

Acoustic Behavior of *Amblycorypha parvipennis* (Orthoptera: Tettigoniidae)

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ABSTRACT The sounds made by *Amblycorypha parvipennis* Stål (Tettigoniidae: Phaneropterinae) consist of sequences of phrases produced at rates of 7-9/min with phrases 4-5 s long consisting of an average of 24 phonatomes (20-25°C). Phonatomes consisting of three or four pulse trains generated during a single wingstroke were produced at average rates of 4.5-5.5/s. Adjacent singing males alternate and overlap phrases and, where phrases overlap, phonatomes are synchronized. Although males of several phaneropterine species alternate production of phrases, and one species has been reported occasionally synchronizing lips, no other orthopteran is known to alternate overlapped phrases and to synchronize phonatomes. Male song-phrase intervals are longer during paired chorusing than when males sing alone; this suggests that phrase alternation is the result of one male being inhibited during most of the phrase of another singing katydid. Phaneropterine females typically produce single, short sounds ("ticks") at species-identifying intervals of 17-1,130 ms following male phrases. Females of *A. parvipennis* are unique in producing an average of 3.2 ticks/male phrase (range, 1-17; mode, 1) and ticks falling between the phonatomes of male phrases. The only or last female tick usually falls just before (49%) or after (46%) the last phonatome of a male phrase. Sequences of female ticks fall between male phonatomes, and ticks are initiated an average of 120 ms following initiation of the previous male phonatomes. Male phonatome synchrony may have evolved so that females could time their responses and males could perceive female responses.

KEY WORDS Insecta, chorusing, acoustic behavior, Phaneropterinae

INSECT CHORUSES consist of spatially aggregated males whose temporally aggregated song has been described as "statistically significant temporal interaction involving the acoustic signals of neighbors" (Greenfield & Shaw 1983). Chorusing can involve synchronous or alternate production of song phrases (Alexander [1967]; consisting of one or more phonatomes [Walker & Dew 1977] which are sounds produced by single wing strokes) by two or more males, or males simply singing during the same time period without rhythmic relationships of sound components between or among males (unison or unison bout singing) (Fig. 1). Males of *Amblycorypha parvipennis* Stål are unique among chorusing Orthoptera in that adjacent males alternate phrases and synchronize phonatomes where phrases overlap (Fig. 1). Alternation of phrases with infrequent overlap has been reported for a number of orthopteran species (e.g., *Ephippiger bitterensis* (Finot) (Busnel et al. 1956); *Pholidoptera griseoptera* (DeGeer) (Jones 1966); *Pterophylla camellifolia* (F.) (Shaw 1968); *Chorthippus brunneus* (Thunberg) (Young 1971); *Lea floridensis* (Beutenmuller) (Greenfield & Shaw 1983). However, these species produce relatively short phrases (85-250 ms, 20-27°C) and intervals (600-2,020 ms) that are 3-20 times longer than their phrases. In contrast, *A. parvipennis* males produce phrases (e.g., 4,500 ms) that are longer than their intervals (e.g., 3,500 ms), and both phrases and intervals are longer than

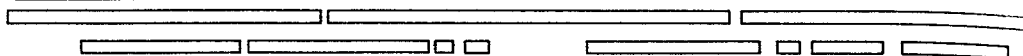
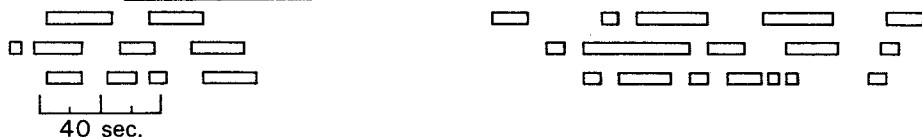
those of nonoverlapping alternaters (Greenfield & Shaw 1983).

Some *Orchelimum* (Tettigoniidae: Conocephalinae) species produce phrases as long or longer than those of *A. parvipennis* with intervals that are considerably shorter (Alexander 1956, Feaver 1977). When a conspecific male intrudes upon another male's singing territory, the males may adopt a relatively consistent alternating of overlapping phrases; however, synchrony of phonatomes has not been reported (Feaver 1977). Among all the singing Orthoptera, synchrony of phonatomes has been reported only for *Platycleis intermedia* (Serville) (Samways 1976), a species that also synchronizes phrases.

Like other species of the subfamily Phaneropterinae, *A. parvipennis* females produce short "ticks" which attract sexually responsive males. Phaneropterine females typically respond to conspecific males by ticking at a species-specific interval following a male's phrase (Alexander 1960, Spooner 1968, Heller & von Helversen 1986). Our listening records suggest a different response pattern for *A. parvipennis* females.

Phonatome synchrony of *A. parvipennis* was first reported by Fulton (1928, 1934). Overlapping alternation of phrases was reported by Shaw et al. (1981). We have not found any published reports on the nature of the acoustic response of *A. parvipennis* females. The purpose of our study was to

CHORUS TYPES

UNISON (*Neoconocephalus ensiger*)UNISON BOUT (*Neoconocephalus affinis*)SYNCHRONY (*Neoconocephalus nebrascensis*)ALTERNATION (*Pterophylla camellifolia*)OVERLAP (*Amblycorypha parvipennis*)

- phonatome
- phrase
- L leader
- F follower

Fig. 1. Chorus types of singing Orthoptera.

analyze the sounds of *A. parvipennis* males and females, the nature of male chorusing, and the acoustic interaction between males and females.

Materials and Methods

We have been recording the sounds of *A. parvipennis* since 1978. Most of the data used in this study came from recordings made during the summers of 1983-1986.

Katydidids were collected from approximately the last week in June until the first week in August from a prairie preserve bordering the west side of Ames High School, Ames, Iowa. The insects were housed in wire mesh cages (10 by 10 by 18 cm) and maintained in the laboratory or Percival environmental chambers (Percival Refrigeration and Manufacturing Co., Boone, Iowa) in a 16:8 (L:D) photoperiod and at 23°C. Chicken starter feed, leaves of wild grape (*Vitis* sp.) or horsemint (*Mentha longifolia* (L.)) and water (in small, cotton-plugged vials) were provided ad lib.

All sound recordings were made in an acoustic isolation chamber (4.6 by 5.3 by 2.4 m) (Industrial

Acoustics Company, Bronx, NY). Recordings of male solo songs were made with a PI-6204 instrumentation recorder (Precision Data, Santa Clara, Calif.) and a B&K 0.6 (4 Hz-100 kHz) or 1.3 (4 Hz-40 kHz) cm microphones (Brüel & Kjaer Instruments, Cleveland). Male-male and male-female acoustic interactions were recorded with a pair of GC Electronics #30-2374 microphones (GC Electronics, Rockford, Ill.) and a Sony TC-6300 stereo tape recorder (Sony Corporation, Sun Valley, Calif.). Because *A. parvipennis* males sing at night, all recordings were made at very low light levels (just sufficient for the investigator to move around the room) using a rheostat-controlled 1,000 W lamp (Hub Electric Co., Chicago, Ill.) covered with red celluloid.

Temporal and frequency parameters of the songs were determined from physiograph tracings (Model 4B, Narco Biosystems, Houston, Tex.), oscillograms (Grass Instrument Co., Model C4-12 Kymograph camera, Quincy, Mass.; Tektronix, model 5110 and 5111 storage oscilloscopes, Beaverton, Oreg.), sonographs (Kay Elemetrics Corp. 7029A Sonagraph, Pine Brook, N.J.) and printouts from a

B&K type 2033 frequency analyzer. Accurate upper-level frequency measurements were limited to 40 kHz. Sonograms were made from solo songs recorded with the 0.6-cm B&K microphone. Although the amplifying system (Tektronix type 122 in conjunction with a Tektronix type 160A power supply) was not linear above 40 kHz, sound frequencies up to 128 kHz were recorded with the 0.6-cm B&K microphone (Fig. 2B). The recordings used for frequency analysis with the B&K type 2033 frequency analyzer were made with the 1.3-cm B&K microphone and there was little reproduction of frequencies above 40 kHz (Fig. 4). Temporal song parameters and phase relationships of chorusing male pairs were determined using a Commodore 128 computer (Commodore Business Machines, Westchester, Pa.) and a specially designed tape recorder-computer interface and software. Sound level measurements were made with a B&K type 2203 sound level meter equipped with a B&K type 1613 octave filter set.

To determine the relationship of wing strokes to phonatome structure, singing males were photographed at 48 frames/s using a 16 mm camera (Arriflex Corporation, Elmsford, N.Y.) with a 15–150 mm, F-2.8, T-3.1 zoom lens (P. Angenieux, Paris, France). Three 650W Omni-lights (Lowell-light Manufacturing, New York, N.Y.) were focused on a singing male. The films were viewed with a Kodak Pageant projector (model AV-126-T12) at 18 frames/s.

All specimens used in this study were labeled and placed in the collection of the Iowa State Museum of Entomology, Department of Entomology, Ames.

Results

Solo Song. Phonatomes. Analysis of wing movement during sound production by slow-motion photography indicated that each song phrased unit (Fig. 1) was the result of a single wingstroke and therefore could be termed a phonatome. Each phonatome consists of three or four pulse trains and the pulses ("any sound that seems unitary"; Alexander [1967]) in the pulse trains correspond to tooth strikes (Morris & Walker 1976) (Fig. 2). The first two or three pulse trains are the result of the scraper striking one to five file teeth, whereas the last pulse train is considerably longer, consisting of 10 to 24 tooth strikes (each tooth strike produces a highly damped sound wave) ($n =$ two phrases from 13 males) (Fig. 2). Each progressive pulse train is longer; the last pulse train is approximately three times the length of the preceding one ($\bar{x} \pm$ SE for lengths [l] and intervals [i] between successive pulse trains [PT] from solo calling songs of *A. parvipennis* males: PT1 no. 1, 5.98 ± 1.44 ms; PT1 no. 1, 15.56 ± 2.20 ms; PT1 no. 2, 8.85 ± 2.39 ms; PT1 no. 2, 14.97 ± 2.58 ms; PT1 no. 3, 13.76 ± 4.10 ms; PT1 no. 3, 12.96 ± 4.68 ms; PT1 no. 4, 36.70 ± 2.67 ms; $n = 10$ phonatomes selected from the begin-

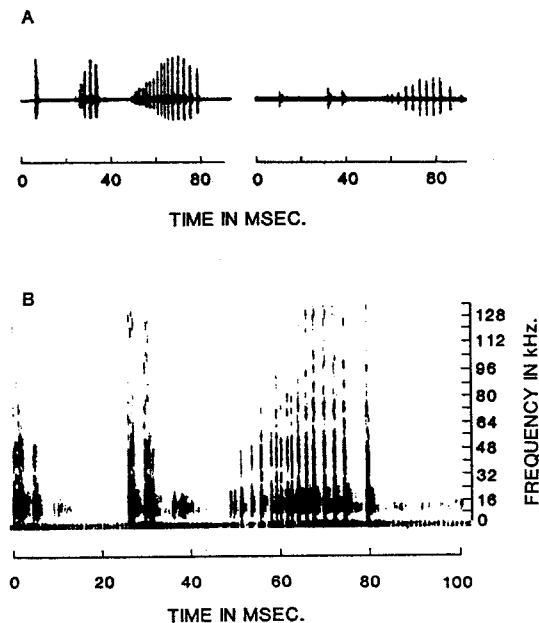


Fig. 2. Temporal and frequency characteristics of phonatomes of the calling song of *A. parvipennis* males at 24–25°C. (A) Oscillograms of phonatomes from two different males. (B) Sonogram of male phonatomes.

ning, middle, and end of one phrase for eight katydids.)

Phonatome lengths and intervals averaged 105.9 ± 10.5 and 111.6 ± 13.3 ms, respectively ($\bar{x} \pm$ SE for eight katydids, 10 phonatomes from 1 phrase/katydid; phonatomes sampled from beginning, middle, and end of phrase; 20–22°C). Phonatome rate averaged 4.5–5.5/s over a temperature range of 20–25°C (Table 1). Phonatome rate was not constant throughout the length of a phrase but usually increased after phrase initiation and slowed near the end of the phrase (Fig. 3).

Phrases. Phrases consisted of an average of 24.1 ± 4.2 phonatomes ($\bar{x} \pm$ SE for 12 katydids, 10 phrases/katydid), whereas means for individual katydids ranged from 17.6 to 31.5 and individual phrases for all katydids contained from 14 to 46 phonatomes. Phrase length averaged 3.9 and 5.4 s with intervals shorter than phrases, resulting in mean periods of 7.1 s (24–25°C) and 8.7 s (20–22°C) (Table 1). This converts to phrase rates of 6.9/min and 8.5/min, respectively. Occasionally, a male produced an exceptionally long phrase (e.g., 9–10 s, 21°C) or short intervals (e.g., 2.5 s, 22°C).

Frequency. The mean principal or dominant frequency determined from male solo calling songs was $10,585 \pm 1,643$ ($\bar{x} \pm$ SE, $n = 50$, frequencies determined from one representative phrase for each male). Like many tettigoniids, the raucous sound of *A. parvipennis* males usually consists of a continuous band of frequencies reaching beyond 100 kHz (Fig. 2B). The frequency spectra were quite

Table 1. Comparison of temporal parameters ($\bar{x} \pm SE$) of solo songs and songs produced during paired singing of *A. parvipennis* males

Year	Temp	Phrase length, s			Phrase interval, s			Phrase period, s			Phonotome rate/s						
		Solo	Chorus	t	n	Solo	Chorus	t ^a	n	Solo	Chorus	t	n				
1984-1985	20-22°C	5.235 ± 0.793	5.362 ± 0.763	-0.52	20	3.461 ± 0.985	4.165 ± 1.008	-2.23*	20	8.686 ± 0.894	9.527 ± 0.890	-2.94***	20	4.563 ± 0.349	4.539 ± 0.349	0.22	20
1986-1987	24-25°C	3.864 ± 0.523	3.861 ± 0.436	0.03	46	3.221 ± 0.554	3.960 ± 0.686	-5.68***	46	7.085 ± 0.539	7.821 ± 0.543	-2.41**	46	5.579 ± 0.491	5.584 ± 0.366	-0.05	46

^a *, $P = 0.05$, **, $P = 0.01$, ***, $P = 0.001$.

variable among males. Some males showed a gradual decline in frequency amplitude for frequencies higher than the dominant frequencies; others showed one to four higher frequency amplitude peaks, which approximated harmonics of dominant frequencies (Fig. 4). Mean \pm SE values for frequency amplitude peaks higher than the dominant frequencies were as follows: peak 2, 19,242 \pm 2,438 ($n = 40$); peak 3, 28,606 \pm 4,078 ($n = 28$); peak 4, 36,356 \pm 3,516 ($n = 6$); peak 5, 45,502 \pm 3,273 ($n = 2$) (frequencies determined from one representative phrase for each male).

Male Chorusing. If one stands between two males in the field or laboratory, it is apparent that the males tend to alternate phrases. A male frequently starts its phrases before the other male ends its phrases, and the two males synchronize their phonotomes where phrases overlap (Fig. 3A). An analysis of chorusing by nine pairs of katydids (30-40 phrases/interaction) yielded the following mean percentages of types of overlap: phrases overlapped on beginning or end, 70.1% (range, 21.2-93.8%) (Fig. 3B), phrases overlapped on both ends, 25.6% (range, 0-78.8%) (Fig. 3A), and no overlap, 4.3% (range, 0-12.5%). As the ranges indicate, the percentage of overlap was quite variable between katydids within a chorusing pair and between pairs. Phrase phase relationships during a paired interaction could be quite variable, or sequences of consistent differences in phase relationships could occur (Fig. 3B). Although the average overlap was 1.4 s (Fig. 5A), overlap occurred most frequently during the first or last 1.0 s of katydid's phrase (Fig. 5B). Also, when overlap did not occur, the interval between the end of one katydid's phrase and the beginning of the phrase of the other katydid was usually very short, averaging 0.4 s (Fig. 5A).

When males switched from soloing to chorusing, phonotome rate and phrase lengths did not change (Table 1). However, phrase intervals lengthened, resulting in longer periods (Table 1) and therefore slower phrase rates.

On six occasions of acoustic interaction of two *A. parvipennis* males, one male suddenly changed to a softer, more ticklike song. This represents less than 1% of interactions to which we have listened. One such interaction was recorded, and we examined the sounds on the storage oscilloscope. In addition to reduced amplitude, the last pulse train of each phonotome consisted of only four to five tooth strikes (i.e., similar to the penultimate pulse train of some males) (Fig. 2A).

Female Sounds. Like other phaneropterine species, *A. parvipennis* females produce short sounds (ticks) in response to male phrases (Spooner 1968, Heller & von Helversen 1986). Female ticks are produced by rubbing together knobs and spines distributed over much of the lower and upper surfaces of the wings (Fulton 1933). The result is ticks showing considerable variation in length ($\bar{x} \pm SD = 25.8 \pm 11.8$ ms; $n = 25$ ticks, five ticks from five females) (Fig. 6) and in number of ticks (Fig. 7).

A. PARVIPENNIS MALES
ACOUSTIC INTERACTION

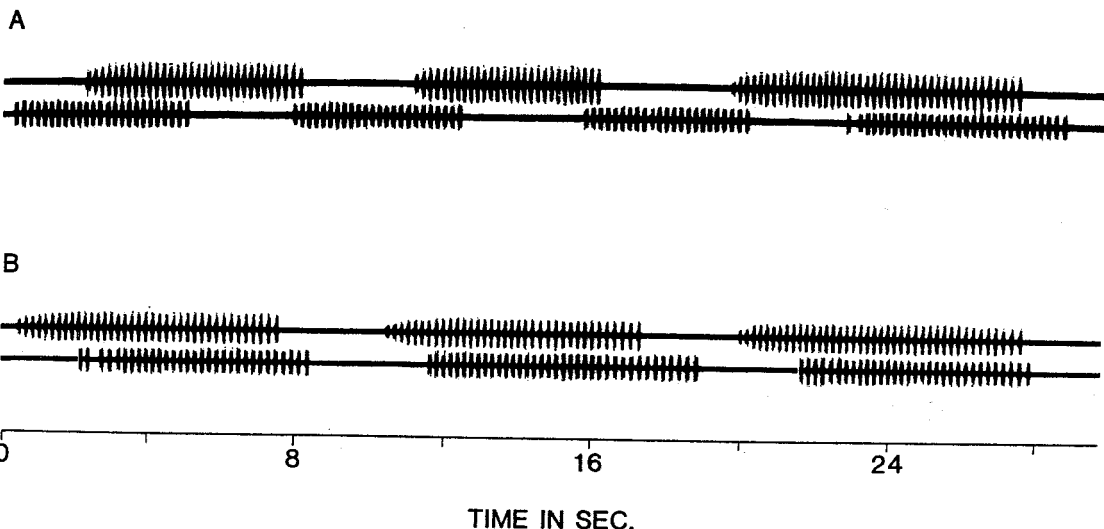


Fig. 3. Chorusing of two *A. parvipennis* males placed 3.34 m apart in an acoustic chamber at 24–25°C. (A) Beginning and end of each male's phrases overlapped by phrases of other male. (B) Only beginning or end of a male's phrase overlapped by phrases of other male.

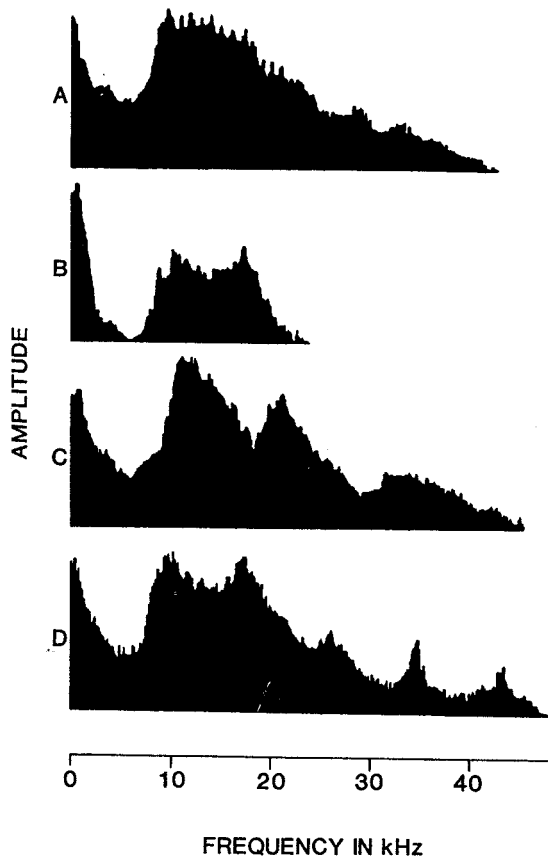


Fig. 4. Frequency spectra of solo calling songs of *A. parvipennis* males. (A) Single peak amplitude. (B) Two peaks. (C) Three peaks. (D) Four peaks.

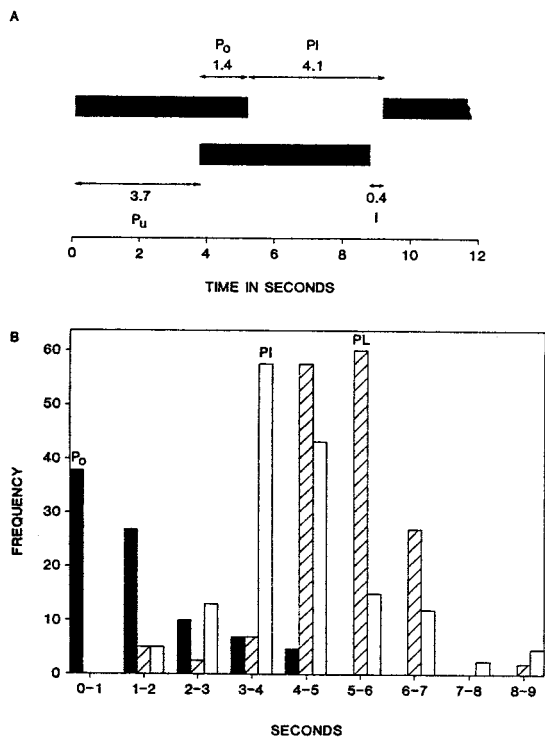


Fig. 5. Mean and distribution frequency of temporal parameters during chorusing by pairs of *A. parvipennis* males at 20–22°C. (A) Mean temporal parameters. (B) Frequency distribution of temporal parameters. P_u , un-lapped portion of chorusing male's phrase; P_o , portion of male's phrase overlapped by phrase of other male; P_i , phrase interval; P_L , phrase length ($=P_u + P_o$).

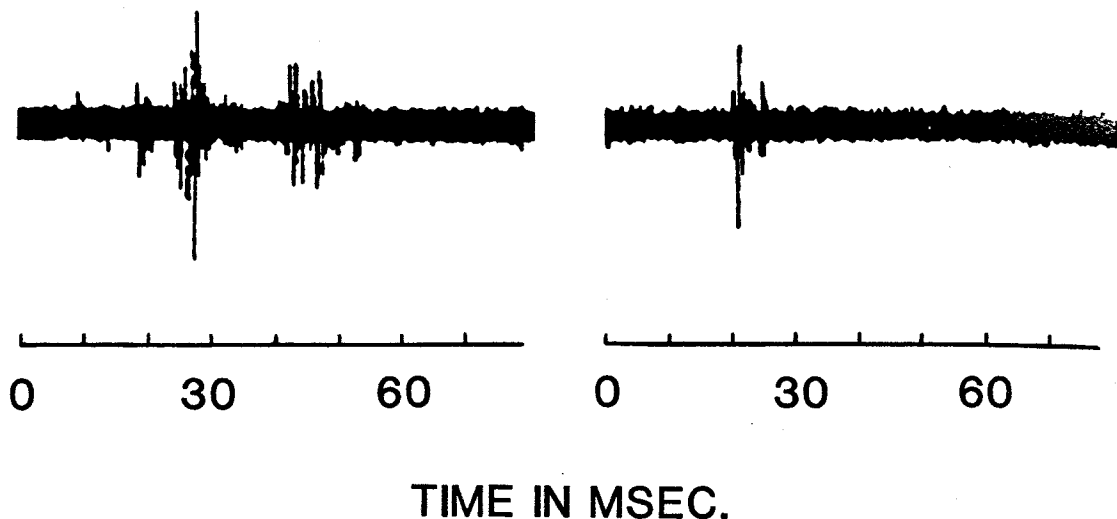


Fig. 6. Sounds of *A. parvipennis* females at 24–25°C.

Male-Female Acoustic Interaction. Females typically produce ticks during male phrases, and female ticks fall between male phonatomes 96% of the time (Fig. 7). Of 251 ticks produced during 77 male phrases, only 11 ticks overlapped male phonatomes. Because phonatome intervals are approximately the same length as phonatomes, females singing independently of males should overlap male phonatomes approximately 50% of the time. Six of the overlapping ticks were produced by the same female, which produced exceptionally long ticks (e.g., left oscillogram in Fig. 6) started just before male phonatome initiation. The interval between the beginning of a male phonatome and the beginning of a following female tick averaged 120.3 ± 13.7 ms ($\bar{x} \pm SE$) ($n = 60$, 10 measurements from each of six females; 24–25°C). The number

of female ticks per male phrase was variable, averaging 3.2 ± 2.92 ticks/phrase with a range of 1–17. The modal tick number was one, occurring 26% of the time. Ticks occurred immediately before or after the male's last phonatome 75% of the time (before: 38 of 77, 49% [Fig. 7A]; after: 28 of 77, 36%; before and after: 8 of 77, 10% [Fig. 7B]). Occasionally, females produced ticks at the same rate as males produced phonatomes, resulting in an alternating pattern (Fig. 7B).

Discussion

Phaneropterine songs range from sequences of simple phonatomes through a range of songs of varying complexity, culminating in the song of *Amblycorypha uhleri* Stål, the most complicated

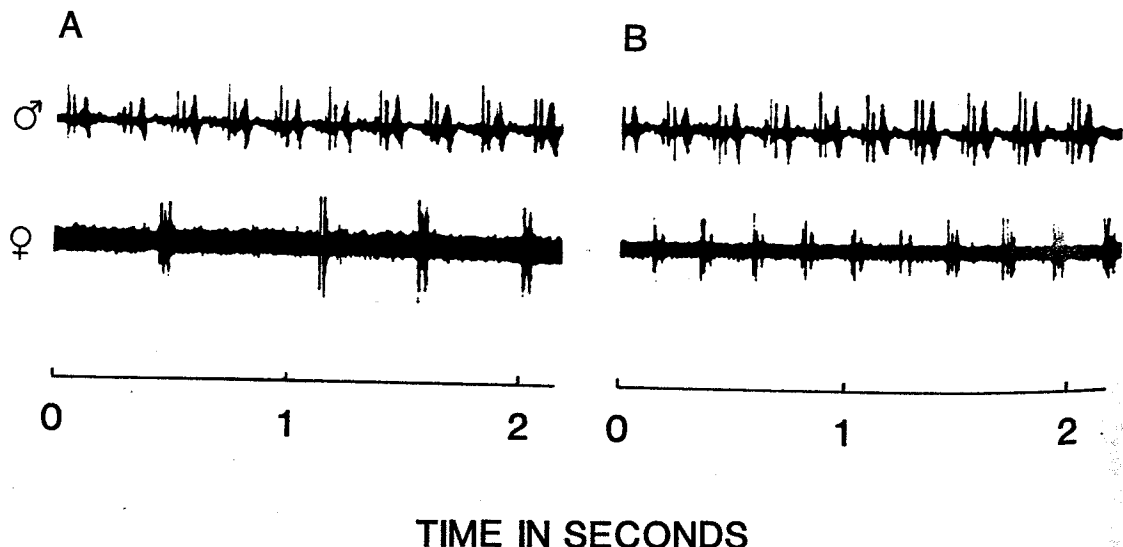


Fig. 7. Acoustic interaction of male and female *A. parvipennis* at 24–25°C. (A) Last female tick occurs before last male phonatome. (B) Last female tick occurs after last male phonatome.

song produced by any orthopteran species (Alexander 1956, Walker & Dew 1972). According to Alexander (1956) and Spooner (1968), phaneropterine songs consist of two basic types of pulses or pulse trains: ticks, consisting of one to a few tooth strikes and lisps, consisting of a large number of tooth strikes.

It is not uncommon among sound-producing Orthoptera for opening wing strokes to produce no sound or short (sometimes soft) ticks and for closing wing strokes to produce longer and frequently louder pulse trains or lisps (Dumortier 1963). Walker's (1975) analysis of *Neoconocephalus* (Tettigoniidae: Conocephalinae) sounds verified the production of one or two pulse trains during simple open-close wing cycles; however, Walker's and other studies (Morris & Pipher 1972, Walker & Dew 1972) showed that males of some species produce multiple pulse trains generated during two to eight hesitations during wing closure. Thus, production by *A. parvipennis* of three or four pulse trains per wing stroke is not unique. In fact, another phaneropterine, *A. uhleri*, produces a phonatome type that also consists of three or four pulse trains per wing stroke (Walker & Dew 1972).

Regular synchrony or alternation of sound components by uniformly spaced conspecific males appears to be uncommon among the Phaneropterinae. Males of *Microcentrum rhombifolium* (Saussure) and *Amblycorypha oblongifolia* (De Geer) alternate short phrases (0.10 and 0.18 ms) and relatively long intervals (2.61 and 2.97 ms; 23 and 26°C); however, alternation may be a result of chance (Shaw 1968). Spooner (1968) describes alternation of lisps and ticks for a number of species, but these probably represent aggressive interactions occurring only at close range. Consistent overlapping phrase alternation is unique to *A. parvipennis*; the only other report of phonatome synchrony involved occasional synchrony of males of *Scudderia curvicauda* (De Geer) housed in a laboratory in close proximity (Spooner 1968).

Phrase alternation in other alternating katydid songs is the result of one male being inhibited from singing during the phrase of a nearby male (Jones 1966, Shaw 1968, Samways 1976, Latimer 1981). Inhibition also appears to be involved in phrase alternation by *A. parvipennis* males. In analyzing chorusing of *A. parvipennis* males and the response of males to computer-generated phrases, Smith (1986) found that intervals between male phrases were longer when an artificial sound or the sound of another katydid occurred during the interval than when no sound occurred during a phrase period or occurred only during the katydid's phrase. Phrase inhibition during overlapping alternation probably explains why phrase intervals are longer during paired chorusing than during solo calling (Table 1).

It has been suggested that synchrony of song units by adjacent males may be achieved and maintained by one of two mechanisms. An anticipatory

(Buck & Buck 1968) or homeepisodic (Walker 1969) mechanism is involved when one male cues on the initiation of the concurrent phrase of another male. A male also might time the interaction of its phrases on the start or end of previous song units of another male, a mechanism termed anticipatory (Buck & Buck 1968) or proepisodic (Walker 1969). Walker (1969) analyzed synchrony of song phrases in pairs of the snowy tree cricket, *Oecanthus fultoni* Walker, and suggested that only a proepisodic mechanism could produce such a rapid rate. Snowy tree cricket males produce phrases at approximately 2.5/s (25°C, Walker [1969]), and intervals between initiations of synchronized phrases averaged 27 ms.

Recent studies of male-female response times of phaneropterines have indicated intervals between initiation of male and female phrases of 20 ms or less (Heller & von Helversen 1986, Robinson et al. 1986), and Greenfield (1988) reported intervals of 10-30 ms between phrase initiations of *Neoconocephalus spiza* Walker & Greenfield males after several seconds of silence. These recent results suggest that *O. fultoni* males might be capable of a homeepisodic mechanism of synchrony.

Phonatome rates of *A. parvipennis* males averaged 4.5-5.5 s (20-25°C), and phrase initiation phase differences averaged 32 ms. Smith (1986) suggested that synchrony of phonatomes in *A. parvipennis* is proepisodic because males start some phrases by beginning their first phonatome before the concurrent phonatome of their acoustic partners.

In the analysis of alternation and synchrony of pairs of males for some katydid species, males have been designated "leaders" and "followers." Leaders typically spend more time singing per unit time (i.e., expend more energy) than followers. Leaders in alternating chorusing sing more phrases per unit time; they may sing at a faster rate while soloing (Busnel et al. 1956, Jones 1966, Shaw 1968) and preferentially attract females (Busnel 1967). In the synchronizing katydid *Neoconocephalus nebrascensis* (Bruner), leaders, in addition to always starting synchronous phrases, first produce longer phrases and also sing at a faster rate during chorusing (Meixner & Shaw 1986). As indicated in Fig. 3B, an *A. parvipennis* male does not always overlap the end of the phrases of its partner. In a study of mate choice, P.L.G. & K.C.S. (unpublished data) found that females chose males that "outcompeted" their chorusing partners by initiating more phrases after the end of their partners' phrases than vice versa. These leader males also produced longer phrases and shorter intervals between phrases, and they sang louder. Thus, competitor males and choosy females have a number of cues to use in decision-making during mate competition.

The rare but distinctive reduction in song intensity by *A. parvipennis* males is an enigma. Variation in song intensity is characteristic of phaneropterine males (Spooner 1964, 1968). Reduction in sound intensity may serve to reduce competition of males for females. Because female phanero-

pterines produce sounds in response to songs of conspecific males, it is not uncommon for several nearby singing or silent males or both to approach a ticking female. *Scudderia texensis* Saussure and Pictet males may produce a softer sound after perceiving a ticking female. The softer sound apparently inhibits female ticking and may make it difficult for competitor males to locate the female (Spooner 1964, Otte 1977). Spooner also reports low-intensity songs for *Inscudderia strigata* (Scudder) males at times of low acoustic activity. Many males of the field cricket *Gryllus integer* Scudder produce soft calling sounds during the hours around sunrise. Cade (1979) suggests that because females no longer show directional orientation and positive phonotaxis to long-distance calling songs at this time, the soft sounds may serve to arouse nearby females sexually and reduce the possibility of attracting parasitoid flies. Because it is so rare, the soft ticking sound of *A. parvipennis* males probably does not reduce competition from nearby males, attract nearby sexually receptive females, or reduce likelihood of attack by phonotactically positive parasitoids.

Phaneropterine females respond to male calling phrases at specific intervals which identify the species of the female and elicit phonotaxis by the male (Alexander 1967, Spooner 1968, Heller & von Helversen 1986, Robinson et al. 1986). These acoustic response times range from 17–1,130 ms. *A. parvipennis* male–female response time is approximately 120 ms. However, females of *A. parvipennis* are unique in that female responses fall between the phonatomes of male phrases, with the most frequent responses falling before the last phonatome. Female ticks did occur after the last male phonatome but only in 46% of the phrases examined.

The characteristic of female ticking between phonatomes and male overlapping phrases suggests that males synchronize phonatomes so that females can clearly perceive male phonatomes and males can perceive female ticks. It is possible there may be a competitive aspect to phonatome synchrony; e.g., males attempting to start phonatomes first or to end last (Greenfield in press). Whatever the adaptive significance of phonatome synchrony, its maintenance is important to male *A. parvipennis*. Smith (1986), in attempting to analyze the acoustic response of *A. parvipennis* males to computer-generated signals, found that males stopped singing if overlapped by signals that did not synchronize with their phonatomes.

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