Choice of singing sites by male bushcrickets (*Tettigonia viridissima*) in relation to signal propagation

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Summary. The spatial dispersion of singing male bushcrickets (*Tettigonia viridissima*) in a marshland habitat was found to be significantly clumped. Males clustered in patches of taller vegetation, but within such clusters, males were regularly spaced with a mean distance of 6 m between nearest-neighbours. Males occupied perches on plants that were, on average, 0.3 m above the top of surrounding vegetation. Physical and acoustical interactions between males were observed more frequently when males were singing from higher sites. Excess attenuation of the male song was found to increase with frequency but decreased markedly with increasing elevation of the singing male above the ground. The maximum detection range of the song, realized when the insect was singing > 1 m above the surrounding vegetation, was estimated as 60 m for the fundamental frequency (10 kHz), 38 m for the 1st harmonic (20 kHz) and 14 m for the second harmonic (30 kHz). By contrast, when males sang from the middle of dense reed beds, the estimated detection distance was only 8 m, 6 m and 4 m for each frequency band, respectively. Males could have increased the detection range of their songs almost three fold by singing from higher positions than those usually observed in the field. This suggests that there may be a cost of singing at higher elevations such as an increased risk of predation and/or increased aggression from neighbours. We suggest the spacing strategy adopted by males reflects a compromise between maximizing the range over which their songs can be detected and accurately localized by females and minimizing interference from competing males.

Introduction

The use of songs to attract mates from a distance is widespread among many birds (Eriksson and Wallin 1986), frogs (Littlejohn 1977), and insects (Ewing 1989). In such species, selection is expected to influence both the behaviour of the signaler and the form of the songs in such a way to maximize the signaler's reproductive success. One simple way that a signaler may increase its reproductive success is to increase the broadcast range, or "active space" (Marten and Marler 1977), of its song, thus increasing the probability that prospective mates detect the signal. However, to increase the broadcast range, animals have to cope with two important constraining factors, the physical properties of the habitat and the co-occurrence of competing signalers.

Physical properties of the environment cause the attenuation and degradation of songs. At some distance from the source, essential features of the song may be degraded beyond recognition or be too weak to be detected by prospective mates. Attenuation and degradation of acoustic signals may occur for a number of different reasons, the most important being geometric spreading, absorption and scattering of sound by vegetation and the atmosphere, and refraction of sound waves due to wind and temperature gradients (Michelsen 1978; Wiley and Richards 1978; Richards and Wiley 1980; Michelsen and Larsen 1983; Michelsen 1985).

Most of the early work on the propagation of animal sounds has been carried out on signals with frequencies in the range commonly utilized by birds and mammals, i.e. 50 Hz–10 kHz (e.g. Marten and Marler 1977; Marten et al. 1977; Michelsen and Larsen 1983), but the attention paid to the propagation of insect sounds with frequencies above 10 kHz is increasing (e.g. Popov et al. 1974; Schatral et al. 1984, 1985; Bailey et al. 1990).

Sound emission by insects is very inefficient at low frequencies, due to the small size of their sound-radiating structures. Consequently, many insects produce high frequency signals, but this involves other constraints, because the attenuation of signals increases markedly as the frequency increases (Michelsen and Nocke 1974).

There are two ways in which animals may minimize signal attenuation. First, they can utilize signals with optimum properties for transmission in the kind of habitat that they favour (e.g. Nottebohm 1975; Waser and
Waser 1977; Hunter and Krebs 1979; Waas 1988). Alternatively, they may adjust their behaviour by choosing appropriate microhabitats and times of the day for singing (Bailey and Roberts 1981; Prozesky-Schulze et al. 1975; Henwood and Fabrick 1979). Behavioural adaptations for efficient sound transmission, although rarely investigated, are widespread among insects that use acoustical signals to attract mates (e.g. Paul and Walker 1979; Doolan and MacNally 1981; Gwynne and Edwards 1986).

The co-existence of conspecific signalers may also reduce the efficiency of advertising for mates, either through mutual acoustical interference between competing signals (Römer et al. 1989) or because songs produced by competitors are more attractive to potential mates. A common strategy adopted by many advertising species is to maintain an individual distance to other signalers by acoustical or physical interactions (e.g. Alexander 1961; Fellers 1979). This behaviour allows individuals to broadcast within a zone which is free from competitors.

Environmental and biological constraints on an animal’s broadcasting strategy have usually been the subject of separate studies. However, because animals rarely advertise for mates in total acoustic isolation from their competitors, it is clear that both factors will interact to some degree. In this paper, we have combined two approaches to investigate the spatial dispersion of singing male bushcrickets, *Tettigonia viridissima*, in the field. We first describe the observed dispersion of signalers and report their preferences for different vegetational types as broadcasting sites. Secondly, we measure the extent to which songs are attenuated when males sing from different positions in the habitat and estimate the range over which their songs can be heard by females in each situation.

**Methods**

**Habitat.** A population of bushcrickets, *T. viridissima*, was studied at Dagnäsjön Nature Reserve, Björnlunda, approximately 90 km southwest of Stockholm, Sweden. The study area (1.8 ha) consisted of a low-lying marshland habitat on a peninsula extending into Lake Bäven. The vegetation was highly stratified and could be classified into three distinct layers. The lowest layer (< 1 m maximum height) covered approximately 70% of the study site and was dominated by the sedge *Carex acuta*, reeds, *Juncus conglomeratus*, and the grass *Deschampsia cespitosa*. Patches of taller vegetation, including thick stands of meadow sweet, *Filipendula ulmaria*, scattered fennels, *Peucedanum palustre*, and small alders, *Alnus glutinosa*, formed a layer of vegetation of intermediate height, the tips of these plants extending up to 3 m above the ground. Taller bushes and trees, mainly alder, sallow, *Salix* sp. and birch, *Betula pendula*, formed the highest layer of vegetation, reaching a maximum elevation of 15 m above ground.

**Estimate of spacing.** We censused the study site on 5 days during the period September–October, 1987. All surveys were conducted during periods of continuous sunshine between 1300 and 1700 hours, the period of peak singing activity at our study site. All singing males were located and their positions marked by attaching a numbered piece of yellow reflective tape on the upper part of the male’s singing perch where it was clearly visible from a distance. At the same time we noted the species of plant on which the male was sitting, the elevation of the singing male above the ground and the mean height of the vegetation surrounding the male’s singing perch. Even if this procedure silenced the males, they resumed singing in approximately the same position after a short period of time. In what follows, the vertical position of a singing male is expressed in relation to its height above or below the top of the surrounding layer of vegetation.

Distances between males and their nearest singing neighbours were measured in the field. The position of all singing perches were plotted onto a detailed map of the habitat in the morning after each census day. The dispersion of singing males was analysed using the Clark and Evans (1954) nearest-neighbour techniques. The parameter R is a measure of the degree to which the observed mean nearest neighbour distance between singing males departs from the expected in an infinitely large, random distribution of the same density. The value R ranges from 0 (maximum aggregation) through 1.0 (random distribution) to 2.149 (maximum regularity). Statistical tests for significant differences from R = 1 were carried out using the method described in Clark and Evans (1954).

In cases in which a clumped distribution was found, the analysis of male distribution within each of the clumps required a subjective and somewhat arbitrary demarcation of their boundaries. We followed the procedure adopted by Bailey and Thiele (1983) in their study of male spacing in the tettigonid, *Mygalopsis marki*. After determining the mean nearest-neighbour distance in the field we referred to our maps of the habitat, and with a pair of compasses set at this distance, we circled each individual. Individuals whose circles overlapped were considered as belonging to the same clump. Clumps so defined consisted of 2–18 individuals; however, only those clumps consisting of > 5 individuals were used in the analysis of intraclump spatial patterns.

**Description of song.** The song of *T. viridissima* has been described previously by Rheinlaender and Römer (1980), Ahlén (1981) and Keuper et al. (1988). It consists of a train of disyllabic pulses repeated monotonously for long periods. The first syllable of each pulse is emitted during the opening phase of the wings and the second syllable during the closing phase (Fig. 1, insert). The power spectrum of the song is shown in Fig. 1. The distribution of energy falls into three more-or-less distinct frequency bands: a low frequency band (fundamental frequency) centered around 10 kHz, and two higher frequency bands (1st and 2nd harmonics) centered...