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Male spacing behaviour and acoustic interactions in a field cricket: implications for female mate choice

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Males of several acoustically communicating orthopteran species form spatially and temporally structured choruses. We investigated whether male field crickets of the species *Plebeiogryllus guttiventris* formed choruses in the field. Males formed spatial aggregations and showed fidelity to a calling site within a night, forming stable choruses. Within aggregations, the acoustic ranges of males overlapped considerably. We tested whether males within hearing range of each other interacted acoustically. The chirps of simultaneously calling males were aphasic with respect to each other and showed no significant alternation or synchrony of calls. Some individuals changed temporal features of their calling songs such as chirp durations and chirp rates in response to a simultaneously calling neighbour. The implications of these results for female mate choice are discussed.

Male crickets use calling songs as long-distance mate attraction signals (Alexander 1967). Although males of most cricket species are solitary, calling males of a number of species form spatial aggregates or 'choruses' rather than being uniformly distributed in available habitat. Spatial aggregation or chorus formation may be a form of resource defence polygyny or resource-based lek (Gerhardt & Huber 2002). Aggregation may also be driven by the advantage that it might offer in predator avoidance: individuals within aggregations may be less conspicuous to parasites and predators than individuals calling in isolation (Burk 1982; Greenfield 1994). A more controversial hypothesis for aggregate formation is that of increased female attraction to calling male aggregates as opposed to solitary callers (Gerhardt & Huber 2002).

At a more local scale, however, both experimental evidence (Arak et al. 1990; Farris et al. 1997) and theoretical considerations (Forrest & Green 1991; Forrest & Raspet 1994) suggest that males pay a cost in terms of reproductive success if they allow their acoustic ranges to be overlapped by those of others. Males with overlapped acoustic ranges attract fewer females than if they do not allow overlap, particularly if they produce low-intensity song (Forrest & Raspet 1994; Farris et al. 1997). This leads to the expectation that even when males aggregate on a larger spatial scale they should attempt to prevent or reduce acoustic range overlap with their neighbours.

Female crickets, on the other hand, use calling song not only to locate potential mates but also to discriminate between them by using specific features of their calling songs (reviewed in Gerhardt & Huber 2002). Females might therefore prefer to compare males with others in a population before making a decision to mate and this could drive the formation of aggregates (Alexander 1975; Bradbury & Gibson 1983). Thus, at local scales, males and females appear to drive the spatial patterning of calling males in opposite directions (Farris et al. 1997).

The spacing of calling males and the intensity of their calling songs determine whether males can hear their calling neighbours. Male spacing thus determines the possibility and nature of acoustic interactions between calling individuals. Acoustic interactions between calling males can result in the alternation or synchronization of calls, as reported in a number of species of crickets and frogs (frogs: Brush & Narins 1989; Schwartz 1993; tree crickets: Walker 1969; Forrest et al. 1998; bushcrickets: Sismondo 1990; Greenfield & Roizen 1993; Hartbauer et al. 2005). Females of some species have been observed to prefer the calls of males that lead their neighbour's calls by a few milliseconds (Snedden & Greenfield 1998), as a consequence of the sound localization mechanism used by ensiferans (Römer et al. 2002). Males interacting with each other would therefore be expected to readjust the timing of their calls in response to those of their neighbours in an attempt to lead them (Greenfield & Roizen

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1993), giving rise to the phenomenon of synchronous choruses. Since a sound localization mechanism similar to that of bushcrickets is used by field crickets (Horseman & Huber 1994a, b), acoustically interacting field crickets may also be expected to synchronize their calls.

Female crickets are known to prefer calls with higher chirp rates and longer chirps (Tuckerman et al. 1993; Wagner 1996; Berg & Greenfield 2005). Males would therefore be expected to alter the temporal structure of their calling songs, producing longer chirps at higher rates, in response to the song of a competing neighbour.

Studies on field crickets have principally concentrated on demonstrating that the distributions of crickets on large spatial scales show aggregation as well as regularity within aggregates (Campbell & Shipp 1979; Cade 1981; Campbell 1990). These studies do not, however, address the question of whether a female cricket in such an aggregate can perceive multiple males. Most previous studies of female preference for call characters have used either single or simultaneous stimulus call presentation paradigms (Gerhardt & Huber 2002). The ecological relevance of data from such experiments is difficult to evaluate unless information is available on whether a female cricket of the species being studied is likely to hear males simultaneously or singly in the field.

In addition, as has been pointed out by Gerhardt & Huber (2002), field studies on all aspects of chorusing behaviour, such as spacing within a chorus, the relation of spatial pattern to acoustics, and fine temporal structuring of choruses, have never been carried out in a single system. Often, where detailed information about spacing behaviour and its relation to call intensity is available, no information is available about the temporal structuring of choruses (Römer & Bailey 1986). Other studies provide information on the spacing behaviour and temporal structuring of choruses but not on call intensity (Greenfield & Snedden 2003).

In this study, we examined whether (1) males of the field cricket species *Plebeiogryllus guttiventris* form stable aggregations in the field, (2) these aggregations form choruses from the point of view of a female and (3) simultaneously calling males interact acoustically.

GENERAL METHODS

Plebeiogryllus guttiventris is a field cricket species that is widely distributed on the Indian subcontinent (Chopard 1969). Sound recordings for song analysis, measurements of sound pressure level and observations on spacing and movement patterns were carried out on adult males located in the field in and around Bangalore, India. For the laboratory experiments on female hearing threshold and interactions between calling males, we used adult males and females from a laboratory culture of *P. guttiventris* established in 2002, into which wild-caught adult males and females were introduced every year. Breeding cultures were maintained in large plastic barrels at room temperature on a 12:12 h light:dark cycle. The crickets were reared on a diet of Nutripet Dog Chow and water was provided ad libitum. Male and female larvae were separated at the last instar for use in experiments and reared separately to ensure virginity of females. Males and virgin females were tested 3–4 weeks after the final moult.

SONG STRUCTURE

Methods

Calling song characterization

We recorded calling males in the field, with a Sony WM-D6C Professional Walkman and Sony ECM-MS957 microphone (frequency response: 1–12 kHz ± 3 dB), between December 2002 and March 2003. Ambient temperatures close to the ground at the time of recording were measured with a Kestrel 3000 Pocket Weather Station. Recordings of the calling songs of 57 males were made at temperatures of 11.3–27°C. The recordings were made on analogue tape and digitized with a Creative SoundBlaster A/D card at a sampling rate of 44.1 kHz. Spectral analysis was carried out with the software SpectraPlus Version 3.0 (Pioneer Hill Software, Poulsbo, WA, U.S.A.).

Temporal features of songs (number of syllables/chirp and chirp and syllable period, i.e. the time from the start of one chirp/syllable to the start of the next) were measured for 20 s of song (which had been down-sampled to 16 kHz) for each male by using custom-written signal analysis programs (S. Chandrasekhar, unpublished software) for Matlab Version 6.5 (The Mathworks Inc., Natick, MA, U.S.A.) and were regressed against the temperature of the recording. Frequency distributions of chirps with different syllable numbers (chirp types) were also computed and the average proportion of each chirp type was calculated for each individual. The proportions of each chirp type were arcsine transformed and analysed with a one-way repeated measures ANOVA to test whether there were significant differences between chirp types pooled across individuals. Post hoc Tukey highly significant difference (HSD) tests were used for pairwise comparisons of the proportions of different chirp types between individuals. Statistical analyses were carried out with Statistica (Statsoft Inc., Tulsa, OK, U.S.A.) software.

Results

Temporal features of calling song

Calling song consisted of short chirps that varied considerably in duration because of differences in the number of syllables per chirp (Fig. 1a). In a typical five-syllable chirp (Fig. 1b) the amplitude of succeeding syllables increased and usually reached a maximum at the third syllable. The different chirp types were produced in varying proportions (one-way ANOVA: $F_{6,318} = 52.67$, $P < 0.0001$; Fig. 2a). The most common chirp was the five-syllable chirp, followed by chirps with two and four syllables each (Fig. 2a). The mean number of syllables per chirp was not dependent on temperature ($R^2 = 0.00$, $N = 54$, $P = 0.72$; Fig. 2b).