Interspecific Differences in Frequency and Other Physical Parameters of Pair-forming Sounds of Bush Katydids (Orthoptera: Tettigoniidae: Phaneropterinae)[1]

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ABSTRACT

Comparison of frequency spectra of pair-forming signals of *Amblycorypha floridana, Microcentrum rhombifolium, Scudderia cuneata, S. furcata,* and *S. texensis* showed (1) the dominant frequencies in the signals differ from species to species with little intraspecific variation and (2) the sounds of males and females of each species have similar frequency spectra. Upward frequency modulation occurs in the male tick song of *M. rhombifolium.* Intensity changes occur at the end of male songs of *A. floridana* and *S. texensis.* Female sounds of the 5 species differ in time delay, duration and waveform. At least some of these differences may be adaptive.

Most species of ensiferan Orthoptera regularly employ sound during sexual pair-formation. These pair-forming signals are produced when individuals are not in physical contact with one another. Selection should enhance differences in those parameters of species-specific songs that promote more effective use of time and energy in forming conspecific sexual pairs.

Parameters of pair-forming signals that might convey information to the receiver and be exposed to selection are frequency, intensity, amplitude modulation, frequency modulation, transients, pulse rate, and chirp rate (Alexander 1967, Dumortier 1963). The roles of pulse rate and chirp rate have been studied by Walker (1957) and reviewed by Alexander (1960) and Walker (1964), but only recently has attention been given to other features of sound. Frequency spectra of insect sounds have been analyzed extensively by only five workers (Busnel 1953, Morris 1970, Morris and Pipher 1972, Pipher and Morris 1974, Suga 1966, Webb et al. 1976).

Among crickets and katydids, two pair-forming signal systems operate, called signal systems I and II by Lloyd (1971). In signal system I, a stationary male signals acoustically, and females move to the sound. All crickets and most katydids use this system. In signal system II, a mobile male produces a sound to which a nearby female responds with a sound of her own. The male then moves to the responding female. All species of the subfamily Phaneropterinae, the bush katydids, that have been studied (n=18) and perhaps some species of the subfamily Ephippigerinae (Hartley, Robinson, and Warne 1974) use this system in pair formation—though sometimes in combination with signal system I (Spooner 1968).

Because of the sporadic nature of their acoustic behavior, bush katydid sounds have received little attention. The sounds of bush katydids are not continuously repeated for long periods of time, making measurement of physical parameters of their signals much more difficult. Although the signals of male bush katydids are usually distinctive and often very complex (Walker and Dew 1972), the signals of females sound the same, at least to human ears, and consist of one or a few brief ticks in response to the male signal. The species-specific time delay between the male song and the female response has been studied (Spooner 1964, 1968).

Here I compare the frequency spectra of both male and female signals of 5 sympatric, synchronic species of bush katydids. During the analysis of frequencies, interspecific differences in other parameters became apparent. These parameters included time delay, duration and waveform of female signals, and amplitude modulation, frequency modulation, and transients of male signals. I report these interspecific differences and discuss their possible adaptive significance.

MATERIALS AND METHODS

Five species were studied: *Amblycorypha floridana* Rehn and Hebard, *Microcentrum rhombifolium* Saussure, *Scudderia cuneata* Brunner, *S. furcata* Morse, and *S. texensis* Saussure and Pictet. Virgin adults were used in most cases, since females of most species usually stop responding acoustically after mating. Virgin specimens were obtained by rearing eggs or field-collected nymphs. In cases where specimens were difficult to obtain (e.g., females of *Microcentrum rhombifolium*), field-collected adults were used. Each specimen was kept individually in a screen-top, wide-mouth, quart Mason jar with a water vial, a piece of Purina® dog chow, and some lettuce. Individuals that produced pair-forming signals in their jars were placed in special cages in the spectrum analysis recording chamber and recorded 5–20 h later.

Recordings and frequency spectrum analyses were made in the sound laboratory at the Insect Attractants and Basic Biology Laboratory, U.S.D.A., in Gainesville, Florida. The sound laboratory consisted of an instrument room and a commercial anechoic chamber built by Cahill Corporation. The chamber had an inside working space of 10′×9′×7.5′ and was acoustically baffled with 24″ fiberglass wedges.

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A small Faraday box, 3′×3′×2′, was placed inside the anechoic chamber. This box was lined with copper screen and styrofoam strips to reduce the possibility of interference from stray electrical signals and attenuate any spurious sounds that might be generated within the anechoic chamber. With this arrangement of a box-within-a-box, ambient noise above 150 Hz was lower than the recording sensitivity of the instruments.

A male and a female were placed in separate cages within the Faraday box, which was left open on one side. The cage containing the male was a screen (16×18 meshes/inch) cylinder, 7.5 cm high × 12.5 cm diameter, placed 30 cm beneath the cage of the female. The cage containing the female was a smaller screen cylinder, 12.5 cm high × 7 cm diameter, with a pivoting central axis so that the cage could be rotated to permit the observer to position the female with minimal disturbance and ensure the correct spatial geometry for recording each species. This cage was mounted on a stand 7.5 cm below the recording microphone.

The positions of the male and female were noted before recordings were made. The desired position for the female was upright directly beneath the microphone. This position could be maintained by very slowly rotating the cage about its axis and moving the stand forward or backward. The female usually remained stationary durnig recording sessions. Because males seldom are stationary while singing, analyses of male sounds were made only of those males that were placed in isolation in the cage usually occupied by the female and rotated into proper position.

Recordings were made at 27±3°C. A low intensity lamp illuminated the Faraday box with light reflected off the wall of the anechoic chamber. Although time of day varied, all recordings were begun within 2 h after the overhead lights in the chamber were turned off.

A Bruel & Kjaer half-inch condenser microphone (cartridge Type 4133) with a B & K 2619 cathode follower was suspended through the top of the Faraday box. The microphone was connected to a Bruel & Kjaer frequency amplifier, Type 2107, which functioned both as an amplifier and a sound level meter.

The output signal from the frequency amplifier passed through a variable electronic filter (Spencer-Kennedy Laboratories, Inc., Model 308A) which filtered out frequencies below 120 Hz and attenuated the signal by about 55%.

The filtered signal then passed to a Saicor SAI-52 Real Time Spectrum Analyzer-Digital integrator, connected in parallel to a Tektronix R5031 Dual Beam storage oscilloscope which monitored the actual signal and displayed the frequency spectrum stored in the memory of the SAI-52 Analyzer. The memory portion of the SAI-52 was connected to a Tektronix oscilloscope Type 3A3 Dual-Trace differential amplifier which could monitor or display waveforms of the signal held in the memory of the SAI-52.

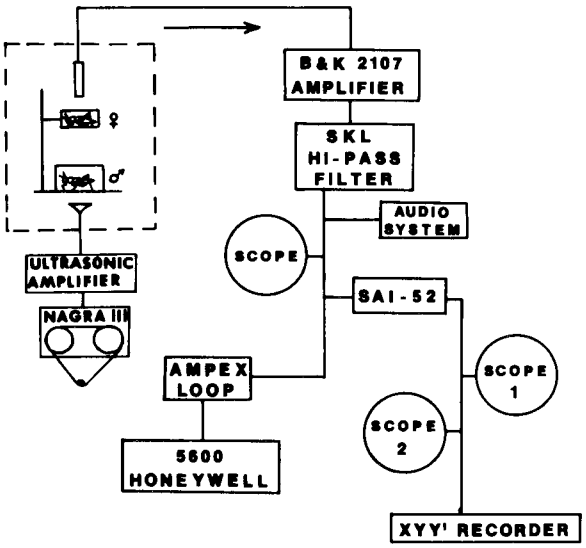

FIG. 1.—Schematic diagram of record-analysis apparatus. Faraday box is indicated by dotted lines. Enclosed in box are katydid cages, ½″ condenser microphone, and speaker from Naga III tape loop.

The signals were recorded on an Ampex FB-450 BinLoop recorder at 60 ips (inches per second) and then transferred for storage to a Honeywell Model 5600 portable tape recorder/reproducer at the same recording speed. All audible signals were monitored with a Rotel stereo amplfier RA-110A. The record-analysis apparatus is schematically diagrammed in Fig. 1.

Signals to be analyzed were taken from storage from the Honeywell 5600 and transferred to the Ampex 450 at 60 ips. The tape speed on the Ampex was then reduced to 7½, 3¾, or 1⅞ ips and the signals fed into the SAI-52 Analyzer.

Oscillographs of female sounds of each species were made with a Honeywell 2106 Visicorder. Signals from the Ampex Loop Recorder/Reproducer were fed at 3¾ ips into the Visicorder (Fig. 2).

Males of 3 of the species were reluctant singers in the cages, but they could be induced to sing when presented with an attenuated, recorded male pair-forming song on a loop of ¼″ tape played on a Nagra III tape recorder, fed into an ultrasonic amplifier and passed into the anechoic chamber where the signal was broadcast at about 40 dB (at 30 cm). Males of *Amblycorypha floridana*, *Microcentrum rhombifolium*, and *Scudderia cuneata* were usually induced to sing within 2 min of stimulation. As soon as the male began to sing, the sound from the tape loop was reduced in intensity and then turned off. Once induced to sing, males usually continued to sing intermittently for at least one hour.

The number of recordings analyzed for each species is indicated in the results by 2 values in brackets: [x = number of individuals of that species that were recorded, and n = the total number of songs analyzed].

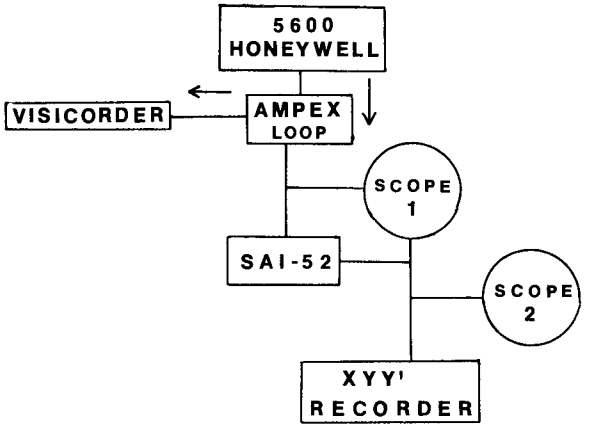

FIG. 2.—Schematic diagram of reproduce-analysis apparatus.

RESULTS

The pair-forming song produced by males of *Amblycorypha floridana* consists of a series of ticks followed by a buzz. Spooner (1968) divided the song into 3 parts: Part I, a series of 4–12 ticks that are produced initially at a slow rate of 1–2 per second and gradually increasing in rate to 3–4 per second; Part II, 1–2 ticks preceding the buzz, produced at a more rapid rate than the previous ticks; and Part III, the buzz. Each tick in Part I consists of a 3-pulse train at a rate of 50 pulses/second; the ticks in Part II are single pulses; while the buzz is a series of 7–10 pulses delivered at a rate of 35–45 pulses/second. The female answers with a single tick about 140 msec after the buzz.

The most intense range of frequencies is 7–19 kHz for both sexes. The dominant frequency is 9.9±1.2 kHz ($\bar{x}\pm SD$) for males [x=14, n=21], and 9.6±1.3 kHz for females [x=5, n=21], with a 2nd intense peak near 17 kHz for both sexes. Little sound energy occurs below 7 kHz (Fig. 3A, B). The female tick has a duration of 32±5 msec and consists of a complex 4-pulsed waveform (Fig. 4A).

Temporal changes are evident in the frequency spectrum of a typical male pair-forming signal of *Amblycorypha floridana* (Fig. 5). Because the time duration of the buzz was longer than the analyzing time of the SAI-52 Analyzer, the buzz was analyzed 2 equal segments. The frequency spectra of each Part differed. Ticks in Part I were variable in intensity, and the frequency spectrum range was 8–14 kHz. Beginning in Part II and becoming very apparent in the buzz, an intensity increase occurred at 17 kHz. The buzz was much more intense and

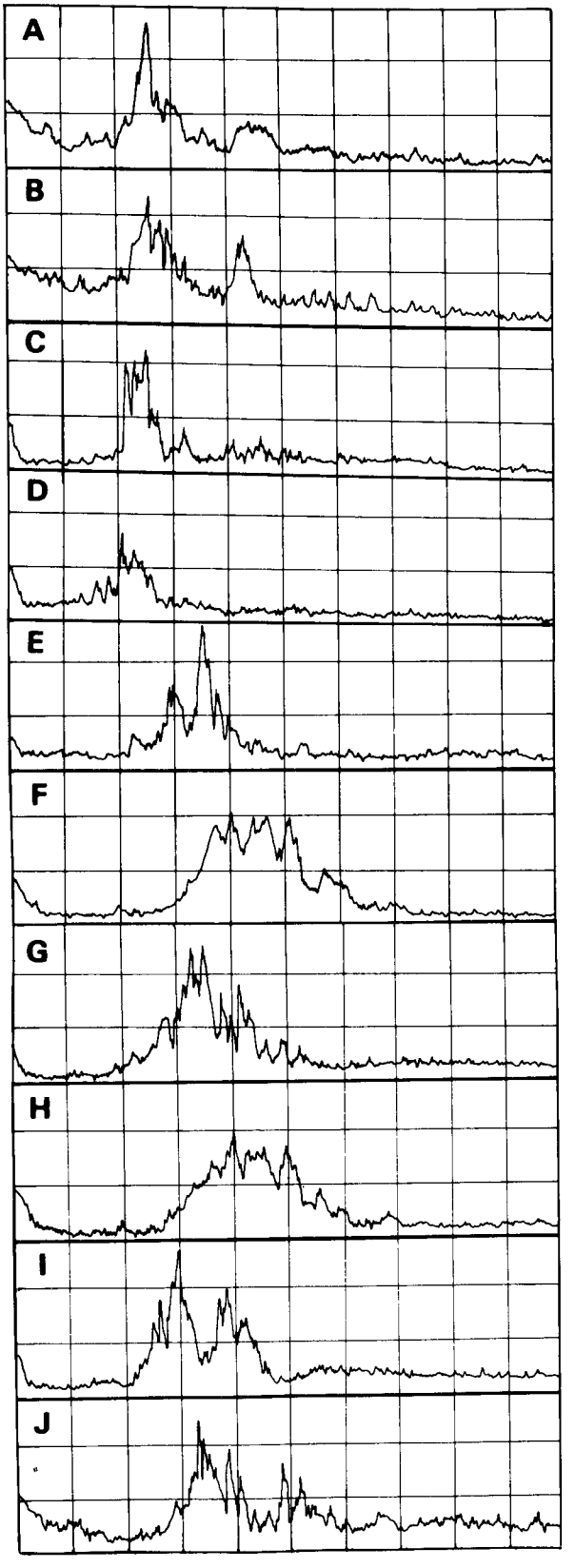

FIG. 3.—Frequency of pair-forming signals of 5 species of bush katydids: *Amblycorypha floridana,* A. male, B. female; *Microcentrum rhombifolium,* C. male, D. female; *Scudderia cuneata,* E. male, F. female; *S. furcata,* G. male, H. female; *S. texensis,* I. male, J. female. Frequency spectrum range is 40 kHz. One horizontal division is 4 kHz.

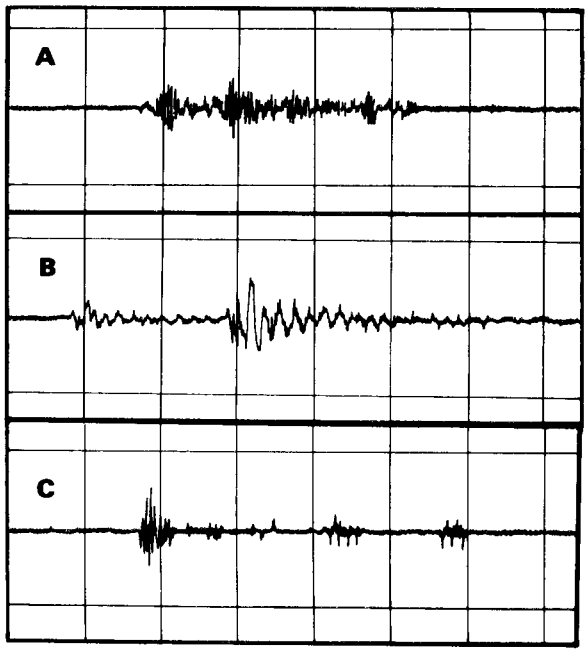

FIG. 4.—Oscillograms of female tick sounds of 3 katydid species. A. *Amblycorypha floridana;* B. *Microcentrum rhombifolium;* C. *Scudderia texensis.* One horizontal division is 8 msec. Vertical scales are linear and in arbitrary voltage units.

had a broader spectrum of frequencies than either Part I or II.

Microcentrum rhombifolium males produce two kinds of signals, a lisp and a series of ticks. The females respond acoustically to the tick series only. Males produce an average of 22–25 ticks/series at a rate of 9 ticks/second (25°C), each tick corresponding to one toothstrike. At 25°C females respond with 1 or 2 ticks about 249±27 msec after the last tick of the male song.

Microcentrum rhombifolium has the lowest frequency spectrum of the 5 species studied. Male and female signals have similar frequency spectra, with a range of the most intense frequencies of 6–12 kHz [♂: x=3, n=20; ♀: x=2, n=20]. The dominant frequency in both sexes is 9.2–9.5 kHz (Fig. 3C, D).

Female ticks of *M. rhombifolium* have a complex waveform of 2 parts (Fig. 4B). The 1st part is about 8 msec in duration and is less intense than the 2nd part, which has a low frequency component at the beginning. The total duration of the female tick is 37±9 msec.

Temporal changes are observed in the spectrum of frequencies with each successive toothstrike in the male tick series (Fig. 6). Changes in intensity occur from tick to tick with an increase infrequencies below 7 kHz near the end of the tick series. There is a consistent trend toward higher dominant frequencies during the tick sequence from 8 kHz in the 1st toothstrike to 12 kHz in the last. This upward frequency modulation was observed in all samples of the male tick song (n=3).

The pair-forming signals of males of *Scudderia cuneata* and *S. furcata* are so similar that they may be difficult to distinguish by ear since they vary in duration with temperature. Both produce a series of 3–6 lisps of short duration, followed by long periods

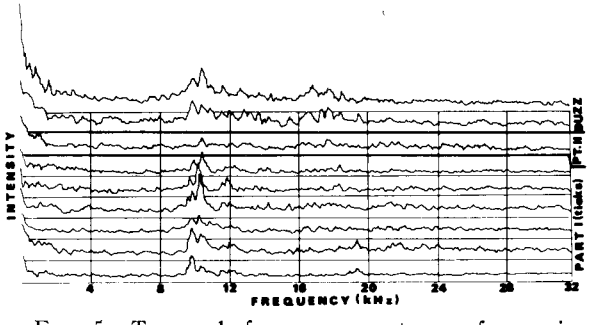

FIG. 5.—Temporal frequency spectrum of a pair-forming song of male *Amblycorypha floridana.* Parts I, II, and III are delineated. Each tick of Part I was analyzed separately at 8 spb. Part III, the buzz, was analyzed in two equal parts at 8 spb, since the duration of Part III was greater than analysis time. Frequency spectrum is 32 kHz. Intensity is linear. Vertical scales are linear and in arbitrary voltage units.

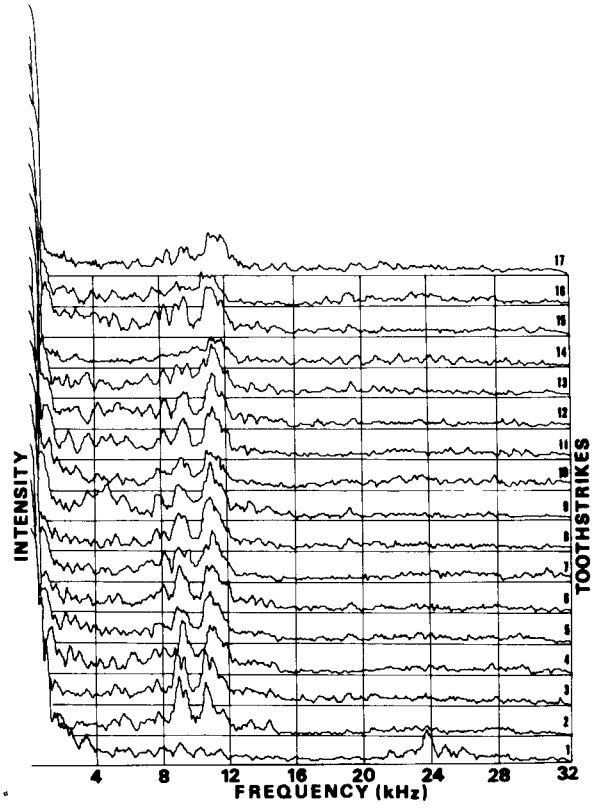

FIG. 6.—Temporal frequency spectrum of a pair-forming song of male *Microcentrum rhombifolium.* Each toothstrike of a tick series (n=17) was analyzed at 8 spb to 32 kHz. Intensity is linear and in arbitrary voltage units.

of silence. Spooner (1968) found them to be distinct. The lisp duration for *S. cuneata* at 25°C is 16±3 msec, while that for *S. furcata* at 25°C is 65±9 msec. Female response time is also distinct for each species. Timing of the female tick after the male lisp is about 350 msec for *S. cuneata,* and 1100 msec for *S. furcata.*

Scudderia cuneata and *S. furcata* have similar frequency spectra (Fig. 3E–H). The most intense frequencies in both species occur between 7–24 kHz. The dominant frequencies in females are consistently higher than in males for both species. The dominant frequency in males of *S. cuneata* is 14.0±1.7 kHz [x=2, n=5]; in females, 17.4±2.4 kHz [x=4, n=5]. In males of *S. furcata* it is 14.6±1.5 kHz [x=5, n=12]; in females, 16.0±2.0 kHz [x=6, n=3].

The duration of the female tick of *S. cuneata* averages nearly twice as long as that of *S. furcata:* 3.97±0.35 msec for *S. cuneata,* 2.34±0.56 msec for *S. furcata.* Typical waveforms of female ticks for these species indicate that the tick of *S. furcata* is double- or single-pulsed, while that of *S. cuneata* consists of 3 pulses (Fig. 7A, B). With samples of 15 ticks from 3 individuals for each species, the greatest variation in waveforms occurred with *S. furcata* in which an individual produced both two-pulsed and single-pulsed ticks, in no apparent order. *S. cuneata* usually produced 3-pulsed ticks, but 2 of 15 were two-pulsed.

Although *Scudderia texensis* males produce 2 songs, the fast-pulsed and the slow-pulsed songs, females answer only the slow-pulsed song (Spooner 1964). This usually consists of 2 phrases, a short one of 5–7 wingstroke cycles in duration and a longer one of 15–22 wingstrokes. The wingstroke rate at 25°C is 11.4 wingstrokes/second. Females answer with one or a few ticks after about 1300 msec.

Frequency spectra for male and female signals are similar for *S. texensis.* The range of most intense frequencies is 10–24 kHz. The dominant frequency occurs at 12.8±1.9 kHz for males [x=3, n=12] and 13.5±1.7 kHz [x=2, n=4] for females. Other peaks of high intensity occur at 16 kHz (for both sexes) and 20 kHz (for females) (Fig. 3I, J). The duration of the female tick is 28±6 msec and consists usually of 3 pulses, of which the first is most intense (Fig. 4C).

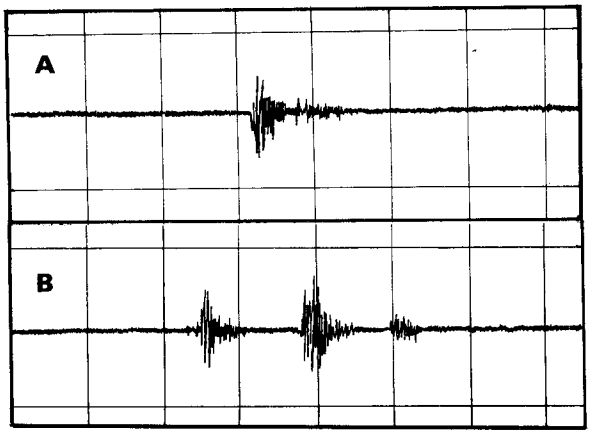

FIG. 7.—Oscillograms of female tick sounds of 2 katydid species. A. *Scudderia furcata;* B. *S. cuneata.* One horizontal division is 1 msec. Vertical scales are linear and in arbitrary voltage units.

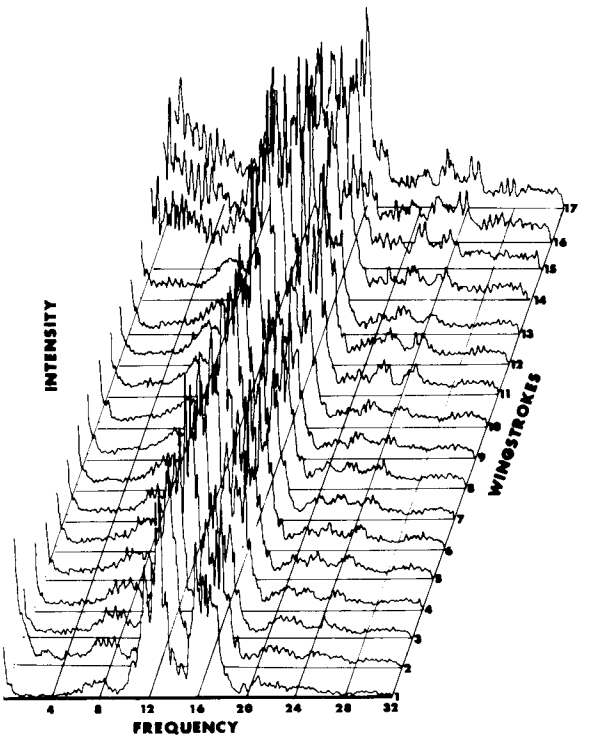

FIG. 8.—Temporal frequency-spectrum analysis of a slow-pulsed, pair-forming song of *Scudderia texensis.* Each analysis corresponds to one complete wing closure of a 17-pulsed song. Frequency range is 0–32 kHz, and intensity is linear and in arbitrary voltage units.

Temporal changes occur in the frequency spectrum of each wing closure of the slow-pulsed song of the male of *S. texensis* (Fig. 8). Although the dominant frequency does not change from beginning to end, changes in intensity at the end of the signal are obvious, with an increase in frequencies below 10 kHz.

DISCUSSION

Frequency spectrum analyses indicate that frequency spectra of pair-forming sounds differ interspecifically but are similar for conspecific males and females. Whether or not interspecific differences and intraspecific similarities are adaptive has not been demonstrated. Spectral differences may be a by-product of morphological differences that evolved in another context; or selection for spectral differences may have stimulated the evolution of differences in the sound-producing structures. The carrier frequency seems to vary inversely with the size of the katydid; the greater the size, the lower the carrier

frequency. *Microcentrum rhombifolium,* the largest species examined, has the lowest carrier frequency, followed by *Amblycorypha floridana,* the second largest species. That *Scudderia cuneata* and *S. furcata* are so similar in both morphology and frequency spectra also suggests a relationship between tegminal morphology and song frequency.

A number of hypotheses has been introduced to explain frequency in terms of physical features of the tegmina. Pierce (1948) suggested that carrier frequencies are a function of the natural resonant frequency of the mirror or disc of the right tegmen. However, destruction of parts or all of the right tegminal mirrors did not appreciably alter the frequency spectrum, although intensity was reduced (Broughton 1964, Morris and Pipher 1967).

Morris and Pipher (1967) and Bailey (1970) suggested that the vein framework surrounding the mirror acted as a cantilever vibrating about the vestigial file of the right tegmen. By plotting the observed carrier frequencies of katydid songs against the reciprocal of the square of the lengths of the mirror lattice, they obtained a straight line passing through the origin. The plot suggested a relationship which supported their model. Using their model, I plotted values for the 5 species of bush katydids. Although *M. rhombifolium* and *A. floridana* fell on the line, all species of *Scudderia* fell above the line (though parallel to it), perhaps because their tegminal lattices are considerably more complex than any of the other species plotted, with smaller lattices to the left of the mirror (Fig. 9). Possibly by multiplying the L value (length of the mirror) by a correction factor to take into account possible additive effects of the small lattice frames, the values for these species may conform more closely with the model.

If the frequencies of a signal are produced by the mirror frame set into vibration, the way in which it is set into vibration will determine, in part, the frequency spectrum produced. Bailey and Broughton (1970) list 4 methods by which a sound emitter may be thrown into vibration:

(1) Each stimulation may throw the emitter into vibration at its natural frequency of free vibration, producing a pulse, or train of waves at this frequency, and decaying more or less rapidly before the next stimulation. (2) The stimulating mechanism if regularly periodic, may drive the emitter into forced vibration at a frequency equal to the number of stimulations per second, and unrelated to the emitter's own natural frequency of free vibration. (3) A combination of the above 2 cases. The number of stimulations per second almost coincides with the natural frequency of the emitter, so that each stimulation now evokes one wave, reinforced by the next before any decay can set in; this has the effect of greatly amplifying the total energy emitted. The condition is resonance," and the frequency of the resonant vibration is marginally higher than that of free vibration. Each wave is a monocyclic pulse but the whole series of monocyclic pulses now simulates a simple homogeneous train or the conventional pulse. Because the true resonance phenomenon tends to produce smoothly rising and decaying "pulses," lacking in initial or final transients, the sound has a more musical quality than type (1), which has numerous transients. (4) A 4th system is possible, in which the tegminal emitter has no particular natural frequency of vibration of its own but emits a damped pulse of something approaching "white noise" at each impact.

Most crickets and some katydids use Type 3, while most katydids probably use Type 1 or 2 to set the mirror frame into vibration.

Morris and Pipher (1972) found 2 contrasting frequency spectra emitted by the same apparatus of *Metrioptera sphagnorum,* and indicate that not only tooth size and spacing on the file, but also the way in which the file is struck influence the frequency spectrum of the songs.

Whatever the mechanism is that produces the characteristic frequency spectra of male katydids, it is difficult to explain similar frequency spectra for female katydids, since they lack a mirror in their right tegmina. Structures that may operate to emit carrier frequencies are the areas between the transverse veins (Nickle and Carlysle 1975). An explanation of frequency spectra of female signals in terms of morphology, however, has not been resolved.

There is evidence to suggest that the ears of crickets and katydids are frequency sensitive and that crickets and katydids may perhaps be able to discriminate frequencies. Katsuki and Suga (1960) showed that in 5 species of crickets and katydids the dominant frequency range involved in stridulation agreed well with the frequency range to which the tympanal organ of the same insect was most sensitve. Using neural response thresholds of carrier frequencies in crickets (*Teleogryllus commodus* and *T. oceanicus*), Loftus-Hills et al. (1971) demonstrated that neural elements of the afferent auditory pathways of these crickets were closely tuned to the carrier frequencies of the crickets' calling songs (which differed from each other), though the mechanism responsible was unclear. Similarly, Nocke (1972) observed hearing thresholds in *Gryllus campestris* at 4 kHz and 14 kHz, corresponding to the frequencies of that species calling song and courtship song, respectively. Wever and Vernon (1959) demonstrated frequency sensitivities in 2 species of katydids, *Neoconocephalus retusus* and *Conocephalus strictus,* that correspond to the carrier frequencies of their songs. Michelson (1968) demonstrated that in an isolated locust (Acrididae) ear frequency discrimination occurred and that it was mediated by four receptor cells located on different parts of the tympanum corresponding to different modes of vibration. The intensity required to stimulate the auditory nerve of *Gryllus* species decreased sharply at 5 kHz, which is the frequency of the male calling song (Wever and Vernon 1959). The mole cricket *Scapteriscus acletus* responded to a narrow range of frequencies with species-specific pulse rates maintained, and

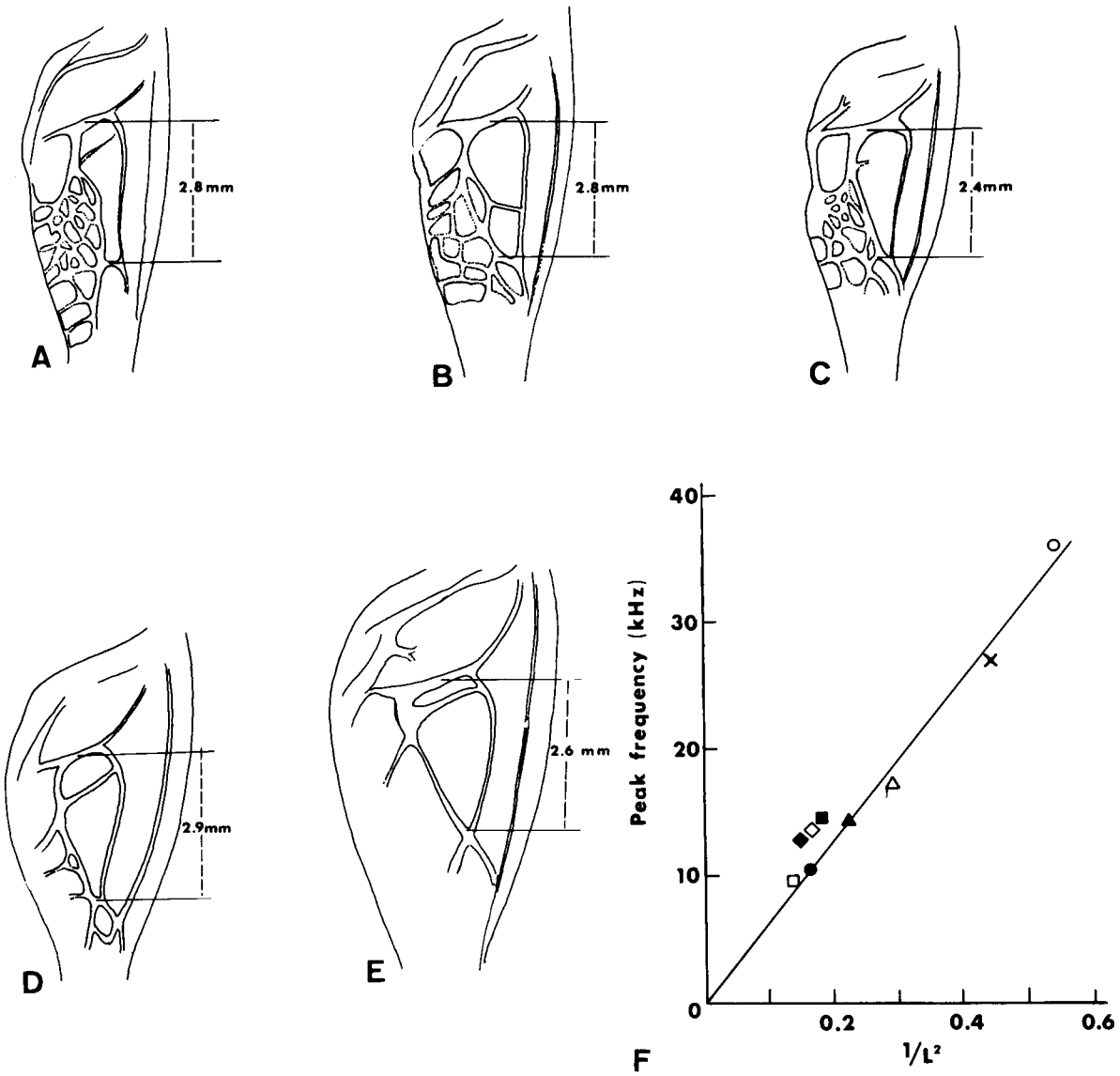

FIG. 9.—A-E, mirror lattices of male right tegmina of bush katydids, dorsal view: A. *Scudderia cuneata;* B. *S. furcata;* C. *S. texensis;* D. *Amblycorypha floridana;* E. *Microcentrum rhombifolium.* F. Plot suggesting the feasibility of a cantilever model. Points for *Conocephalus nigropleurum* (○) and *Orchelimum gladiator* (△) (Morris and Pipher, 1967, *Homocoryphus nitidulus* (▲) and *Conocephalus discolor* (×) (Bailey, 1970), *Amblycorypha floridana* (●), *Microcentrum rhombifolium* (□), *Scudderia cuneata* (◇), *S. furcata* (◆), and *S. texensis* (■). Coefficient of linear correlation for all values is 0.9711.

Gryllus rubens, Oecanthus celerinictus, Neoncmobius cubensis, and *Scapteriscus acletus,* with similar pulse rates, have non-overlapping frequency spectra (Ulagaraj and Walker 1973, 1975), suggesting that the carrier frequency of each species acts to reduce nonproductive encounters among these species.

The acoustic environment of any singing insect consists of the total sound-producing fauna within broadcasting range of the singing individual and all environmental factors affecting the sounds produced. The 5 species of katydids in this study sometimes sing at the same site at the same time in Gainesville. In addition to these singers, frogs, crickets, and other katydids add their sounds to the evening chorus. To communicate effectively in this situation, these insects should be expected to have evolved a mechanism that would enhance the effective range (i.e., the maximum distance a signal may carry the species-specific information to the listener) of their signals. To be heard, the signal has to be distinguished by the receiver from the ambient noise of the environment. Receiving and decoding acoustic signals might be more difficult if all organisms broadcasted at the same time producing their songs at the same fre-

quency. For example, suppose 2 individuals of different species were singing at the same time at the same intensity. If one produced a single-pulsed song every 2 sec while the other sang continuously at a rate of 60 pulses/second, the effective range of the first insect would be less than the second, because the 60 p/s signal would mask to some extent the temporal pattern of pulses of the insect singing at 0.5 p/s. On the other hand, if the signals differed in their frequency spectra, discrimination of the signals would be possible, and masking effects would not operate. Bailey and Robinson (1971) suggest that information in the song patterns of species of *Homorocoryphus* (Tettigoniidae) is carried on a limited frequency band, thus avoiding message jamming from ambient environmental noise, i.e., insects with tuned receivers might be better able to decode information from the high noise level of insects in tropical regions.

Saby and Thorp (1946) measured ambient ultrasonic noise in 2 jungles in Panama and found a diurnal cycle of noise in both places. The frequency spectral distribution of each jungle was characteristic and reflected in part the fauna of each site. No study has determined which species are singing together in any one area and how the frequency spectral distribution of their songs relate to one another. If there were considerable non-overlap of carrier frequencies among vicinal species singing at the same time, it would suggest that the carrier frequency of a signal might act to facilitate information decoding by the receiver, which would decode only that information being received within a narrow band of sound energy.

The possible adaptive significance of the other parameters is less clear. Sliding frequency modulation is observed in the male tick song of *Microcentrum rhombifolium*. Pipher and Morris (1974) report that sliding FM of prolonged pulses is invariably downward, coinciding with increasing tegminal overlap. In *M. rhombifolium*, however, successive rapid decay pulses have on upward modulation of 4 kHz. The upward modulation perhaps is due to tooth size and shape or to the fact that only the more central 15–25 teeth of the file are being struck during the signal such that the effects of total wing-stroke or wing closure do not come into account here.

Intensity changes at the end of the male song of both *Amblycorypha floridana* and *Scudderia texensis* could act to switch on the timing mechanism for the female response at the appropriate time delay. Female tick duration may convey some species-specific information in *Scudderia* species. *S. furcata* and *S. texensis*, with similar time delays and frequency spectra, have very different tick durations. With such well-defined interspecific differences, the information-conveying potential of these calling signal parameters should not be overlooked.

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