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EFFECT OF INTERMALE DISTANCE AND FEMALE PRESENCE ON THE NATURE OF CHORUSING BY PAIRED *AMBLYCORYPHA PARVIPENNIS* (ORTHOPTERA: TETTIGONIIDAE) MALES

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ABSTRACT

Pairs of chorusing *Amblycorypha parvipennis* Stål males alternate the production of 3-5 s long phrases with frequent partial overlap of phrases. To determine the effect of intermale distance and the presence of a sexually receptive, sound-producing ("ticking") female on the nature of paired male chorusing, pairs of males were recorded, with and without the presence of a ticking female placed midway between the caged males, chorusing 3.3 m and 40 cm apart. The presence of a ticking female elicited a shortening of intervals between phrases (increase in phrase rate) and an increase in the extent of phrase overlap. In contrast, shortening the distance between males in the absence of a ticking female resulted in a lengthening of phrase interval (decrease in phrase rate) and a reduction in phrase overlap. Possible proximate and ultimate causes of these chorusing changes are discussed.

RESUMEN

Pares de machos de *Amblycorypha parvipennis* Stal, cantando en coro, alternan la produccion de frases de 3-5 segundos de duracion, con la frequente sobreposicion parcial de las frases. Para determinar el efecto de la distancia entre machos y la presencia de una hembra sexualmente receptiva y productora de sonido en la naturaleza del par de machos cantando en coro, los pares de machos fueron grabados, con y sin la presencia

de la hembra la cual estaba situada a 3.3m y 40 cm de distancia de los machos en jaula. La presencia de la hembra produjo un acortamiento entre los intervalos entre frases (incremento en la produccion de frases) y un incremento en la sobreposicion de estos. En contraste, al acortar la distancia entre machos y en la ausencia de una hembra, resulto en la extension del intervalo de frases (la produccion de frases decrecio) y en una reduccion en la sobreposicion de las frases. Se discuten las causas inmediatas y ultimas para estos cambios en los coros.

Available evidence suggests that both inter- and intrasexual selection are important in the evolution of chorusing between and among male singing Orthoptera (see reviews by Alexander 1975, Otte 1977, Greenfield & Shaw 1983, Greenfield 1990). Male competition for females is expressed in uniform spacing of singing males resulting from movements away from and/or towards the songs of adjacent males (Campbell & Shipp 1979, Thiele & Bailey 1980, Bailey & Thiele 1983, Latimer & Schatral 1986, Latimer & Sippell 1987). Associated with spacing dynamics, singing orthopteran males may alter their songs when another singing conspecific male moves closer (Alexander 1957, 1961, Fever 1977, Otte 1977, Meixner & Shaw 1986, Shaw 1968). If uniform spacing serves to reduce male competition for females, then a reduction in distance between neighboring males should represent an increased threat to both males' abilities to acquire mates. An obvious reaction to such a threat would be to increase energy output by increasing sound output and/or entering into physical combat. Males of many field cricket species may increase length of chirps, reduce intervals between chirps and/or increase sound level of chirps (Alexander 1957, 1961). This also is true of males of at least some species of the pseudophylline katydid, *Pterophylla* (Shaw 1968, Shaw & Galliart 1987, Barrientos 1988). Males of several species of the concocephaline genus, *Orchelimum*, increase the rate, length, and/or intensity of the "tick" component of their calling sounds when a conspecific intruder approaches (Feaver 1977).

In contrast, a study utilizing males of the Australian conocephaline katydid *Mygalopsis marki* Bailey suggests that males of this species may reduce the number of pulses/phrase and reduce phrase rate by increasing intervals between phrases in response to a reduction in distance between neighboring males. Reduction in distance between an apparent intruder and a territorial male was simulated by increasing the sound level of playbacks of a *M. marki* male song and recording the response of territorial males in the field (Dadour 1989).

Since females of most species of singing Orthoptera move toward males that are 1 m or more from other singing males, male acoustic interaction in competition over a nearby female is seldom seen. Such encounters have been reported between cricket males in terraria (e.g., Alexander 1961, Burke 1983), but there has been no report that the nature of sounds or the acoustic interaction differs from that when a female is present. In species of the subfamily Phaneropterinae, females produce simple sounds in response to male calls and the males move to the female (Spooner 1968). This method of bringing the sexes together should increase the opportunity for male-male acoustic interaction at close range. Although Spooner (1968) indicates that phaneropterine males sing differently in groups than in isolation, we know of no investigation of the effect of change in intermale distance or the presence of a female on the nature of acoustic interaction of males in any species of this subfamily.

The phaneropterine katydid, *Amblycorypha parvipennis* Stål is unique among chorusing Orthoptera in that males alternate overlapped phrases and, where phrases overlap, phrase subunits (phonatomes) are synchronized (Shaw et al. 1990) (Fig. 1). This study asks whether the nature of sound production and acoustic interaction of paired males are affected by moving the males closer together in the absence and presence of a sound-producing female.

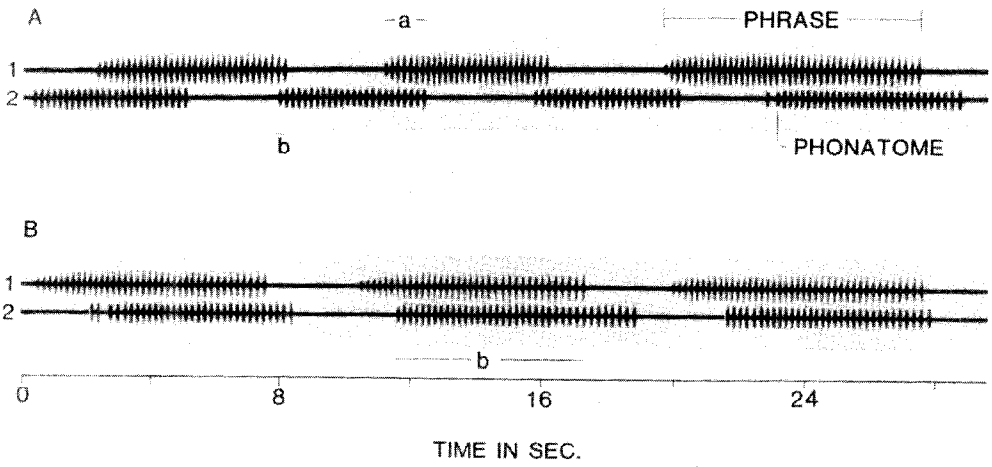

Fig. 1. Oscillographs of chorusing by paired *A. parvipennis* males. A - the initial part of the phrase of each male overlaps the latter part of the phrase of the other male. B - in this selection, katydid 2 overlaps katydid 1 but 1 does not overlap 2. a - indicates the time that the phrase of 1 overlaps the phrase of 2. b - indicates the time that the phrase of 2 overlaps the phrase of 1.

Materials and Methods

Subjects and Housing

A. parvipennis males and females were collected at night using flashlights during June and July, 1986-1989. Most virgin females were collected during the first week of singing. Males were collected as needed throughout the testing period. Specimens were marked with fingernail polish. Males were isolated in 10x10x17 cm wire screen cages and females were housed together in 34x34x31 cm wire screen and wood cages. The insects were housed in a laboratory maintained on a 14L:10D light schedule at 24-25°C. The insects were fed leaves of horsemint (*Mentha longifolia* (L)). or wild grape (*Vitis* sp.), and water was provided in cotton-capped vials.

The Effect of Intermale Distance and Female Presence on Paired Male Chorusing

In order to investigate the effect of intermale distance and female presence on male chorusing, we compared 10 min recordings of paired males singing under four different conditions: 1) two caged males 3.3 m apart (within the range of common, field nearest neighbor distances [Shaw et al. 1981]), 2) males 40 cm apart (a proximity which should elicit male-male competition for space), 3) males 3.3 m apart with a sexually receptive (ticking) female placed midway between the two males, and 4) males 40 cm apart with a ticking female midway between the males. The recordings were made using two unidirectional dynamic microphones (GC Electronics, #30-2374), each placed 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 song phrase phase relationships of pairs of chorusing males were determined using a Commodore 128 computer in conjunction with a computer interface and software designed for this analysis.

The data used in this paper are taken from studies originally designed to determine which acoustic and other factors affect mating success and male competition. Data for conditions 1) and 3) were taken from 114 males used in 57 two-choice discrimination

trials run in 1986 and 1987. In these trials males were recorded chorusing 3.3 m apart in the absence of a female and with a ticking female placed midway between the two caged males. After the recordings, the males and female were released in order to determine which male eventually mated with the female (Galliart & Shaw 1991). In 1988, we obtained data for conditions 1) and 2) during male competition trials. In 22 trials, 44 males were recorded chorusing at 3.3 m and 40 cm prior to release from the cages to determine which male stayed and which left the immediate area (unpublished data). In 1989, we returned to two-choice discrimination trials during which we obtained data from 66 males for conditions 1), 3) and 4). These 33 trials were the same as in 1986 and 1987 except that pairs of males were recorded at 40 cm apart following a recording at 3.3 m and then released (unpublished data).

Data Analysis

Because of the difficulty in collecting specimens, especially females, males and females were used in more than one trial. Males were used in up to three different trials (85% males used once, 10% used twice, 5% used three times); however, reused males were never matched with the same male twice. As discussed later, this source of males does not affect the experimental error values used in performing tests of probability. Females were used up to five times but, unlike two-choice discrimination tests, using females more than once as aa source of ticking sounds should have little effect on the results analyzed in this paper.

The 10-min. segments of paired males chorusing under each condition were examined in relation to temporal sound parameters (phrase number, phrase length, phrase interval, phrase period [phrase length + phrase interval], total sound produced in 10 min [phrase number x phrase length]) and nature of phrase overlap (number of phrase overlaps, mean overlap time and total overlap in 10 min [number of phrases overlapped x mean time of overlap]). Phrase overlap for each katydid was measured from the time that a katydid initiated its phrase during the phrase of another katydid until the other katydid terminated its phrase (Fig. 1). Phrase overlap does not include the latter portion of a katydid's phrase that is overlapped by the initiation of the other katydid's phrase.

In order to combine data from different years and compare data across years, we performed an analysis of combined experiments (Cochran & Cox 1957) (see Table 1 for example). This analysis treats the mean value for each condition during each year as a different measurement (e.g. condition 1 is treated as four measurements, one each year, not as 224 measurements over four years). Therefore the experimental error values used in all statistical tests involve between year variation rather than variation within any condition during one year. The four conditions were considered the treatments. The treatments were regarded as a factorial combination of the factors of intermale distance

TABLE 1. Use of analysis of combined experiments to analyze the effect of intermale distance and female presence on the phrase intervals of paired chorusing males.

Source	df	Mean Square	P > F
Year	3	0.12306	0.0022
Intermale Distance	1	0.04079	0.0066
Female Presence	1	0.64659	0.0004
Distance*Female	1	0.12681	0.0021
Error	2	0.00027	

and presence or absence of a female. The response variables are the acoustic parameters listed above. This analysis allowed us to look at the main effect of female presence, the main effect of distance and the interaction between these two factors. When the interaction between female presence and distance was significant, least square means for the appropriate singing categories were compared using two-tailed Student's t-tests. Least square means were used to adjust means for differences among years and to enable comparison of chorusing at 40 cm in the absence and presence of a female, two conditions which were recorded during different years.

Results

The presence of a female had an excitatory effect on male singing behavior; following introduction of a ticking female, males increased their phrase rate. At both intermale chorusing distances, the phrase period (reciprocal of phrase rate) was less when a ticking female was present (Fig. 2; $F = 68.73$; $df = 1,2$; $p = 0.014$). The reduction in phrase period was a result of a shortening of phrase interval (Fig. 3; $F = 118.38$; $df = 1,2$; $p = 0.008$).

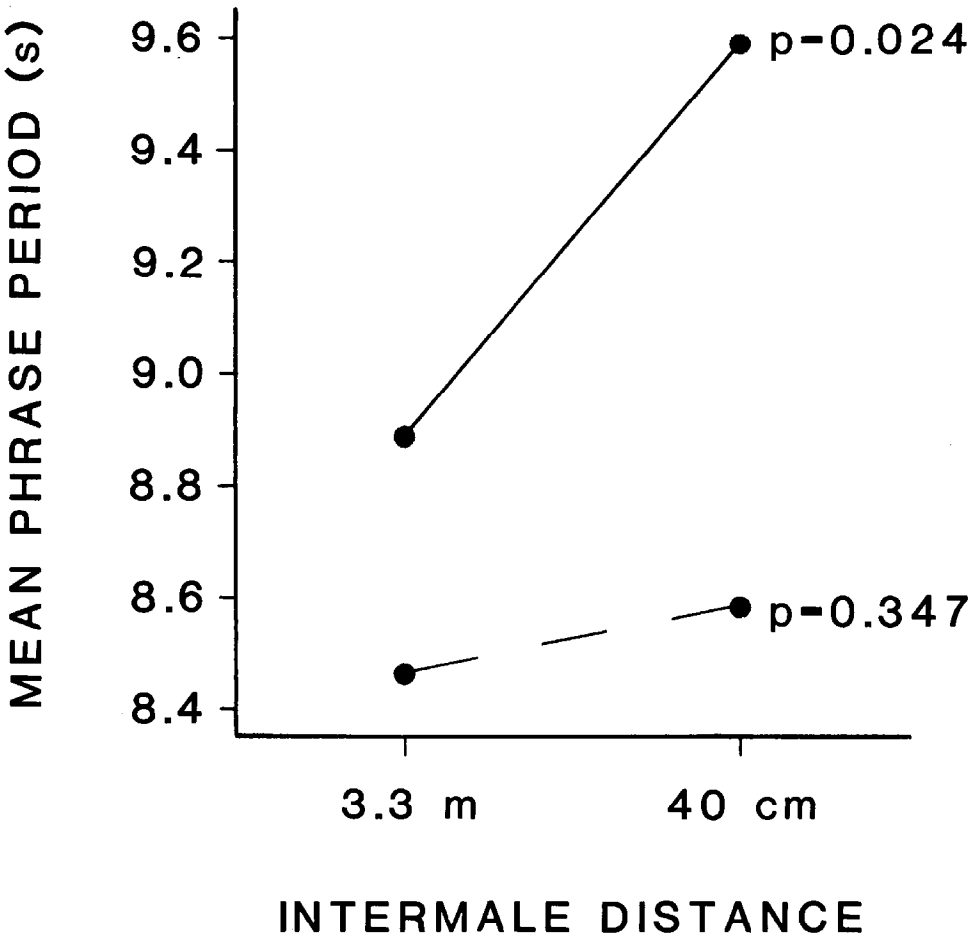

Fig. 2. The effect of intermale distance and female presence on the phrase period of pairs of chorusing *A. parvipennis* males. Males were recorded in the absence (solid line) and presence (dotted line) of a ticking female. P values from Student's t-tests.

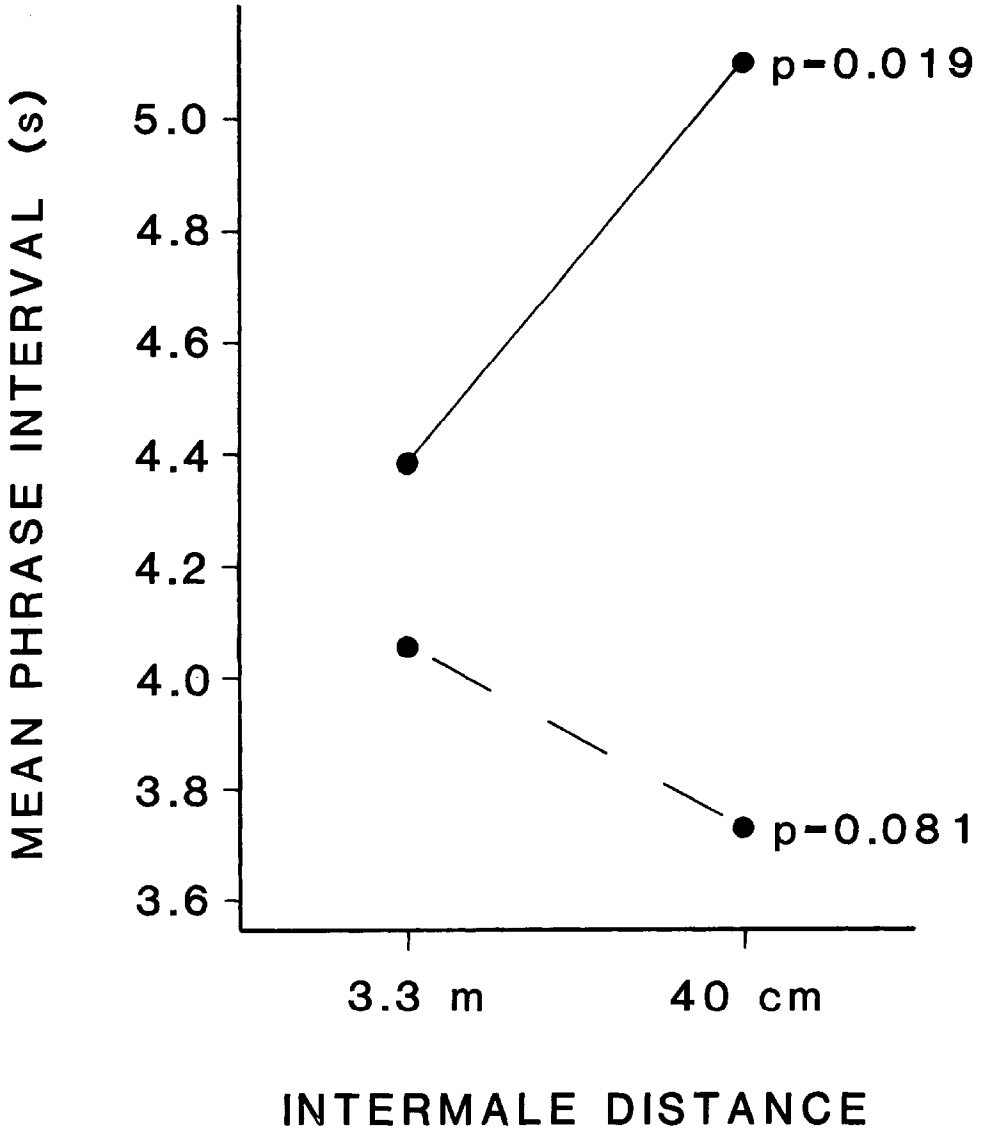

Fig. 3. The effect of intermale distance and female presence on the phrase intervals of pairs of chorusing *A. parvpennis* males. Remainder as in Fig. 2.

The effect on the nature of chorusing of moving males closer together was contingent upon female presence. There was a significant interaction between intermale distance and female presence for phrase interval (Fig. 3; $F = 56.92$; $df = 1,2$; $p = 0.017$) and the interaction for phrase period approached significance (Fig. 2; $F = 15.17$; $df = 1,2$; $p = 0.060$). In the absence of a female, the effect of moving chorusing males closer together was opposite to that of female presence, i.e., there was an inhibitory effect expressed as a reduction in phrase rate. Both mean phrase period (Fig. 2) and interval (Fig. 3) increased significantly when intermale distance was reduced from 3.3 m to 40 cm. The presence of a ticking female not only elicited an increase in phrase rate of the chorusing males, it eliminated the effect of distance reduction between chorusing males (Figs. 2, 3).

Female presence and the reduction in intermale distance also affected the degree of phrase overlap by chorusing males. The presence of a female resulted in an increase in mean phrase overlap (Fig. 4; $F = 2371.61$; $df = 1,2$; $p = 0.0004$) and total overlap (Fig. 5; $F = 45.65$; $df = 1,2$; $p = 0.021$) at both intermale distances. As for phrase rate, decreasing the distance between chorusing males in the absence of a female had effects opposite to that of introducing a female. There was a significant interaction between female presence and intermale distance for both phrase overlap (Fig. 4; $F = 465.13$; $df = 1,2$; $p = 0.002$) and total overlap (Fig. 5; $F = 18.74$; $df = 1,2$; $p = 0.049$). When males were moved closer together in the absence of a female, there was a decrease in both mean (Fig. 4) and total (Fig. 5) phrase overlap; however, the latter difference was not statistically significant. As in the case of phrase rate, the presence of a female eliminated (Fig. 5) and even reversed (Fig. 4) the effect of reducing distance in the absence of a female.

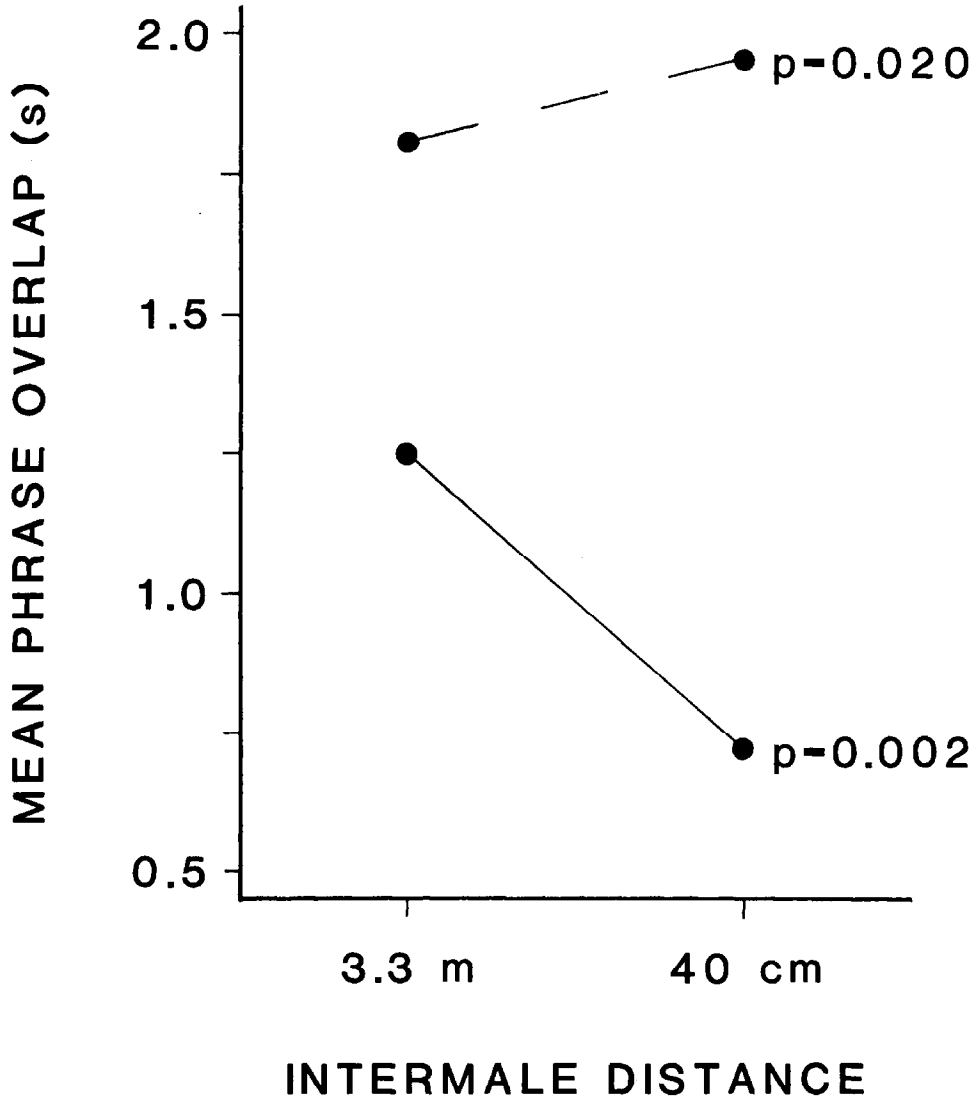

Fig. 4. The effect of intermale distance and female presence on the extent to which each of a pair of *A. parvipennis* males overlapped the phrases of their chorusing partner. Remainder as in Fig. 2.

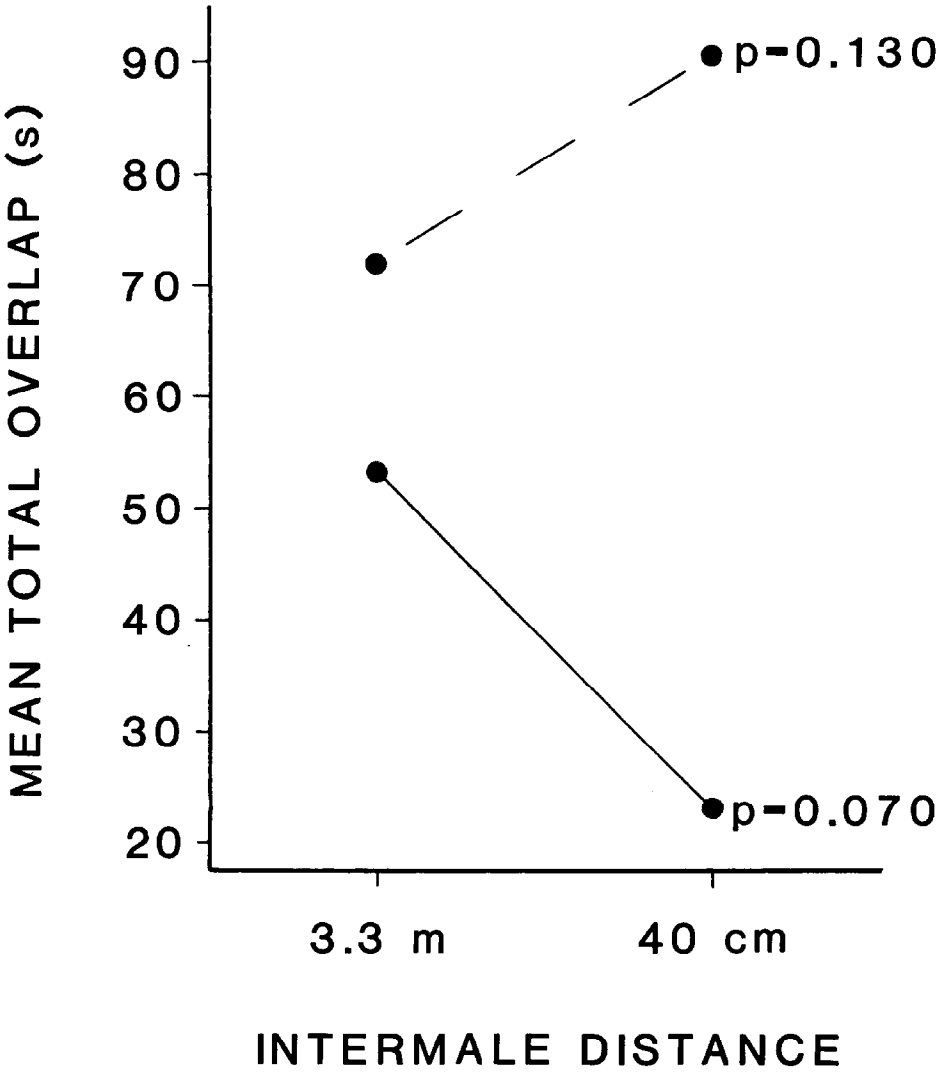

Fig. 5. The effect of intermale distance and female presence on the total period of time (number of phrases produced in 10 min x mean phrase overlap) that a pair of *A. parvipennis* males overlapped one another's phrases. Remainder as in Fig. 2.

Discussion

In analyzing the nature of chorusing by pairs of katydid males, several investigators have provided evidence that alternation is the result of one male being inhibited during the phrase of another male (Jones 1966, Shaw 1968, Samways 1976, Latimer 1981). Because the phrase intervals of *A. parvipennis* males are longer during acoustic interaction than when males sing alone, Shaw et al. (1990) suggested that alternation of overlapped phrases results from one male being inhibited for some period during the song phrase of another katydid. Smith (1986) showed that electronically produced imitations falling between an *A. parvipennis* male's phrases increased phrase interval when compared to males singing alone or when imitations occurred during a male's phrases. Moving two *A. parvipennis* males closer together than 3.3 m appeared to enhance inhibition, i.e., increased phrase interval was associated with reduced phrase overlap,

the latter resulting in more of the phrase of one katydid falling in the phrase interval of the other katydid. This increased inhibitory effect could have been the result of the increased intensity with which one katydid heard the sound phrases of the other.

Spooner's (1968) analysis of male-female and male-male acoustic interaction of a number of phanopterine species suggests that inhibition may not be uncommon in the acoustic interaction of conspecific males. In congregations of *Inscudderia strigata* (Scudder) and *Amblycorypha floridana* Rehn and Hebard males, phrases (lisps or buzzes) produced by one male or a playback, resulted in a cessation of phrases by other males.

If acoustic interaction is involved in spacing dynamics, and if reduction in distance between two conspecific males increases the competition between the males, why would males reduce rate of sound output under the latter conditions? If, as Dadour (1989) suggests for *M. marki* males, increasing phrase interval between phrases enhances a male's ability to monitor an intruder (and, we assume, an intruder's ability to monitor a resident), then an increase in phrase interval, as well as a reduction of phrase overlap by *A. parvipennis* males, may facilitate the decision as to which male leaves the area of confrontation.

This reduction in rate of sound output is contrasted to an increase in rate of sound output evidenced when chorusing males were exposed to a ticking female (Fig. 2). The presence of a female also negated the effect of reduction in distance. Thus, the importance of competing for a sexually receptive female completely superseded the effect of male-male competition in the absence of a female.

In addition to increasing phrase rate in the presence of a ticking female, males increased phrase overlap. This phenomenon, which has been discussed in detail previously (Galliart & Shaw 1991), will only be summarized here. In the data utilized in this study to compare the nature of chorusing of male pairs in the absence and presence of a female, the male that usually succeeded in copulating with the female (the winner), overlapped the phrases of the other male (the loser) less than vice-versa (e.g., Fig. 1B). In fact, the total number of phrases overlapped for both katydids decreased in the presence of a female, but the decrease was principally due to a decrease on the part of the winner (Galliart & Shaw 1991). Thus, although the number of phrases overlapped decreased, the mean length of phrase overlap increased suggesting that this increase is a byproduct of males adjusting their phrase rates in an attempt to reduce the number of phrases they overlap. A preliminary analysis of three paired interactions has indicated that a male's extent of phrase overlap is greater when his chorusing partner does not overlap the male's previous phrase than when the chorusing partner does overlap it (unpublished data) (e.g., compare extent of phrase overlap by katydid 2 in Figs. 1A and 1B).

The question remains as to why males of some species increase sound output and others decrease it when distance between singing males is decreased. A number of factors could be involved. The importance of specific singing sites may determine the degree of energy expended. Field crickets occupy a burrow or equivalent which they defend and which may be important to success in mating with a female. In *Orchelimum* spp., the position within a resource patch may be important in controlling female access to the patch (Feaver 1977, 1983). In contrast, in other species, specific areas may be important because of an increased chance of encountering females, but occupation of specific sites within these areas may not be important. For example, in *A. parvipennis*, male and female density is related to density of preferred host plant (Shaw et al. 1981). However, because females tick in response to male sounds and two or more males may move to a ticking female, specific sites within a resource patch may not be important to defend.

Also, a mechanism of intermale communication which involves a reduction in energy output in the absence of a female may be favored by selection in order that energy is

conserved for male-male and male-female competitive communication in the presence of a sexually receptive female. In the presence of a ticking female, *A. parvipennis* males encounter one another physically and acoustically and male-male and male-female encounters may last for many hours. During one night's observation, we intermittently observed three females, each being courted by 4-5 males, from our initial observation (between 10 P.M. and 12 midnight) until dawn. None of the females mated (Shaw et al., unpublished observations) before dawn. In the laboratory, we have run 114 mate choice trials with two males and one virgin female and, in 24 of these trials, copulation had not occurred in the 4-hour limit given to the trials. During the mate choice trials, males lost up to 12% of their body weight (Galliart & Shaw, unpublished observations).

With the emphasis on male-male and male-female strategies and the application of game and economic theory to an understanding of animal reproductive behavior, (Krebs & Davies 1984; Maynard Smith 1989) changes in acoustic interaction of conspecific males with change in intermale distance and presence of absence of females should be of special interest to animal behaviorists. The ease with which sounds can be recorded and analyzed make such analyses relatively easy. In some species, quantitative and/or qualitative changes, termed aggressive and courtship (Alexander 1967, Otte 1977) are obvious. This and Dadour's (1989) study have shown that interesting and significant changes in calling songs, which may not be obvious to the unaided ear, may be taking place in many species not characterized by the production of obvious aggressive and courtship songs.

Acknowledgment

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