

ROLE OF WEIGHT AND ACOUSTIC PARAMETERS,
INCLUDING NATURE OF CHORUSING, IN THE MATING
SUCCESS OF MALES OF THE KATYDID, *AMBLYCORYPHA*
PARVIPENNIS (ORTHOPTERA: TETTIGONIIDAE)

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ABSTRACT

Amblycorypha parvipennis Stål males are unique chorusers; adjacent males alternate 4-5 s phrases frequently overlapping the end of a partner's phrases, and where phrases overlap, phonotomes (phrase subunits) are synchronized. We explored the effect of weight and a number of sound parameters, including frequency, intensity, temporal parameters and phrase phase relationships during chorusing, on male mating success using laboratory tests in which single females were exposed to pairs of chorusing males. Females mated with males that were heavier, louder, and overlapped their partner's phrases less when in the presence of a sexually-receptive (sound-producing) female. Male spermatophore weight was correlated with male body weight; this suggests that females may choose heavier males to obtain larger spermatophores (10-20% of male's wet body weight) upon which females feed. Sound level rather than sound frequency may be important in mating success because competing males produce sounds in close proximity to competitors and females and this proximity negates the environmental degradation of sound level over greater distances. The reduction in the rate at which eventual successfully mating males overlap unsuccessful males in the presence of a female suggests that males compete to reduce the rate at which they overlap the end of a competitor's phrases. This ability, as well as weight and sound level, appears to be utilized by females or competitors in determining the "superior" male.

RESUMEN

Los machos de *Amblycorypha parvipennis* Stal conforman un coro unico; los machos producen 4-5 frases alternas las cuales sobreponen en el final de la frase emitida por otro macho, y cuando estas frases estan sobrepuestas, los tonos foneticos (subunidades de frase) se sincronizan. Se investigo, en experimentos de laboratorio, utilizando hembras expuestas a un coro de machos, el efecto del peso y varios parametros del sonido (los cuales incluyen, frecuencia, intensidad, parametros temporales y fases de frases y sus relaciones durante el coro), y su efecto en el exito del apareamiento. Las hembras se aparearon con machos que eran mas pesados, mas sonoros, y los que sobreponian menos las frases en las de sus companeros, cuando estaban en la presencia de una hembra receptiva (productora de sonido). Se relaciono el peso del espermatoforo del macho con el peso del cuerpo; esto sugiere que las hembras escojen machos mas pesados con el fin de obtener espermatoforos mas grandes (10-20% del peso fresco del macho) de los cuales ellas se alimentan. El nivel del sonido fue mas importante que la frecuencia en el exito del apareamiento, porque los machos que estan compitiendo producen sonidos junto a otros competidores, y junto a las hembras, y esta proximidad reduce la degradacion ambiental del sonido en largas distancias. La reduccion de la proporcion en que los machos se aparearon con exito sobrepasa a los machos sin exito de apareamiento en presencia de una hembra, sugiere, que los machos compiten para reducir la velocidad a la cual ellos sobreponen frases a el final de las frases de los competidores. Esta habilidad, asi como el peso y el volumen del sonido, paracen ser utilizados por las hembras o por los competidores con el fin de determinar el macho "superior".

The males of many species of singing Orthoptera aggregate spatially (Campbell & Clarke 1971, Cade 1976, Campbell & Shipp 1979, Shaw et al. 1981, 1982) and perform communal sexual displays, i.e., exhibit temporal aggregations of song which Walker (1983) termed "sprees." Alexander (1960, 1967, 1975) called such spreeing aggregations "choruses" and considered them analogous to male anuran choruses which attract conspecific males and females to breeding waters (Wells 1977). There are a variety of chorus types classified on the basis of the temporal relationships of the song components of adjacent males (Greenfield & Shaw 1983).

The songs of Orthopteran males are undoubtedly involved in determining mating success whether by intrasexual competition or intersexual mate choice. Males may compete for singing sites and chorusing is involved in spacing dynamics (Shaw 1968, Greenfield & Shaw 1983, Latimer & Schatral 1986, Meixner & Shaw 1986). There is experimental evidence that male spacing within choruses is affected by males hearing the sounds of neighbors (Campbell & Shipp 1979, Thiele & Bailey 1980, Bailey & Thiele 1983, Latimer & Schatral 1986, Latimer & Sippel 1987).

Orthopteran songs function to attract sexually receptive females (Alexander 1960, 1967, Dumortier 1963, Otte 1977, Forrest 1980, 1983) and attract or repel competing polygamous males (Morris 1972, Cade 1979, Forrest 1980, 1983). Studies of male acoustic cues involved in mating success have shown that females mate with males that produce louder songs (Cade 1979, Forrest 1980, 1983, Gwynne 1982, Bailey 1985), lower song frequencies (Bailey 1985, Latimer & Sippel 1987), and that initiate song and sing more during collective calling bouts (Busnel 1967).

Only Busnel's (1967) studies implicated some aspect of chorusing in mating success. He studied three species of katydids of the genus *Ephippiger* in which adjacent males tend to alternate production of phrases. In paired interactions, the male which initiated more calling bouts and sang more phrases during calling bouts attracted more females.

Male weight is another apparently important factor in male mating success of singing Orthoptera (Gwynne 1982, 1983, Forrest 1983, Simmons 1986a,b). This may be related to heavier males producing larger external spermatophores upon which females feed (Gwynne 1982, 1983).

Our study of the acoustic and reproductive behavior of a phaneropterine katydid, *Amblycorypha parvipennis* Stål (Shaw et al. 1990) suggested that this would be an excellent species to investigate regarding the role of song and chorusing in mating success. In paired interactions, males alternate 4-5 s phrases, which frequently overlap the end of the partner's phrases, and, where phrases overlap, phonotomes (sounds produced by a single cycle of wing movement: Walker & Dew 1972) are synchronized (Fig. 1). During paired interactions, males differ in the number of times the beginnings of their phrases overlap the phrase endings of the other katydid (Fig. 1) (Shaw et al. 1990). Unlike most katydids, phaneropterine females produce short "ticking" sounds in response to male sounds, and one or more males move to the ticking female (Shaw et al., 1990). When near the female, *A. parvipennis* males frequently encounter one another and may kick or push with front or hind legs, crawl over, or mount one another. Males court by ceasing singing, raising their wings, and backing toward a female or another male. These interactions can last for hours and may result in some males abandoning courtship and leaving the area (Shaw et al., 1990).

This study was designed to observe mating under controlled laboratory conditions where acoustic parameters could be readily measured and physical interactions easily observed. This involved a series of trials where individual females were given a choice of two chorusing males. The following questions were asked. 1) Do acoustic differences between males, including phrase phase relationships during acoustic interaction, reflect differences in the males' abilities to achieve mating success? 2) Do females mate with heavier males and, if so, is male size correlated with spermatophore size? 3) if more

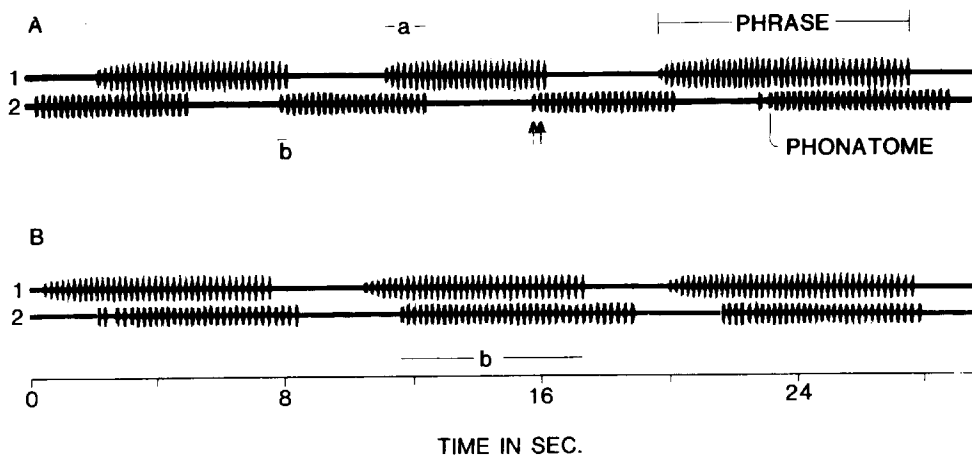


Fig. 1. Oscillographs of two paired acoustic interactions (choruses) by *A. parvipennis* males. A—several phrases recorded from each of a pair of chorusing males. The initial part of the phrase of each male overlaps the latter part of the phrase of the other male. In this selection, both katydids overlap the other katydid three times, i.e., the overlap number of each katydid is three. The mean length of overlap, i.e., the mean length of time that each katydid overlaps the other katydid is the sum of the period that each phrase is overlapped divided by three. B—several phrases recorded from another pair of chorusing males. In this selection, katydid 2 overlaps katydid 1 but 1 does not overlap 2. Therefore, the overlap number and mean overlap time for 1 is zero. 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. † † designates the initial phonatomes of katydid 2 that are out of phase with the terminal phonatomes of katydid 1.

than one parameter is related to mate choice, are these parameters correlated with one another?

METHODS

Subjects and Housing

Specimens of *A. parvipennis* were collected from a prairie west of Ames High School, Ames, Iowa. Using flashlights, individuals were collected at night from 1 July to 6 August 1986 and 22 June to 21 July 1987. Singing males were easily collected as needed throughout the testing period. Females were much more difficult to collect. Most females were collected by searching food plants, especially horsemint (*Mentha longifolia*) and wild grape (*Vitis*), at night. A few nymphs were collected by sweeping food plants with an insect net during the day. In order to ensure that females were receptive (assumed virgin), they had to be captured as nymphs or adults prior to the second week of male singing. Only 13% of the sexually receptive females maintained in the laboratory were captured after the first week of male singing. The approximate age range for females used in trials was 1 to 4 weeks. Female nymphs were reared in the laboratory in environmental chambers (Percival Refrigeration and Manufacturing Co.) (14L:10D, 24-25°C).

Males were individually marked using colored nail polish and isolated in 10x10x17 cm wire screen cages and placed around the laboratory which was maintained on the same light-dark and temperature regimes as the environmental chambers. Females were housed together in 34x33x31 cm wire screen and wood cages inside an environmental

chamber. This isolated them from male sounds until they were used in a mate choice trial. After they were used in a trial, females were housed collectively in a separate cage. All insects were fed leaves of horsemint or wild grape and chicken starter feed. Water was provided in cotton-capped vials.

Two-Choice Discrimination Tests

Two-choice discrimination tests enabled individual females to listen to and interact with two males. Receptive females were chosen by placing a cage of females in the laboratory of singing males and selecting a ticking female. We ran 24 trials using a different female and different pair of males in each trial. The number of trials was limited by the difficulty in finding receptive females. Females were weighed before and after every trial; males were weighed before and after the first 10 trials but only following the last 14 trials. Handling males prior to a trial greatly reduced the probability that they would sing again that day.

All trials were performed in an acoustic isolation chamber (4.6 x 5.3 x 2.4 m; Industrial Acoustics Co., Inc.) at room temperature (24-25°C). Caged males were placed 3.4 m apart (within the range of the most common nearest neighbor distances in the field [Shaw et al. 1981]) at the ends of three tables placed end-to-end. After males began to sing, sound level was measured approximately 5 cm above each male's stridulatory apparatus. This close-range measurement was taken because sound level at the intermale midpoint could vary several dB (re: 0.002 dynes/cm²) depending upon the position of the male in the cage. Maximum sound levels were measured at frequency bands centered at 8 and 16 kHz using a Bruel & Kjaer (B & K) type 2203, precision sound level meter in conjunction with a B & K, type 1613, octave filter set. Following sound level measurements, a 30 s recording (B & K, type 4133, microphone; B & K, type 2615, microphone preamplifier; B & K, type 2801, power supply; Tektronix, type 122, preamplifier; Tektronix, type 160A, power supply; Precision Data, type PI-6204, instrumentation tape recorder) was made for frequency analysis. Frequency spectra of song samples were determined using a B & K, type 2033, frequency analyzer. The upper frequency limit of the recording equipment was 40 kHz. Although the upper frequency limit of the B & K frequency analyzer is 20 kHz, by recording the songs at 37.5 in/s on the Precision Data recorder and playing the songs at 15 in/s on a Nagra III tape recorder, frequencies up to 40 kHz could be analyzed.

The frequency spectra of *A. parvipennis* male sounds are analyzed elsewhere (Shaw et al., 1990). Although sound frequencies extend beyond 100 kHz, most sound energy is below 50 kHz with maximum energy occurring at a mean frequency of 10.5 kHz. However, male sounds may show one to three lower energy peaks between 10 and 40 kHz, the latter being the upper frequency range we used in the analysis of male sounds. In this study, we asked whether pairs of males differed in the lower two peak frequencies ($\bar{x} = 10585 \pm 1643$ and 19330 ± 1458 Hz, Shaw et al. 1990).

Following the recordings for frequency analysis, 10-min recordings were made of the males chorusing, without and then with a sexually receptive (ticking) female (within a circular screen cage, 10 cm in diameter) placed between and equidistant (1.7 m) from each male. The singing males were recorded using two uni-directional dynamic microphones (GC Electronics, #30-2374), each placed approximately 6 cm from the cage of a singing male, and a Sony TC-6300 2-channel tape recorder. The temporal parameters of each male's song and the phase relationships of pairs of acoustically interacting males were determined using a Commodore 128 computer in conjunction with a computer interface and software designed for this experiment.

After completing the 10-min recordings, both males and female were released by opening their cages. In order to obtain spermatophores, copulations were terminated by the observer as soon as the male's spermatophore was visible. Fifteen of the 24 males

continued to emit the whole spermatophore after separation from the female. When this happened the spermatophore was removed and weighed. Males and females were weighed following the end of the trial. When a male emitted a spermatophore, the spermatophore weight was included in determining each male's weight following initiation of copulation. In order to increase the sample sizes for determining the relationship between male body weight and spermatophore weight, spermatophores were collected from 26 other males placed with females already utilized in two-choice discrimination trials.

Data Analysis

Male mating success was examined in relation to male weight, sound level (8 kHz and 16 kHz), sound frequency, temporal sound parameters, phase relation of the sound phrases of the two males during chorusing, and number of physical interactions. Temporal parameters included number of phrases, mean phrase length, mean phrase interval, mean phrase period (phrase length + phrase interval) and total sound produced (number of phrases x mean phrase length). Phrase phase relations were determined by recording the number of phrase overlaps (the number of times the beginnings of a katydid's phrases overlapped the ends of the phrases of the other katydid [Fig. 1]), mean phrase overlap time (the mean length of time that the phrase beginnings of both katydids overlapped the phrase endings of their chorusing partner's phrase endings; this does not include phrases that were not overlapped [Fig. 1]) and total overlap time (number of overlaps x mean overlap time). Physical interactions measured included number of male mountings and mounts by other male, individual male mountings by the female, males kicking or being kicked by the other male, male crawling on or being crawled on by the other male, separating other male and female by backing into (courting) or crawling over them, males jumping away, and males walking away. Temporal sound parameters were examined for two conditions (treatments): chorusing with and without a ticking female in the acoustic chamber.

Weight, sound level and number of physical interaction differences between males that achieved copulation (successful males = $S\delta$ s) and those that did not (unsuccessful males = $U\delta$ s) were analyzed by paired-comparison Student's *t*-tests ($S\delta - U\delta$). A split-plot analysis, with male mating success ($S\delta$ or $U\delta$) as the whole plot treatment and female absence or presence as the split-plot treatment, was used to analyze the temporal sound parameters and phrase phase relationships. Since temporal sound parameters and phrase phase relationships were measured for each male in the absence and presence of a female, the split-plot factor in this analysis was regarded as a repeated measure. This ANOVA enabled us to examine male mating success regardless of the presence of the female, the effect of the presence of the female on both males as well as the effect of the female on $S\delta$ and $U\delta$ separately. Based on the results of previous studies (see Introduction), we hypothesized that females would mate with heavier males, louder males, males with lower song frequencies, and males that produced more sound energy either in more or longer phrases and/or total sound produced. Pearson's correlation coefficients were determined for the parameters implicated in mate choice. The peak frequencies of winner and loser sounds were compared using chi-square tests.

RESULTS

Females mated more often with males that produced louder sounds before the trials and that were heavier following the trials (Table 1). Of special interest, there was a significant interaction between male mating success and female presence for the number of times a male's phrases were overlapped ($F = 8.98$, $df = 1, 44$; $p < 0.0045$). Eventual

TABLE 1. COMPARISON OF MEAN DIFFERENCES (S-U) IN WEIGHT AND SOUND LEVEL OF SUCCESSFUL (S♂) AND UNSUCCESSFUL (U♂) *A. PARVIPENNIS* MALES IN TWO-CHOICE DISCRIMINATION TESTS.

Parameter	Difference		Means		N	t	p ^c
	S-U	S.E. ^a	S♂	U♂			
Weight (g)	0.04	0.02	0.73	0.69	24	1.77	0.05
SI-8kHz ^b (dB)	1.73	0.97	71.73	70.00	24	1.79	0.04
SI-16kHz ^b (dB)	1.63	0.83	73.27	71.65	24	1.97	0.03

^aS.E. = standard error

^bSI-8kHz—sound intensity at 8 kHz filter band; SI-16kHz—sound intensity at 16 kHz filter band

^cp—probability that the mean (S-U) difference equals zero using one tailed, paired-comparison Student's t-test

S♂s overlapped U♂s more when a female was absent but the situation was reversed when a ticking female was present (Fig. 2). Paired-comparison t-tests indicated that differences between males approached a p-level of < 0.05 under both conditions (female absent: $t = -1.94$, $p = 0.070$, two-tailed test; female present: $t = 2.02$, $p = 0.055$, two-tailed test). With a female absent and omitting ties, S♂ overlapped U♂s more in 14 of 21 trials; in contrast, S♂s overlapped U♂s less in 14 of 21 trials with a female present. The presence of a female resulted in a reduction in total number of phrases overlapped in 15 of 21 trials and this was accompanied by S♂s overlapping U♂s less in

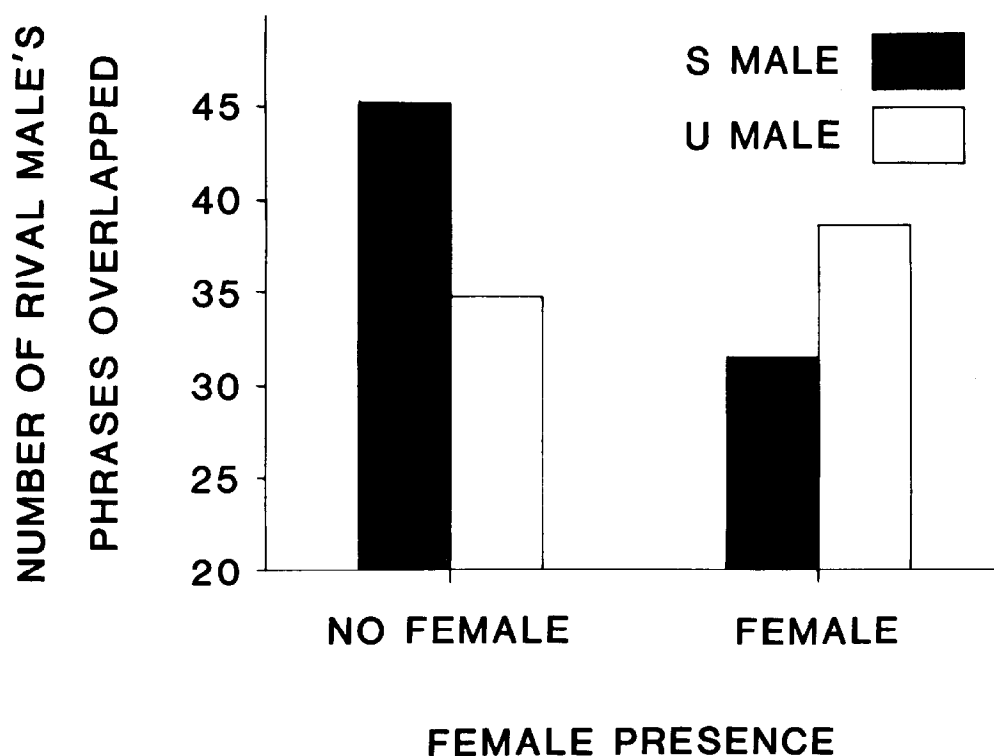


Fig. 2. Comparison of the mean number of times each of two chorusing males overlapped his chorusing partner when a sexually receptive ("ticking") female was absent and present. S Male—male that eventually mated with female; U Male—male that did not mate with female. N = 24.

18 of 22 trials after the female was added. In contrast, S♂s were overlapped more in 13 of 23 trials after the female was added.

The repeated-measures ANOVA also indicated that the presence of a female increased the length at which the phrase of each katydid overlapped the phrases of the other katydid (female absent [\bar{x} S.E.]: 1.27 ± 0.71 s; female present: 1.83 ± 0.74 s; $F = 21.35$; $p = 0.0001$).

Pearson's correlation coefficients were run using the three parameters most likely involved in determining mating success, i.e., male weight, sound level and phrase overlap number in the presence of a female. From the six paired comparisons, there were four correlations with a $p < 0.05$ and one with $p < 0.10$ (Table 2).

Of all the physical interactions recorded, only one was significantly higher for S♂s; females mounted eventual S♂s more than U♂s (S♂: $\bar{x} \pm$ S.E. = 8.63 ± 1.26 ; U♂: 5.43 ± 0.94 ; $t = 3.02$; $p = 0.006$, two-tailed test).

Unlike Latimer and Schatral's (1986) and Latimer and Sippel's (1987) findings for *Tettigonia cantans*, we found no relationship between frequency of male sounds and whether or not they achieved copulation. Peak frequencies were quite variable among males (Shaw et al. 1990) and S♂s did not produce lower or higher peak frequencies than U♂s (first peak frequency: chi-square = 0.17, $p > 0.50$, $df = 1$, $N = 24$; higher peak frequency; chi-square = 0.05; $p < 0.80$, $df = 1$, $N = 18$).

A. parvipennis males produce large spermatophores ($\bar{x} \pm$ S.E. = 95.20 ± 4.83 mg, $N = 41$) which comprise an average of 12% (range = 10-20%) of the males' body weights ($\bar{x} \pm$ S.E. = 768.30 ± 9.00 mg, $N = 41$). Following spermatophore extrusion, males do not sing for 1-5 days. Male weight is correlated with spermatophore size ($r = 0.454$, $P < 0.005$) (Fig. 3).

DISCUSSION

As has been determined for some other species of sound-producing Orthoptera (see Introduction), *A. parvipennis* males successful in achieving copulation were heavier and produced louder sounds. Spermatophore weight was correlated with body weight and proteins in spermatophores are known to enhance the fitness of female Orthoptera (Gwynne 1988). Females took hours to choose between competing males usually mounting each male a number of times and the number of mountings was correlated with mate choice. This would be an opportune time to determine male size.

In two-choice discrimination tests utilizing artificially-generated sounds, Latimer & Sippel (1987) found that differences in sound frequency were more important than sound

TABLE 2. CORRELATION MATRIX FOR PARAMETERS INVOLVED IN MATING SUCCESS.

	SI ^c 8kHz	SI 16kHz	OVN-f ^d
Weight	0.34 ^a 0.019 ^b	0.35 0.016	-0.20 0.172
SI-8kHz		0.77 0.0001	-0.31 0.035
SI-16kHz			0.073

^aPearson's correlation coefficients

^bp values

^cSI—as in Table 1

^dOVN-f—number of times S♂ overlaps end of phrases of U♂ in presence of a ticking female

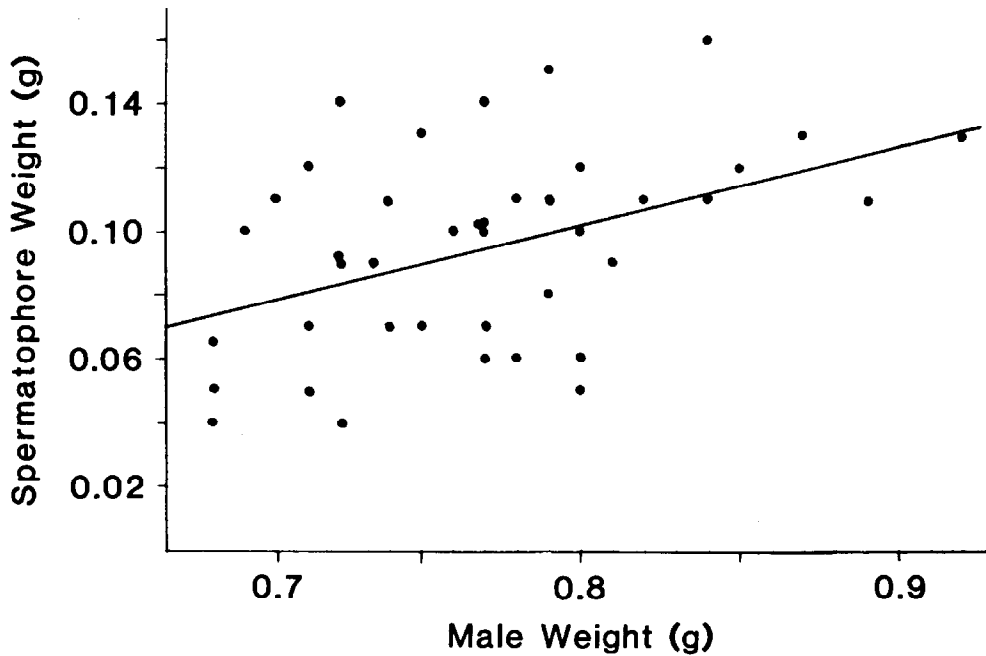


Fig. 3. The relationship between spermatophore weight and male weight.

level in attracting females of the katydid *Tettigonia cantans*. Latimer & Sippel argue that, because of variation in sound level caused by differences in vegetation density, male body orientation, etc., frequency differences would be more effective in communicating male status. The failure to find any correlation between sound frequency and mating success for *A. parvipennis* may be related to the differences in mating systems between *T. cantans* and *A. parvipennis*. *T. cantans* females move toward a particular singing male; the mating success of *A. parvipennis* males may be determined after they have moved to a female.

An especially interesting finding of this study was that females preferentially mated with males who reduced the number of times they overlapped the phrase beginnings of their competitors in the presence of a ticking female. If eventual S♂s overlapped eventual U♂s more in the absence of a female, the situation was usually reversed when a ticking female was perceived. A closer examination of the data indicated the total number of phrases overlapped for both katydids decreased in the presence of a female and that the major reason for this was a reduction in the number of times the S♂ overlapped the U♂ in 18 of 22 trials. This evidence suggests that S♂s adjusted their phrase rates in order to avoid overlapping the ends of the eventual U♂s' phrases and thereby, probably because of limitations on U♂s' ability to adjust phrase rate, forced the U♂s to overlap S♂s phrases more. In fact, the mean length of phrase overlap actually increased in the presence of the female. These data suggest that the ability of a male to adjust its phrase rate so that he can initiate his phrase following the end of the other male's phrase, communicates, either to competing males or to the female, that he is the superior male. Greenfield (in press) suggests that the nature of chorusing is the evolutionary result of males adjusting their phrase rate so that the loudest portion of their song is free of jamming, i.e., not overlapped by the song of another katydid. Generalizing from Greenfield's hypothesis, it is the portion of the phrase carrying the most information relating to male-male competition or female choice that males should attempt to free from jamming by the sounds of other males.

The most rapidly produced and loudest phonatomes of *A. parvipennis* occur during the middle of the phrase and this is the portion of the phrase usually free of overlap during acoustic interaction of pairs of males. During the first few phonatomes of the phrase, phonatome rate and sound level increased; during the last few phonatomes, phonatome rate decreased (Fig. 1). Unlapped middle portions of phrases may be important in male-male communication (e.g., in maintaining uniform spacing between adjacent males; Shaw et al., 1981) and in male-female communication, (e.g., in attracting conspecific females to the vicinity of one or more males prior to the female beginning to tick). However, in the field, chorusing may involve more than one male and females may perceive considerably more overlap between songs of neighboring males. If phonatome rate enables females to identify conspecific males and release phonotaxis, then selection would favor synchrony. This rhythm preserving model of synchrony function has been proposed for sound-producing insects (Walker 1969, Alexander 1975, Otte 1977, Greenfield & Shaw 1983) and light-flashing fireflies (Lloyd 1973a,b, Otte & Smiley 1977, Otte 1980, Buck 1988).

Because, like firefly females, phaneropterine females characteristically respond to male signals at species-identifying intervals (Spooner 1968, Heller and von Helverson 1986) and because *A. parvipennis* is unique in that females produce short sounds (= ticks) that may fall between the latter phonatomes of a male's phrase (Shaw et al., 1990), males may synchronize phonatomes in order to detect a female, to recognize her as a conspecific (female detection and delay recognition models of Otte & Smiley [1977]), and to better perceive the location of the female. If synchrony enables males to perceive and identify the species and location of conspecific, sexually receptive females, then why the apparent adjustment of a male's phrase rate to avoid overlapping the end of another male's phrases in the presence of a ticking female? This also may enhance the perception of female ticks. Unlike fireflies, synchronizing male Orthoptera may be unable to detect the signals of conspecifics while simultaneously producing signals (see discussion by Greenfield, in press). Males may attempt to avoid overlapping an adjacent male to better detect the location of a ticking female. Although males typically synchronize phonatomes, the rate of the last few phonatomes slows rapidly and the phonatomes tend to be out of phase with the other male's phonatomes (see Fig. 1). This could result in overlapping (jamming) of male phonatomes and the ticks of a nearby female. Unjammed female ticks may be especially important to males who, as in this experiment, have not yet moved to the location of the ticking female. It also is possible that there is information in the rapidly changing initial portion of a male's phrase that relates to his ability to compete for females. If this is true, then using Greenfield's (in press) logic, males should compete to avoid overlaps.

Although the correlation coefficients are not very large, most of the correlations between parameters implicated in mate choice are significant at $p \leq 0.05$ or close to it (Table 2). This indicates that competitor males and/or females can use one or a combination of these cues in determining a "superior" male. Male size or weight could be determined during male-male or male-female physical interactions. Males continue to chorus as they move toward the female and when in proximity to the female or other male. Future experiments will examine what is happening to sound level, temporal parameters and phrase phase relationships when males are in proximity.

As with many studies of sexual selection, it is impossible to state whether mating is the result of male competition or female choice, and it is very possible that both processes are involved (Halliday 1978, Burk 1983). In 10 of the 24 trials, one male did not encounter the female, i.e., he either did not leave the opened cage or left the vicinity of the female after encountering the other male acoustically and physically. These data suggest mating success resulting from male competition. As indicated above, future experiments will examine what is happening to male acoustic parameters after release from the cages.

The long period of time that females spent interacting with one or both males suggests that females are in a process of actively making a choice. Females spend up to 10 min on the back of some males while continually pulling their abdomens away from the male and, not infrequently, they separated and resumed ticking in response to the singing of the competitor male. All of this is difficult to comprehend if mating success is strictly the result of male competition.

This type of observational/correlative study raises many questions and provides few answers. Are all of these or any of these factors crucial to mating success? Are these the important factors or are they simply correlated with the yet undiscovered crucial factors? We are in the process of designing experiments to explore the role of these factors, separately and in various combinations, in mate mating success and female mate choice.

ACKNOWLEDGMENTS

We wish to thank Dr. Michael Greenfield, Department of Biology, UCLA, Dr. Darryl Gwynne, Department of Zoology, Erindale Campus, University of Toronto, and anonymous reviewers for critiquing drafts of this manuscript. Drs. David Cox and Paul Hinz, Department of Statistics, Iowa State University served as consultants for the statistical analysis. A special thanks to Mike Reilly, a student in the Department of Electrical Engineering, Iowa State University, for designing the computer program and interface used in our data analysis. This work was partially funded by a grant from the Iowa Science Foundation.

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