in the presence of light.
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For studying the effects of photoperiod, the freshly emerged males and females were reared under a short daylength (8L–16D) for 5 days. Thereafter, single pairs of males and females were released on a cotton leaf for 30 min. The sexual responses of the insects were then compared with the same responses of the insects reared under a long daylength (13L–11D).

For studying the effects of surface continuity on the sexual behaviour, ten pairs of 5-day-old males and females were released in a clear plexiglass chamber (40 x 20 x 20 cm) having one or four cotton leaves, each with its petiole immersed in water in a separate glass vial, such that they were neither touching each other nor the walls of the chamber. The insects were observed for 60 min in each test. The percentages of insects arriving and copulating on the leaf or leaves were calculated.

RESULTS

As reported before (Saxena and Kumar, 1984), the males of A. devastans emit 'croaking' sounds which are transmitted through the plants on which they are feeding. The females, if present on the same plant, respond to such croaks by emitting their own substrate-borne 'cooing' sounds. The coos stimulate the males to emit their croaks more frequently and to commence 'dancing' movements during which they approach the females. The sounds of the two sexes alternate with each other throughout. On reaching the females, the males are arrested by the side of the females, extend their genitalia towards those of the females (copulatory attempt) and finally copulate. In view of this, the effects of various factors on the following responses of the insects were studied: (1) percentages of males and females emitting their sounds, (2) the number of croaks and coos emitted by the males and females respectively, (3) percentage of males showing dancing movements, (4) percentage of males reaching the females and arrested by them, (5) percentage of males showing copulatory attempts and (6) percentage of pairs copulating. The first three responses were observed when the two sexes were kept confined under their respective PVC covers for the entire observation period whereas the remaining types of responses were observed after removing the PVC covers subsequent to the onset of dancing movements by the males.

Temperature effects

Figure 1 shows that the percentages of the males and females emitting croaks and coos respectively at the low temperature (18 ± 1°C) were as high as those at the optimum temperature (28 ± 1°C). The numbers of acoustic signals emitted by the sexes at the low temperature were significantly lower than those at the optimum temperature. Despite the low rate of sound emission at the low temperature, the percentages of the males 'dancing' arrested by the females and showing copulatory attempts were as high as at the optimum temperature. But, all the females did not accept the males and, consequently, the percentage of pairs copulating at 18 ± 1°C was reduced significantly in comparison to that at the optimum temperature.

At the high temperature (38 ± 1°C), on the other hand, the percentage of the males singing was as high as at the optimum temperature. But, the percentage of females singing was declined significantly. The numbers of sounds emitted by the males and females at the high temperature were significantly lower than those at the optimum temperature. Consequently, the percentages of the males dancing, arrested by the
Fig. 1. Sexual responses of male and female Amrasca devastans held in pairs on a watered cotton leaf, in relation to temperature (percent responses based on 30 insects and no. of sounds based on no. of insects in each column; observation time = 30 min). Single vertical bars represent standard errors and each double vertical bar represents l.s.d. at \( p=0.05 \) (ANOVA test) for all the columns immediately on its left.

Table 1. Sexual responses of male and female Amrasca devastans held in pairs on a watered cotton leaf, in relation to humidity (percent responses based on no. of 30 insects and no. of sounds based on no. of 10 insects in each row (observation time = 30 min)

<table>
<thead>
<tr>
<th>Relative humidity (%)</th>
<th>% males croaking</th>
<th>% females cooing</th>
<th>( \bar{X} ) croaks per male</th>
<th>( \bar{X} ) coos per female</th>
<th>% males arrested by females</th>
<th>% males showing copulatory attempts</th>
<th>% pairs copulating</th>
</tr>
</thead>
<tbody>
<tr>
<td>30-40 (low)</td>
<td>100 a</td>
<td>100 a</td>
<td>609±25 a</td>
<td>508±28 a</td>
<td>100 a</td>
<td>100 a</td>
<td>100 a</td>
</tr>
<tr>
<td>≥80 (high)</td>
<td>60±6 b</td>
<td>50±6 b</td>
<td>73±40 b</td>
<td>66±36 b</td>
<td>47±3 b</td>
<td>37±7 b</td>
<td>33±9 b</td>
</tr>
</tbody>
</table>

Croaks were 2-6 pulsed phrases.
Two means in a column followed by different letters are significantly different \( (p<0.05) \).

females, showing copulatory attempts and copulating were reduced significantly at the high temperature in comparison to those at the optimum temperature. Thus it is significant to note in Fig. 1 that every phase in the sexual behaviour of this leafhopper was affected by the high temperature.

**Humidity effects**

Table 1 shows that all the males and females sang and the number of sounds emitted by each sex was very high under the low humidity (30-40\% r.h.). Consequently, all
the males exhibited dancing, reached the females and mated with them. Under the high humidity (80% r.h.), on the other hand, the percentages of the males and females singing as well as the numbers of sounds emitted by each sex were significantly lower than those under the low humidity. This reduced acoustic stimulation between the sexes under the high humidity, resulted in the low percentages of the males dancing, reaching the females and copulating (Table 1).

**Light effects**

Table 2 shows that the percentages of the males and females singing in complete darkness were as high as in the presence of light. The number of sounds of the females also remained the same though that of the males in the dark was significantly lower than that in the presence of light. The percentage of the males dancing in the dark, as indicated by the loud thundering noise, was also statistically identical to that in the

Table 2. Sexual responses of male and female *Amrasca devastans* held in pairs on a watered cotton leaf, in relation to light (percent responses based on no. of 30 insects and no. of sounds based on no. of 10 insects in each row; observation time=30 min)

<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>% males croaking</th>
<th>% females cooing</th>
<th>X croaks per male</th>
<th>X coos per female</th>
<th>% males dancing</th>
<th>% males arrested by females</th>
<th>% males showing copulatory attempts</th>
<th>% pairs copulating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light present</td>
<td>100 a</td>
<td>100 a</td>
<td>621±35 a</td>
<td>501±47 a</td>
<td>100 a</td>
<td>100 a</td>
<td>100 a</td>
<td>100 a</td>
</tr>
<tr>
<td>Light absent</td>
<td>90±10 a</td>
<td>90±10 a</td>
<td>455±45 b</td>
<td>368±46 a</td>
<td>90±10 a</td>
<td>70±6 b</td>
<td>67±7 b</td>
<td>43±7 b</td>
</tr>
</tbody>
</table>

Croaks were 2–6 pulsed phrases.
Other explanations as in Table 1.

Table 3. Sexual responses of male and female *Amrasca devastans* held in pairs on a watered cotton leaf, in relation to photoperiod (percent responses based on no. of 30 insects and no. of sounds based on no. of 10 insects; observation period=30 min)

<table>
<thead>
<tr>
<th>Photophase</th>
<th>% males croaking</th>
<th>% females cooing</th>
<th>X croaks per male</th>
<th>X coos per female</th>
<th>% males dancing</th>
<th>% males arrested by females</th>
<th>% males showing copulatory attempts</th>
<th>% pairs copulating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Short daylength (8L–16D)</td>
<td>100 a</td>
<td>100 a</td>
<td>670±42 a</td>
<td>519±45 a</td>
<td>97±3 a</td>
<td>97±7 a</td>
<td>93±7 a</td>
<td>93±7 a</td>
</tr>
<tr>
<td>Long daylength (13L–11D)</td>
<td>100 a</td>
<td>100 a</td>
<td>601±30 a</td>
<td>506±41 a</td>
<td>100 a</td>
<td>100 a</td>
<td>100 a</td>
<td>100 a</td>
</tr>
</tbody>
</table>

Croaks were 2–6 pulsed phrases.
Other explanations as in Table 1.
presence of light. But, the percentages of the males arrested by the side of the females and showing copulatory attempts in complete darkness, as indicated by their snoring and pattering sounds respectively, were significantly lower than those in the presence of light. Finally, the percentage of the pairs copulating as indicated by the drumming sounds was also significantly lower than that in the presence of light.

Photoperiod effects

Table 3 shows that adults maintained under a short daylength (8L–16D) emitted their sounds in almost as high percentages as those kept under a long daylength (13L–11D). Similarly, the numbers of sounds emitted by the males and females maintained under the two daylengths were the same. Consequently, the percentage of the short daylength- males showing the remaining sexual responses culminating in their copulation with the females was statistically as high as that of the long daylength individuals.

Surface continuity effects

Table 4 shows that when a single leaf was offered to the unmated individuals in a plexiglass chamber, about 53% of the males and 40% of the females arrived on the leaf and in about 78% of the arrived pairs, the males showed dancing and copulated with females. On presenting 4 leaves in the test chamber, 80% males and 80% females arrived on one or the other leaf. The sexes mostly arrived at different times on different leaves except for about 30% cases in which the sexes arrived on the same leaf during the same time. In all these pairs, the males exhibited dancing and copulated with the females.

DISCUSSION

Several investigators have examined the effects of various environmental stimuli on the sexual behaviour of different groups of insects (Engelmann, 1970; Saunders, 1982). So far as the auchenorrhynchous homopterans are concerned, no detailed investigation has been conducted yet. In the leafhopper, Doratura stylata, for example, the effect of temperature on the calling songs of the male but not on its sexual behaviour has been reported by Ossiannilsson (1949). In the beet leafhopper, Circulifer tenellus, on the other hand, the effects of different temperatures on the sexual activity but not on the sound emission have been reported by Perkes (1970). There is hardly any information on the role of other environmental factors in influencing the sexual com-
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munication and behaviour of the homopterans. The results given in this paper thus advance our knowledge by providing information on the roles of various environmental factors in determining the acoustic communication as well as the sexual behaviour of the leafhopper, *A. devastans*.

The present work shows that the sound emission and sexual behaviour of *A. devastans* are governed by the fluctuations in the temperature and humidity but will be independent of photoperiod. This suggests the following: (1) In summer months of May and June in North India, when the temperature reaches 40°C during the noon hours, the sexual activity of *A. devastans* would be restricted to the early and late hours of the day when the temperature and humidity remain considerably optimum. (2) In the winter months of December and January, on the other hand, the sexual activity of this leafhopper would occur mostly after sunrise when the temperature and humidity start becoming optimum, because the temperature remains pretty low during the early and late hours of the day. These adaptations enable this leafhopper to reproduce and build up its population enormously both during the peak summer as well as winter months in India.

The present work also demonstrate that in complete darkness singing by the sexes would be as high as in the presence of light. However, the other sexual responses in the dark e.g. arrest of the male by the female leading to copulation would be lower than those in the presence of light due to non-perception of the visual signals from the females by the males as described by us previously (Saxena and Kumar, 1984). Thus this leafhopper would differ from certain planthoppers which have been reported to sing as well as mate equally high in the presence and absence of light (Ichikawa, 1977).

In many orthopterans, the air-borne sound of the male can attract the females from a large distance (Haskell, 1974). Unlike these insects, the present work shows that the mating activity of *A. devastans*, the sexes of which have been reported to pair together through substrate-borne acoustic signals (Saxena and Kumar, 1984), would be determined by the presence of males and females on a common surface. This has been proved in this work by using a simple model by presenting to the sexes 1 or 4 cotton leaves inside a plexiglass chamber. When there was one leaf, both the sexes arrived on it and because of the acoustic continuity of its surface, showed sexual behaviour and copulated. But, when there were four leaves, the insects would be attracted to any of them with almost equal probability. Consequently, the chances of the males and females arriving on the same leaf were reduced so that the communication and copulation between them also declined. Thus, the reproduction and population build-up of the leafhopper would be limited by the number of acoustically continuous or discontinuous areas in a locality.

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REFERENCES

EUSCELIS-ARTEN

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