

SEXUAL SIGNALING IN PERIODICAL CICADAS, *MAGICICADA* SPP. (HEMIPTERA: CICADIDAE)

by

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Summary

Periodical cicada (*Magicicada* spp.) sexual pair formation takes place in dense aggregations and involves intense male-male competition for limited mating opportunities. Pair-forming behavior in these species has been poorly understood because of limited knowledge of sexual communication. We have found that sexually receptive female *Magicicada* flick their wings in timed response to an individual chorusing male; this previously unrecognized female response is hereafter referred to as a 'wing-flick' signal. We document the nature, timing, and species-specificity of this signal as well as its absence in both immature and mated females. We also document changes in male chorusing and searching behavior in response to wing-flick signals and male responses to the signals' visual and acoustical components. We test the hypothesis that female sensory psychology has shaped the evolution of -decim calls by

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favoring frequency-modulated male calls that are more readily distinguishable in an intense background chorus. Within mating aggregations, male *Magicicada* attempt to usurp ongoing courtships and also engage in interference competition by acoustically obscuring the calls of potential interlopers, reducing the likelihood of a female response.

Keywords: Cicadidae, communication, *Magicicada*, periodical cicada, playback experiments, receiver psychology, sexual pair formation, signal evolution, specialized chorusing behavior.

Introduction

The adult behavior of periodical cicadas (Insecta: Hemiptera: *Magicicada* spp.) has been considered enigmatic because of incomplete knowledge of these species' sexual communication. Several species are typically present in a *Magicicada* emergence, usually one from each of the cognate groups '-decim,' '-cassini,' and '-decula' (Table 1). Both sexes are attracted to conspecific calling song and form dense, mixed-species mating congregations (Alexander & Moore, 1962; Alexander, 1975; reviewed in Williams & Simon, 1995). Within these aggregations, chorusing males alternate short (*ca* 3-15 s) bouts of 1-3 calls with short flights of a few centimeters to several meters ('sing-fly' behavior). Males approach females while making call phrases similar to those in chorusing, but without intervening flights (CI courtship of Dunning *et al.*, 1979), and they court stationary females with an unusually complex acoustical repertoire, which in most species includes at least two acoustic signals in addition to the calling song (Alexander & Moore, 1958, 1962; Alexander, 1968, 1975; CII and CIII courtship of Dunning *et al.*, 1979; Table 2, Fig. 1).

TABLE 1. *Magicicada* species and cognate groups

Cognate group	Species	Life cycle (yrs)
'-decim'	<i>M. neotredecim</i> (Marshall & Cooley)	13
	<i>M. tredecim</i> (Walsh & Riley)	13
	<i>M. septendecim</i> (L.)	17
'-cassini'	<i>M. tredecassini</i> (Fisher)	13
	<i>M. cassini</i> (Alexander & Moore)	17
'-decula'	<i>M. tredecula</i> (Alexander & Moore)	13
	<i>M. septendecula</i> (Alexander & Moore)	17

TABLE 2. *The sexual sequence in Magicicada cognate species groups*

Cognate group	Chorus calling	Female signal	Courtship CI calling	Female signal	Male behaviours	CII calling	Female signal	Male behaviours	CIII calling	Female signal	Male behaviours
M. -decim	2-3 phrases between flights	After each phrase	phrases similar to those used in chorusing and separated by silent gaps	After each phrase	walking, flying between phrases	repeated, shortened phrases of the same type as in court I, without intervening silence	At end of CII	sometimes walking during calling, sometimes foreleg vibrate at transition to CIII	repeated staccato buzzes	No	Foreleg vibrate, mount, engage genitalia
M. -cassini	1-2 phrases between flights	After each phrase	phrases similar to those used in chorusing and separated by silent gaps	After each phrase	walking, flying between phrases	repeated, shortened phrases of the same type as in court I, with shorter intervening silences and with additional ticks after the downslur	At end of CII rarely during CII	sometimes walking during calling, sometimes foreleg vibrate at transition to CIII	repeated staccato buzzes	No	Foreleg vibrate, mount, engage genitalia
M. -decula	1 calling bout between flights	During call	calls similar to those used in chorusing	During call	walking, flying between phrases	none known	-	none known	repeated staccato buzzes	No	Foreleg vibrate, mount, engage genitalia

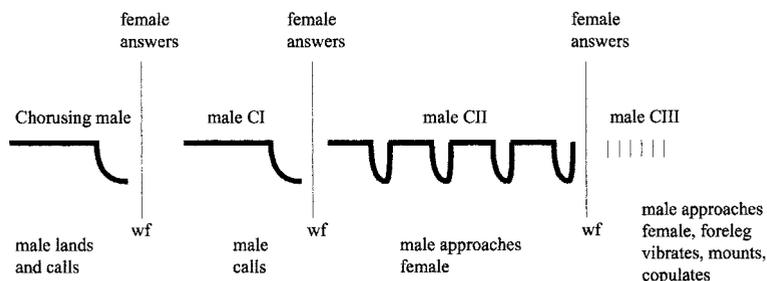


Fig. 1. Stylized sonogram of male call/female wing flick courtship duet for *M. -decim*. The male begins with court I (CI) calls; the female answers each call with a wing flick. After several such interactions, male begins court II (CII) calling. After the male ceases CII calling, the female wing flicks in response, and the male begins court III (C III) calling. Number of call phrases in each stage of the sexual sequence varies. See Table 2 for descriptions of the signals.

Until now, the cues causing males to switch from chorusing (not directed at a specific individual) to courtship (directed at an individual female) have remained unknown, and females have been regarded as signaling readiness to mate only through motionlessness (Alexander, 1968; Dunning *et al.*, 1979; Karban, 1983; Lloyd & Karban, 1983). This mode of male-female pairing has no known equivalent among acoustically signaling organisms and raises several questions (Alexander, 1975): How do individuals manage to court primarily conspecific females even when multiple species are present? Why do males always combine calling with flight? Why, even in the densest choruses, do males always signal while searching? Clarification of each sexes' role in pair-formation is necessary in order to fit these unusual organisms into general theories of pair-formation and sexual communication.

While studying caged *Magicicada septendecim* in 1995, we observed unmated females responding to nearby (≈ 25 cm) individual conspecific male calls with single rapid, audible wing movements (here called 'wing-flicks'). Similar female signals have been observed in other cicadas (see Discussion). In the first part of this paper, for *Magicicada septendecim* and other *Magicicada* species, we demonstrate that the female signal is timed to individual conspecific male call phrases in a species-specific manner and that the signal is produced only by sexually receptive females. We then describe experimental tests of new hypotheses for the functional design of male chorusing behavior, male calling song structure, and a newly recognized inter-male acoustic interference behavior.

Functional design of male chorusing behavior

The discovery of the female signal in *Magicicada* suggests that many aspects of chorusing behavior can be explained in terms of males 'trolling' acoustically for female wing-flick responses, in a manner observed by Gwynne (1987) for Australian tick-tock cicadas. Several predictions follow from this view of male behavior: (1) Perception of wing-flick signals should cause chorusing males to cease 'sing-fly' behavior and immediately approach the stimulus; (2) A male that perceives a wing-flick signal but does not immediately locate the signaling female should localize his chorusing effort; (3) Upon reaching the source of the signal, the male should complete acoustic courtship and attempt to mate; (4) Males should respond to call/wing-flick exchanges of other pairs and attempt to displace other courting males.

Functional design of -decim calling song

-Decim calling song consists of a short (≈ 1.5 -4 s) phrase containing a constant-pitch 'main component' of between 1.1 and 1.7 kHz depending on species and a terminal 'frequency downslur' ending approximately 35% lower in pitch. The discovery of female wing-flick signaling suggests an explanation for the two-part structure of these calls. In dense *Magicicada* choruses, the nearly pure-tone main components of -decim calls blend into a uniform drone. Only the calls of nearby males stand out (to a human ear) from the background chorus, with the downslurs most noticeable; this pattern suggests that the downslur has evolved to improve females' ability to time their responses to the ends of male calls in dense aggregations. Three predictions follow: (1) Increasingly intense background choruses should decrease female responsiveness to playbacks of whole male calls, and this decreased responsiveness should be even more noticeable for playbacks of call fragments lacking terminal downslurs; (2) Downslurs alone should be insufficient to elicit wing-flick signals, unless the background chorus is loud enough to take the place of the main component in stimulating the female; (3) Neither the downslur nor the rest of the call alone should be as effective as the intact call in eliciting the female response at any background chorus intensity.

Functional design of acoustic inter-male interference competition

The close proximity of competing males within dense *Magicicada* aggregations and the dramatically male-skewed operational sex ratio (most females mate just once; White, 1973; Cooley & Marshall, unpubl. data) foster an intense scramble competition for mates. Knowledge of the female wing-flick signal has revealed a previously unrecognized sound apparently used by males in a novel form of acoustic interference competition.

When engaged in extended courtship, -decim and -cassini males may produce short (≈ 0.25 s) ‘buzzes’ with frequency content roughly comparable to that of the calling song main component (Fig. 2). These sounds are always produced during the downslurs of a nearby chorusing male’s calls. Because our experiments suggest that the downslur is important in eliciting a female wing-flick (see below), these sounds may reduce the likelihood that the courted female will hear the downslurs and reveal her presence with a wing-flick before the newly-arrived potential interloper completes his short calling bout and leaves. This hypothesis predicts (1) that such ‘interference buzzes’ should be elicited only in circumstances surrounding the arrival of a competitor male during a courtship interaction, not during chorusing behavior, and (2) that appropriately-timed playbacks of model buzzes should reduce female response rates to male calling songs. Alternatively, since males sometimes mistakenly court other males, males might use the buzz to signal their

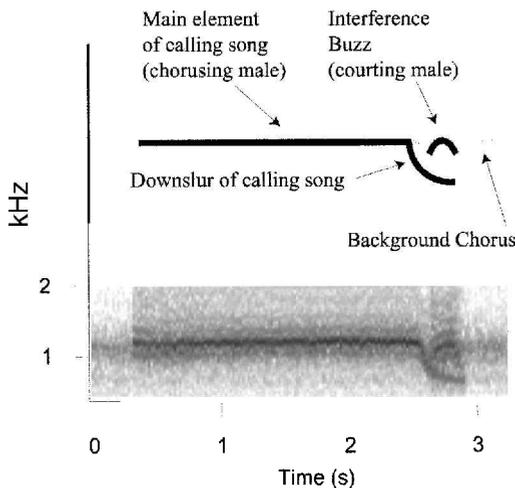


Fig. 2. Sonogram of male *M.* -decim call and interference buzz of nearby male, with stylized explanatory sonogram above.

sex and thereby discourage misdirected sexual attention, a function proposed for a 'flick-tick' signal observed in *M. cassini* males (Dunning *et al.*, 1979). This hypothesis predicts that the buzzes should be observed most often when males are crowded and encounter one another commonly in the chorus.

Materials and methods

General methods

We observed male-female interactions and conducted experiments on sexual signaling from 1995-2000 (Table 3), using both 13- and 17-year cicadas. Because of their greater availability, we concentrated on the -decim species but included others when sufficient numbers were available. Within any of the three periodical cicada cognate species groups, the sexual behaviors of 13- and 17-year species are extremely similar, and for the -cassini and -decula groups, appear identical. Thus, findings for any one periodical cicada species are likely applicable to all other species in the same cognate group. Periodical cicadas remain teneral for several days after their final moult (Karban, 1981; Maier, 1982; Young & Josephson, 1983); during this period they do not mate and are identifiable by their dull color and soft bodies. Although mated females commonly have a hardened white seminal plug in the genital opening (White, 1973), this plug is occasionally absent or difficult to detect in mated females and is therefore an imperfect indicator of mating status. Except as noted below, we used only females that had been captured and sequestered as teneral adults in our studies.

Tape recordings were made using a Sony WM-D6C cassette recorder and a Sony ECM-909A microphone with ambient air temperatures between 21-34°C. Acoustical analyses were conducted using a Macintosh computer and Canary software (versions 1.2.1 and 1.2.4; Cornell Bioacoustics Laboratory, Ithaca, NY), and model songs were synthesized

TABLE 3. *Study sites, 1995-2000*

Year	Brood	Life cycle	Location	County	State	Characteristics
1995	I	17	Alum Springs	Rockbridge	VA	Logged site
1996	II	17	Horsepen Lake SWMA	Buckingham	VA	Logged site
1997	III	17	Siloam Springs SP	Brown, Adams	IL	Old field
1998	XIX	13	Harold Alexander WMA	Sharp	AR	Recently cleared field
1999	V	17	Tar Hollow State Forest	Ross	OH	Recently cleared hillside
2000	VI	17	Private property	Burke	NC	Logged site

Periodical cicadas in different regions emerge in different years; the year-classes are called 'broods.' The broods are largely allopatric, and each brood (except VI and VII) contains a -cassini, -decula, and at least one -decim species. The 17-year broods are numbered I-XVII in order of their emergence, the 13-year broods XVIII to XXX.

with SoundEdit software (Macromedia, San Francisco, CA). Sounds were digitized at 22 kHz and signal timing and frequency content were measured from sonograms. Synthetic *M. septendecim* calls for playback experiments contained pure-tone (sine wave) sound only and consisted of a 1.7 s tone (1.38 kHz carrier frequency) followed by a downslur (ending at 0.860 kHz) for a total call length of 2.1 s. These model calls mimicked the form of natural calls but lacked pulse structure. In developing these models, we have found that females respond similarly to playbacks of recorded and pure-tone model calls; therefore pulse structure is not necessary to evoke a female response. Natural calls used in some playback experiments were chosen for clarity and lack of background noise from archived recordings at the University of Michigan Museum of Zoology. Playback equipment consisted of a Sony WM-D6C cassette player or a Macintosh computer connected to a Radio Shack SA-155 amplifier (frequency response 0.02-25 kHz) driving a Radio Shack 40-243 3 midrange speaker (range 0.135-18 kHz) for -decim calls or a Radio Shack 40-1219 piezo tweeter (range 1.8-30 kHz) for -cassini calls. During playbacks, the speaker was placed between 20-50 cm from the cicadas and playback call intensity was maintained at natural levels (≈ 72 dB at 20 cm from the sound source as measured by a Radio Shack 33-2050 sound level meter set to 'A' weighting). In all years, cicadas were kept in captivity, but within their natural environment, by placing them in ≈ 200 liter cages made by enclosing living vegetation with black fiberglass screen or white nylon tulle. Some observations were completed in small $22 \times 24 \times 22$ cm screened test chambers or in larger $3 \times 3 \times 2.5$ m 'flight cages' placed over living woody vegetation. All statistical analyses were conducted using Systat 5.0 for the Macintosh.

The nature, timing, and species-specificity of the female signal

In 1995-1998, we observed sexual interactions between caged male and female *Magicicada* of all species except *M. tredecula*, which we were unable to collect in sufficient numbers for study. We observed the effects of the female wing-flick signal on male behavior and measured the timing of the signals in relation to male calling and courtship songs (details of these signals are in Table 2). Although signal timing was measured under a range of ambient temperatures, all measurements were made under conditions appropriate for chorusing, as judged by the occurrence of active singing and flying in the surrounding vegetation.

To demonstrate the species-specific nature of the wing-flick response, in 1996 we played recorded, alternating *M. septendecim* and *M. cassini* calls to 25 caged, unmated *M. septendecim* females and noted their responses. We also included three unmated *M. cassini* females as controls. We tested the *M. septendecim* females in groups of five, playing a series of 15 alternating *M. septendecim* and *M. cassini* calls (30 calls total) and recording female responses.

The relationship of female signals to sexual receptivity

To confirm that teneral females are sexually inactive and do not wing-flick, in 1998 we made daily collections of approximately 25 newly-emerged female *M. tredecim* and *M. neotredecim* for six days, caging each collection separately. We then played recorded conspecific male calls to the day-cohorts for two minutes and recorded any wing-flick signals.

White (1973) stated that periodical cicada females mate only once. To determine whether mated females are sexually unreceptive and do not wing flick, in 1997 we allowed 22 individually-marked (marking methodology in Cooley *et al.*, 1998) female *M. septendecim* to

mate once and divided them between two cages along with 22 marked, unmated females of the same age. We played recorded *M. septendecim* calls to the females for two minutes and noted the number of mated and unmated females responding.

The effects of female signals on male chorusing behavior

In 1996 and 1997, we examined how female signals influence male *M. septendecim* chorusing behavior by producing sounds and movements imitating female wing-flick signals. Before we identified a suitable device for producing simulated wing-flicks, we used a strip of paper that we flicked with our fingers. Later, we discovered that snapping our fingers or toggling an ordinary household electric light switch was less disruptive and more repeatable. All of these methods produce clicks that are similar to actual wing flicks in duration and frequency (Fig. 3). Because males appeared to respond in the same manner to the various stimuli and to actual females, we combined trials using the different methods in our analyses.

To document the importance of correct timing in eliciting male *M. septendecim* courtship, we produced simulated wing-flicks in response to the calls of males that had landed and begun calling on nearby vegetation, placing the flicking device within 25 cm of the male along the branch on which he had just landed and timing the signals either (1) during the main component of the call, (2) during the downslur, or (3) after the downslur (see Introduction for definitions). In control trials, the experimenter approached in the same fashion while holding the flicking device, but without producing simulated wing-flicks. We scored a male as responding positively if he moved toward the stimulus and began late-stage courtship behaviors including CII or CIII calling, foreleg-vibration, or sexual mounting (see Table 2). Each trial ended when the male responded positively, flew or walked away from the stimulus, or when the male remained inactive longer than 20 seconds. After each trial, the experimenter chose a different chorusing male for the next trial.

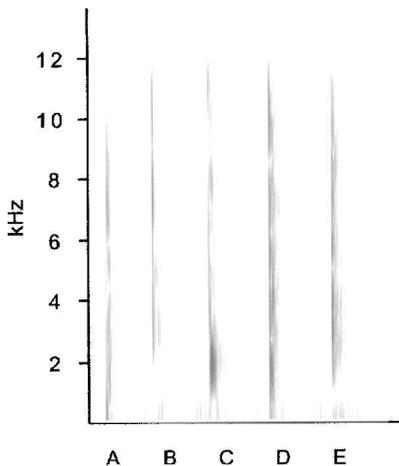


Fig. 3. Sonograms of *M. septendecim* wing flick (A) and synthetic wing flicks produced by a 12 V electric relay (B), a finger snap (C), a piece of paper flicked rapidly (D), and an ordinary electric light switch (E).

To examine male responses in a scenario involving weak and/or inconsistent female responses (such as in situations where responding females were distant), we presented individual chorusing males that had just landed with a single nearby (25 cm) or distant (1.3 m) simulated wing-flick with timing appropriate for the species. We included control trials in which the experimenter approached in the same manner but did not produce a signal. In each trial we recorded the number of calls the male made in his current bout (call number), the nature of his next action (sit, walk, fly), and the direction and distance of movement. In all experiments, direction of movement was estimated as a value from 1-12 as on a clock face with the observer at 12. To avoid biased interpretation of ambiguous lateral movements, only males that moved in directions 11, 12, 1 (toward stimulus) or 4, 5, 6 'away from stimulus' were considered. When vegetation permitted, flight distances were measured with a meter stick. Males that paused for longer than 20 seconds were not monitored further.

Male responses to visual and acoustical components of the female signal

Female wing-flick signals contain visual and broad spectrum acoustical stimuli (Fig. 4). It is possible that different *Magicicada* species perceive different aspects of female signals; although high-frequency sounds are within the range of maximal hearing sensitivity of *-cassini*, much of the acoustic content of wing-flick signals is above the range of maximal hearing sensitivity for male *-decim* (Simmons *et al.*, 1971; Huber *et al.*, 1980, 1990).

To examine the effects of timed flick sounds alone on male chorusing behavior, in 1997 we constructed a clicking device by attaching a 12-volt relay to the end of a 1-meter wooden pole, covering all wires and dark (cicada-colored) parts of the relay with white masking tape; this device produced a sharp, broad-frequency click. In test trials, we identified a chorusing male *M. septendecim* or *M. cassini* that had just landed, placed the relay 25 cm from him along the same branch, and clicked the relay in response to each call in his next two calling bouts with timing appropriate for the species. We avoided making any sound-synchronized movements observable by the male. In control trials, we placed the device in the same manner without clicking the relay. For each male, we measured the number of calls in the next calling bout and the distance moved after the bout.

In 1998, to investigate the effects of visual signals (sound-synchronized movements of cicada-like objects) without sound, we presented individual chorusing male *-decim* that had just landed with a model consisting of a white plastic ballpoint pen with a black cap or with an identical cap painted white, holding the pen 25 cm away so that the male faced the cap. In response to each of the male's calls, and without making sound, we twitched the model once rapidly back and forth about 2 cm with the appropriate timing for a female signal (see Figs. 1, 4), or we held it still. In controls we presented the model in the same manner but did not move it. We recorded all courtship behaviors directed toward these models, discontinuing recording if the male moved away, climbed onto the model, or remained motionless longer than 20 s. The black model was similar to an adult cicada in size, shape, color, and contrast to the background, while the white model differed in color and contrast.

To determine whether combined visual and acoustical stimuli are more potent than either alone, in 1997 we captured males of *M. septendecim* or *M. cassini* from the surrounding chorus and placed each male in a 22 × 24 × 22 cm test chamber. Two opposite walls of the chamber consisted of three layers of dark, opaque cloth to allow sound, but not light, to penetrate; the remaining walls consisted of fiberglass screen. In one treatment, we suspended a motionless model cicada constructed of a thimble covered with black cloth inside the

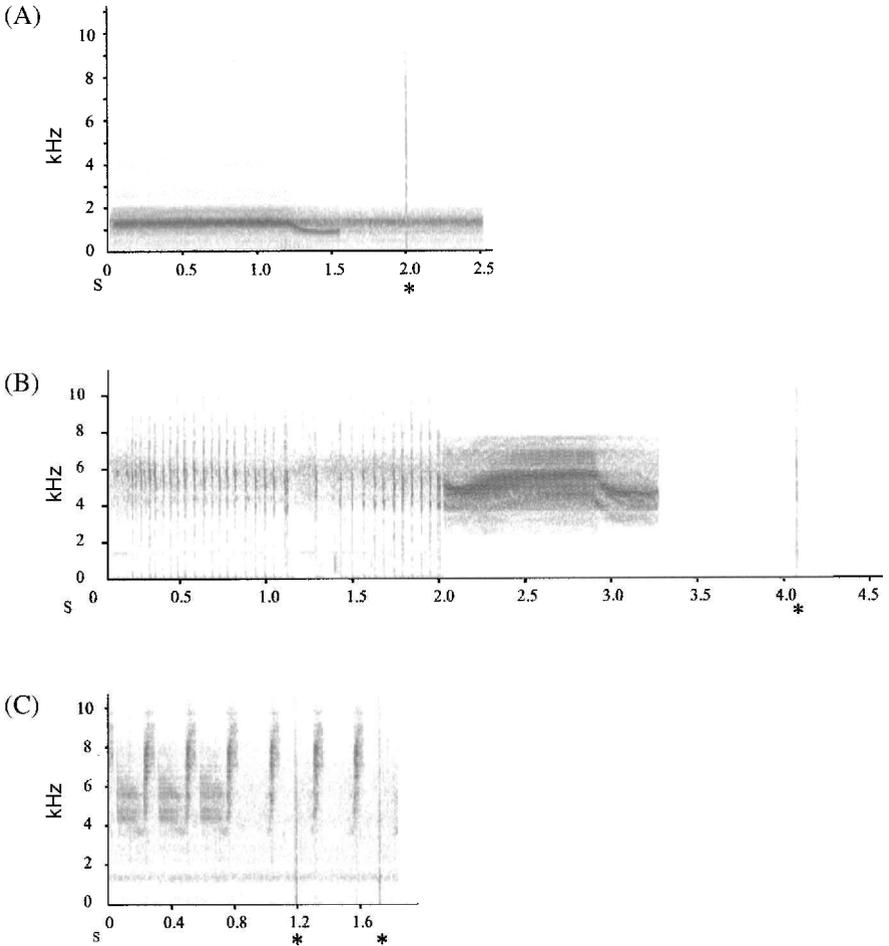


Fig. 4. Sonogram of male *M. -decim* call phrase (A), *M. -cassini* call phrase (B) and fragment of *M. -decula* calling song (C) with female wing flick response. Female response (marked with asterisk) is a broad-frequency sound. Wing flick sounds enhanced and extraneous background noise removed for clarity.

test chamber and responded to the male's calls with light-switch clicks produced behind the opaque chamber sides. We found holding the model to be inappropriate because of our inability to keep the model absolutely still with one hand while clicking a switch with the other. In the second treatment, the experimenter held the model inside the chamber and responded with appropriate timing to the calling male by twitching the model slightly with the appropriate timing (see Figs. 1, 4), without making clicks. In the third treatment, we responded by simultaneously producing clicks and moving the model. After the start of each trial, we recorded the male's behaviors for the next two minutes. Male *M. septendecim* and

M. cassini were scored as responding positively to the model if they exhibited any of the following behaviors during the five minute trial: CII or CIII call, extrusion of genitalia, foreleg vibration, mounting attempts, or copulation attempts.

The functions of M. -decim call components

In 1997, to test the hypothesis that the -decim call downslur functions to distinguish the call from the background chorus, we noted the wing-flick responses of female *M. septendecim* to playbacks of pure-tone model whole calls, pure-tone main components, and pure-tone downslurs. The call fragments were created by removing either the main portion or the slur portion of the pure-tone model. Thus, while the playback treatments differed in duration, they were realistic depictions of actual sounds made by *M. septendecim*. We played each of these calls or call fragments five times at an intensity of 72-79 dB (call intensity varied within the test chamber) against each of four continuous pure-tone background 'choruses' differing in intensity (0 dB, 58-62 dB, 63-77 dB, 65-80 dB). We tested 19 groups of five females each. The experiment was conducted in a quiet field away from the natural *Magiicada* chorus.

Male-male acoustical interference behavior

We conducted two experiments in 1997 to evaluate the hypotheses for the function of -decim buzzing behavior. In the first experiment, we simulated the events involved in the appearance of a potential interloper during courtship by presenting 22 males one at a time with the following series of stimuli: First, we confined the male in a small (22 × 24 × 22 cm) screened test chamber. We then played one to five minutes of recorded calling song from a speaker positioned ≈25 cm away at an intensity of approximately 75 dB at 10 cm (Stage 1). Males often began to call during this treatment, but if the playbacks did not stimulate calling, we produced simulated wing-flick signals in response to the speaker by toggling an electrical switch held outside the cage but within view of the male; signals from the switch always induced a call-walking approach (see below) from the male (Stage 2). Once the male began calling, we turned off the speaker and responded to the male's calls with the switch as he approached (Stage 3); once he reached a position nearest the switch (held outside the cage), we ceased responding to his calls. Once the male stopped his calling or courtship songs (some males began CII or CIII calling during this duet), we resumed playbacks of calling song (Stage 4). We noted the context of any buzzes produced by the male during the trial. Under the hypothesis that the male buzz signal functions by acoustically obscuring buzzes of rival males during courtship, we expected the focal male to buzz only in Stage 4 of each trial.

In the second test, we confined four unmated female *M. septendecim* in the test chamber and played a sequence of 30 call pairs each consisting of (a) one model pure-tone call phrase (main component pitch 1.4 kHz) played from one speaker followed by (b) one model call played from the same speaker along with a 0.25 s 1.4 kHz pure-tone model 'buzz' played from a second, identical speaker and superimposed over the model call downslur. We recorded the number of females responding with wing flick signals to each call and repeated the experiment six times, using different females each time. We compared the number of females responding to obscured and unobscured calls using a Friedman two-way analysis of variance.

Results

The nature, timing, and species-specificity of the female signal

A *Magicicada* female signals in response to a calling conspecific male by moving her wings in a single, quick motion which produces a broad-frequency sound of less than 0.02 s duration (Fig. 4). The timing of the signal in relation to the male's call is species-specific. In *M. septendecim*, under weather conditions appropriate for chorusing, females signal an average of 0.387 ± 0.106 s ($\bar{x} \pm$ SD, $N = 235$ wing flicks from 171 females) after the end of the male calling phrase (Fig. 4a). Ambient air temperature appears to have little influence on the timing of the signal in *M. -decim* (Fig. 5), suggesting that *M. -decim*, like *M. -cassini* are able to thermoregulate. The delay in *M. cassini*, 0.705 ± 0.112 s ($\bar{x} \pm$ SD, $N = 16$), is nearly twice as long under similar conditions (Fig. 4b). Observations of *M. neotredecim*,

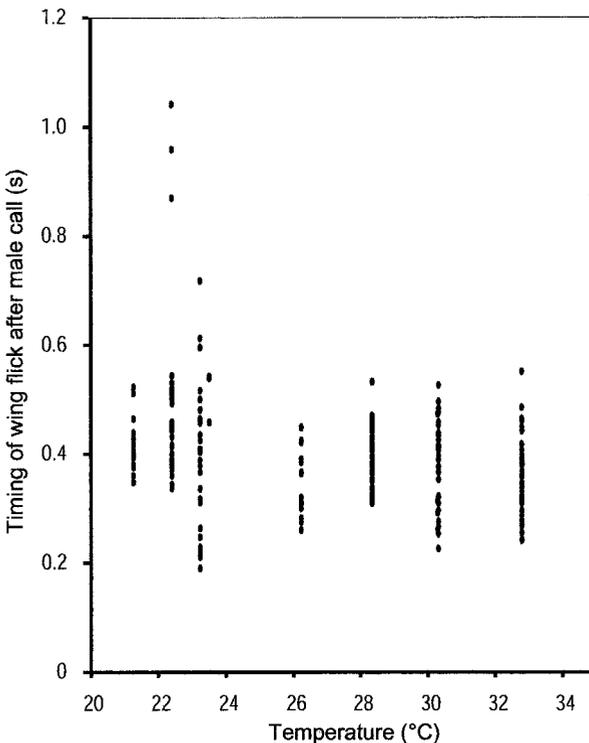


Fig. 5. Timing of female wing flick after end of male call at different ambient air temperatures. 222 individual wing flicks produced by 161 individual females were measured.

M. tredecim and *M. tredecassini* indicate that the female signal timing of these species is similar or identical to that of their 17-year counterparts. *M. septendecula* females produce individual wing-flick signals in one or more of the brief silences between subphrases (Fig. 4c).

In all species studied, once a chorusing male has perceived wing-flick signals, he approaches the signaling female, who wing-flicks in response to each of the male's call phrases (Fig. 1). In the -decim and -cassini species, this 'duet' continues until the male switches to CII courtship. We have not determined what stimuli cause a male to begin CII courtship; he usually does so once he approaches to within 1-15 cm of the female, perhaps upon making close visual contact. Female -decim and -cassini only rarely produce wing-flicks during CII; however, if a -decim male ceases CII courtship, leaving a silent gap, the female may respond with a timed wing-flick. In -decula, no homologous CII courtship song is yet known. In all species the male switches to CIII courtship soon after positioning himself next to the female, at which point he attempts to mount her, usually while vibrating his foreleg and using it to make first contact. Females do not wing-flick during CIII; wing-movements after the onset of mounting interrupt courtship and apparently indicate mating rejection by the female. Sexual pair formation always occurs in this stereotyped sequence unless (1) the male fails to locate the female or (2) the female ceases wing-flicking at any point during CI or (3) the female rejects the male upon his attempt to mount (see also Table 2 and Fig. 1). In situations #2 and #3 the courtship may become prolonged, involving long waits, repeated series of CI calls, and occasional attempts to mount with or without CII and CIII courtship calling.

In the playbacks of conspecific and heterospecific calls, *M. septendecim* females routinely responded to the *M. septendecim* call phrases in each trial. Only one of 25 *M. septendecim* females ever responded to a heterospecific playback; the responsiveness to conspecific and heterospecific calls was significantly different (Fisher's exact two-tailed test: $p \leq 0.01$). The three *M. cassini* females in the experiment responded only to *M. cassini* calls and never responded to heterospecific playbacks. Females of *M. tredecim* and *M. neotredecim* have also been shown to respond preferentially to models of conspecific calls (Marshall & Cooley, 2000).

Female signals and sexual receptivity

Females in the mixed *M. tredecim*/*M. neotredecim* sample first signaled 6.5 ± 1.1 ($\bar{x} \pm SD$ for six collections) days after emerging, consistent with

previous reports of the *Magicicada* teneral period (Karban, 1981; Maier, 1982; Young & Josephson, 1983). In the playbacks to mated and unmated females, none of the 22 mated females responded, while 9/17 unmated, mature females responded ($p \leq 0.001$, Fisher's exact test). These results demonstrate that females wing flick signal only during periods in which they are expected to be sexually receptive.

The effects of female signals on male chorusing behavior

Only simulated wing-flicks produced after the downslur caused male *M. septendecim* to respond positively (Table 4). Males usually responded to such stimuli by walking toward the stimulus while calling. In this behavior, termed 'call-walking,' males stopped walking for approximately one second immediately following each downslur. This pattern is distinct from chorusing behavior, which involves bouts of stationary calling alternating with flights or silent walks. Males were unresponsive to the control treatment and to simulated wing-flicks produced during the main component or during the downslur (Table 4).

Male *M. septendecim* responded to single nearby and distant simulated wing-flick signals in a manner suggesting an attempt to localize the stimulus (Table 5). Both kinds of stimuli caused males to increase the number of calls in the current calling bout compared to control males, but, as in chorusing behavior, most males then flew to a new calling perch instead of call-walking toward the stimulus. Whether walking or flying after the calling bout, males presented with either stimulus were more likely to move in the direction of the stimulus than were control males. In control trials, males were more

TABLE 4. *Responses of individual male M. septendecim to simulated wing-flick signals produced at different times in relation to their calls*

Timing	N	Response		p (vs Control)
		(+)	(-)	
Control	46	6	40	
After slur	83	66	17	≤ 0.001
During call	41	3	38	≤ 0.498
During slur	13	0	13	≤ 0.326

Fisher's exact two-tailed tests were used to compare treatments to 46 controls in which the clicking device was presented to the male, but no click was made.

TABLE 5. *Effect of single nearby (25 cm) or distant (1.3 m) artificial wing-flick signal on male M. septendecim chorusing behavior*

	Control	With signal, <i>p</i>
Single nearby simulated wing-flick signal		
Call number	2.28 ± 1.16 (<i>N</i> = 43)	<i>z</i> = 3.247, ≤ 0.001 (Wilcoxon rank sum)
Likelihood of flight	(<i>N</i> = 43)	
<i>Flight after signal</i>	36	
<i>No flight after signal</i>	7	<i>p</i> ≤ 0.223 (Fisher's exact test)
Distance of flight (cm)	25.75 ± 19.4 (<i>N</i> = 40)	<i>z</i> = -0.926, <i>p</i> ≤ 0.355 (Wilcoxon rank sum)
Movement direction	(<i>N</i> = 19)	
<i>Toward Observer</i>	3	
<i>Away from Observer</i>	16	<i>p</i> ≤ 0.003 (Fisher's exact test)
Single distant simulated wing-flick signal		
Call number	1.94 ± 0.83 (<i>N</i> = 17)	<i>z</i> = 2.838, <i>p</i> ≤ 0.005 (Wilcoxon rank sum)
Likelihood of flight	(<i>N</i> = 17)	
<i>Flight after signal</i>	13	
<i>No flight after signal</i>	4	<i>p</i> ≤ 1.000 (Fisher's exact test)
Distance of flight (cm)	35.76 ± 26.55 (<i>N</i> = 13)	<i>z</i> = -1.225, <i>p</i> ≤ 0.221 (Wilcoxon rank sum)
Movement direction	(<i>N</i> = 7)	
<i>Toward Observer</i>	0	
<i>Away from Observer</i>	7	<i>p</i> ≤ 0.02 (Fisher's exact test)

See text for details.

likely to move away from the stimulus than toward it, probably because the presence of the experimenter tended to disturb the cicadas.

Male responses to components of the female signal

Timed click sounds alone did not affect chorusing male *M. septendecim* behavior, but male *M. cassini* flew significantly shorter distances between calls when timed click sounds were made (Table 6); no males of either species attempted courtship in response to the clicks. Male *M. septendecim* courted pen cap models that were moved silently to imitate wing-flick signals, but they were less likely to engage in late-stage courtship with white colored caps than with black colored caps (Table 7), indicating that while movement alone is sufficient to provoke male responses, males also respond to color or contrast components of the stimulus. A small number of observations with *M. tredecassini* in a flight cage confirmed that males of this species will also court the silent moving pen model. In the trials directly comparing movement and sound stimuli, the model that moved and clicked simultaneously was most attractive to *M. septendecim* and *M. cassini* (Table 8).

The functions of M. -decim call components

Although call fragments elicited some female responses, *M. septendecim* females were more likely to respond to whole calls than to partial calls at all

TABLE 6. Changes in male *M. septendecim* and *M. cassini* chorusing behavior in response to simulated wing-flick sounds

	<i>M. septendecim</i>		<i>M. cassini</i>		
	<i>N</i>	mean	<i>N</i>	mean	
Number of calls					
With click	64	3.3 ± 2.1	24	1.4 ± 0.93	
Control	46	3.0 ± 2.5	26	1.3 ± 0.45	$H_{11} = 311.0,$ $p \leq 0.980$
Flight distance (cm)					
With click	50	25.2 ± 25.3	23	7.8 ± 5.6	
Control	37	24.8 ± 17.0	25	31.0 ± 33.9	$H_{11} = 458.5,$ $p \leq 0.001^*$

Results were analyzed with Kruskal-Wallis one-way analysis of variance.

TABLE 7. *Male M. tredecim courtship behaviors directed toward black- or white-colored models held at 25 cm distance*

Contrast	Early stage courtship	Late stage courtship
	(Call-Walk)	(Court II, Foreleg-Vibrate)
Black/move vs black/still	15/22 vs 3/22 ($p \leq 0.001$)*	10/22 vs 2/22 ($p \leq 0.001$)*
Black/move vs white/move	15/22 vs 9/22 ($p \leq 0.129$)	10/22 vs 3/22 ($p \leq 0.045$)*
White/move vs white/still	9/22 vs 0/21 ($p \leq 0.001$)*	3/22 vs 0/21 ($p \leq 0.233$)
Black/still vs white/still	3/22 vs 0/21 ($p \leq 0.233$)	2/22 vs 0/21 ($p \leq 1.00$)

The models were held still (controls), or moved in a manner that simulated a female wing flick signal. Male responses were compared using Fisher's exact 2-tailed tests.

TABLE 8. *Responses of individual male M. septendecim to actions of a model*

Model action	Species						
	<i>M. septendecim</i>			<i>M. cassini</i>			
	<i>N</i>	<u>Response</u>		<i>N</i>	<u>Response</u>		<i>p</i>
	(+)	(-)		(+)	(-)		
Move	16	4	12	16	5	11	
Click	17	2	15	16	2	14	
Move and Click	17	12	5	15	14	1	
<i>Move vs Click</i>							NS
<i>Move vs Move and Click</i>							≤ 0.015
<i>Click vs Move and Click</i>							≤ 0.001

Males were scored as responding positively to the model if they produced Court II or Court III songs, or if they attempted to mount and copulate with the model. Fisher's exact 2-tailed test used for all comparisons.

background chorus intensities (Fig. 6). As the background chorus intensity increased, female responsiveness to whole calls and main components of whole calls declined, while females became more responsive to slurs (Fig. 6), such that at the highest intensity, females were more responsive to slurs alone than to main components alone.

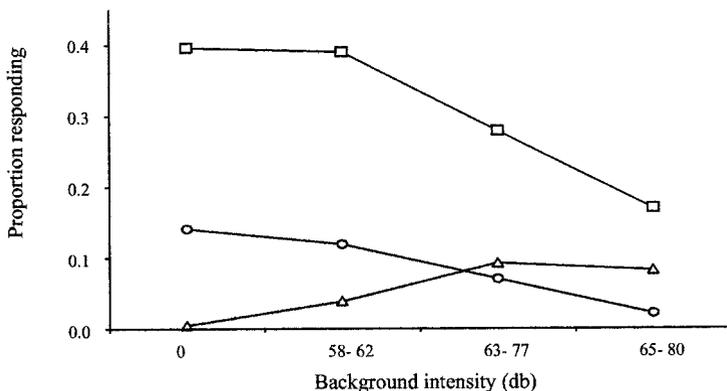


Fig. 6. Responses of female *M. septendecim* to playbacks of artificial, pure tone calls and portions of calls against artificial background choruses of different intensities. Females were scored as responding positively if they produced one or more wing flick signals in response to a playback. Data are presented as proportion of positive responses for specific call and background condition given the total number of trials with those experimental conditions. At all background intensities, whole calls (squares) were more likely to elicit responses than either main portion only (circles) or slur portion only (triangles). At higher background intensities, the effectiveness of whole calls was reduced (Kruskal-Wallis One Way ANOVA $z = 420$, $p \leq 0.001$), as was the effectiveness of main portion only (Kruskal-Wallis One Way ANOVA $z = 64$, $p \leq 0.001$), while the effectiveness of slurs alone was increased (Kruskal-Wallis One Way ANOVA $z = 44$, $p \leq 0.001$).

Male-male acoustical interference behavior

In the first experiment, simulating the appearance of an interloper during courtship, males never produced buzzes in response to the initial series of speaker playbacks (Stage 1), never produced buzzes during artificial duets between the speaker and the experimenter (Stage 2), and never produced buzzes while duetting with the experimenter (Stage 3). In contrast, in 16 of the 22 trials, the male began producing buzzes once playbacks had resumed following the termination of his duet (Stage 4), usually in response to the first or second playback call, but sometimes not until three or four calls had played. The responses of males before and after simulation of an interloper were significantly different (Fisher's exact two-tailed test, $p \leq 0.001$). Males producing buzzes did so only during the downslur of the recorded calling song phrases. In five of the trials, we again began producing simulated wing-flick signals to the speaker while the male buzzed; in four of these five cases this caused the male to cease buzzing and begin call-walking near

TABLE 9. *Effects of M. -decim 'interference buzz'*

Replicate	Buzz	Average number of females responding to each call (mean \pm SD)	p (Friedman two-way ANOVA)
A	Yes	1.13 \pm 0.86	$F = 12.033, p \leq 0.001$
	No	2.23 \pm 0.77	
B	Yes	0.57 \pm 0.57	$F = 26.133, p \leq 0.001$
	No	2.43 \pm 0.68	
C	Yes	0.80 \pm 1.00	$F = 10.800, p \leq 0.001$
	No	1.73 \pm 1.08	
D	Yes	1.27 \pm 1.93	$F = 7.500, p \leq 0.006$
	No	1.93 \pm 0.58	
E	Yes	0.93 \pm 0.87	$F = 4.033, p \leq 0.045$
	No	1.53 \pm 0.78	
F	Yes	0.47 \pm 0.57	$F = 17.633, p \leq 0.001$
	No	2.07 \pm 0.98	

See text for details.

the simulated wing-flick stimulus. In the fifth case the male walked while buzzing after each playback call.

In the second experiment, females were significantly less likely to respond to calls obscured by model buzzes than to unobscured calls (Table 9). Under the conditions of this experiment, buzzes halved the likelihood of a female response.

Discussion

Wing-flick signals in Cicadidae

Communicative wing-flicking (sometimes called wing-tapping, -banging, -clapping, -clacking, or -clicking) may be widespread in cicadas. We use the term 'wing-flick' in this paper because it connotes movement and sound, both of which are perceived by male *Magicicada*; other terms emphasize only the acoustic component of the signal. Although McAtee (in Myers, 1929) mentions wing flicking in *Magicicada*, this appears to be a reference to the click sounds that are components of -cassini male calls. Male wing-flicking during close-range courtship interactions with females has been re-

ported in New Zealand *Kikihia* and *Amphipsalta* (Dugdale & Fleming, 1969; Lane, 1995), North American *Okanagana* (Davis, 1919; Alexander, 1957; Cooley, 2001), and European *Tibicina* (Fonseca, 1991), while males combine wing-flicks with long-range calling song in Asian *Cicadetta* (Popov, 1981), New Zealand *Amphipsalta* (Dugdale & Fleming, 1969; Lane, 1995), and Western North American Platypediinae (Moore, 1968). Female wing flick signaling is known in North American *Magicicada* (this study) and *Okanagana* (Davis, 1919; Cooley, 2001), Australian *Cystosoma* (Doolan, 1981; Doolan & Young, 1989), *Cicadetta* (Gwynne, 1987), and *Amphipsalta* (Dugdale & Fleming, 1969), and New Zealand *Amphipsalta*, *Kikihia*, *Maoricicada*, *Notopsalta*, *Rhodopsalta* (Dugdale & Fleming, 1969; Lane, 1995), and *Melampsalta* (Myers, 1929). The most detailed published reports of female wing-flick signaling involve *Kikihia* spp. (Lane, 1995), *Amphipsalta cingulata* (Lane, 1995), *Cystosoma saundersii* (Doolan, 1981; Doolan & Young, 1989), and *Cicadetta quadricinctata* (Gwynne, 1987). In the few species studied in detail, female wing-flick signals elicit male courtship behavior and appear to have a specific temporal relationship to the male's song, although in some species female wing-flick signals are apparently not always required for mating: Both sexes of *Okanagana canadensis* and *O. rimosa* may use wing-flicks to signal their presence, but females more often signal receptivity simply by approaching stationary calling males (Cooley, 2001).

The *Magicicada* wing flick signal consists of synchronized visual and acoustical stimuli that are more effective in eliciting male responses than either sounds or visual cues alone. The timing of the signal appears to be more important than its other characteristics, since the appropriately-timed flick of a scrap of paper or the click and movement of an ordinary electric light switch are sufficient to provoke the entire male courtship sequence. Timing may be the most significant feature distinguishing *Magicicada* female wing-flick signals from other wing-movements previously recognized as indicating mate rejection by the female.

Pair-formation and specialized search behavior in Magicicada

The *Magicicada* pair-forming system lies at one extreme of the range of systems found in acoustically signaling insects (see Alexander, 1960; Ewing, 1989; Robinson, 1990), with males alternating unusually brief bouts of calling and unusually short call phrases (for cicadas) with short flights.

Only one other well-studied cicada species, the Australian tick-tock cicada (*Cicadetta quadricinctata*) appears to have a similar system, although calling bouts in this species are still three to four times longer in duration than those of *Magicicada* (Alexander & Moore, 1962; Gwynne, 1987). The *Magicicada/Cicadetta* pair-forming system is similar to that found in many fireflies (see Lloyd, 1966, 1979), acridid grasshoppers (von Helversen & von Helversen, 1983) and phaneropterine katydid (Spooner, 1968; Heller, 1990; Heller & von Helversen, 1993), in which females answer male calls and require males to complete the approach. Alexander (1968) remarked that female signals are a likely component of pair-formation whenever males adopt an active, locomotory role. In noting the similarities of male behavior in *Magicicada* and *Cicadetta quadricincta*, Gwynne (1987) all but predicted that female wing-flick signals would be found in *Magicicada*. In some phaneropterine species, the female approaches the male part-way before responding (Spooner, 1968), paralleling the initial entry into a chorus by a *Magicicada* female. Similar pair-forming systems are also found in substrate-vibrating leafhoppers (Claridge, 1985; Hunt & Nault, 1991; Hunt *et al.*, 1992) and lacewings (Wells & Henry, 1992; Henry, 1994).

At the other extreme are cicada species such as North American *Okanagan canadensis* and *O. rimosa* (Cooley, 2001) in which males advertise continuously (with or without separate call phrases) from a single location for hours or days at a time. In such species males remain stationary while females approach males without responding. The mating systems of some katydid species (*e.g.* *Neoconocephalus* spp., Greenfield, 1990) as well as those of some frogs are characteristic of this end of the continuum. Other cicadas, such as those in the genus *Tibicen*, exhibit intermediate patterns of call length, flight frequency, and flight distance, although the nature of female signaling (if any) remains unknown. The ecological factors underlying these variations are still largely unexplored, but may include factors such as the relative risk of exposure to predation for the two sexes (Heller & von Helversen, 1993; Alexander *et al.*, 1997).

The behavior of *Magicicada* males within choruses appears consistent with a strategy in which males acoustically 'troll' for wing-flick responses of stationary, receptive females. Males call, even in the loudest choruses, because female wing flick signals are made in response to nearby calling phrases. Males alternate calls with flights because females within choruses are relatively stationary, so males must search for them. Male -decim and

-cassini produce calls with delays between phrases or delays before flight that are only slightly longer than the timed delay of the female's wing-flick. The short average flight distance likely reflects the limited area within which a male can be perceived by a female and perceive any response she may give, although this remains to be tested.

Signal structure and function in Magicicada

The nature and timing of the female signal allows insight into the functional design of *Magicicada* call phrases. The intense intraspecific acoustic interference in a *Magicicada* chorus, along with the requirement for species-specific timing in the female response, places a premium on male signal discriminability (see Guilford & Dawkins, 1991). The decreasing responsiveness of females to an artificial call as the intensity of the background chorus is increased suggests that female *M. septendecim* have difficulty detecting and responding to male calls within a loud chorus. One solution to the problem of increasing discriminability is the evolution of multicomponent signals (Rowe, 1999). Female *Magicicada* become (1) increasingly responsive to the downslurs alone, and (2) less responsive to calls lacking downslurs, as the chorus intensity increases, even though calls without downslurs contained more total sound energy than downslurs alone. This finding suggests that the terminal frequency-modulated downslur of -decim (and possibly -cassini) calls has evolved to increase the discriminability of the call terminus.

A different but related solution to call discriminability appears in some phaneropterine katydids, which use amplitude modulation to accentuate call components (such as the beginnings or ends of calls, or certain call syllables) that are timing cues for females (Heller, 1990). Interspecific background interference forces males of some *Neoconocephalus* katydid species to call only when males of a related species are silent (Alexander, 1956; Greenfield, 1990). These findings underscore the importance of considering tactical design (effectiveness of the signal in conveying information through the environment) as well as strategic design (appropriateness of a signal as an indicator of information, such as freedom from parasites) in studies of signal evolution (Guilford & Dawkins, 1991; Endler, 1992, 1993; Römer, 1993).

A specialized acoustic defense against interloping

The competitive environment of a chorus places courting males in jeopardy of displacement by interlopers, as observed when wing flick duets attract

the attention of nearby males (JRC, DCM, pers. obs.). The risk to a male of displacement during courtship has apparently led to the evolution of an acoustic defensive strategy related to the female wing-flick signal: In the -decim (and, apparently -cassini) species, when a close-range male-female duet or a prolonged courtship is interrupted by the arrival of a calling male competitor, the courting male emits short buzzes coincident with the downslurs of his rival's calls. These buzzes obscure the rival's call downslur, reduce the likelihood that the female will perceive them and respond, and thereby increase the likelihood that the interloper will continue chorusing and depart without detecting the female. One potential objection to this hypothesis is that the buzz itself could reveal to the interloper the presence of the nearby receptive female. However, male *M. septendecim* and *M. cassini* hearing sensitivity is reduced 5-15 dB during calling by the action of muscles that reduce tension on the tympana (Simmons *et al.*, 1971). Suppression of hearing during calling has been described for other cicada species (*e.g.* Pringle, 1954; Hennig *et al.*, 1994) and for other singing insects (see Greenfield, 1990). Thus calling interlopers may have difficulty perceiving that their signals are being jammed by buzzing males, as suggested by the fact that buzzing males terminate the signal precisely at the end of the interloper's song (Fig. 2). The reduced hearing ability of calling cicadas and the specific timing of the buzz argue against the alternative hypothesis that the buzz is used by a male to deflect mistaken courtship attention from another male by revealing the sex of the courted individual.

Competitive acoustic interactions are well-documented in insects, but these commonly involve the calling song or a part of the calling song and most are thought to function primarily in territorial interactions (*e.g.* Shaw, 1968; Feaver, 1983; Greenfield & Roizen, 1993). Specialized acoustic behaviors such as the *Magicicada* interference buzz are rarer. Some male phaneropterine katydids produce accessory ticks that are timed in relation to their own calls in the same manner as female responses; observers have suggested that these signals might confuse potential interlopers (*Microcentrum*: Grove, 1959; Alexander, 1975; *Scudderia*: Spooner, 1968; *Isophyra*: Heller, 1990), possibly in the later stages of sexual approach when the male is close to locating the female. A related function could be served by male wing-clicking during calling in cicadas such as *Amphipsalta cingulata*, in which males appear to imitate female clicks to their own calling songs (Lane,

1995). Similarly, rapid 'wing-flutters' (typically more than five rapid wing-beats) produced by some male *Magicicada* under conditions similar to those that elicit the interference buzz (JRC, DCM, pers. obs.), and timed to occur after the expected timing of a female wing-flick signal, might serve to confuse potential rivals. Male-male interaction sounds have been reported in two other cicadas, *Fidicina mannifera* (Cocroft & Pogue, 1996) and *Cicada barbara lusitanica* (Fonseca, 1991), but the signals are not yet well understood. The *Magicicada* interference buzz appears unique in that the sound apparently reduces competition from rival males by preventing an unwitting courted female from signaling.

Conclusion

The discovery of the female wing-flick signal clarifies the adaptive design of the *Magicicada* behavioral repertoire, including calling song structure, chorusing pattern, and competitive behaviors, given the selective context of dense *Magicicada* choruses. Intense scramble competition may partly explain why the wing-flick signal remained undiscovered for so long in such a well-studied genus: With so many active males present, newly signaling females may be detected, courted, and mated almost immediately. Most females mate once (White, 1973; JRC, DCM, unpubl. data), further decreasing the likelihood that an observer will notice the brief pair-formation stage. Finally, wing-flick signals are easily confused with other wing movements used by females to reject unwanted contact; the special timing of the wing-flick signal is easily overlooked.

The discovery that *Magicicada* females actively signal sexual receptivity promises greater progress in studies of *Magicicada* mating behavior. The *Magicicada* mating system played a role in the development of the non-resource-based lek concept (Alexander, 1975), critical for studies of female choice and lek evolution, such as comparisons of insect and vertebrate leks (e.g. Bradbury, 1985). Knowledge of the female wing flick signal has already played an important role in the discovery of a new species, 13-year *Magicicada neotreddecim* (Marshall & Cooley, 2000), the demonstration of lack of gene flow between this species and its closest 13-year relative *M. treddecim* (Simon *et al.*, 2000; Cooley *et al.*, 2001), and the discovery of reproductive character displacement in calling song pitch and female song pitch preference where the two 13-year -decim species overlap geographically (Marshall & Cooley, 2000).

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