EFFECT OF MALE-DEPRIVATION ON FEMALE PHONOTAXIS IN FIELD CRICKETS (ORTHOPTERA: GRYLLIDAE; *GRYLLUS*)

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Abstract

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The effect of depriving female field crickets of conspecific male contact upon the frequency of phonotaxic response to conspecific mating song was tested in *Gryllus integer* Scudder and *G. veletis* Alexander and Bigelow (Orthoptera: Gryllidae). In both species, positive phonotaxis was 5 to 9 times more frequent in male-deprived females than in females kept with males. Increased phonotaxis in the former group was apparent with 3 days separation. Addition of *G. veletis* males to the female-only culture greatly reduced subsequent phonotaxis. As female field crickets sometimes occur in male-free areas in the field, such increased phonotaxis may well be of adaptive importance.

Introduction

The calling songs of male crickets attract females and lead to matings (Alexander 1967). Although various factors influence the frequency and intensity of female phonotaxis, the single most important variable from an evolutionary perspective is the species-specificity of the song. Preferential phonotaxis by females to conspecific song was first demonstrated by Walker (1957) in tree crickets (Gryllidae; Oecanthinae), and has since been demonstrated experimentally in field crickets (Gryllidae; Gryllinae) (Hill *et al.* 1972; Moiseff *et al.* 1978; Popov and Shuvalov 1977; Zaretsky 1972), ground crickets (Gryllidae; Nemobiinae) (Paul 1976), and mole crickets (Gryllotalpidae) (Ulagaraj and Walker 1973). In these crickets, the rate at which individual song pulses are delivered (Popov and Shuvalov 1977; Ulagaraj and Walker 1975; Walker 1957; Zaretsky 1972) and the carrier frequency of the song (Loftus-Hills *et al.* 1971; Ulagaraj and Walker 1975) contribute to the phonotactic specificity. With the exception of the field studies of Ulagaraj and Walker (1973, 1975), studies of cricket phonotaxis have been conducted using females isolated from males in laboratory containers. Although it is generally believed that such male-deprivation promotes increased female phonotaxis, there is, in fact, no evidence that this is the case (Paul 1976). As a component of previous and on-going studies on cricket reproductive behaviour and phonotaxis, it became necessary to quantify the effect of male-deprivation on female phonotactic response. I here report experimental evidence which indicates that male-deprivation does result in a significantly increased frequency of positive phonotaxis by females of two species of field crickets, *Gryllus integer* and *G. veletis*.

Methods of Study

Adult *G. integer* were collected in Austin, Texas, under electric street lights where they had flown on 12 July 1974. Fifty females and 25 males were placed in a terrarium for 5 days. Twenty-five females were removed and placed in a terrarium without males. Both terraria (41 cm × 92 cm × 30 cm) contained pans of moistened vermiculite for oviposition, corn meal, pieces of apple, and cotton-plugged test tubes containing water. Although not controlled, laboratory lights were generally switched on from 0800 to 2000 h, thus approximating the normal photoperiod. Female phonotaxis was tested at night in a box (80 cm × 80 cm × 120 cm) lined with acoustical tile, and with a circular cardboard arena (72 cm × 14 cm) inside. A 20-watt incandescent red bulb was suspended above, and a high frequency loudspeaker (Radio Shack — Realistic 40-1224) was placed on one side of the arena. A Uher 4000 Report L tape recorder broadcasted previously recorded *G. integer*

calling song through the loudspeaker at 78-81 db (A scale) as measured with a General Radio Sound Level Meter – 1565 B held 10 cm in front of the loudspeaker[1]. A single female was placed under an inverted beaker in the centre of the arena. After the female became quiescent (usually within 2 min), the beaker was removed and song broadcasting commenced. A trial lasted until a positive response was recorded, until 5 min had elapsed, or until the female left the arena. A positive response involved a female climbing on and remaining motionless on the front of the loudspeaker for at least 30 sec. Twenty females from each group were tested once each night. Tests were conducted on the first 8 days and then again on day 14 following separation.

With the following exceptions, the same procedure was used with 30 *G. veletis* females collected as adults on the campus of Brock University, Niagara Region, Ontario on 29 and 31 May 1978. All 30 were housed in a common terrarium with 10 adult males for 10–12 days. Fifteen females were then placed in a separate terrarium without males. Crickets were exposed to a photoperiod of 12:12 h with light and dark periods opposite those of an outdoor cycle. Trials were conducted in a circular arena (105 cm × 15 cm) constructed of expanded polystyrene (Styrofoam®). A Uher 240 CR cassette tape recorder and a loudspeaker embedded in the wall of the arena at a height of 3 cm were used. Individual females from both groups were tested for 6 days. After trials on day 5, seven male *G. veletis* were placed in the female-only terrarium.

Results

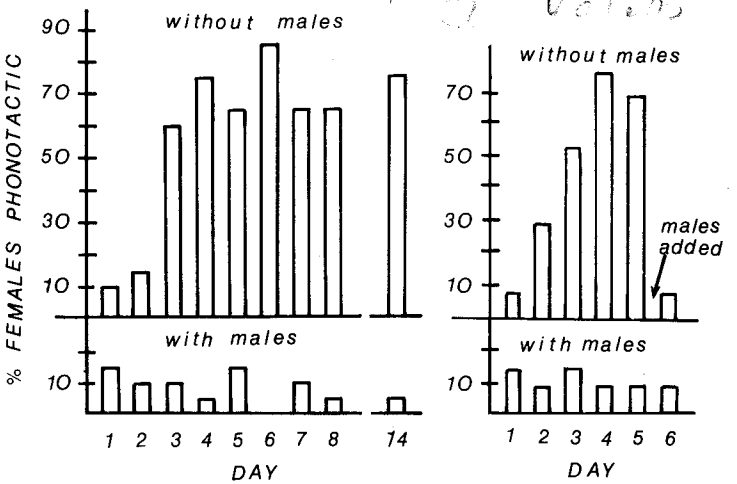
Percentages of females showing positive phonotaxis are summarized for *G. integer* (Fig. 1) and for *G. veletis* (Fig. 2). Chi-square tests (Snedecor and Cochran 1967) on the actual frequencies indicate that for male-deprived females of both species, the frequency distributions depart significantly from uniformity (for *G. integer*, $\chi^2 = 19.37$, d.f. = 8, $p < 0.02$; for *G. veletis* excluding day 6, $\chi^2 = 10.39$, d.f. = 4, $p < 0.05$). Females kept with males, however, have frequency distributions which do not depart from uniformity.

The relative degree of phonotaxis between conspecific groups on each day was also compared. For *G. integer*, females deprived of males and those kept with males did not differ significantly on days 1 and 2. A significantly greater phonotactic response was observed for male-deprived *G. integer* females on day 3 ($\chi^2 = 7.1$, d.f. = 1, $p < 0.01$) and for each day thereafter (χ^2 values range from 17.0 to 6.25, $p < 0.001$ to $p < 0.02$, d.f. = 1). In *G. veletis* no significant differences between the two groups were observed on day 1 or 2. Females deprived of males, however, demonstrated significantly greater phonotaxis than did females kept with males on days 3, 4, and 5 ($\chi^2 = 3.6$, 8.3, and 7.4; $p < 0.05$; d.f. = 1). After the addition of conspecific adult males, *G. veletis* females showed a very reduced level of phonotaxis to the tape song.

Discussion

The experiments reported here clearly demonstrate that male-deprived female field crickets are more readily attracted to conspecific mating songs than females exposed continuously to males. In both *G. integer* and *G. veletis*, the increased level of phonotaxis was not evident until day 3 following separation. One day of exposure to conspecific males, however, greatly depressed the incidence of phonotaxis in *G. veletis*. Although it is not known if these females mated when males were added to their terrarium, Hörmann-Heck (1957, as cited in Engelmann 1970)

[1]This sound intensity is well within the range observed for *G. integer* males in the field ($\bar{X}$ = 76.5 db, range = 46-92 db, S.D. = 11.14, N = 24; see Cade 1979*a*).



FIGS. 1–2. Percentage (N = 20) of positive phonotactic responses by female *Gryllus integer* and percentage (N = 15) of positive phonotactic responses by female *G. veletis* kept with and without conspecific males.

demonstrated that female *G. campestris* L. remate more readily following a period of male deprivation. Also, Morris *et al.* (1975) showed that mating eliminated the subsequent phonotaxis of female *Orchelimum gladiator* Bruner (Orthoptera: Tettigoniidae). Interestingly, a few *O. gladiator* females became phonotactic 3 days after mating, a time period corresponding to that required to produce increased phonotaxis in male-deprived crickets.

Gryllus veletis and *G. integer* are very different congeneric species. Differences between these species involve the number of generations per year, geographic distribution, and wing-length polymorphism (Alexander 1968). It is, therefore, somewhat surprising that such similar results were obtained for *G. integer* and *G. veletis*. In field studies with *G. integer* I observed females in areas not populated by calling males, suggesting that male-deprivation routinely occurs. It is, however, difficult to explain the adaptive significance of increased phonotaxis following male-deprivation. Flying *G. integer* females are generally inseminated (Cade 1979*b*) and exposure to males in laboratory containers should have increased the likelihood of insemination for females of both species. In ovipositing female insects, females become more receptive to males as the sperm supply is depleted (Englemann 1970). Sperm depletion is, however, unlikely to occur in only 3 days. Moreover, in the field female *G. integer* which oriented to taped conspecific song were later shown to have spermatozoa in their spermathecae (Cade 1976, 1979*a*). If increased phonotaxis following male-deprivation results in remating, the benefits accruing to individual females may involve additional genetic diversity in progeny, the acquisition of nutrition through consumption of male spermatophores, and the correction for the possibility that previous matings did not result in maximum insemination (Sakaluk and Cade unpub.). At any rate, workers interested in female cricket phonotaxis should consider the possibility that male-deprived females are unusually phonotactic.

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