

# EVIDENCE FOR SONIC COMMUNICATION IN THE GERMAN COCKROACH (DICTYOPTERA: BLATTELLIDAE)

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## Abstract

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Our objective was to test the hypothesis that late-instar nymph, male, and (or) female German cockroaches, *Blattella germanica* (L.), use sonic signals for intraspecific communication. A digital-recording system was assembled that consisted of a computer equipped with data-acquisition hardware and software, microphones sensitive to sonic and ultrasonic frequencies, and speakers capable of emitting sonic and ultrasonic sound. Sound was repeatedly recorded from groups of five nymphs, five virgin males, or five virgin females. Click-type sounds were commonly present in recordings from nymphs, and consisted of sound pulses of about 10-ms duration and peak frequencies of 7, 9, 11, and 14 kHz. Similar “clicks” were found in recordings from females. In replicated binary choice arena bioassays with individual laboratory-reared insects, played-back “clicks” from nymphs or females or computer-generated artificial clicks attracted nymphs but not males or females. These results provide the first evidence that sonic signals are part of the complex *B. germanica* communication system.

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## Résumé

Nous avons éprouvé l'hypothèse selon laquelle les larves de stades avancés, les mâles et (ou) les femelles de la Blatte germanique, *Blattella germanica* (L.), utilisent des signaux sonores pour communiquer les uns avec les autres. Un système digital d'enregistrement a été mis au point : un ordinateur muni d'équipement et de logiciels d'acquisition de données, des microphones sensibles aux fréquences sonores et aux ultra-sons et des hauts-parleurs capables d'émettre des sons et des ultra-sons. Des groupes de cinq larves, ou de cinq mâles vierges, ou de cinq femelles vierges, ont été enregistrés de façon répétée. Des sons de type claquement se sont avérés communs dans les enregistrements de larves et étaient composés de pulsations sonores d'environ 10 ms et de fréquences maximales de 7, 9, 11 et 14 kHz. Des claquements semblables s'entendaient dans les enregistrements de femelles. Au cours de tests de choix binaires répétés sur des insectes élevés individuellement en laboratoire, les claquements de larves ou de femelles, ou des claquements artificiels générés par l'ordinateur attiraient les larves, mais n'attiraient ni les mâles, ni les femelles. Ces résultats constituent une preuve inédite que des signaux sonores font partie intégrante du système de communication complexe de *B. germanica*.

[Traduit par la Rédaction]

## Introduction

The communication ecology of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae), is complex. Aggregation, mate attraction, mating, and dispersal are mediated by pheromones (Nishida and Fukami 1983; Sakuma and Fukami 1990; Liang and Schal 1993; Rust *et al.* 1995). Aggregation pheromones are produced

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by nymphs, as well as by adult males and females (Ishii and Kuwahara 1967, 1968). They are secreted with the feces (Sakuma and Fukami 1990) and consist of components that cause attraction and arrestment of conspecifics (Ishii 1970; Roth and Cohen 1973).

Sexually receptive "calling" females release sex pheromone to attract males. When releasing pheromone, they stilt their legs to raise the body above the substrate, tilt the thorax down, and raise the tegmina and flight wings (Liang and Schal 1993). Contact sex pheromones are produced by both males and females. Males excrete a pheromonal substance from the tergal glands that is lapped up by receptive females during mating (Rust *et al.* 1995). Virgin females have a contact pheromone in their cuticular wax that elicits wing-raising behavior in a male that attempts to mate (Nishida and Fukami 1983). Dispersal pheromones are nonvolatile and perceived on contact. They are produced in the saliva by juveniles and adults and act as an antagonist to aggregation pheromones (Rust *et al.* 1995). Released by early instar nymphs, they may serve to protect them from cannibalism by adults (Ross and Tignor 1986).

Potential sonic communication by *B. germanica* has not been thoroughly studied, although there is evidence for sound production and reception in various cockroach species. Cockroaches of the genus *Gromphadorhina* Brunner (Dictyoptera: Blaberidae) produce sound by expelling air from the tracheal system, whereas many other cockroaches stridulate by rubbing cuticular files on the pronotum against costal regions of the tegmina (Guthrie and Tindall 1968). The American cockroach, *Periplaneta americana* (L.) (Dictyoptera: Blattellidae), has sound receptors in the metathoracic legs that are most sensitive to frequencies near 1.8 kHz, comparable with other insects' auditory organs (Shaw 1994a, 1994b). Whether sound produced by cockroaches plays a role in intra- or inter-specific communication systems is yet to be investigated.

The objective of this study was (1) to test the hypothesis that *B. germanica* produce sonic signals and, (2) if so, to (a) characterize recorded signals, (b) bioassay the recorded signals, (c) computer-generate the signals, and (d) bioassay the computer-generated signals.

## Materials and Methods

**Rearing of Experimental Insects.** *Blattella germanica* were reared in Plexiglas™ cages (30 × 60 × 45 cm high) lined with paper towels and maintained at 25 ± 1°C, 40–70% RH, and a photoperiod of 14L:10D. Insects were given a diet of ground Purina dog chow (Ralston Purina Company, St. Louis, Missouri), apple slices, and water. Cages with final-instar nymphs were checked daily for eclosed adult males and females (Cornwell 1968), which were removed and kept in separate cages. Virgin adults 4–14 d post eclosion and late-instar (5th–6th) nymphs were used as experimental insects. Virgin females that had started to form an ootheca were not used in bioassays.

**Acquisition of Sonic Signals.** Software with monitoring, recording, and triggering capabilities was developed with Labview 4.0 – Graphical Programming for Instrumentation (National Instruments Corporation, 11 500 North Mopac Expressway, Austin, Texas). Signals were recorded for 1-s intervals, when the monitoring software (a virtual oscilloscope) detected sound that exceeded the baseline threshold of 0.1 mV. This software was used in combination with National Instruments AT-MIO-16E-1 and PCI-MIO-16XE-10 data acquisition cards in a Pentium 166 computer, to record digitally at sampling frequencies of 48, 100, and 200 kHz. Potential signals in the sonic range (0–24 kHz) were recorded, using an AKG CK 61-ULS condenser microphone (AKG Acoustics, Nashville, Tennessee) and a sampling rate of 48 kHz. The signal-to-noise ratio was improved by pre-amplifying (National Instruments SC-2040

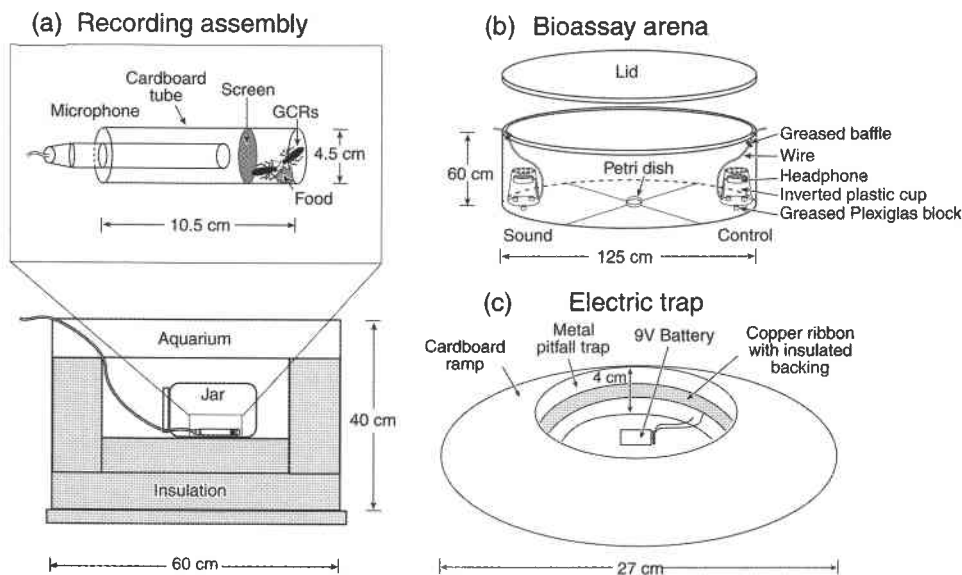


FIGURE 1. (a) The assembly for recording sound from groups of *Blattella germanica*, either five nymphs, five virgin males, or five virgin females. (b) The arena used in binary-choice bioassays to test *B. germanica* responses to sonic stimuli; the plastic cups were 11 cm high and 15 cm in diameter at the opening. (c) The electric trap used to capture *B. germanica* in bioassays conducted throughout the scotophase.

amplifier) signals before recording them on computer. Signals with ultrasonic frequencies (20–100 kHz) were not detected in preliminary recordings (condenser microphone, type 4138, Brüel & Kjær, Division of Spectris Technologies Inc., Pointe Claire, Quebec).

For sound recordings, five insects, either nymphs, virgin males, or virgin females, were placed in a jar within an insulated aquarium (Fig. 1) to eliminate background noise. Recordings took place about 3 h before the scotophase, coinciding with peak food-foraging behavior (Fuchs and Sann 1981). The triggering software for audio recording was designed to (1) stream audio data through a circular buffer at a user-defined sampling (scan) rate, (2) take user-defined numbers of pre- and post-trigger scans to acquire and place the signal in a file, (3) append subsequent audio data to that file, and (4) continue data acquisition until a user-defined time limit between trigger events was exceeded or the procedure was stopped manually. A slight discrepancy between user-defined and actual hardware scan rates (48 kHz) was corrected by setting the user-defined scan rate at 47.619 kHz. This correction ensured that recorded and played-back signals were identical.

The intensity of the sonic signals produced by *B. germanica* was measured by a 1551-C sound level meter (GenRad, Inc., Westford, Massachusetts) attached to either microphone, so that signal intensities during bioassays could be set at similar levels.

**Characterization of Sonic Signals.** Recordings were analyzed with National Instruments Joint Time–Frequency Analyzer. This software can display and analyze the frequency and intensity of sound(s) over specified periods of time. Low-amplitude, high-frequency signal components that might have been overpowered by relatively strong, low-frequency signal components during analyses were magnified by setting the “subband option” to the most sensitive level.

TABLE 1. Stimuli tested with *Blattella germanica* in binary-choice bioassays.

| Exp. | Dates                  | Treatment*           | <i>B. germanica</i> tested |                     |
|------|------------------------|----------------------|----------------------------|---------------------|
|      |                        |                      | <i>n</i> <sup>†</sup>      | Developmental stage |
| 1    | 23 Jul. – 1 Aug. 1997  | Female sonic signals | 28                         | Late-instar nymphs  |
| 2    | 11–15 Aug. 1997        | Female sonic signals | 19                         | Virgin males        |
| 3    | 18–22 Aug. 1997        | Female sonic signals | 20                         | Virgin females      |
| 4    | 24 Aug. – 3 Dec. 1997  | Nymph sonic signals  | 31                         | Late-instar nymphs  |
| 5    | 25 Jan. – 12 Mar. 1998 | Nymph sonic signals  | 32                         | Late-instar nymphs  |
| 6    | 17 Mar. – 15 Jun. 1998 | Female sonic signals | 26                         | Late-instar nymphs  |
| 7    | 24–27 Aug. 1998        | White noise          | 20                         | Late-instar nymphs  |
| 8    | 16–25 Jul. 1998        | Artificial signals   | 32                         | Late-instar nymphs  |

\* See Fig. 2 for female and nymphal sonic signals. Artificial signals were computer-generated and resembled those produced by females. Silence was the control stimulus in Experiments 1–8.

<sup>†</sup> Six and eight insects in Experiments 5 and 6, respectively, were not electrified and captured in traps associated with treatment or control stimuli.

Recurring signals in bioactive but noisy audio files were extracted (spliced) and placed in smaller files, employing a “splicing software program.” This procedure was conducted to increase the number of signals per time interval and reduce the overall noise level, anticipating an enhanced attractiveness of the audio file in bioassays.

Edited *B. germanica*-produced sonic signals were played back using developed software with AT-MIO-16E-1 or PCI-MIO-16XE-10 data-acquisition cards in a Pentium 166 computer and Sennheiser HE 60 headphone speakers (Sennheiser electronic, GmbH & Co. KG, D-30900, Wedemark) capable of emitting sound in the range of 6 Hz to 35 kHz. Identical scan rates during the recording and playing back of signals ensured that sonic signals were played back at the same frequencies at which they were recorded. The program continued to replay the same sound until stopped manually.

**Bioassays of Sonic Signals.** Edited sonic signals were tested with individual *B. germanica* in binary choice arena bioassays (Fig. 1). Software to play back recorded sonic signals was developed using Labview 4.0. Sennheiser HE 60 headphone speakers that played back sonic signals (treatment) or “silence” (control) were housed in inverted plastic cups. Output from the speakers was set at 50 dB, similar to the level during signal recording. Plastic cups were set on greased Plexiglas blocks to prevent *B. germanica* from contacting cups or speakers. Greased Plexiglas baffles around the speaker wires prevented *B. germanica* from descending on these wires and contacting the plastic cups or speakers from above.

Bioassays, like recordings, were conducted about 3 h before the scotophase and at steady barometric pressure. *Blattella germanica* were isolated at least 1 h before the onset of bioassays. For each replicate, a petri dish housing a single *B. germanica* was placed in the center of the bioassay arena (Fig. 1). After 15 min, the 30-min test was initiated by carefully lifting the lid of the petri dish. The accumulated time, in seconds, that the insect spent under or near (<15 cm) the plastic cups was recorded for each replicate. The positions of the speaker/plastic cup assemblies were rotated 90° in the arena before each replicate, to compensate for potential positional effects. Also, the speaker emitting the treatment signal was alternated between replicates.

**Bioassay Experiments.** Experiments 1–3 (Table 1) tested the response of nymphs (Exp. 1), virgin males (Exp. 2), and virgin females (Exp. 3) to recorded sonic signals from virgin females or silent controls. Experiments 4 and 5 tested the response of nymphs to recorded sonic signals from nymphs. Experiment 6 tested the response of

nymphs to recorded signals from females. For Experiments 5 and 6, the design was modified. The test was run throughout the scotophase, and responding nymphs were electrified and captured in traps (Fig. 1) beneath the plastic cups. The traps consisted of a cylindrical metal receptacle with a cardboard ramp and were designed so that individual *B. germanica* dropped into the trap when an appendage touched an insulated copper ribbon, thereby completing a 9-V circuit and electrifying and trapping the *B. germanica*. The metal pitfall traps were cleaned with ethanol and hexane before each replicate. The electric trap/speaker assemblies (Fig. 1) were rotated 90° before each replicate and the headphones emitting treatment and control stimuli were alternated between replicates.

Experiment 7 tested the response of individual nymphs to a source of “white noise” (a signal uniformly distributed at all frequencies within the sonic range) or silence played back for 30 min. This experiment was conducted to test whether nymphs were attracted to random sound (white noise) played back at the same intensity and duration as recordings of *B. germanica* signals. Experimental design and protocol were exactly the same as for Experiments 1–3, except that National Instruments Arbitrary Waveform Generator software was used to emit 10 ms of white noise every second from the treatment speaker.

Experiment 8 tested the response of individual nymphs to computer-generated artificial signals (Fig. 4) and to silent control stimuli. Peak frequencies and the waveform properties of female-produced click-type signals served as a template for the artificial waveform. The artificial signal was constructed using the Arbitrary Waveform Generator (National Instruments) by combining three 10-ms triangle waveforms with frequencies of 7, 9, and 12 kHz (Fig. 4) and adding a trapezoid function to generate a “ramping” effect.

**Statistical Analyses.** Differences in mean cumulative time spent in or near treatment or control stimuli were assessed with a paired sample *t* test. Differences in the proportion of insects trapped in electric traps associated with treatment or control stimuli were assessed with a binomial-distribution test for proportions ( $\alpha < 0.05$ ; Microsoft Excel 97, Microsoft Corp.).

## Results

**Characterization of Sonic Signals.** Joint time–frequency analyses of signal recordings from eight groups of five nymphs revealed a variety of signals, including a recurring click-type signal (Fig. 2) that lasted about 10 ms and had a frequency range that spanned 2–24 kHz. Peak frequencies appeared to be at 7, 9, 11, and 14 kHz. Joint time–frequency analyses of signal recordings from six groups of five virgin females also revealed many sonic signals, including a recurring click-type signal (Fig. 2) that was similar to that produced by nymphs (Fig. 2); about 10 ms in duration with a frequency range of 2–24 kHz and peak frequencies at 7, 9, and 12 kHz. Because recurring signals were not found in signal analyses from virgin males, only recorded signals from nymphs and virgin females were tested in bioassay experiments.

Ultrasonic signals could not be detected in any recording.

**Bioassay Experiments.** In experiment 1, late-instar nymphs spent significantly more time in or near plastic cups housing a headphone that emitted clicks from females (Fig. 2) than in or near silent control cups (Fig. 3). The sonic signal that attracted or arrested nymphs in experiment 1 had no effect on males in experiment 2 or on females in experiment 3 (Fig. 3).



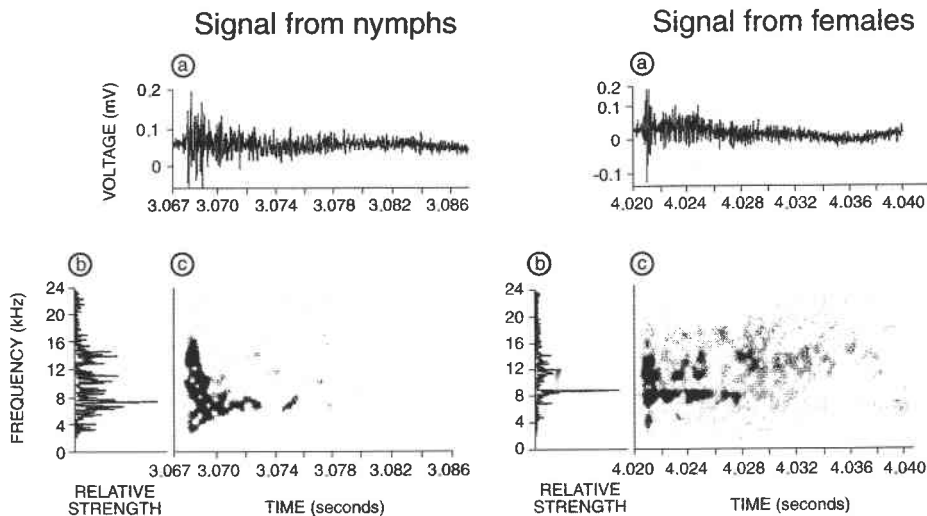


FIGURE 2. Analyses of waveform (a), frequency (b), and time–frequency/sound intensity (c) of click-type sonic signals recorded from nymph and female *Blattella germanica*. In c, the more intense the shading, the more intense the frequency component of the signal.

In Experiment 4, late-instar nymphs also spent significantly more time in or near plastic cups housing a headphone that emitted clicks from nymphs (Fig. 2) than in or near silent control cups (Fig. 3). More late-instar nymphs were electrified and caught in traps beneath a plastic cup housing a headphone that emitted clicks from late-instar nymphs (Exp. 5) or females (Exp. 6) than in respective control traps (Fig. 4). There was no difference in mean cumulative time spent by nymphs in Experiment 7 in or near cups housing a headphone that emitted either white noise or “silence” (Fig. 4). Computer-generated artificial signals that resembled the click-type signals from nymphs or females (Fig. 2) attracted or arrested more late-instar nymphs than did silent control stimuli (Fig. 4; Exp. 8).

## Discussion

Pheromone-based aggregation (Sakuma and Fukami 1990), mate attraction (Liang and Schal 1993), mating (Rust *et al.* 1995; Nishida and Fukami 1983), and dispersal behavior (Rust *et al.* 1995) have been intensively investigated in *B. germanica*. Our study is the first to report that sonic signals are also part of the *B. germanica* communication system. Evidence for sonic communication in *B. germanica* includes (1) recurring click-type signals produced by nymphs and females (Fig. 2), (2) significant attraction in binary-choice bioassays of late-instar nymphs to clicks recorded from females (Fig. 3; Exp. 1) and nymphs (Fig. 3; Exp. 4), (3) significant captures of late-instar nymphs in electric pitfall traps emitting clicks recorded from nymphs or females (Fig. 4; Exps. 5 and 6), and (4) significant attraction of late-instar nymphs to computer-generated artificial clicks (Fig. 4; Exp. 8).

A combined use of chemical and acoustic sensory modalities by *B. germanica* for communication may be of adaptive significance. In closed foraging sites that are inundated with food volatiles or pheromone(s), olfactory receptor cells and the central nervous system may become adapted and habituated, respectively. Alternatively, foraging nymphs that enter a new, as yet unexplored, habitat may use sound to signal the location of both food sources and potential shelters, without having to rely on the delayed

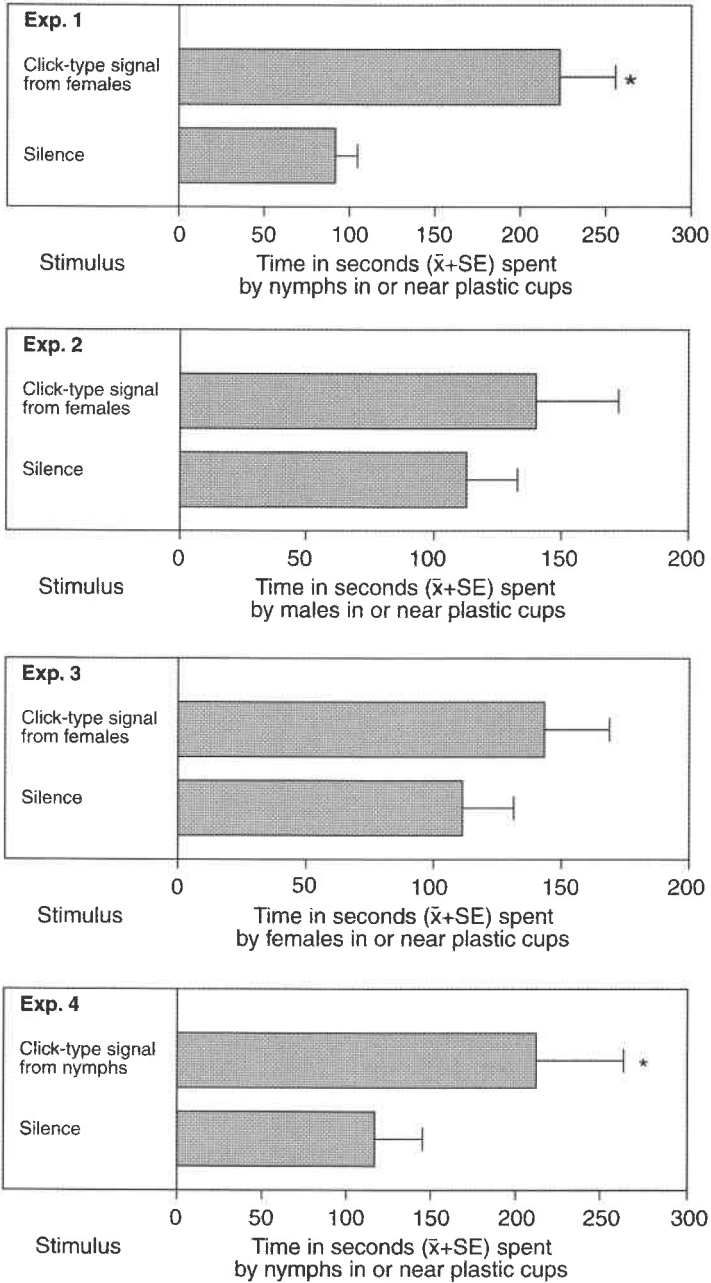


FIGURE 3. Time spent by experimental *Blattella germanica* in or near (<15 cm) plastic cups associated with a click-type signal recorded from females (Exps. 1–3) or nymphs (Exp. 4). An asterisk indicates a significant preference for a test stimulus at  $P < 0.05$ .

presence of frass-derived aggregation pheromone. Aggregations of nymphs are associated with increased survivorship of individuals (Rust *et al.* 1995). The attraction of nymphs but not of males or females to nymph-produced “clicks” (Fig. 2) suggests that sonic signals from nymphs may help them to form aggregations, such as those

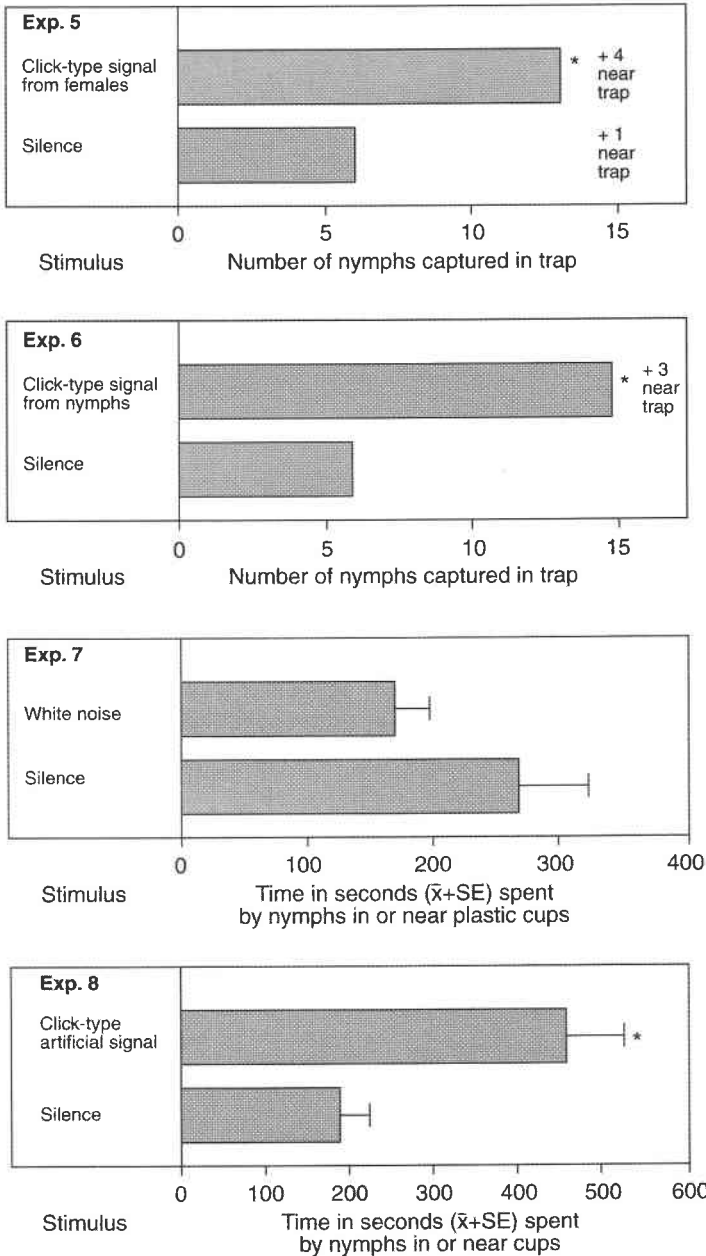


FIGURE 4. Experiments 5 and 6. The number of *Blattella germanica* nymphs captured in electric traps (see Fig. 1) associated with either a silent control stimulus or click-type signals from females (Exp. 5) or nymphs (exp. 6). Experiments 7 and 8. Time spent by nymphs in or near (<15 cm) cups associated with either a silent control stimulus or test stimuli. For each experiment, an asterisk indicates a significant preference for a particular stimulus at  $P < 0.05$ .

commonly observed in rearing cages. Nymphal aggregations, without adults, may help reduce competition for food or cannibalism by males, or both.

Click-type sonic signals have also been reported in other insect orders and may be generated by tymbal organs. For example, click-like sounds in *Drosophila fasciculisetae*



(Hardy) (Diptera: Drosophilidae) range from 500 Hz to 10 kHz (Hoy *et al.* 1988). Cicadas (Hemiptera) and katydids (Orthoptera) produce high-frequency clicks using stridulation or muscle-activated tymbals (Michelsen and Nocke 1974). Pentatomids and reduvids (Hemiptera) employ tymbal-like organs for sound production (Ewing 1989). Finally, the greater wax moth, *Galleria mellonella* (L.) (Lepidoptera: Pyralidae), has a tymbal organ on each tegula that generates sound with frequencies up to 75 kHz (Spangler 1986).

“Clicks” might not be the only sonic signal produced by *B. germanica*. Recordings from nymphs, males, and females gathering around a food source contained a wide variety of sounds, one or more of which may constitute a communication signal. When handled, male and female *B. germanica* fan their wings, generating low-frequency sound (Mistal 1999) that resembles the alarm calls of the cockroach *Henschoutedenia epilamproides* Shelford (Dictyoptera: Blaberidae) (Guthrie and Tindall 1968). Moreover, the possibility of ultrasonic communication in *B. germanica* cannot be excluded. Potential ultrasonic signals produced by *B. germanica* may be at intensities too low to be detected by the Brüel & Kjær type 4138 condenser microphone, which has a frequency range of <150 kHz and moderate sensitivity. If a microphone were to be designed that combines high sensitivity with a wide frequency range, a re-analysis of *B. germanica*-produced sound would be warranted.

There was no apparent interaction between frass-derived aggregation pheromone and click-type sonic signals (Mistal 1999). The many possibilities from combining semiochemical stimuli (pheromone and food volatiles) with bioacoustic signals for enhanced attractiveness are yet to be explored.

From a pest-management perspective, traps emitting sonic signals could be used to supplement or replace semiochemical-baited traps, or to induce aggregations on pesticide-treated substrates. Alternatively, acoustic devices that interfere with *B. germanica*-produced clicks could be investigated. Moreover, if they are repellent, computer-generated *B. germanica* distress or alarm calls in combination with semiochemical repellents (Rollo *et al.* 1995) may render otherwise suitable habitats inhospitable for *B. germanica*.

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