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**ACOUSTIC SIGNALS OF *GRAMINELLA NIGRIFRONS*
(HOMOPTERA: CICADELLIDAE)**S. E. Heady and L. R. Nault¹**ABSTRACT**

The deltocephaline leafhopper, *Graminella nigrifrons*, produces low intensity substrate transmitted vibrations (signals) to facilitate location of virgin females by males during courtship. In the laboratory, signals produced on maize leaves were received by a phonographic cartridge, amplified, and analyzed on an oscillograph and sonograph. Male calls, that are produced spontaneously, are complex, consisting of three consecutive sections. Section 1 consists of ca. 3 sec of irregular clicks. Section 2 has ca. 4 sec of repeated phrases consisting of a continuous series of 0.4 sec chirps and a roll. Section 3 consists of ca. 5 sec of an intermittent series of 0.2 sec chirps and a roll. Female calls are produced in response to male calls. Female calls are simple compared to male calls and consist of ca. 4-5 sec of low frequency clicking. Signal patterns of *G. nigrifrons* are compared to those of other leafhoppers and evolutionary scenarios are presented to account for the observed gender differences in signals.

The blackfaced leafhopper, *Graminella nigrifrons* (Forbes), is one of the most common leafhoppers occurring in grasslands of the Eastern United States (Kramer 1967). *G. nigrifrons* is the primary vector of the virus causing one of the most important stunting diseases of maize (*Zea mays* mays) in the United States. The pathogen, initially described as the 'Ohio corn stunt agent' by Rosenkranz (1969), was later identified as maize chlorotic dwarf virus (MCDV) (Gingery 1988 and references therein). In the corn belt states, MCDV has been reported in Ohio, Illinois, and Indiana, but is generally a problem only in areas where its alternate host, johnsongrass (*Sorghum halepense* L.), occurs (Gordon et al. 1981). Use of tolerant maize genotypes can reduce losses in some years and locations. MCDV remains the most destructive and widespread maize virus in the Southeastern and adjacent maize growing regions of the United States (Gordon and Nault 1977).

The biology of *G. nigrifrons* and its role as the vector of MCDV are well documented. Studies have been conducted on field biology (Boyd and Pitre 1968, Stoner and Gustin 1967), host range (Boyd and Pitre 1969), host utilization (Hunt and Nault 1990, Larsen et al. 1990), distribution (Douglas et al. 1966, Durant 1968, Durant and Hepner 1968), and vector relationships (Nault et al. 1973, Choudhury and Rosenkranz 1983, Knoke et al. 1983). The reproductive biology of *G. nigrifrons* has been studied in terms of laboratory life tables (Sedlecek et al. 1986); however, studies on the mating behavior were lacking. Leafhoppers were discovered to produce low intensity substrate signals by Ossiannilsson (1949). These signals are integral in courtship and facilitate males locating virgin females for copulation. To aid

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our understanding of the mating behavior of *G. nigrifrons*, male and female signals are described herein. Other aspects of the mating behavior, particularly those that may influence vector movement and disease spread, were conducted concurrently (Hunt 1988).

MATERIALS AND METHODS

Acoustic recordings were made using adults taken from laboratory colonies kept in rearing cages (D'Arcy and Nault 1982) at 26–28°C with a photoperiod of 12:12 (L:D). Late-instar nymphs were individually separated to obtain virgin adults for recording (Heady et al. 1986). To record signals, a leafhopper was placed on a maize leaf piece (ca. 15 cm length) and quickly covered with a plastic dome (1 cm diam) (Heady 1987). The leaf piece was laid over a phonographic cartridge (ElectroVoice 5146) so that it lightly touched the needle. Signal output from the cartridge was sent to a preamplifier (Omega EQ-25), a DC amplifier at 100x (Dana 3640), displayed on an oscilloscope (Dumont/Fairchild 766), monitored with earphones, and recorded on a tape recorder (Nagra E) using magnetic tape (3M 250) set at 19 cm/s. Recordings were made in a laboratory where temperatures ranged from 25 ± 2°C. Calls on acoustic tape were printed using a pen and ink polygraph (Grass Model 7, D.C. driver amplifier)(Heady et al. 1986). For male *G. nigrifrons*, the average duration of a spontaneous call was measured from 30 randomly chosen individuals. Characterizations of portions of the male signals were analyzed from oscillograms of five calls per individual and 10 individuals using a repeated measures analysis of covariance, with temperature as the covariable. Calls of female *G. nigrifrons* were analyzed from eleven individuals. Frequency spectra were printed using a DSP Sona-Graph (Model 5500, Kay Elemetrics Corp.).

Call terminology is described based on onomatopoeic interpretation and by pulse structure (Alexander 1967, Booij 1982, Heady et al. 1986, Huber et al. 1989). Leafhopper call repertoire includes male calling signals and male and female courtship signals. These calls are made up of sections composed of phrases, which are themselves made up of chirps, clicks, rolls, and intervals of silence. Chirps are distinct sounds to the human ear and are composed of simple or complex pulses of sound. Clicks have shorter durations than chirps. A roll is composed of a chirp and 3–6 pulses.

RESULTS

G. nigrifrons males spontaneously produced calling signals with mean durations of 15.2 (S.E. = 1.4, N = 30) sec. In the presence of a responding female, the male would call almost continuously as he walked to the female and joined genitalia. The male calling signal of *G. nigrifrons* was composed of three sections (Fig. 1A). Section 1 consisted of irregular clicks which were produced with increasing frequency over ca. 3 sec. Section 2 consisted of ca. 4 sec of repeated phrases consisting of a continuous series of 5–9 chirps and a roll (Fig. 1B). Section 3 has ca. 5 sec of repeated phrases consisting of an intermittent series of 1–4 chirps and a roll (Fig. 1C). The repeating phrase in section 2 was longer than the repeating phrase in section 3, 0.4 and 0.2 sec, respectively (Table 1). The rolls found in section 2 and 3 were not significantly different in duration and pulse rate (Table 1). Additionally, the rate of roll production (rolls/msec) in section 2 and 3 was not significantly different ($P > 0.20$). Thus the main difference between section 2 and 3 was the chirping before rolls. When the chirps, rolls, and silent interval between phrases were totaled (Table 1, phrase duration + phrase interval) and compared for section 2 and 3, section 3 phrases ($\bar{x} = 597.8$, S.E. = 9.9) were only slightly longer than section 2 phrases ($\bar{x} = 537.5$, S.E. = 17.2). Temperature did not significantly ($P >$

Table 1. — Male calling signal variables of *Graminella nigrifrons*.

	\bar{x} (S.E.)	
	Section 2 ^a	Section 3 ^a
Phrase Duration (msec)	449.4 (15.7)	215.8 (4.5)
Phrase Interval (msec)	88.1 (10.2)	382.0 (10.6)
Chirp Rate (chirps/sec) ^b	0.02 (0.0003)	—
Roll Duration (msec)	64.6 (1.1)	64.6 (0.9)
Roll Pulse Rate (pulses/sec) ^b	0.15 (0.0044)	0.15 (0.0066)
Roll Rate (rolls/sec) ^b	2.00 (0.043)	1.87 (0.064)

^a Corresponds to Fig. 1.

^b Values are temperature corrected for 24°C.

0.20) affect duration of phrases or intervals between phrases, but did impact on the pulse rate of chirping in section 2, pulse rate in the rolls, and rate of roll production ($P < 0.05$). The variation in calls among individuals for all variables analyzed was 2–7 times higher than the variation in calls within individuals. The frequency spectrum of calls of male *G. nigrifrons* consisted of frequency bands of energy concentrated between DC to 2000 Hz, with dominant frequencies at ca. 250 and 390 Hz.

In courtship, male calling began with section 1 type calls followed by section 2 and section 3 type calls which were repeated until copulation. Females called only when males produced section 2 and 3 calls. Calls of female *G. nigrifrons* consisted of low frequency (dominant frequencies at 170 and 250 Hz) clicking sounds. Average durations of female pulses were 15.4 msec (S.E. = 0.8, $N = 11$) and average intervals of 778.1 msec (S.E. = 106.3, $N = 11$) (Fig. 2).

DISCUSSION

Leafhoppers and planthoppers produce vibrational signals by means of a sound-producing organ similar to the cicada timbal organs in the first and second abdominal segments (Ossianni1sson 1949, Mitomi et al. 1984). The signals are transmitted through the plant substrate on which the insect is sitting (Ichikawa and Ishii 1974, Michelsen et al. 1982). Males and females alternate calls and the male walks to the female whereby copulation may occur. The mechanism for male mate location has been described as phonoklinotaxis for the leafhopper, *Ammrasca devastans* (Dist.) (Saxena and Kumar 1984). In contrast, Michelsen et al. (1982) theorized that signal frequency-time domain information might be used to determine the direction, distance, or both to a female. Claridge (1985) proposed that no directional information is received by the male, rather female calling elicits spontaneous random searching movements by males. Hunt (1988) proposed that male *Graminella nigrifrons* receives information on distance but not direction to females. Additionally, Hunt (1988) has demonstrated that phototactic responses in addition to acoustic signaling facilitate male location of females.

When a male *G. nigrifrons* flies or hops to a plant it will produce a call spontaneously. This signal, designated as a calling signal, attraction call, or common call (Ossianni1sson 1949, Heady et al. 1986), is complex and consists of three distinct sections (Fig. 1). The *G. nigrifrons* call becomes more patterned over time. The first portion of the call contains irregularly spaced clicks that increase in amplitude as section 2 calls are produced. In section 3 the signal pattern is well defined. A similar pattern of irregular clicking that changes to a patterned signal is found in the leafhoppers *Aphrodes trifasciatus* (Fourer.) (Ossianni1sson 1949), *Nephotettix nigropictus* (Dist.) (Claridge 1988), and short-winged forms of *Macrostes fascifrons* (Stål) (Purcell and Loher 1976). In the latter species, the male call was described as a trill with gradual transition to chirping. However, other leafhoppers

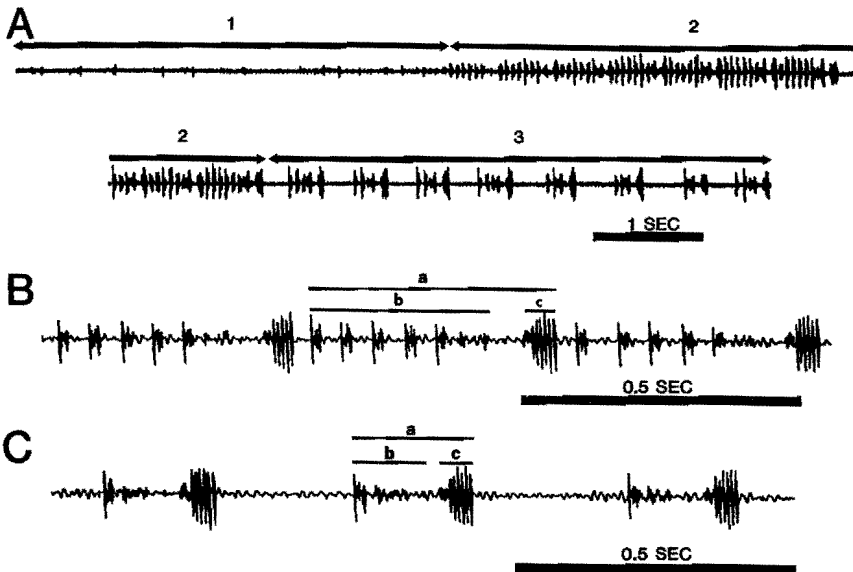


Figure 1. *Graminella nigrifrons* male calling signal. (A) Entire calling signal composed of three labeled sections. (B) Expanded Section 2 type calls with three repeated phrases. A phrase (a) consists of chirps (b) and a roll (c). (C) Expanded Section 3 type calls with three repeated phrases (a) consisting of chirps (b) and a roll (c). There are 6 pulses in the labeled roll.

studied do not produce a long building call, but rather, discrete chirps. *Amrasca devastans* (Distant) was described as producing "croaking" sounds (Saxena and Kumar 1984). Males of 10 *Dalbulus* species spontaneously produced calls composed of chirps (Heady et al. 1986). For example, *D. maidis* (DeLong and Wolcott) emitted 1-11 repeated chirps spontaneously. Male common calls of 10 *Dalbulus* species were analyzed using cluster analyses and the resulting phenogram was similar to groupings of species based on cladistic analysis of morphological characteristics (Heady et al. 1986). Although calls of members within a genus appeared similar in *Dalbulus*, calls of members among related tribes do not seem similar using the characteristics examined here. *Dalbulus* and *Macrosteles*, members of the tribe Macrostelini, have very different calls. The call of *G. nigrifrons* is similar to *N. nigropictus*, yet they are members of different Deltocephalinae tribes, Deltocephalini and Euscelini, respectively. Thus calls may be useful in resolving phylogenetic relationships within genera but not at higher taxonomic levels.

Female calls of *G. nigrifrons* were very simple in structure compared to male calls, and were produced only when males were producing section 2 and 3 signals. Section 1 male clicks do not elicit female calling nor any other obvious behaviors such as walking, perhaps because they are not patterned and are not species specific, or because their low amplitude may not be received by the female. Female calls of other leafhoppers are also less complex (lacking different patterned sections) compared to male calls. Examples are *Dalbulus* species (Heady et al. 1986; Heady, unpublished data); *Nephotettix* species (Claridge 1988); *M. fascifrons*, whose female call was described as a buzz (Purcell and Loher 1976); and *A. devastans*, whose call was described as cooing (Saxena and Kumar 1984).

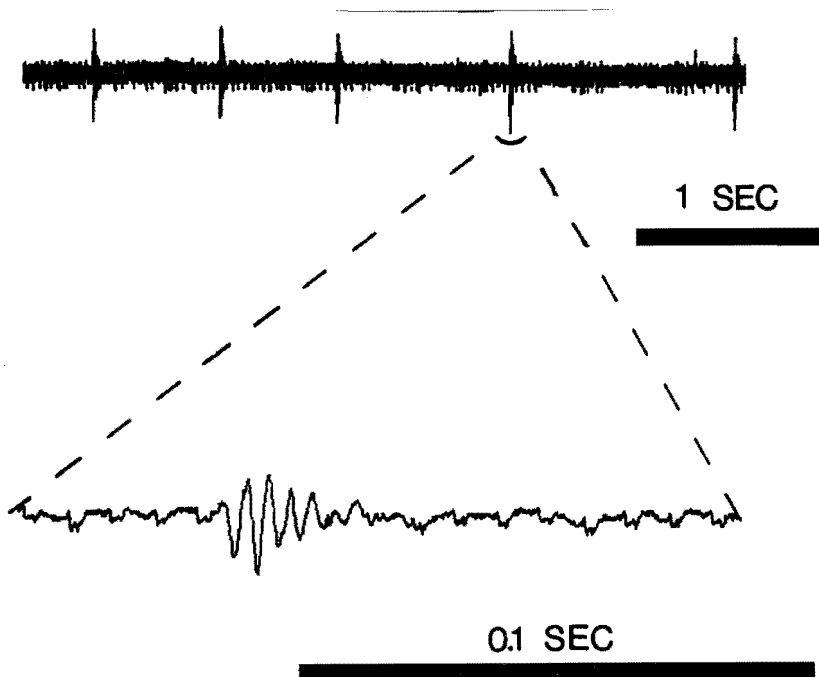


Figure 2. *Graminella nigrifrons* female calling signal produced during male section 2 or section 3 signalling.

The differences in call complexity between males and females may have evolved as a result of (1) the energetic cost of calling, (2) the risks associated with searching for mates, and/or (3) runaway sexual selection. Integral to these three hypotheses is the inherent asymmetry of reproductive roles between the sexes (West-Eberhard 1984). Male leafhoppers, like many insects, produce large numbers of small gametes (sperm) and multiply mate, whereas females invest more in gametes (large eggs), produce relatively few of them, and mate once or twice. In most crickets, katydids, and cicadas, males alone bear this energetically expensive activity of calling while a mute female finds him (Alexander 1967). In leafhoppers, males bear most of calling expense by producing more or longer calls than females.

Acoustic communication is the most energetically expensive of all forms of communication, i.e., chemical, visual, and tactile (Alcock 1989) and is known to be exploited by predators and parasites due to the ease of locating the signaller. A tachinid fly, *Euphasiopteryx ochracea* (Bigot), was attracted to taped songs of the field cricket *Gryllus integer* Scudder (Cade 1975) and a vertebrate predator (domesticated cat) was observed locating male crickets using their acoustic signals (Walker 1964). Additionally, the sarcophagid fly, *Colcondamyia audirix* Shewell, acoustically intercepts calling male cicadas (Soper et al. 1976). Specific predators of the leafhopper, *G. nigrifrons* have not been identified. Parasites identified from *G. nigrifrons* include three pipunculid flies, one strepsipteran, two dryinid wasps and one encyrtid wasp (Freytag 1987); however, their host-finding strategies have not been elucidated. Generalist insect and spider predators may be attracted to calling male leafhoppers by detecting the vibrations on the plant and by cuing on the

movement of males as they walk to females. Predators and parasites probably exert selective pressures on general male reproductive behaviors including song characteristics (Cade 1975, Zuk 1987a, b). Several studies of insect mating systems have shown that males suffer greater predation and parasitism as a result of their conspicuous displays and movements through habitats in search for females (Gwynne 1987, Thornhill 1978, Burk 1982, Walker and Masaki 1989). Hunt (1988) found that male *G. nigrifrons* flew plant-to-plant, calling on each, until landing on a plant that harbored sedentary but calling virgin females. This "call-and-fly" tactic was previously found in tick-tock cicadas, *Cicadetta quadricincta* and explained the higher incidence of males than females caught in spider webs (Gwynne 1987).

Lastly, the complex calls of males could be the result of rapid or "runaway" evolutionary change (Fisher 1958). If superior signalling is at a premium then there is selection on females to favor superior signallers as mates, because they will produce sons who are superior signallers. This leads to increasing selection on signalling ability and a genetic correlation between female preference and male signalling ability which will accelerate the evolution of both. Runaway change would end when natural selection against too costly or too risky displays balances sexual selection in favor of traits that are appealing to females (Alcock 1989). We expect that male calls of *G. nigrifrons* contain different section types and are elaborate compared to female calls due to female preference and yet are likely constrained by the energetics of calling and the risks associated with mate-finding.

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