

The Relation of Male and Female Acoustic Parameters to Female Phonotaxis in the Katydid, *Amblycorypha parvipennis*

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Adjacent males of *Amblycorypha parvipennis* Stal alternate 4-5 s phrases. Phrases of different males overlap frequently and, where overlap occurs, phrase subunits are synchronized. Females "tick" in response to male phrases and males move to ticking females. In previous two-choice discrimination tests, in which males were free to move to ticking females, females preferentially mated with louder and heavier males and males that were more successful in initiating phrases without overlap. The current study involved two-choice discrimination tests in which females moved to sound-producing, caged males. We suggested that if females use the same parameters in determining phonotaxis, these parameters would be implicated in female mate choice. The results were that females moved to louder males, males that produced longer phrases, and males that overlapped their competitors' phrases for a shorter period of time than vice-versa. Since movement to louder males may indicate a mechanism by which females move toward larger (= louder) groups of males, we have provided no convincing evidence for female mate choice. The finding that females tick more in response to the male they eventually move toward uncovers another potential signal for the mating game. [Key Words: *Amblycorypha parvipennis*, phonotaxis, chorusing, mate choice]

Although the males of a number of species of singing Orthoptera chorus (i.e., song components of adjacent individuals show temporal interaction such as alternation, synchrony, etc.; Greenfield and Shaw 1983), males of *Amblycorypha parvipennis* Stal are unique chorusers. Neighboring males alternate 4-5 s phrases and most phrases are overlapped; where phrases overlap, phrase subunits (phonatomes) are synchronized (Greenfield and Shaw, 1983, Shaw et al. 1990).

Male-female acoustic interaction also is unique. Phaneropterine females typically produce soft "ticks" at species-specific intervals following the ends of males' song phrases (Spooner 1968, Heller and von Helversen 1986). However, *A. parvipennis* females alternate varying numbers of ticks (mean = 3.2 ± 2.92 ; range 1-17 with the last tick typically occurring just before or after the last phonatome) with male phonatomes (Shaw et al. 1990).

Differences in males' ability to chorus have been implicated as important in sexual selection (Alexander 1975, Otte 1977, Greenfield and Shaw 1983). However, only Busnel (1967) and Galliart and Shaw (1991a) have published experimental results which support this hypothesis. Busnel studied *Ephippiger provincialis*, a species in which adjacent males alternate chirps (Busnel et al. 1956). The results of her two-choice discrimination phonotaxis experiments indicated that approximately 65% of females were attracted to males that initiated more (65%) acoustic bouts than their competitor (Busnel 1967). Busnel also implied that the successful (termed dominant) males also

produced more phrases during alternating bouts. In *E. provincialis*, the male that initiates calling bouts more frequently also intermittently sings two or more chirps before the alternating partner responds (Busnel et al. 1956).

In our study (Galliart & Shaw 1991a), the experimental endpoint was not termination of female phonotaxis, but the initiation of copulation. Our experimental design was similar except that the two caged males and a centrally located caged female were released at the same time and the males moved toward the ticking female. The results of this study indicated that females preferentially initiated copulation with heavier and louder males and with males they had mounted more frequently (females typically mounted each male one or more times prior to accepting a male in copulation). Our 1991 results also suggested that females chose males that initiated more phrases that did not overlap the ends of their rival's phrases than vice-versa (Fig. 1). A repeated-measures ANOVA indicated a significant interaction between male mating success and female presence (male acoustic interaction was recorded with and without a ticking female present) for the number of times that the males overlapped one another's phrases. Eventual successfully mating males overlapped unsuccessful males more when the female was absent, but the situation was reversed when a ticking female was present, i.e., the successful males initiated more phrases free of overlap than the unsuccessful males (Fig. 2). Student t-tests indicated that these differences were close to statistical significance in the absence ($p = 0.070$)

and presence ($p = 0.55$) of the female.

If, like most singing Orthoptera, silent females moved to and copulated with, stationary, singing males, this would be evidence that *A. parvipennis* females are utilizing sound level and overlap number differences in male songs to choose mates. However, like many other Phaneropterinae (Grove, 1959, Spooner, 1968), *A. parvipennis* males move to sound-producing (ticking) females. In the proximity of a ticking female, males interact physically and continue to interact acoustically, while trying to mate with the female (Shaw et al. 1990). In this type of mating system, it is difficult to determine whether the male parameters implicated in mating success are involved in male competition, female choice, or both.

During our mating success trials, we noted that some females would begin moving to one of the singing males if at least one of the males had not reached her within a given time period. We reasoned that, if we could show that females use all or some of the same parameters in determining which male to move toward, we would have evidence that females could use these parameters in mate choice. This paper reports the results of two-choice discrimination experiments, similar to those of Busnel (1967), in which the response measured was the cage to which the female moved and contacted.

We also suspected that females may be communicating their choice of males. During our earlier two-choice discrimination tests, it appeared that females were ticking more in response to the phrases of one male than the other. Therefore, we measured the number of ticks that were associated with each male's phrases.

Materials and Methods

Subjects and Housing

Specimens of *A. parvipennis* were collected from prairie areas north and west of Ames High School, Ames, IA. Individuals were collected at night from 21 June to 23 July in 1990 and from 20 June to 14 July in 1991. Females were located with difficulty by searching the tops of food plants with a flashlight. Some of the females and males were captured as nymphs and reared in the laboratory in Percival environmental chambers under a light regime of 14L: 10D and a temperature of 24-25°C. Adult females were captured within 10 days of the onset of male singing and were determined receptive (ticked in response to singing males) the day after capture. More males were captured as singing adults by moving toward their sounds and eventually spotting them with a flashlight.

Males were individually marked using colored nail polish, housed separately in 10

$\times 10 \times 17$ cm. wire screen cages and placed around the laboratory which was maintained at the same light-dark and temperature regimes as the environmental chambers. Adult females were housed separately in coded 16 cm. (h) \times 13 cm. (d) cylindrical cardboard and mesh cages in the environmental chamber. This setup served to isolate the sexes from the sounds of the opposite sex until they were used in a female phonotaxis trial. All insects were fed leaves of horsemint or wild grape daily and provided with water in cotton-capped vials.

Female Phonotaxis Experiments

Females were allowed to listen to and acoustically interact with a pair of chorusing males, and then to choose between the males by moving to one of them. A pair of males was chosen for each trial by selecting two males singing in the laboratory and moving them into an acoustic isolation chamber (4.6 \times 5.3 \times 2.4 m; Industrial Acoustics Co. Inc.). A receptive female was then chosen by placing a tray holding the individual female cages in the laboratory of singing males and selecting a ticking female. We ran 25 trials (12 in 1990 and 13 in 1991) using a different female and a different pair of males in each trial. Due to the difficulty in collecting females, we reused females to run 34 additional trials (26 in 1990 and eight in 1991; four females used once, nine females used twice, 11 females used three times, and one female used four times). Because using females more than once violates the statistical criterion of independence required for ANOVA and Student's *t*-tests, the focus of our analysis is on the results of the initial 25 trials. However, in the Discussion, we compare the results from the 59 trials with the results from the initial 25 trials and with the results obtained in our earlier mating success experiments (Galliard and Shaw 1991a). In the reuse trials, females were never exposed to the same male more than once; a different pair of males was used in each of the 59 trials.

All trials were performed in the acoustic isolation chamber at the same temperature (24-25°C) maintained in the environmental chambers. Caged males were placed 3.4 m apart (within the range of the most common nearest neighbor distances recorded in the field [Shaw et al. 1981]) at the ends of three tables placed end to end. After the males began to sing, 10-min recordings were made of the males chorusing, without and then with a sexually receptive (ticking) female (within a cylindrical screen cage 10 cm in diameter) placed midway between and equidistant from the two males. The singing males were recorded using two unidirectional dynamic microphones (GC Electron-

ics, #30-2374) each placed approximately 3 cm from the cage of each male and a Racal (Store 4 DS) 4-channel tape recorder. The ticks of the female during the second 10-min recording were recorded on a third channel of the tape recorder using a Brüel & Kjaer (B&K), type 4133, microphone; B&K, type 2615, microphone preamplifier; B&K, type 2801, power supply; Tektronix, type 122, preamplifier; and Tektronix, type 160A, power supply.

Following the second 10-min recording, a 30-s recording was made of each male's song using the B&K microphone and associated equipment. These recordings were used to determine if the songs of the male differed in frequency spectra. Frequency spectra were determined with a Uniscan II (Multigon Industries, Inc.) spectrum analysis system. Sonographs made with the Uniscan II were used to determine the upper and lower frequencies and the range of frequencies. The upper frequency of the recording equipment was 40 k Hz.

After the 30-s recordings, sound intensity level was measured approximately 5 cm above each male's stridulatory apparatus. Maximum sound intensity levels were measured at frequency bands centered at 8 and 16 kHz using a B&K, type 2203, precision sound level meter in conjunction with a B&K, type 1613, octave filter set. After completing the sound intensity measurements, the female was released from her cage. The trial was terminated when the female touched one of the male's cages. Following the trial all three katydids were weighed.

The temporal parameters of each male's song and the phrase relationships of each pair of acoustically interacting males were determined using a Commodore 128 computer in conjunction with a computer/tape recorder interface and computer software designed for the analysis of *A. parvipennis* songs. Oscillograms were made from the taped female's responses to the chorusing males using a Grass Instruments Co., model C4-12 Kymograph camera and a Tectronix, model 5110 oscilloscope.

Data Analysis

Male success in eliciting female phonotaxis was examined in relation to male weight, sound level (8 and 16 kHz), temporal sound parameters, phase relations of the sound phrases of the two chorusing males and the number of female ticks produced during a male's phrase. Noise on the tape prevented us from accurately determining the number of female ticks during the 13 trials performed in 1991. Temporal parameters included number of phrases, mean phrase length, mean phrase interval, mean phrase period (phrase length + phrase inter-

val) and total sound produced (number of phrases x mean phrase length). Phrase phase relationships were determined by recording the number of phrase overlaps (the number of times that the beginnings of a katydid's phrases overlapped the ends of his rival's phrases), the mean phrase overlap time (the mean length of time that the beginnings of each katydid's phrases overlapped the ends of their rival's phrases; this did not include phrases that were not overlapped), total overlap time (phrase overlap number x mean phrase overlap time) and the percent of phrases overlapped (phrase overlap number/number of rival's phrases) (Fig. 1). Temporal sound parameters and phrase phase relationships were examined for two conditions: chorusing without and with a ticking female in the acoustic chamber.

Weight and sound level differences between males that were successful in eliciting female phonotaxis (successful males - Sms) and those that were not (unsuccessful males - Ums) were analyzed by one-tailed, paired-comparison Student's t-tests (based on our 1991 results (Galliard & Shaw 1991a), we formulated an initial hypothesis that females would move to heavier and louder males). The male acoustic parameter data were analyzed by use of the ANOVA shown in Table 1. This method is an extension of that described by Cochran and Cox (1957). This ANOVA allows us to examine male success regardless of the presence of the female (F test on male success), the affect of the females presence on both males (F test on female presence) and any difference between Sms and Ums in their reaction to the presence of a ticking female (F test on male success x female presence). In the event of significant male success x female presence interactions, Sms and Ums were compared in the presence and absence of a female separately using Student's t-tests.

The ANOVA was used to analyze the data for the 25 trials involving first use of each female, the 59 trials involving reuse of females, and the 12 of the 25 initial trials in which sound level differences between Sms and Ums were 3 dB or less for measurements centered at both 8 and 16 kHz. The latter analysis was performed to determine if phrase phase relationships were more important in determining phonotaxis when sound level differences between males were not great.

Differences between Sms and Ums in the number of female ticks produced during their phrases and in frequency parameters were analyzed using a Chi-square test. Pearson's correlation coefficients were calculated for pairs of male song parameters and for male song parameters and number of female ticks.

Table 1. Sample ANOVA Table. Parameters connected by brackets were components of the same F-test.

source	df	Mean Squares	F-TESTS
year	1	0.0206	
trial (year)	23	2.1057	
male success	1	15.3186	
year+male success	1	1.8415	
male success*trial (year)	23	1.6225	
female presence	1	5.4275	
male success*female presence	1	0.5955	
year*female presence	1	0.0005	
year*female presence*male success	1	0.9932	
error	46	0.7169	

Table 2. Comparison of mean differences (Sm - Um) in weight and sound level of *A. parvipennis* males that were successful (Sm) and unsuccessful (Um) in attracting females to their cages in two-choice discrimination tests. N - 25.

parameter	Sm	Um	Sm - Um	N	P > T
weight (g)	0.77	0.78	-0.01	2	NS
S.I.-8 kHz ^a	72.40	69.50	2.90	2	.057
S.I.-16 kHz	73.36	69.86	3.50	2	.038

^aS.I.-8 kHz - sound intensity at 8 kHz filter band; S.I.-16 kHz - sound intensity at 16 kHz filter band

Table 3. Correlation matrix for parameters implicated in determining female phonotaxis. N - 25.

	S.I.-16 kHz	Phrase Length	Phrase Period	Phrase Overlap
S I 8 kHz ^c	0.91 ^a	-0.11	-0.11	-0.29
	0.0001 ^b	0.48	0.46	0.045
S.I.-16 kHz ^c		-0.01	-0.06	-0.30
		0.96	0.68	0.037
Phrase Length			0.62	0.51
			0.0001	0.0002
Phrase Period				0.42
				0.003

^aPearson's correlation coefficients

^bp values

^cSee table 2

Results

Louder, but not heavier, males were more successful in eliciting female phonotaxis (Table 2). The sound level difference between Sms and Ums was significant ($p < 0.05$) for the sound intensity measurement centered at 16 kHz and nearly so for the 8 kHz measurement ($p < 0.06$). Females also preferentially moved to males with longer phrases (Sm - Um = 0.62 s, $F = 5.14$, $df = 1, 99$, $p = 0.033$) and phrase periods (Sm - Um = 0.56 s, $F = 4.43$, $df = 1, 99$, $p = 0.046$). Average phrase overlap was also related to female phonotaxis with Sms being overlapped for a longer time by their rivals' phrases than vice-versa (Sm - Um = -0.34 s, $F = 5.23$, $df = 1, 99$, $p = 0.032$).

The correlation analysis (Table 3) indicated strong correlations between the measures of sound intensity and among phrase length, phrase period and mean phrase

overlap. Sound level and mean phrase overlap are weakly but significantly negatively correlated, while sound level is not correlated with mean phrase length or phrase period. The number of female ticks was not correlated with any of the song parameters implicated in female phonotaxis.

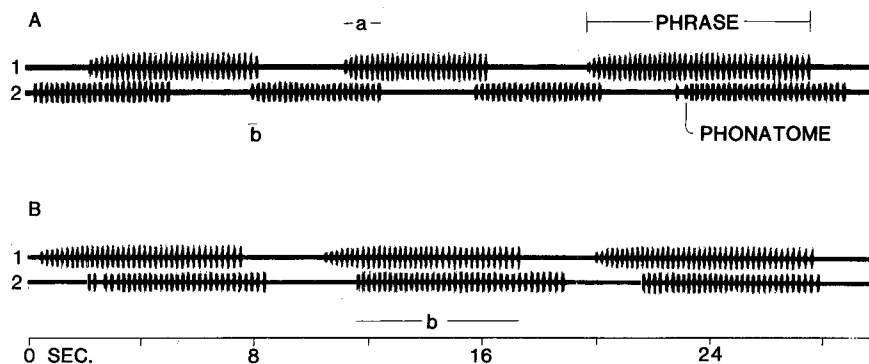
When the 12 trials in which male songs differed by 3 dB or less were analyzed, no song parameters were significantly related to female phonotaxis. However, there were two parameters which showed significant interactions between female presence and mating success. Ums increased both the number of times they overlapped their rivals' phrases ($F = 6.70$, $df = 1, 47$, $p = 0.018$) (Fig. 3a) and the percent of their rivals' phrases that they overlapped ($F = 9.70$, $df = 1, 47$, $p = 0.006$) while both of their parameters remained unchanged for Sms (Fig. 3a). The difference between Sms and Ums is significant for both of these parameters in the ab-

Table 4. Mean female clicks per 10 male phrases for 12 trials in 1990.

trial	clicks during winner's phrase	clicks during loser's phrase	Sm-Um
1	8.6	10.1	
2	18.9	10.0	+
3	3.1	2.0	+
4	34.1	4.9	+
5	11.6	2.6	+
6	7.4	6.0	+
7	13.2	8.6	+
8	15.1	4.6	+
9	16.5	1.7	+
10	21.7	6.6	+
11	6.9	1.6	+
12	32.4	8.6	+

Table 5. Effect of female presence on male song parameters. Mean values are for both males. N = 25, df = 1.

parameter	no female	female	F	P>F
phrase no.	71.16 + 9.38	73.42 + 10.10	3.08	.09
phrase length	4.83 + 1.13	5.30 + 1.23	7.36	.01*
phrase interval	3.84 + 1.01	3.09 + 0.99	31.20	.0001*
phrase period	8.67 + 1.32	8.39 + 1.20	2.06	.16
total sound	338.43 + 53.79	382.25 + 56.60	43.48	.0001*
overlap no.	44.86 + 20.16	51.84 + 14.13	10.33	.002*
phrase overlap	1.50 + 0.69	2.15 + 0.89	53.14	.0001*
total overlap	68.86 + 49.69	110.00 + 51.36	48.66	.0001*
percent overlap	0.64 + 0.27	0.72 + 0.23	7.04	.01*

**Fig. 1.** Oscillographs of chorusing by paired *A. parvipennis*. **A**, the initial part of the phrase of each male overlaps the latter part of the phrase of the other male. **B**, katydid 2 overlaps katydid 1 but 1 does not overlap 2. **a**, indicates the time that the phrase of 1 overlaps the phrase of 2. **b**, indicates the time that the phrase of 2 overlaps the phrase of 1 (from Galliard and Shaw 1991b).

sence of a female (overlap number: $t = 2.69$, $df = 22$, $p < 0.02$; percent overlap: $t = 2.83$, $df = 22$, $p < 0.01$).

In 11 of the 12 trials analyzed, females ticked more often during the phrases of Sms than Ums (Chi-square = 8.33, $p < 0.005$) (Table 4). Sms' and Ums' songs did not differ in minimal, maximal or range of frequencies.

Table 5 affirms our earlier report (Galliard and Shaw 1991b) that the presence of a ticking female has a marked affect on the singing behavior of both caged males. Males produced longer phrases, shorter phrase intervals and more total sound in the pres-

ence of a female. The nature of the acoustic interaction was also affected by the introduction of a female with males increasing the number, mean time of phrase overlaps as well as the total and percent overlap time.

Discussion

Our results indicate that females move toward the male with the louder song, longer song phrases and periods, and the male that overlaps his competitor's phrases for a shorter time than vice-versa. By moving toward louder males and/or males producing longer phrases, a female may be solicit-

ing the more vigorous male, i.e., the male expending the more energy per unit time (Greenfield and Shaw 1983). A number of investigators have shown a positive relationship between male sound intensity and female phonotaxis for singing Orthoptera (Cade 1979, Forrest 1983, Bailey 1985). Hedrick (1986) has shown that *Gryllus integer* females move to the conspecific male producing the longer calling bouts.

Females also initiate copulation with louder males but the ANOVA in our mating success studies (Galliard and Shaw 1991a) did not implicate phrase length. However, when we performed t -tests on the data, Sms produced significantly longer phrases when females were not present (Sm - Um = 0.33 s, $df = 23$, $t = 2.55$, $p = 0.009$). Although mean phrase lengths of Sms were longer in the presence of a female, the differences were not significantly different. The failure of phrase length to be significant in male mating success may be a result of the confounding effect of male weight. Although females initiated copulation with heavier males (Galliard and Shaw 1991a), our phonotaxis experiments failed to implicate male weight in affecting phonotaxis. Obviously, females cannot move to heavier males unless weight is correlated with a song parameter such as sound level or phrase length. Weight was weakly correlated with sound level in our mating success studies and in this study (S.I.8-kHz; $r = 0.310$, $p = 0.032$; S.I. -16kHz; $r = 0.357$; $p = 0.013$) and was not correlated with phrase length in either study. Some other studies of phonotaxis of singing Orthoptera have indicated a correlation between male weight and sound level (Bailey and Thiele 1983, Forrest 1983, Walker 1983); others have not (Latimer and Sippel 1987).

The results of this experiment gives little support for the hypothesis that females determine direction of phonotaxis using the same parameters that were shown to be important in mating success (Galliard and Shaw, 1991a). Only one parameter, sound intensity, was the same and the similar results could have different causes. In some species of Phaneropterinae, a female moves to within a certain distance of one or more males and then the females produce sounds which attract the males (Grove 1959, Spooner 1968) to her. This preference for a higher sound level could be a mechanism for moving toward the largest (= loudest) group of singing males where female choice may occur.

In regard to the other male song parameters implicated in female phonotaxis, phrase period is very likely a reflection of females' preference for longer phrases; the mean difference in phrase period between Sms and Ums was similar (0.56 s) to that between mean phrase lengths (0.62 s). Phrase period

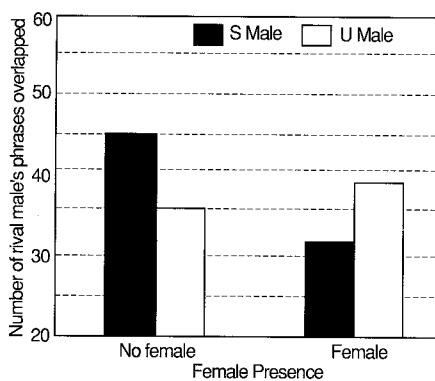


Fig. 2. Comparison of the mean number of times each of two chorusing males overlapped his chorusing partner when a sexually receptive ("ticking") female was absent and present. S MALE - male that eventually mated with female; U MALE - male that did not mate with the female. N = 24 (from Galliard and Shaw 1991a).

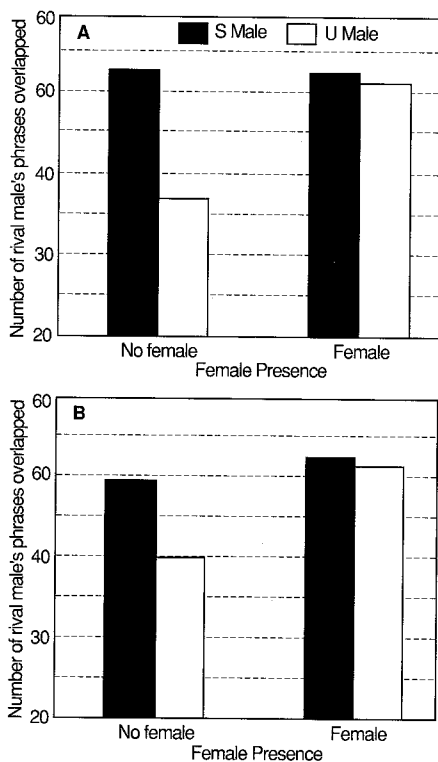


Fig. 3. Same as Fig. 2. **a**, data for trials in which sound intensity differences between the males was < 3 dB (n = 12); **b**, data for trials involving initial use and reuse of females. N 59.

was not significant when we analyzed the 59 trials involving reuse of females.

The actual role of phrase phase relationships in intra and/or intersexual selection continues to be elusive. In our mating success studies, we suggested that the ability of males to avoid overlapping their competitors' phrases might have been a signal to either the competitor or the female that this was the "superior" male. However, there

was no indication of a difference in phrase overlap number in this study. Instead, the mean time that successful males overlapped unsuccessful males' phrases was less than vice-versa. These two measures could be viewed as similar in that the Sm is reducing its degree of overlap or its degree of increase in overlap which characterizes the singing of both males in the presence of a ticking female (Table 5). However, it is also possible that the statistically significant relationship between mean phrase overlap and the direction of female phonotaxis is a type II statistical error. This relationship was not significant when the 59 trials involving female reuse were analyzed. Also, it is difficult to imagine that females would be using a male character that is negatively correlated with sound level of male song (Table 3).

In the mating success trials, the difference in phrase overlap number was the result of a reversal of who overlapped whom the most in the absence and the presence of a ticking female (Fig. 2). Although our analysis of the 25 trials did not show such an interaction, the analysis of the 12 trials in which male dB difference was < 3 dB did show a similar interaction, i.e., indicated a significant increase in overlap number (Fig. 3a), as well as an increase in the percentage of phrases overlapped for the unsuccessful male. The same results were achieved when all female trials (n = 59) were analyzed (Fig. 3b).

Since there was essentially no difference in number of phrases overlapped (Fig. 3) or in percentage of phrases overlapped in the n = 12 and n = 59 trials and the difference in overlap number was not quite statistically significant in the mating success studies, it is possible that females do not utilize this information. However, it also is possible that females might perceive the changes in phrase phase relationships if it occurs over a short period of time after she is introduced into the chamber. We are pursuing this possibility by analyzing the first few minutes of acoustic interaction after a female is introduced and comparing it with the interaction before and after this time. The finding that females tick more in response to the phrases of Sms than Ums supports the possibility of female choice.

It is also possible that males could use the information. If significant phrase phase differences occur in the absence of a female, males could use this information, as well as differences in sound level and phrase length, to establish a dominance-subordination relationship which may eventually express itself. In 10 of the 24 trials in our mating success studies, one of the males failed to leave the cage. In several of the remaining cases, one of the males left the vicinity of the female and other male prior to initiation of

copulation.

The difficulties we have had in implicating phrase phase relationships in determining mating success and direction of phonotaxis are exacerbated by the difficulty in collecting *A. parvipennis* females. Because a number of parameters are used in determining mating success and phonotaxis, and because they are weakly correlated or not correlated at all (e.g. sound level and phrase length in Table 3), larger numbers of trials are demanded to reduce confounding effects of the multiple parameters. Currently we are utilizing computer-generated signals to perform the two-choice phonotaxis trials. This will enable us to vary one or two parameters while holding the others constant. In this way, we hope to clarify the females' use of male song parameters in phonotaxis and in mating success as well.

As in our earlier study, there is no evidence that females are utilizing frequency difference between males. In our mating success studies (Galliard and Shaw 1991a), we argued that *A. parvipennis* females did not have to depend on frequency attenuation over distance to compensate for the problem of differentiating between a softer, closer and a louder, more distant source because males move to the females. In this phonotaxis experiment, females may utilize intensity and frequency as they would if males were in close proximity. Whether frequency attenuation is utilized when females are differentiating between males or groups of males at greater distances is unknown.

Using tape loops made from katydid phrases, Tuckerman (1990) found that females of the phaneropterine, *Scudderia curvicauda*, increased number of ticks as phrase length increased. Although *A. parvipennis* females obviously produced more ticks in response to Sms than Ums (Table 4) and Sms produced longer phrases than Ums, we could find no evidence that females were responding to phrase length. Again, this may be clarified with the use of computer-generated signals.

The evidence that females tick more in response to the male she eventually moves toward suggests another source of information for the mating game. In our mating success experiment (Galliard and Shaw 1991a), the males that failed to leave their cages, or left the vicinity of the female and competitor male prior to copulation, may have received information concerning the female's choice.

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SHORT NOTES

New Status for *Circotettix coconino* (Rehn) (Orthoptera: Acrididae: Oedipodinae)

In 1984 I mistakenly considered Rehn's *Circotettix coconino* to be a synonym of *C. rabula* (Otte 1984: 242). The morphological differences between these nominal species were believed to be too slight to warrant separating them. Specimens assigned to *coconino* are all from northern Arizona, and the majority of them have blue tibiae (*rabula* usually has yellowish tibiae). But the presence of a few northern Arizona specimens with yellowish tibiae led me to believe that *C. coconino* was a synonym.

In October 1990 I encountered this species

a few miles east of McNary, Arizona, and at the summit of Mt. Graham (Pinaleno Mountains). I observed numerous flight displays. These were quite different from those of *C. rabula* in several respects: (a) The wing-beat rate (pulse repetition rate) was much higher—estimated at approximately double that of *C. rabula*; (b) males hovered over one spot during an entire flight; (c) males moved up and down rather than weaving side to side or making wide circling motions.

The habitats of the two species also differ somewhat. *C. rabula* seems to occur only along hillsides and along banks; *C. coconino* occurs in similar situations but also inhabits open patches of level ground.

There is no doubt that *C. coconino* is distinct from *C. rabula* Rehn and Hebard.

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