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The Effect of Variation in Parameters of the Male Calling Song of the Katydid, *Amblycorypha parvipennis* (Orthoptera: Tettigoniidae), on Female Phonotaxis and Phonoresponse

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After being placed equidistant from playbacks of two computer-generated male calls, females of the katydid Amblycorypha parvipennis *preferentially moved toward call phrases that were louder, longer, and "leading" (initiated without being overlapped by other call phrase endings). Because earlier tests with calling males had indicated that male mating success was related to these call parameters, we suggest that mating success is partly a result of female choice. Females also preferentially responded to the initial, rather than the latter, half of male phrases. Results of other tests suggested that females were responding to increased phonatome rate characteristic of the first half of the phrase. Males may compete to lead in order to prevent jamming of initial phrase information. Females also preferentially phonoresponded ("ticked") in response to longer phrases. In earlier studies of male mating success and female phonotaxis using live males, male weight, sound level, and leading were intercorrelated; however, none of these parameters were correlated with phrase length. We suggest that females may respond to different call parameters under different environmental conditions.*

KEY WORDS: katydid; calling song; phonoresponse; phonotaxis; female choice.

INTRODUCTION

According to sexual selection theory, variation in the nature of male signaling is likely to be related to mating success (West-Eberhard, 1984). Gerhardt (1991)

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differentiated between static and dynamic properties of signals. Static properties are likely to be associated with species identification and under stabilizing selection. In contrast, dynamic properties may show considerable within- and between-male variation and be subjected to directional sexual selection. Gerhardt (1991) examined the role of dynamic properties of acoustic signals in eliciting phonotaxis of female tree frogs. In this study, we examine the role of dynamic properties of the acoustic signals of males of the "chorusing" katydid *Amblycorypha parvipennis* Stål in eliciting the attraction and phonoresponse of conspecific females.

Male signaling in acoustic Orthoptera frequently involves some form of chorusing, i.e., statistically significant temporal interaction of call components between or among the acoustic signals of neighbors (Greenfield and Shaw, 1983). Chorusing includes remarkable examples of alternation, overlapping, and synchrony of call units. Even more remarkable is the paucity of studies investigating the role of chorusing in male mating success.

During chorusing of *A. parvipennis*, call phrases of adjacent males frequently overlap, and when phrases overlap, phrase subunits (phonatomes) are synchronized (Fig. 1) (Greenfield and Shaw, 1983; Shaw *et al.*, 1990). During paired interactions, males vary in the frequency with which they "lead" the acoustic interaction, i.e., initiate phrases free of overlap by phrase endings of the other male (Fig. 1). As is characteristic of other phaneropterines, *A. parvipennis* females produce short, soft sounds (ticks) in response to male calls.

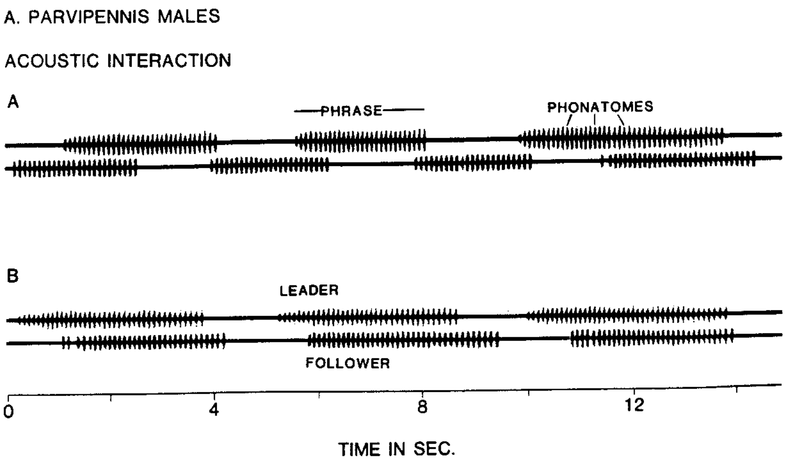

Fig. 1. Chorusing of two *A. parvipennis* males placed 3.34 m apart in an acoustic chamber at 24–25°C. (A) Beginning and end of each male's phrases overlapped by phrases of other male. (B) Only beginning or end of a male's phrase overlapped by phrases of other male; male with beginning of phrase unlapped is "leader," while other male is "follower."

These females produce varying number of ticks during male phrases and ticks fall between (alternate with) male phonatomes (Shaw *et al.* 1990).

As in other phaneropterines, male–female acoustic interactions serve to bring the sexes together (Spooner, 1968, 1995; Heller and van Helverson, 1986). In the laboratory sound-producing males move toward "ticking" females, and females move toward calling males if the males do not arrive at the female within a few minutes. *A. parvipennis* belongs to a category of North American phaneropterines in which males produce a single call which serves to elicit both female phonotaxis and phonoresponse (Spooner, 1995).

In order to determine what differences in call parameters might account for variation in male mating success of *A. parvipennis*, we performed a series of discrimination tests in which females were given a choice of two (caged) calling males (Galliart and Shaw, 1991). The results of these trials indicated that females mated with males that were heavier, louder and led acoustic interactions more frequently. We suggested that phrase beginnings may be more attractive to females or the tendency to lead during the acoustic interaction may signal male dominance (Greenfield and Shaw, 1983).

Phrase length may also be involved in determining *A. parvipennis* mating success. Our mating success studies (Galliart and Shaw, 1991) indicated that males that eventually mated produced longer phrases, but only during paired acoustic interactions in the absence of a ticking female.

Since the sound parameters implicated in mating success could be involved in either male competition or female choice, we performed another two-choice discrimination experiment in which females were forced to move to caged singing males (Galliart and Shaw, 1992). The results of this experiment indicated that females move to louder males, males with longer phrases, and males whose phrase beginnings were overlapped less by the phrase endings of the other male (Fig. 1). In this same experiment, we recorded the number of ticks produced by 12 of the females and discovered that 11 of the 12 females ticked more frequently during the call of the male to which they eventually moved.

Because of variation in call parameters implicated in our studies of mating success and phonotaxis, and in the nature and degree of correlation between these parameters, we decided to present females with computer-generated signals that could be systematically controlled. The experiments were designed to answer the following questions: (1) When females are presented with two sounds in which only one of the acoustic parameters implicated in mating success and/or female phonotaxis is varied, do they respond as they did in our previous mating success or phonotaxis studies? (2) If females preferentially respond to changes in more than one signal parameter, are the effects of the signal alterations additive? (3) Are variations in some signal parameters more effective than others in attracting females? (4) Are phrase beginnings more effective than phrase endings in attracting females, and if so, is the effectiveness related to natural differences in phonotome rate between the two parts of the phrase? and (5) Do females tick more in response to phontactically preferred signals?

MATERIALS AND METHODS

Subjects and Housing

A. parvipennis females are difficult to collect. They are more readily collected, as last-instar nymphs and presumedly virgin adults (females tick in response to playbacks of male calls), by searching the tops of food plants with flashlights at night during the first week after the first male is heard singing. For this experiment, females were collected from prairie areas north and west of Ames High School, Ames, Iowa, from 29 June to 7 July 1992. Females were housed separately in coded 16 cm (h) × 13 cm (d) cylindrical cardboard and mesh cages which were kept in Percival environmental chambers under 14L:10D and at 24–25°C. The insects were fed leaves of horsemint (*Mentha longifolia*) and wild grape (*Vitus* sp.) daily and provided with water in cotton-capped vials.

Construction of Computer-Generated Calls and Experimental Design

Acoustic signals were generated with an Apex 80386SX/25 computer and sound editing hardware and software (Sound FX-Pro, Silicon Shack, Ltd.). The sound editing package allowed us to construct different signals, on two different channels, that could be repeated by any number of times. We created all the calls used in the tests with a single 4-s call phrase [mean call phrase length of the population, 3.861 ± 0.436 s; 24–25°C (Shaw *et al.* 1990)] selected from the call of a male recorded in an acoustic isolation chamber (4.6 × 5.3 × 2.4 m; Industrial Acoustics Co., Inc.) (Table I).

Short phrases (2 s) were constructed by removing every other phonatome (Fig. 1) from the original 4-s phrase. This retained the characteristic increase and then decrease in phonatome rate while producing phrase lengths representing the shortest phrases produced by males (Shaw *et al.* 1990).

All calls were played at a sound pressure level (SPL) of either 70 or 75 dB [0 dB re 20 μPa; Brüel and Kjaer (B&K) Type 2203 sound level meter; B&K Type 1613 octave filter set; frequency weighting, 8 kHz] recorded at the site of female release, 1.7 m from each speaker. These values were similar to the mean decibel levels reported for males that were unsuccessful and successful respectively in attracting females in our previous phonotaxis study (successful males, X = 73.4 dB; unsuccessful males, X = 69.9 dB) (Galliart and Shaw, 1992).

Phrase interval and extent of phrase overlap varied among the tests. This was necessary in order to produce the necessary differences between signals in the parameters being tested (Figs. 2–4). These parameters are quite variable in

Table I. Two-Choice Discrimination Tests Involving Female Phonotaxis in Response to Computer-Generated Simulations of Male Cells Varying in One or Two Parameters

Test	dB	Phrase length (s)	Phrase interval (s)	Phrase overlap (s)[a]	Response[b]	P[c]
1. Loud	75	4.0	2.2	0.9	15	0.02
Soft	70	4.0	2.2	0.9	4	
2. Long phrase	75	4.0	1.0	0.5	15	0.05
Short phrase	75	2.0	3.0	0.5	5	
3. Leader	75	4.0	3.3	0	16	0.01
Follower	75	4.0	3.3	1.8	4	
4. Short overlap	75	4.0	1.6	0.5	12	ns
Long overlap	75	4.0	1.6	2.0	8	
5. Loud/long	75	4.0	1.0	0.5	19	0.001
Soft/short	70	2.0	3.0	0.5	1	
6. Loud/leader	75	4.0	3.3	0	17	0.01
Soft/follower	70	4.0	3.3	1.8	3	
7. Long/leader	75	4.0	2.1	0	19	0.001
Short/follower	75	2.0	4.1	0.9	1	
8. Loud/short	75	2.0	3.0	0.5	10	0.10
Soft/long	70	4.0	1.0	0.5	10	
9. Loud/follower	75	4.0	3.3	1.8	13	ns
Soft/leader	70	4.0	3.3	0	7	
10. Long/follower	75	4.0	2.1	0.9	20	0.001
Short/leader	75	2.0	4.1	0	0	
11. Phrase beginning	75	2.9	5.2	0	14	0.05
Phrase ending	75	2.9	5.3	0	5	
12. Fast phonatome rate	75	3.1	5.4	0	14	0.001
Slow phonatome rate	75	3.3	5.2	0	0	
13. Phonatome rate constant	75	4.1	5.9	0	9	ns
Phonatome rate normal	75	4.0	6.0	0	6	

[a]Each value refers to time of overlap of beginning of designated phrase. Value for other phrase represents time of overlap of end of designated phrase.
[b]Numbers of females moving toward each call.
[c]Chi-square tests.

male chorusing and all values used fall within the normal range of variation during chorusing (Shaw *et al.*, 1990).

Tests 1–4 (Table I, Fig. 2) compared the ability of pairs of computer-generated calls, differing in sound level, phrase length, leading versus following, or degree of overlap of phrase belongings, to elicit female phonotaxis. These are the male call parameters implicated in previous studies as important in male mating success (Galliart and Shaw, 1991) or in eliciting female phonotaxis (Galliart and Shaw, 1992). Tests 5–7 tested whether paired combinations of signal parameter variations preferred in Tests 1–4 were more effective than variations of single parameters (Table I, Fig. 3). Tests 8–10 were designed to

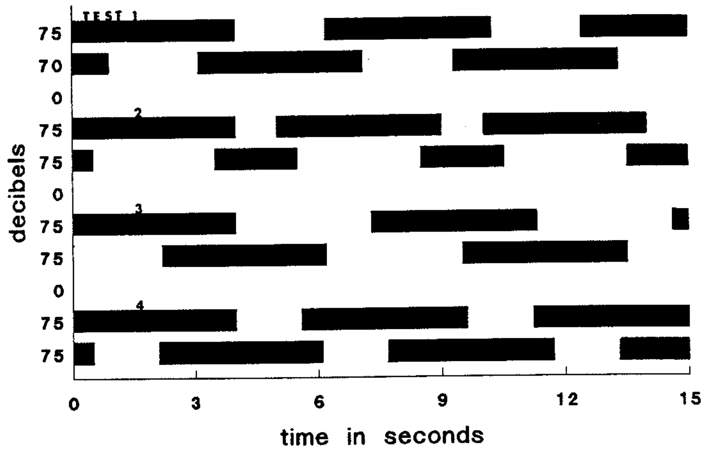

Fig. 2. Diagrams of computer-generated signals used in two-choice discrimination tests: variation in a single call parameter. Test 1, variation in sound level; test 2, variation in phrase length; test 3, leader vs follower; test 4, variation in extent of phrase overlap.

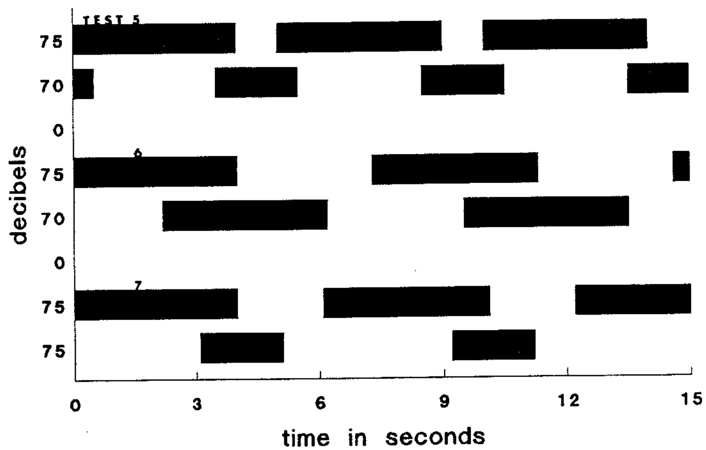

Fig. 3. Diagrams of computer-generated signals used in two-choice discrimination tests: effect of pairing two more preferred and two less preferred variations in call parameters. Test 5, loud/long phrase vs. short/soft phrase; test 6, loud/leading phrase vs. soft/following phrase; test 7, long/leading vs. short/following phrase.

determine if some signals were more effective than others in eliciting female phonotaxis. In each of these two-choice discrimination tests, each of the two calls possessed one preferred and one nonpreferred expression of the two parameters being compared (Table I, Fig. 4).

If, as predicted, females prefer calls with leading phrases, test 11 was designed to determine if females preferentially responded to the beginnings or ends of phrases. The calls used in this test were constructed by retaining only the first 2.9 s of the original phrase for one call and the last 2.9 s of the original phrase for the other call (Table I).

During the phrases of *A. parvipennis* males, phonatome rate increases and reaches its maximum during the first half of the phrase while decreasing during the second half of the phrase (Shaw *et al.*, 1990). Tests 12 and 13 tested whether females were responding to phonatome rate or changes in phonatome rate. Test 12 paired calls with faster and slower phonatome rates (Table I). The calls were constructed from a single phonatome period (0.23 s) from the original phrase. The call with the slower phonatome rate was constructed by repeating the single phonatome period 15 times. The phonatome interval was then shortened slightly, and this shorter phonatome period (0.21 s) was repeated 16 times to serve as the call containing phrase with the faster phonatome rate.

In test 13, a call with a natural change in phonatome rate was paired with

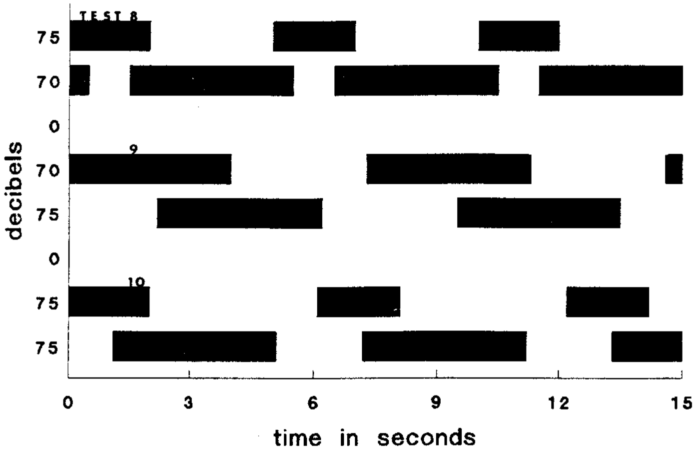

Fig. 4. Diagrams of computer-generated signals used in two-choice discrimination tests: effect of pairing one more preferred and one less preferred variation in call parameters. Test 8, short/loud phrase vs. long/soft phrase; test 9, soft/leading vs loud/following phrase; test 10, short/leading vs long/followed phrase.

Table II. Mean Time Taken for Females to Reach a Speaker in Two-Choice Discrimination Tests (See Table I)

Experiment	Trial No.	Time (s)*
Leader vs follower	3	11.25 A
Loud/leader vs soft/follower	6	9.57 AB
Loud/follower vs soft/leader	9	8.12 AB
Long phrase vs short phrase	2	8.10 AB
Loud/short vs soft/long	8	5.18 B
Loud vs soft	1	5.10 B
Long/follower vs short/leader	10	4.88 B
Loud/long vs soft/short	5	4.80 B
Long/leader vs short/follower	7	4.41 B

*Times followed by different letters are significantly different (Duncan's multiple-range test, $P \leq 0.05$).

a call with a constant phonatome rate. The call with the constant phonatome rate was constructed by removing the shortest phonatome period (0.19 s), which occurs during the first half of the phrase (Smith, 1986; Shaw *et al.* 1990), from the original phrase and repeating that phonatome period 21 times. Therefore, the phonatome rate of the constructed call was the peak phonatome rate of the other call, the normal katydid phrase.

In addition to preferentially moving toward signals, females could express attractiveness of a signal by the rate at which they moved toward the signal and the frequency at which they acoustically responded to it. Therefore, we also determined the average time for females to move toward various signal types (Table II) and the ticks/phrase second (t/ps) during a 3-min recording [number of ticks/(mean phrase length × number of phrases)] prior to moving toward a speaker. The parameter t/ps identifies changes in number of ticks per unit of phrase length, i.e., changes that are not merely a result of a proportional change in phrase length.

Female Phonotaxis Tests

The trials were performed within the acoustic isolation chamber at the same temperature as the environmental chamber. Each female was placed midway between a pair of Realistic, high-frequency (Super Tweeter) speakers placed 3.4 m apart at the ends of three laboratory tables placed end to end. The female was entrapped under a screen cover, 10 cm in diameter and 3 cm high. The SPL of each call was measured 10 cm in front of each speaker at a frequency band centered at 16 kHz using the B&K sound level meter and octave filter set. The SPL was then set at each speaker by adjusting the volume of two Realistic Model MPA-45 PA amplifiers, each of which controlled a single speaker. The highest frequency produced by the sound editing package was 22 kHz, and the frequency range of the PA amplifiers was 67–20,000 Hz ± 3 dB. The calls presented to the females contained a dominant frequency of 10,585 Hz, the mean frequency for male calls recorded by Shaw *et al.* (1990).

Each female was exposed to the calls for 5 min prior to being released. During that period, a 3-min recording was made of the female's acoustic response to the calls. A unidirectional dynamic microphone (GC electronics No. 30-2374) was placed in front of each speaker while female ticks were recorded with a B&K Type 4133 microphone (in conjunction with a B&K Type 2615 microphone preamplifier, B&K Type 2801 power supply, Tektronix Type 122 preamplifier, and Tektronix Type 160A power supply). Each trial was terminated when the female touched one of the speakers. The time it took the female to move to a speaker (interval between initiation of female movement and touching of a speaker) was recorded for each trial.

Twenty females were used in these tests. Each female was to be used once in each test, however, some females died before they were used in all of the tests. The order in which experimental tests were performed on each insect was randomized, and females were not used in more than one trial on a given day.

Data Analysis

Female phonotactic discrimination was examined using chi-square tests. ANOVA was used to determine if the time taken by females to reach a speaker varied between tests involving various levels of sound intensity, phrase length, and leader–follower interaction (tests 1–9). Duncan's multiple-range test was used to compare pairs of tests.

To determine the numbers of female ticks produced during the generated calls, oscillograms (from a Grass Model C4-12 kymograph camera and a Tektronix Model 5110 oscilloscope) were made of the 3-min recordings of the female's responses to the generated calls. The differences in t/ps for each of the pairs of calls were examined using binomial tests. In all tests in which the calls overlapped, female ticks produced during the overlap period were assigned to both calls.

RESULTS

Effect of Variation in Selected Parameters of Simulated Male Calls on Female Phonotaxis

Tests 1–4: Effect of Variation in Single Call Parameters (Table I, Fig. 2). Females moved significantly more often to louder calls, calls with longer phrases, and calls with leading phrases. Change in the length of phrase overlap at phrase initiation had no significant effect on female phonotaxis.

Tests 5–7: Effect of Pairing Preferred Values of Two Call Parameters (Table I, Fig. 3). Calls in which two parameters have preferred values (tests 5–7) are more attractive to females (55/60 females) than calls in which only one parameter has a preferred value (tests 1–3: 46/59 females).

Tests 8–10: Effect of Pairing More Preferred and Less Preferred Values of Two Call Parameters (Table I, Fig. 4). If the three parameters implicated in attracting females were equally effective, one would predict that pairing more and less preferred values would result in signals that were equally effective in attracting females. Females did not show a significant preference for loud/short over soft/long calls or loud/follower over soft/leader calls. However, all 20 females chose long/follower over short/leader calls.

Tests 11–13: Effect of Phrase Part and Phonatome Rate (Table I). Females preferred phrase beginnings to phrase endings. In response to the calls with constant but differing phonatome rates, females preferentially moved to the call with a faster phonatome rate. However, given a choice between phrases consisting of constant, very fast phonatome rate and those showing typical changes in phonatome rate, females showed no preference.

Effect of Parameter Variations on Speed of Female Phonotaxis (Table II). There was significant variation between females in the amount of time it took to reach a speaker ($F = 10.35$, $P < 0.0001$) and between tests ($F = 3.25$, $P < 0.0019$). However, Duncan's multiple-range test indicates significant differences only between the experiment with the slowest mean phonotaxis time, leader versus follower, and the five tests with the shortest times. Although they were not significantly different, the two shortest phonotaxis times occurred in response to calls made up of two preferred parameter values, whereas the second and third longest times occurred in response to calls involving combinations of more and less preferred parameter values.

Effect of Parameter Variations on Female's Acoustic Response (Table III). The results of this analysis suggest that only changes in phrase length and phonatome rate of male calls elicit changes in female t/ps. In all four tests (2, 5, 7, 10) involving differences in phrase length, females' t/ps were higher in response to longer phrases; however, differences were significantly different in only three tests.

Females' t/ps also were higher in response to phrases with faster phonatome rates (test 12) and to the increasing phonatome rate of the first half of male phrases (test 11). The latter was only close to significance ($P = 0.08$).

DISCUSSION

The results of this study indicate that male mating success in *A. parvipennis* is, at least in part, a result of female choice. Our 1991 studies (Galliart and

Table III. Numbers of Females Acoustically Responding More Frequently During Phrases (t/ps; See Text) of the More Attractive and Less Attractive Calls During Experiments in Which Females Demonstrated Significant Phonotactic Discrimination (Binomial Tests; See Table I)

Experiment	More attractive	Less attractive	*P*
1. Loud vs soft	8	8	ns
2. Long phrase vs short phrase	14	4	0.05
3. Leader vs follower	11	7	ns
5. Loud/long vs soft/short	12	6	ns
6. Loud/leader vs soft/follower	5	11	ns
7. Long/leader vs short/follower	16	1	0.01
10. Short/leader vs long/follower	18	0	0.01
11. Phrase beginning vs phrase end	12	5	0.08
12. Fast phonatome rate vs slow phonatome rate	10	2	0.05

Shaw, 1991) indicated that successfully mating males produced louder calls and longer call phrases and/or were leaders more frequently than followers (Fig. 1B). The results of this study indicate that females preferentially moved to computer-generated calls with these same characteristics. Our 1992 phonotaxis studies (Galliart and Shaw, 1992) supported female preference for louder calls and longer phrases of caged males but did not support a female preference for call leaders. Instead the results suggested that females preferentially moved toward males whose phrase beginnings were overlapped less by the phrase endings of the other male; these results were not confirmed in this study. This is not surprising; we previously suggested that the statistical significance of the trait was probably a type II statistical error (Galliart and Shaw, 1992).

One would expect that females would preferentially move toward pairs of preferred parameters, and assuming equal attractiveness, pairing of more preferred and less preferred parameters should result in no phonotactic preference. These predictions were supported for every pairing except calls involving short leading versus long following phrases (Table I). The overwhelming preference for long following phrases may have been the result of using an exceptionally short phrase.

The Role of Sound Level

In *A. parvipennis*, the primary function of responding to male call sound level may be to bring females within ticking distance of more than one male. Since adjacent *A. parvipennis* males synchronize phonatomes where phrases overlap, females should generally perceive larger groups of males as louder. Because ticking females may attract numerous males from which they apparently choose a mate (Shaw *et al.* 1990), it would seem important that they move toward groups of males rather than single individuals.

Once females move within a male aggregation and begin to tick, they could use sound level in eventually choosing a mate. More than one male may move to the ticking female and males continue to sing until the female mounts them. In our mating success studies (Galliart and Shaw, 1991), sound level was positively correlated with male weight and number of times that a female mounted a male. This suggested that females could be actively choosing heavier males. When two males approached a ticking female, she multiply mounted both males and spent long periods of time on the backs of the males continually pulling her abdomen away whenever the males attempted to engage genitalia. Such a process took up to 4 h (the maximum length of the trials), and in addition to choosing heavier males, females eventually mated with males they had mounted more frequently (Galliart and Shaw, 1991).

Male weight may be an important factor for females to assess because it is correlated with weight of spermatophores (Galliart and Shaw, 1991) upon which females feed following copulation (Shaw *et al.* 1990). Proteins in spermatophores are known to enhance fitness of female Orthoptera (Gwynne, 1988). Heavier males not only tend to sing louder, but also sing a greater proportion of the time (Galliart and Shaw, 1994). Females are therefore more likely to hear them and to encounter them.

The Role of Phrase Phase Relationships

Phrase phase relationships of leaders and followers could be used by females to differentiate between pairs of males within aggregations but not between larger and smaller groups of males. A number of factors could explain why song phrase initiations free of overlap are important in passive attraction of females. Early work on the grasshopper *Chorthippus brunneus* showed that male phonoresponse and female phonotaxis were elicited by sound transients, i.e., rapid rate of increase in song amplitude at the initiation of each sound (Busnel and Loher, 1961). Response to transients may be a component of the ''precedence effect'' (Wyttenbach and Hoy 1993), namely, that female phonotaxis is directed toward the first of two sounds initiated as close as 13 ms apart (Greenfield, 1994a,b). Although chorusing *A. parvipennis* seldom initiate songs within such a short time interval (Shaw *et al.*, 1990), song initiation may be important in focusing female attention on the source of the signal and in eliciting movement toward the leading male.

Greenfield (1990, 1994a,b) also suggests that chorusing involving alternation of phrases may evolve when the initial portion of the male's phrase carries the most important information in male–male and/or male–female communication. Greenfield's hypothesis is supported by evidence from this study which indicates that females are focusing on the initial portion (half) of the phrase, i.e., they preferentially moved toward beginnings rather than endings of male phrases (Table I). The initial sections of male *A. parvipennis'* phrases are characterized by increasing amplitude and phonatome rate (Shaw *et al.*, 1990). Hearing the initial portion of a male's phrase free from jamming by the end of another male's phrase may be important in determining which male is louder.

Other trials suggested that females are also preferentially responding to the more rapid phonatome rate. If so, one would expect that males might compete for females by attempting to produce more rapid phonatome rates. However, our previous two-choice discrimination experiments using living males did not implicate phonatome rate as a significant character in either mating success or phonotaxis. We speculated that phonatome rate was a species-identifying character (i.e., exhibiting static properties) and possibly subject to stabilizing selection. However, females preferentially responded to a constant phonatome rate equivalent to the fastest rate achieved by a male when paired with a typical male song.

Whatever the basis for female preferential response to the initial portion of a male's phrase, it appears that males actively compete to free the initial portion of their phrase from overlap by a competitor's phrase while overlapping or jamming the significant portion of the competitor's phrases. In our mating success experiments (Galliart and Shaw, 1991), males successful in mating led fewer times than their chorusing partners in the absence of a ticking female but were leaders more frequently in the presence of a ticking female. Thus males can change their phrase phase relationships and the ability to do so appears to be important in attracting females and eventually in mating success.

Competition for initiation of phrases free of overlap may make it difficult for females to utilize this parameter in female choice. Pairs of males may produce long series of phrase interactions in which neither male leads (Fig. 1A), and both males may lead at different times. The difficulty females may have in using this parameter in phonotaxis and possibly mate choice may be reflected in our data on the time it took females to reach a speaker after beginning to move. The three longest female response times and the only response time significantly longer than the five shortest times involved leading and following phrases (Table III). In this experiment, longer response times were associated with phrase phase relationships that did not change; when pairs of competing males are involved, females may have to discern phrase phase relationships that are continually changing.

The Role of Phrase Length

If female preference occurred in the population of females used in 1991, too little between-male variance (Wagner *et al.* 1995) or too much within-male variance (Wagner and Sullivan, 1995) in call phrase length could make female preference difficult to demonstrate. In our 1991 mating success studies, phrase length differences averaged 0.86 ± 0.74 s (range: 0.07–3.11 s), which would appear to be sufficient for differentiation. However, individual phrase length is quite variable, and a female's ability to average phrase lengths of two males over time is probably a difficult task.

It also is possible that females prefer different male call characteristics under different environmental conditions. Male weight, sound level of male calls, and ability to lead during paired chorusing were all positively correlated (although the correlation between male weight and frequency of leading was not statistically significant) in our mating success studies (Galliart and Shaw, 1991).[3] In contrast, phrase length was not correlated with sound level in our 1992 phonotaxis study and analysis of our 1991 data indicated that phrase length was not correlated or significantly negatively correlated with male weight, call sound level, and a male's ability to lead. Therefore, it is possible that females prefer louder and leading males under certain environmental conditions and longer phrases at other times. For example, females may be more responsive to song parameters correlated with male weight when spermatophores may contain nutrients missing in female's diet (as may occur under laboratory conditions).

Females also produced higher t/ps in response to longer phrases; there was no such significant relationship between t/ps and call sound level or a male's ability to lead. Tuckerman (1992) found that females of the congeneric katydid *Scudderia curvicauda* responded to more phrases with more ticks when phrase of male calls were lengthened. Does this announce female mate preference or is this simply a characteristic of the stimulus–response system designed to attract males?

In conclusion, the mating system of *A. parvipennis* is complex and apparently involves female choice. It is also possible that one or more of these call parameters could be involved in male competition. In 10 of 24 trials in our mating success studies (Galliart and Shaw, 1991), unsuccessful males failed to physically encounter the female because they either did not leave their opened cage or they left the vicinity of the female after hearing the other male and/or actually encountering him. Like many other studies, the results of this study make it difficult to pinpoint which selective factors are involved in mating success and, as may be true in many other cases, suggest that more than one selective factor may be operating.

[3] In the 1991 study we categorized leading as a reduction in "overlap number," i.e., the number of times that the phrase endings of one male overlapped the phrase beginnings of another (Fig. 1). This is the antithesis of leading, so that a negative correlation of overlap number and another call parameter is equivalent to a positive correlation with leading.

REFERENCES

Busnel, R. G., and Loher, W. (1961). Déclenchement de phonoréponses chez *Chorthippus brunneus* Thunb. (Acridinae). *Acoustica* **11:** 65–70.

Galliart, P. L., and Shaw, K. C. (1991). Role of weight and acoustic parameters, including nature of chorusing, in the mating success of males of the katydid, *Amblycorypha parvipennis* (Orthoptera: Tettigoniidae). *Fla. Entomol.* **74:** 453–464.

Galliart, P. L., and Shaw, K. C. (1992). The relation of male and female acoustic parameters to female phonotaxis in the katydid, *Amblycorypha parvipennis. J. Orthopt. Res.* **1:** 110–115.

Galliart, P. L., and Shaw, K. C. (1994). The relationship of weight and sound level to continuity of male calling in the katydid, *Amblycorypha parvipennis. J. Orthopt. Res.* **2:** 43–45.

Gerhardt, H. C. (1991). Female mate choice in treefrogs: Static and dynamic acoustic criteria. *Anim. Behav.* **42:** 615–635.

Greenfield, M. D. (1990). Evolution of acoustic communication in the genus *Neoconocephalus*; Discontinuous songs, synchrony and interspecific interactions. In Bailey, W. J., and Rentz, D. C. F. (eds.), *The Tettigoniidae: Biology, Systematics and Evolution*, Springer-Verlag, Berlin, pp. 71–97.

Greenfield, M. D. (1994a). Cooperation and conflict in the evolution of signal interactions. *Annu. Rev. Ecol. Syst.* **25:** 97–126.

Greenfield, M. D. (1994b). Synchronous and alternating choruses in insects and anurans: Common mechanisms and diverse functions. *Am. Zool.* **34:** 605–615.

Greenfield, M. D., and Shaw, K. C. (1983). Adaptive significance of chorusing with special reference to the Orthoptera. In Gwynne, D. T., and Morris, G. K. (eds), *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*, Westview, Boulder, CO, pp. 1–27.

Gwynne, D. T. (1988). Courtship feeding and the fitness of female katydids (Orthoptera:Tettigoniidae). *Evolution* **42:** 545—555.

Heller, K. G., and von Helversen, D. (1986). Acoustic communication in phaneropterid bushcrickets; Species-specific delay of female stridulatory response and matching male sensory time window. *Behav. Ecol. Sociobiol.* **18:** 189–198.

Shaw, K. C., Galliart, P. L., and Smith, B. (1990). The acoustic behavior of *Amblycorypha parvipennis* (Orthoptera: Tettigoniidae). *Ann. Entomol. Soc. Am.* **83:** 617–625.

Smith, B. (1986). *Acoustic Behavior of Amblycorypha parvipennis in Response to Natural and Artificial Sounds* M.S. thesis, Iowa State University, Ames.

Spooner, J. D. (1968). Pair-forming acoustic systems of phaneropterine katydids (Orthoptera: Tettigoniidae). *Anim. Behav.* **16:** 197–212.

Spooner, J. D. (1995). Pair-forming phonotaxic strategies of phaneropterine katydids (Tettigoniidae, Phaneropterinae). In *Proceedings of the 6th International Meeting of the Orthopterists Society* pp. 127–129.

Tuckerman, J. F., Gwynne, J. T., and Morris, G. K. (1992). Reliable acoustic cues for female mate preference in a katydid (*Scudderia curvicauda*, Orthoptera, Tettigoniidae). *Behav. Ecol.* **4:** 106–113.

Wagner, W. E., Jr., and Sullivan, B. K. (1995). Sexual selection in the Gulf Coast toad, *Bufo valliceps*: Female choice based on variable characters. *Anim. Behav.* **49:** 305–319.

Wagner, W. E., Jr., Murray, A., and Cade, W. H. (1995). Phenotypic variation in the mating preference of female field crickets, *Gryllus integer. Anim. Behav.* **49:** 1269–1281.

West-Eberhard, M. J. (1984). Sexual selection, competitive communication and species-specific signals in insects. In Lewis, T. (ed.), *Insect Communication*, Academic Press, London, pp. 283–284.

Wyttenback, R. A., and Hoy, R. R. (1993). Demonstration of the precedence effect in an insect. *J. Acoust. Soc. Am.* **94:** 777–784.