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**FEMALE
RESPONSE
AND MALE
SINGING
STRATEGIES**

IN TWO ORTHOPTERAN SPECIES

FEMALE RESPONSE AND MALE SINGING STRATEGIES IN TWO ORTHOPTERAN SPECIES

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ABSTRACT

The response behaviour of females and the singing of males was studied in two species of orthoptera: the great green bushcricket Tettigonia viridissima and the common green grasshopper Omocestus viridulus. The study involved direct observation in the field and laboratory experiments.

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The spacing of males in the two species is very different. T. viridissima males space out regularly within areas where the males can elevate themselves above the surrounding vegetation. In contrast, O. viridulus males move about frequently and do not seem to stay in any individual zone. They adjust their singing behaviour according to the presence of other males and sing shorter songs if they have heard a nearby male sing recently. The reason for this may be that singing short songs increases the probability that the male will detect a female response when singing in competition with other males.

The singing systems of these two species differ in that the males of one space out in favorable positions and sing continuously, while males of the other are mobile and adjust the duration of individual songs. This difference reflects the difference in female response behaviour.

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- II. Arak, A. and Eiríksson, T. 1992. Choice of singing sites by male bushcrickets (Tettigonia viridissima) in relation to signal propagation. Behav. Ecol. Sociobiol. 30: 365-372.
- III. Eiríksson, T. Singing and associated behaviour in the grasshopper Omocestus viridulus. Manuscript.
- IV. Eiríksson, T. In press. Female preference for specific pulse duration of male songs in the grasshopper, Omocestus viridulus. Anim. Behav.
- V. Eiríksson, T. In press. Song duration and female response behaviour in the grasshopper Omocestus viridulus. Anim. Behav.
- VI. Eiríksson, T. In press. Density dependent song duration in the grasshopper Omocestus viridulus. Behaviour.
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INTRODUCTION

Orthopteran insects are among the most prominent singers in the animal world, and they are frequently used in research on various aspects of acoustic communication. The most important groups in these studies are crickets (Gryllidae), mole-crickets (Gryllotalpidae), bushcrickets (Tettigonidae) and grasshoppers (Acrididae) (see Otte 1977; Ewing 1989 for reviews).

Most species have a unique type of song. A much studied question is the species-specificity of song pattern and the function of song in separating species (Perdeck 1958; Reynolds 1980; Heller 1984; Ragge 1986, 1987) and the difference between populations (Walker 1980; Ragge 1981; Ritchie 1991), but the variation in song pattern within a population is receiving increased attention (Cade 1980; Walker 1980; Cade and Cade 1992; Ritchie 1992). Orthopterans are now widely used as model species when studying function of acoustic communication in the sexual context, including both male-male competition and female choice (e.g. Butlin et al. 1985; Latimer and Schatral 1986).

Orthopteran insects are in many ways very suitable for these kinds of studies. They are relatively small, it is possible to perform realistic experiments in the laboratory, and many species are easy to breed (Moriarty 1969; Kelly-Stebbins and Hewitt 1972). They are also large enough to study their behaviour in the field and to perform experiments in semi-natural and natural environments. In addition, males and females readily respond to playbacks of song, permitting investigations on the function of song.

Advances in technology have also promoted research. Ever since Regen (1914) did his experiment on crickets with the help of a telephone, studies have been performed with more and more advanced equipment. Computers have made sound analysis easier and synthetic calls have become a valuable tool to study the functional significance of signal properties (Dörrscheidt and Rheinlaender 1980). Furthermore, results from other fields of research have proved valuable. Orthopterans have been used in research on the physiology of sound production (Bennet-Clark 1970; Forrest 1991) and hearing (Michelsen and Larsen 1978). Also the physical aspects of acoustic signalling, such as the propagation of sound in the environment, have been studied (Römer and Bailey 1990). Furthermore, investigations of the neural control of singing are often conducted on orthopterans and neuroethology is an expanding field of orthopteran research (Hedwig 1986 a,b; Harrison et al. 1988).

The mating systems of orthopteran insects are very diverse, making it possible to find suitable species for research of different aspects of communication. Males often attract females from a distance, both flying (mole-crickets: Ulagaraj and Walker 1975) and walking (crickets: Shuvalov and Popov 1973). In some species the males are territorial with males defending either singing sites or resources important to females (grasshoppers: Wang and Greenfield 1991) and using sound to signal to other males. In some species the female responds to the male with stridulation and then the male approaches the female (bushcrickets: Hartley and Robinson 1974; Zimmermann et al. 1989). Sometimes the female approaches and stridulates in response to male song (grasshoppers: Haskell 1958). The male can also actively search for the females (Butlin and Hewitt 1986).

This thesis deals with singing and associated mate searching behaviour in two orthopteran species, the great green bushcricket Tettigonia viridissima and the common green grasshopper Omocestus viridulus. The studies were conducted through observations in the field and by experiments, both outdoors and in the laboratory.

The calling song of T. viridissima is a more or less continuous trill and the females are attracted to males from considerable distances. The males are mainly stationary, but when two males get close to each other they start singing different songs and the interaction can result in a fight (personal observation, see also Schatral et al. 1985).

The grasshopper O. viridulus has a very different mating system. Females not only show phonotaxis to singing males, but also respond with a stridulation of their own. The establishment of mating pairs usually involves stridulation by solitary males and the approach of sexually receptive females, or the alternation of male and female songs followed by both sexes approaching each other (e.g. Jacobs 1953; Haskell 1958). Males may also find females by direct searching, but females are more likely to copulate if they respond with stridulation (Hartmann and Loher 1974). Males do not appear to engage in any form of physical contests for singing sites.

SONG STRUCTURE

The song of orthopteran insects is relatively simple. It is mainly amplitude modulated and formed through stridulation. The stridulatory apparatus varies among the different groups. Bushcrickets make sound by rubbing the wings together. When the plectrum on the right wing strikes a tooth of the file on the left wing, a short impulse results.

Gomphocerin grasshoppers rub the femur of the hind leg, where the file is located, against the wing (see Ewing 1989 for review).

The terminology of sound elements is not standardized and different authors use slightly different terms to describe orthopteran songs. The basic sound element is an impulse resulting from the impact of one stridulatory peg. Such an impact elicits a heavily damped oscillation. The fundamental unit of song is the pulse (Haskell 1957; syllable: Broughton 1972; chirp: Skovmand and Pedersen 1983). A pulse is the train of impulses produced by a complete movement of the stridulatory apparatus, i.e. an upstroke phase and a downstroke phase (syllable: Elsner 1974). Pulse duration, inter pulse interval and pulse rate are all terms used to describe pulse structure. When inter pulse interval is zero, the pulse rate is the reciprocal of pulse duration. A song is a continuous train of pulses (echeme: Broughton 1976).

The song repertoire of a species often includes many song types (Meixner and Shaw 1986) and songs are sometimes combined in a sequence (Ragge 1986). The most usual song type in most species is presumably intended to attract females and is referred to as the calling song or proclamation song. There are also other song types, such as rivalry or aggression song used in close encounters of males (Jacobs 1953; Young 1971). Copulation is not achieved immediately when a female is found and many different songs are used in courtship, especially in grasshoppers (Bull 1979; von Helversen 1986; Riede 1986).

The frequency spectrum of a single impulse determines the general spectral envelope of the complete pulse. The spectrum often peaks at a certain frequency, called the carrier frequency (Skovmand and Pedersen 1978). This frequency is usually relatively constant within each species, but as it partly depends on the impulse rate, which in turn depends on the speed of the stridulatory apparatus, there can be frequency shifts within pulses and between different song types.

Similar to many other bushcrickets, *T. viridissima* males sing with high frequency (Ahlén 1981). The carrier frequency is around 10 kHz, but the harmonics around 20 kHz and 30 kHz are prominent, and frequencies as high as 40 kHz can be detected (II). The song from *O. viridulus* has a carrier frequency around 16 kHz but the harmonic structure is more blurred than in *T. viridissima* (IV, see also Kutsch and Schiolten 1979).

FEMALE PREFERENCE

A basic question is which characters of male song are most important in evoking female response. Many different song parameters have been identified. These can be divided into two main categories: static, where females show preference close to the natural mean of that parameter, and dynamic, where the female preference is highly directional (Gerhardt 1991). There are reasons to believe that static parameters are associated with species recognition, whereas dynamic parameters signal male quality or how easy it is to localize the male. Information in the song about the quality of the individual, such as size, may be contained in frequency parameters of the song (Latimer and Lewis 1986), or magnitudes such as intensity, song duration or song rate (e.g. Latimer and Schatral 1986; Bailey et al. 1990).

Pulse duration or repetition rate often codes for species identity (e.g. Perdeck 1958; Bailey and Robinson 1971; von Helversen 1972; Pollac and Hoy 1979; Butlin et al. 1985; Doherty and Hoy 1985), but the frequency characteristics of a pulse or song are also important as female sensitivity is not equal for all frequencies (Counter 1977; Skovmand and Pedersen 1978; Butlin and Hewitt 1987).

Female grasshoppers respond to male songs in a regular manner. First there is an alert posture, followed by orientation towards the sound. Then the female usually runs or jumps in the direction of the sound and stridulates (see also Skovmand and Pedersen 1978). The whole sequence can be repeated several times. The stridulatory response or phonotaxis of female grasshoppers have been used to estimate the stimulus value of different characters of male songs in several studies (von Helversen 1972, 1984; von Helversen and von Helversen 1975, 1981; Skovmand and Pedersen 1978, 1983; Charalambous 1990). However, stridulatory response and phonotaxis are not necessarily elicited by the same song parameters, since pattern recognition and directional analysis are two processes operating in parallel in the grasshopper's central nervous system (von Helversen 1984; von Helversen and von Helversen 1987).

It is difficult to combine these two measures in one experiment so the preference of female *O. viridulus* for synthetic male songs of different pulse duration was estimated in two separate experiments (IV). In the first, the probability of the female responding with stridulation was measured during presentation of a randomized series of songs of different pulse durations. The second experiment measured phonotaxis of stridulating females towards loudspeakers in two-choice playbacks of songs of different pulse durations.

In both experiments the females preferred songs with an intermediate pulse duration, which coincided with the mean for natural songs. The results indicate the presence of stabilizing selection on pulse duration through female preference, and suggest that this song parameter may be important for species recognition.

Male grasshoppers of the genus Omocestus have a highly species specific duration of the calling song (Ragge 1986). Two playback experiments were conducted to investigate how variation in song duration affected female response (V). The duration of individual songs was varied in one experiment, and both the duration and number of songs was varied in the other.

Females responded more readily and with longer stridulation to longer male songs. There was, however, a diminishing return in the female response, so a male will gain less and less by singing longer songs. Repetition of short songs, with the same total duration as a long song, gave similar or even more intense response. The females also spent more time moving, probably towards the singing male, as a response to longer songs. These results suggest that the duration of individual songs is not important per se in evoking female response, but rather the total amount of singing.

A preference for long songs and many songs might result in a preference for larger males. There is a difference between the song duration of individual O. viridulus males when they sing alone, but the duration of individual songs is not directly related to size (VII). This does however, not mean that the singing is independent of size, since the recovery time needed before males can sing another song of equal duration is negatively correlated with size, smaller males needing longer time to recover.

In T. viridissima, females seem to be attracted by the amount and/or intensity of song. In an experiment on spacing (I), the majority of females released moved from their release points to one of the closest singing males. More distant signallers sometimes attracted females when one of the closest males did not sing, or sang very little, during the period in which females were moving. Comparisons of several characteristics of males successful in attracting females with those of equidistant unsuccessful males showed a significant effect of male weight and male singing activity. The heaviest males were more likely to be successful only because body weight and singing activity are highly correlated. This conclusion is supported by comparisons in which the most active singer was not the heaviest male, in which case the female most often chose the most active singer.

The pattern of female mate selection observed here is compatible with the process termed passive attraction (Parker 1982, 1983; Arak 1988). By approaching the male whose signals are most easily detected (often the closest male), the female will minimize the costs of movement to the source. The males that are most conspicuous are then expected to gain most females (Ryan and Rand 1990).

MALE SPACING

It has been found frequently that signalling males maintain some minimum distance from each other by means of acoustic and physical interactions. This sometimes results in a regular distribution of males within aggregation (e.g., Bushcrickets: Bailey and Thiele 1983; Schatral et al. 1985). The simplest interpretation of such "acoustic spacing" is that it allows males to broadcast their songs to females within a zone that is free from competitors.

As an alternative to spacing out, calling males might clump together, thereby increasing their collective call intensity and perhaps also the number of females attracted per calling male. To investigate the advantage of clumping versus spacing out, a field experiment with *T. viridissima* was performed (I). Clumped males were less successful in attracting females than regularly spaced males within the experimental area. Therefore within a homogenous habitat in which females are randomly distributed, male mating success will be maximized when males space out as far as possible from their competitors.

The natural spatial distribution of singing *T. viridissima* males in a marshland habitat was found to be significantly clumped (II). Males clustered in patches of taller vegetation, but within such clusters, males were regularly spaced with a mean nearest-neighbour distance of 6 m.

The reason for the clumped distribution of males seems to be that suitable singing sites are not evenly distributed over the habitat. Males occupied perches on plants that were, on average, 0.3 m above the top of the surrounding vegetation.

The broadcasting range of male song decreases with frequency, but increases markedly with increasing elevation of the singing male above ground (II). 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 1 st harmonic (20 kHz) and 14 m for the second harmonic (30 kHz). By contrast, when males sang from the middle of dense reed beds,

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 neighbors, as physical and acoustical interactions between males were observed more frequently when males were singing from higher sites (II). The spacing strategy adopted by males seems to be a compromise between maximizing the range over which their songs can be detected and accurately localized by females, and minimizing predation risk and/or interference from competing males.

Q. viridulus males distribute themselves in quite a different manner. Since females do not only approach a calling male but also signal their position, a male would profit by being mobile. In fact Q. viridulus males are not stationary (III), but move frequently and over considerable distance, sometimes several meters in a few minutes. An individual male ranged widely within an observation area of 400 m² where the total number of males was estimated as 150. It could not be seen that the males remained within some smaller area in the total space or maintained any exclusive space (see Young 1971 for discussion of Chorthippus brunneus).

SINGING STRATEGIES

A calling male has the problem of how he should distribute his song over time. In the simplest case, a male does best by singing constantly at a loud volume. T. viridissima appears to be a case where this is true.

A male Q. viridulus needs to take several additional factors into account to achieve an effective singing strategy. First, Q. viridulus females do not necessarily wait for a male song to finish before responding themselves with stridulation. In an experiment a majority of the females had already started to respond before a long song ended (V). There is evidence that grasshoppers are deaf while singing themselves (Hedwig 1986 b; Wolf and von Helversen 1986; see also Römer and Bailey 1990). Thus, in order to maximize the efficiency of his singing, a male must time his songs to decrease the overlap with female response singing, and increase the probability of hearing the female response (see also Greenfield 1990).

Second, grasshopper males are very mobile and may need to adapt their singing according to the presence of other males. Although duration of grasshopper song is species specific, there is also considerable variation within species (VII). One possible reason for this is that males are adjusting their singing tactics in relation to the density of competitors. Males would be expected to sing shorter songs when other males are nearby to enhance the probability of being the first to hear the female response.

To test this hypothesis an experiment was performed by placing different numbers of *O. viridulus* males in large outdoor cages and monitoring their singing behaviour (VI). The results show that males sing on average shorter calling songs as the number of males increases. It was also found that males compensate for singing shorter songs by singing more songs, so the total time spent singing stays similar at all densities. The results suggests that part of the variation in the duration of calling songs reported in several field studies is caused by a change in singing tactics at different densities of males.

In order to further study the influence of other males on the duration of songs *O. viridulus* was studied in the laboratory by recording two males at different distances from each other (VII). The males seemed to monitor the other males singing behaviour constantly and adjust their own singing accordingly. They sang on average shorter songs as the distance to the other male decreased, and the variation in song duration also increased as the distance decreased. Song duration was correlated with the time from the last song emitted by the other male, and the influence of this variable changes with distance. When the other male was not singing or the distance was great the male sang songs of similar duration as he did when singing alone.

This scenario is complicated by the singing of a different very short song type which is mainly, but not exclusively, used in male-male interactions. The probability that males sing such rivalry songs increases with the density of males and the number of these songs increases as male-male interactions get longer (VI). These rivalry songs may function in the spacing of males or may be an extremely short form of the normal calling song used when other males are very close. It seem probable that the songs termed normal calling song and rivalry song are just two ends of a song continuum functioning to stimulate females depending on the presence or absence of other males (VI, VII).

CONCLUSION

Females of the two species respond to male singing in a predictable manner, and are more likely to respond to males that sing more. Female T. viridissima approached the most active singer of those at equal distance, and sometimes bypassed males that were singing little. In O. viridulus, females were more likely to respond to longer or more songs, i.e. higher total amount of singing. The properties of the song are also important. This is exemplified in that O. viridulus females preferred intermediate pulse durations, and in T. viridissima the harmonic content could be important to localize, and to judge the distance to the male.

There is however a difference in the response behaviour. The receptive females in O. viridulus do not only respond to male song with phonotaxis, but also with stridulation of their own, and they do not necessarily wait for the male to end his song before they start responding. The adaptive basis for these differences in female behaviour is poorly understood. However, the differences are likely to influence male behaviour.

Given the female behaviour, a male T. viridissima would benefit from singing almost continuously. In addition he could increase his success by singing from an elevated position around half a meter to one meter above the surrounding vegetation to increase his zone of attraction. If other males come into this zone he should react in a aggressive manner, first with warning sounds and, if necessary, with physical interactions.

For an O. viridulus male the situation is more complex. As for T. viridissima, O. viridulus males should sing as much as possible. Males could also find females through direct searching, but he would be unlikely to find a receptive female in this way. This means that males have to monitor female response stridulation. If a female responds with stridulation she is probably willing to copulate. Thus an actively answering female is much more valuable to the male than a random female, and the mobility of males can be interpreted as foraging for stridulating females.

The main theme in male strategies seems to be similar in the two species. The observed difference in female response behaviour is, however, reflected in the singing behaviour of the males, and the different strategies appropriate to find females may be male adaptations to female behaviour.

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The adaptive significance of acoustic spacing in male bushcrickets *Tettigonia viridissima*: a perturbation experiment

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Summary. A perturbation experiment was carried out in which the spacing between singing male bushcrickets, *Tettigonia viridissima*, was artificially manipulated. The experiment entailed releasing virgin females into an area in which caged males were either spaced evenly or in which a proportion of the males were clumped. There was large variation among males in the proportion of time spent singing (range 39–91% of total singing time). Singing activity was correlated with male body weight, but was not influenced by male spacing. Out of a total of 108 females released during the experiment, the majority ($N=90$) moved from their release points onto the cage of one of the closest singing males. More distant signalers sometimes attracted females when one of the closest males did not sing, or sang very little, during the period in which females were moving. When clumped, males were less successful in attracting females than when regularly spaced within the experimental area. Therefore, within a homogeneous habitat in which females are randomly distributed, male mating success will be maximized when males space out as far as possible from their competitors. As predicted, a regular dispersion of signaling males is the pattern observed in the preferred microhabitats of this species in nature.

Introduction

Choruses of sound-producing insects and anuran amphibians have received considerable attention from behavioral ecologists in recent years. These

choruses consist of aggregations of males producing signals that attract sexually receptive, conspecific females.

The large scale spatial distribution of signaling males may, in many species, reflect the distribution of preferred resources such as foodplants (e.g., grasshoppers: Greenfield and Shelly 1985), oviposition sites (e.g., anurans: Wells 1977), or signaling sites (e.g., bushcrickets: Arak and Eiriksson, submitted). Alternatively, aggregations of males may form at arbitrary places in the habitat, called "leks" (reviewed by Bradbury and Gibson 1983), if clustering per se enhances an individual male's prospects of mating. Two suggestions have been made as to why males that join aggregations might experience increased mating success. Firstly, the combined effect of signaling by many males may increase the broadcast range of signal so that proportionally more females are attracted to larger choruses (Otte 1974; Alexander 1975). We refer to this as the "signal enhancement hypothesis". Secondly, it has been suggested that females may force males to aggregate in order to facilitate mate choice, and as a corollary, refuse to mate with isolated males (Alexander 1975; Bradbury and Gibson 1983). We refer to the latter hypothesis as the "female preference model."

On a smaller scale, it has been frequently found that signaling males maintain some minimum distance from each other by means of acoustic and physical interactions. This may sometimes result in a regular distribution of males within aggregations (e.g., bushcrickets: Bailey and Thiele 1983, Schatral et al. 1984; anurans: Arak 1983, Robertson 1984). The simplest interpretation of such "acoustic spacing" is that it allows males to broadcast their songs to females within a zone that is free from competitors (Arak 1983).

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The overall spatial distribution of signaling males in a habitat may, therefore, reflect a compromise between selective pressures favoring aggregation, which ensures a greater number of available females, and selective pressures to space out, which ensures successful courtship and mating once females have arrived at the aggregation (Doolan 1981). Given that there are many differences in population demography, habitat structure, and display behavior between signaling species, it seems likely that the balance of selective forces favoring either aggregation or dispersal will also vary. It is surprising, therefore, that few studies have been carried out with the aim of discriminating between different hypotheses for male spacing.

In this paper we investigate the optimal spacing pattern in bushcrickets, *Tettigonia viridissima*, by means of perturbation experiments. We have previously shown that the males prefer microhabitats that allow them to broadcast their songs from perches elevated above the dominant layer of vegetation. However, within aggregations, males are spaced evenly and maintain a minimum distance from their competitors both by acoustical and physical interactions (Arak and Eiriksson, submitted). Here we demonstrate that this spacing pattern is optimal for attracting females over short distances. Artificially increasing the degree of aggregation within clumps was found to decrease the ability of individual males to attract females, thus refuting the suggested advantages of signalling in groups.

Methods

All bushcrickets used in the experiments were collected in the field as final instar nymphs and reared to sexual maturity in the laboratory. Males and females were kept individually in well-ventilated plastic boxes (15 × 10 × 10 cm) and were fed daily with fresh grass and dried pellets of dog food. A few days after the final moult, 19 males were taken from the laboratory stock and each placed in a tubular cage (100 × 50 cm) made by suspending a black nylon net between two wire hoops. At each end of the cage, the net was gathered and tied firmly to a central wooden pole, approximately 2 m long, which supported the cage and provided a convenient singing perch for the captive male. The base of the pole was pushed firmly into the ground so that the lower end of the cage came to rest 30–40 cm above ground level. A small amount of fresh grass, a few sprigs of meadow-sweet *Filipendula ulmaria*, and dog food pellets were placed in each cage at 2-day intervals to provide food and cover. Males began singing in the cages within a few hours of acclimatization and sang regularly for several hours each day as long as the shade temperature exceeded 13°C.

Song sections were recorded at a distance of 50 cm above the sound-producing mirror of each male, using an ultrasound detector Model D-960, (frequency range 10–150 kHz, Lars Pettersson, Vretgränd 9D, S-753 22 Uppsala, Sweden) on time-

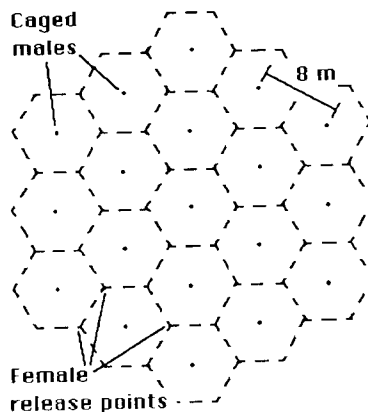


Fig. 1. The experimental design showing how positions of caged males and female release points were determined. Only 3 of the 36 female release points are indicated

expansion mode, linked to a Sony TC-D5M cassette recorder. The time-expanded signals (frequency-reduced 10 times) were analyzed on a Uniscan 4500 sonograph to determine frequency characteristics of songs. Sound pressure levels of songs were measured 50 cm above the mirror, using a Brüel and Kjær 2221 precision sound level meter on peak-recording mode. In this mode, the meter has a linear frequency response from 0.2 Hz to 20 kHz. The peak measurement of the signal, therefore, corresponds to the peak amplitude of the emphasized fundamental frequency of the song (approximately 10 kHz). All males were weighed to the nearest 0.01 g before each experiment began. After completing all experiments, the males were killed, and pronotum length, hind tibia length, and mean diameter of the sound-producing mirror were measured using a Wild binocular microscope with graticule eyepiece.

In preliminary trials, virgin females readily approached singing males 1 week after their final molt. At this time, the 19 caged males were arranged in a field adjacent to the Tove-torp Research Station, 90 km south of Stockholm. This site was chosen because it consisted of fairly homogeneous vegetation, mainly long grasses and clover, and was not colonized by wild *T. viridissima* (the nearest singing males were found approximately 100 m away, beyond the hearing range of the animals used in the experiment; see Rheinlaender and Römer 1986). The experimental area was first mapped out into a honeycomb pattern of 19 perfectly fitted hexagons of equal size (Fig. 1). In Experiment 1, a randomly chosen cage was placed at the center of each hexagon (Fig. 2a). For a fixed number of males in a given area, this arrangement maximizes the distance between adjacent males, each individual having six equidistant nearest-neighbors. The distance between consecutive cages was fixed at 8 m, slightly greater than the mean nearest-neighbor distance of 6 m between regularly-spaced singing males observed in thicker vegetation in the field (Arak and Eiriksson, submitted).

In Experiment 2, we simulated a situation in which a proportion of the males cluster within the habitat. The six cages in closest proximity to the central cage were moved 6 m directly towards the latter. The arrangement (Fig. 2b) then consisted of a central group of seven cages spaced 2 m apart (denoted 'C'), surrounded by an outer group of 12 cages spaced 8 m apart (denoted 'O').

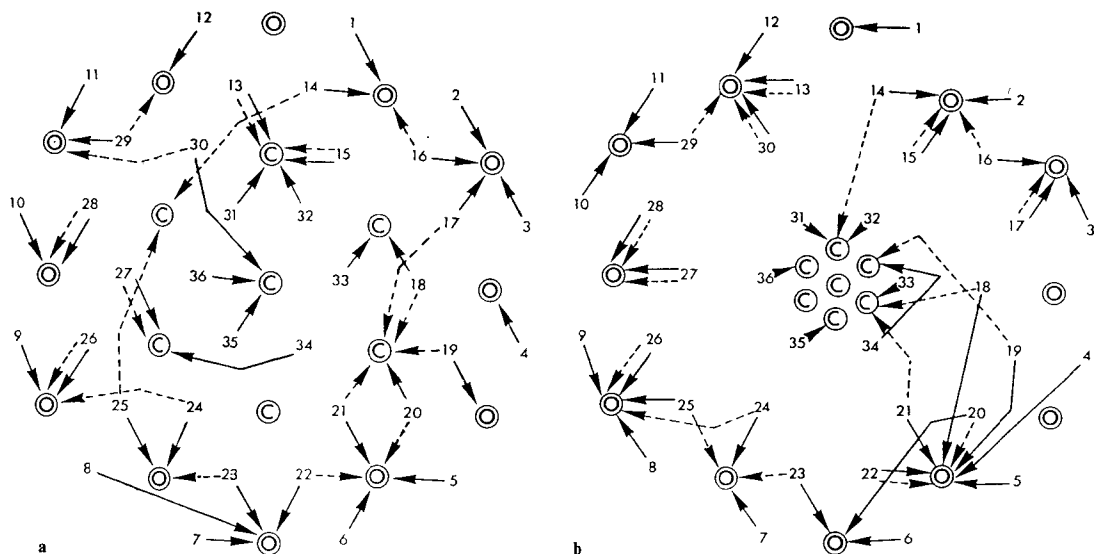


Fig. 2. The arrangement of caged singing males in (a) Experiment 1 and (b) Experiment 2. The letters C and O indicate "central" and "outer" males. The solid arrows show the movements of females from their release points during the first series of experiments; dashed arrows show their movements in the second series. Females were released only from intermediate positions 13–30 in the second series. The position of males was randomized between the two experimental series

In each experiment, 36 virgin females, individually color-coded with paint spots on the pronotum, were placed in plastic rearing boxes and randomly assigned to release points situated at all points of intersection between the corners of adjacent hexagons (see Fig. 1). The experiments took place between 1400 hours and 2300 hours during the last week of August and the first week of September 1987. When all males had been singing for at least 30 min, the lids were carefully removed from the boxes containing the females. Three observers then noted whether or not each male sang for a period of 5 s in successive 3-min intervals. Our observations did not seem to disturb the males. Since males typically produce trills of almost continuous song, interspersed with short, 1–2 s periods of silence, we believe that our point samples of singing activity provide a reliable estimate of the overall singing activity of individual males. Song activity was sampled during at least two periods, each of 30 min duration, within an experimental trial, giving a minimum of 20 point samples of singing activity per male. Females were recovered and placed in plastic bags as soon as they had climbed onto a cage in which a male was singing; their identity and choice of male was noted at the same time. Removal of females from cages occasionally caused the male to stop singing, but in all cases the male began singing again within a few seconds. The experimental trial was terminated when all males had stopped singing for the day, usually when the temperature had dropped below 13° C. Females that had not made choices at this time were sometimes discovered in their release boxes, or quite close to the release point, sitting still or feeding. The experiment was repeated on successive days until a choice had been made by a female from every release point.

The same females were used in Experiments 1 and 2, and as far as possible, they were assigned to the same release points. (This was not always possible since some females released in

Experiment 1 were not recovered.) Thus, the conditions in Experiments 1 and 2 were closely matched, except that the dispersion of the central group of seven males had changed. The whole series of experiments was repeated a second time, but the positions of males were randomized between each series. In the second series, however, females were in short supply, therefore they were released only from positions 13–30, intermediate between the central and outer groups of males. To test for an effect of clumping on female attraction, the relative success of central and outer groups of males were compared between Experiments 1 and 2.

Results

Male singing activity

On average, males were observed singing during 66% of the point samples (range 39–91%, $sd = 13.7\%$, $N = 19$). Male singing activity was highly correlated with body weight ($r = 0.60$, $P < 0.001$, $N = 18$), but not with pronotum length ($r = 0.12$, $P > 0.9$) or femur length ($r = 0.22$, $P > 0.7$). In both Experiments 1 and 2, there was no significant difference between the median singing activity of males in the central and outer groups ($P > 0.4$; Mann Whitney test for difference in median song activity).

We tested the possibility that the cluster of central males in Experiment 2 coordinated their

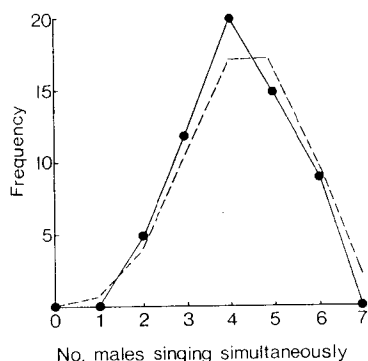


Fig. 3. The frequency at which different numbers of males within the central cluster (C males, Experiment 2) were singing simultaneously within a given song sampling period. The solid line joins the observed frequencies, and the dashed line shows the frequencies expected by chance if males sing independently of each other.

singing activity in such a way that might increase their ability to attract females. Potentially they might achieve this by singing strictly in unison to augment the total intensity of the combined signal, or by alternating song bouts with each other to maximize the total time that a signal is being emitted (see Alexander 1975). During each consecutive 3-min sampling interval, we counted the number of males in the central group of seven that were recorded as singing. The frequencies of sampling intervals in which a given number of males were singing simultaneously is shown in Fig. 3. The observed frequencies at which different numbers of males sang simultaneously did not differ significantly from the frequencies expected by chance if each male sings independently of others in the group ($\chi^2 = 4.05$, $P = 0.54$, $df = 5$). We conclude, therefore, that the males within the central cluster timed the emission of their songs at random. However, it should be noted that during all sampling intervals there were never fewer than two of the seven central males singing at the same time. Thus, when singing alone, even the most persistent signaler (which sang in 91% of all sampling intervals) could not match the combined output of the central cluster of seven males.

Female choice

Out of a total of 108 females that were recaptured on cages in which males were singing, 90 (83.3%) were attracted to one of the closest singing males (i.e., at a distance of 4.6 m from the release point of the female). The furthest distance travelled by

Table 1. Observed and expected number of females choosing equidistant males ranked according to morphological and song characters

Character	No. of comparisons	Observed (expected) number of females choosing male			P
		Rank 1	Rank 2	Rank 3	
Body weight	81	44 (34.7)	31 (34.7)	6 (11.7)	0.02
Pronotum length	69	35 (30)	23 (30)	11 (9)	0.20
Femur length	60	22 (25.7)	30 (25.7)	8 (8.7)	0.52
Mirror diameter	69	34 (30)	28 (30)	7 (9)	0.55
Song frequency	62	29 (27.7)	26 (27.7)	7 (6.7)	0.91
Peak SPL of song	49	22 (21.7)	21 (21.7)	6 (5.7)	0.97
Singing activity	81	60 (34.7)	18 (34.7)	3 (11.7)	0.0001

a female to a singing male was 12.3 m, bypassing one other male on the way.

For those females attracted to one of the closest males, we compared several characteristics of the successful male with those of the equidistant unsuccessful males. The males equidistant from each female's release point were ranked according to the following criteria: body weight, pronotum length, femur length, mean diameter of the sound-producing mirror, fundamental frequency of song, sound pressure level of song, and overall singing activity during the period when the female was making a choice. The male with the highest value of each character was ranked as 1, and the male with the lowest value was ranked 2 or 3 (depending on whether there were 2 or 3 males equidistant from the female's release point). Since we do not have complete data on all males, a maximum of 81 comparisons were possible. The number of females attracted to males of given character rank is shown in Table 1, along with the numbers expected by chance if females are attracted to one of the equidistant males at random with respect to male characters. The only significant departures from random were male weight and male singing activity. Seventy-four percent of all females attracted to one of the closest males chose the male with the highest singing activity ($P < 0.0001$), and 54% chose the heaviest male ($P < 0.05$). The heaviest males were most likely to be successful only because body weight and singing activity are highly

Table 2. Total number of females attracted to central and outer males (both experimental series combined)

	Number of females attracted to:	
	Central males	Edge males
Experiment 1 (central males spaced)	21	33
Experiment 2 (central males clumped)	10	44

$$\chi^2 = 6.07, P = 0.1, df = 3$$

correlated (see preceding section). This explanation is supported by 20 comparisons in which the most active singer was not the heaviest male: In 19 of these cases the most active singer was chosen.

Further evidence of the importance of male singing activity comes from an analysis of those cases in which females did not choose one of the closest males. In 12 out of 18 cases, the female by-passed a male that did not sing at all during the period when the female was moving ($N=8$), or that sang very little (less than 30% of all observations, $N=4$). Only six females passed by males that were singing persistently (during 80–100% of all observations).

Male success in relation to spatial dispersion

In this section we compare the relative success of the central and outer groups of males in both experiments. The combined results from both experimental series show that when all males were evenly distributed (Experiment 1), the central group of seven males attracted 38.8% of all females released during the experiment. When these central males were clumped (Experiment 2), they attracted only 18.5% of females. Although the central males had less success when clumped than when evenly distributed, the difference was not significant ($P=0.1$, Table 2). This was due to the fact that the outer group of 12 females (release points 1–12) were consistently attracted to one of the outermost males, and the inner group of 6 females (release points 31–36) were consistently attracted to one of the centrally situated males in both experimental arrangements of males. Only the choices made by females in intermediate positions (release points 13–30) differed between the two experiments. When only this group of females is considered, 41.7% chose one of the central males in Experiment 1 (when they were evenly distributed), but only 11.1% chose a central male in Experiment 2 (when they were clumped). We conclude, therefore,

Table 3. Number of females released from intermediate positions (13–30) attracted to central and outer males (both experimental series combined)

	Number of females attracted to:	
	Central males	Edge males
Experiment 1 (central males spaced)	15	21
Experiment 2 (central males clumped)	4	32

$$\chi^2 = 11.96, P = 0.0075, df = 3$$

that clumping significantly reduced the ability of the central group of males to attract females from intermediate positions (Table 3, $P=0.007$).

Discussion

In the present study, we tested the effect of male spatial dispersion in *T. viridissima* on the ability of signalling males to attract females. The results show that males were less successful in attracting females when aggregated than when evenly distributed. This effect was primarily caused by the strong tendency of females to be attracted to the closest signaling male. Under these conditions, a male advertising to attract females will maximize his "zone of attraction" when spaced out as far apart as possible from his competitors. Thus, the only stable dispersion of signalling males will be one in which males are evenly spaced within the habitat: Any male who deviates from this pattern will be penalized by reduced mating success.

Alexander's (1975) hypothesis that females prefer to mate only where males are clustered in space, allowing maximum opportunity for mate choice, is not supported by the results of this study. Moreover, female *T. viridissima* showed little evidence of active sampling of several potential mates. On occasions when we observed female phonotaxis, the movements of females were nearly always unidirectional and apparently aimed at a particular signaler. Only six females (5.5%) by-passed a male that was actively singing at the time. The striking tendency of females to choose one of the nearest males is unlikely to be due to their inability to detect more distant signalers. Rheinlander and Römer (1986) and Arak and Eiriksson (submitted) have shown that females can detect male song from a distance of 40–60 m in a grassland habitat when the sound source is elevated above the surrounding vegetation. We conclude from this that all the

caged males in our experiments were placed well within the hearing range of females. However, signals produced by the closest males suffer less attenuation, acoustical interference, and environmental degradation than signals emitted by more distant singers. Directional cues contained in the high frequency components of the song are also better preserved. Thus, closer males transmit their songs to the female with less ambiguity, facilitating species-specific pattern recognition and more accurate source location. Whatever the mechanism responsible, it can be argued from a functional point of view, that there may be an adaptive advantage of choosing the closest signaler if there are significant costs of movement for females (Searcy and Andersson 1986). Such costs might include an increased risk of predation due to conspicuous movements of the female during phonotaxis.

Otte (1974) and Alexander (1975) suggested that larger choruses might attract proportionally more females due to combining signalling effort and thus promote male aggression (but see Bradbury 1981 for objections). However, the need to preserve the species-specific temporal pattern of signals might mitigate against any potential advantages of communal signalling in *T. viridissima*. Since males produce long trills that overlap almost entirely when signalling together, important temporal features of the signal such as rate of amplitude modulation, pulse shape, and pulse duration will become obscured within the combined signal. Hence, any increase in signal amplitude or total broadcasting time experienced by the aggregate of males may be insufficient to counter the effect of increased signal ambiguity. This explanation is supported by experimental work on another bushcricket, *Conocephalus nigropleurum*, with a similar amplitude-modulated song (Morris et al. 1978). When females were offered a choice between the combined, hence louder, sound output of a "group" of two males and the simultaneous broadcast of a single male's song, they significantly preferred the combined song. However, in another experiment, females received the combined two-male song at the same power as that of the single male song, simulating our experimental situation in which the female is closer to the single male than to the group. In this case, females strongly preferred the single male song over that of the group, suggesting that the least ambiguous signal is more attractive when presented at the same amplitude as the combined song.

Most females were attracted to one of the closest signalling males. Among these females, the majority showed a preference for the most active

signaler. It is tempting to suggest that this preference has evolved by sexual selection. The most active signalers were among the heaviest males, and our laboratory studies have shown that there is a strong correlation between male body weight and spermatophore weight in this species ($r=0.81$, $P<0.001$, $N=17$). Further, Gwynne (1984, 1988) has demonstrated that the spermatophore of the bushcricket, *Requena verticalis*, which is consumed by the female after mating, causes a significant increase in the number and size of eggs laid by females and in the hatching success of offspring. The advantage to females of obtaining large spermatophores, though not universal among bushcrickets (Wedell and Arak 1989), may provide an adaptive basis for female discrimination between males observed in *T. viridissima* and other species (Gwynne 1982).

The results presented here differ with the findings of some previous studies. Studies on the prairie chicken leks (Hamerstrom and Hamerstrom 1960), frog choruses (Ryan et al. 1981), singing groups of cicadas (Doolan 1981), and grasshoppers (Shelly and Greenfield 1985) have all shown that larger aggregations of males attract more females per male than do smaller aggregations. However, Cade (1981) found that there was no significant difference between the number of females attracted to songs of male field crickets, *Gryllus integer*, broadcast through single, isolated loudspeaker and the mean numbers attracted to loudspeakers arranged in aggregations. He concluded that although males are aggregated in the field, this cannot be explained by female preference for aggregated males. As far as we know, our study is the first to demonstrate a negative effect of aggregation on the ability of males to attract females. Because our results were obtained in a controlled, experimental situation, we can be sure that this effect was not due to differences in the local densities of females.

Although we do not rule out the possibility of female preference for aggregated males on a larger scale (i.e., females choosing between different clumps of males), the only studies to date that support such an effect are confounded by alternative explanations. For example, in the desert grasshopper, *Ligurotettix coquilletti*, males clump on dispersed creosote bushes (*Larrea tridentata*), their host foodplant, and females congregate on those bushes that contain relatively low amounts of plant secondary compounds (Greenfield & Shelly 1985). In an elegant experiment, Shelly et al. (1987) showed that females whose chemosensory organs had been removed settled on bushes indiscrimina-

tely. Thus, variability among bushes in their plant chemistry alone appears to be sufficient to promote clustering of females on cresote bushes. However, additional observations suggest that females were less likely to leave bushes between successive days if groups of signalling males were present, suggesting that male epigamic displays may play some part in influencing female dispersion as well. In the tungara frog, *Physalaemus pustulosus*, larger choruses of males attract proportionally more females than do smaller choruses (Ryan et al. 1981). Although females do prefer certain males in this species (Ryan 1985), it is by no means certain that females prefer larger groups in order to facilitate mate choice. The effect could come about because individuals in larger groups are relatively safer from predators that are known to specialize on frogs.

In conclusion, we failed to find any evidence for signal enhancement by communal display in *T. viridissima* or for female preference for clustered males within artificial choruses. The results of this study suggest that the optimal spacing pattern is one in which signalling males are evenly dispersed within preferred habitats. This is precisely the distribution that is observed in nature for male *T. viridissima*, and, indeed, many other acoustically advertising animals. Although several authors have suggested that signaling males may benefit by maintaining a distance from their competitors, this is the first experimental demonstration that supports this suggestion.

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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, both 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 signaller and the form of the songs in such a way to maximize the signaller's reproductive success. One simple way that a signaller 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 signallers.

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 signallers 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 signallers 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 signallers 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 Dagnäsön 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 Båven. 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, willow, *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 tettigoniid, *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

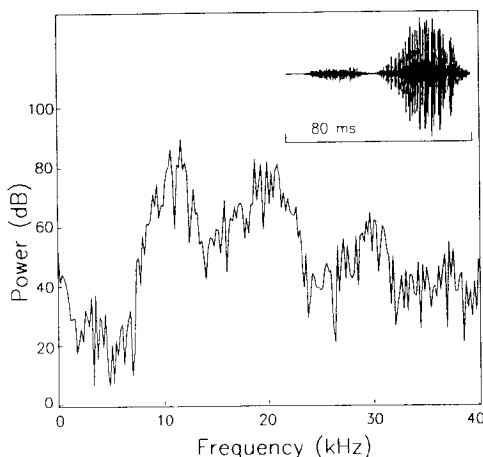


Fig. 1. Power spectrum of the closing phase of the pulse shown in insert. The insert shows oscillogram of one pulse of *T. viridissima* song.

around 20 kHz and 30 kHz, respectively. The sound pressure level of the song was measured 50 cm above the wings of singing males, with a Brüel & Kjær Model 2221 sound level meter, microphone Type 4176, on peak recording mode, RMS fast, and was found to be 93.8 dB re. 20 μ Pa (SD=2.1 dB, $n=19$). The meter has a linear frequency response from 0.2 Hz to 15 kHz. The peak measurement of the signal therefore corresponds to the peak of the fundamental frequency.

Recordings of males. A total of 21 males were recorded at different elevations, within the range -0.3 to +3.0 m relative to the top of the surrounding vegetation. Songs were recorded in the afternoon when most males were active. Care was taken to sample the song when the recording was not disturbed by the singing of neighbouring males; it was sometimes necessary to disturb them slightly to silence them for a moment.

Samples of song were recorded using an ultrasound detector model D-960 (frequency range 10–150 kHz, sensitivity 0 dB at 40 kHz, dynamic range 110 dB, with attached microphone, sensitivity -43 ± 5 dB rel 1V/Pa over 20–100 kHz, directive sensitivity: 30 kHz 15°: -2 dB, 30°: -7 dB, 130 kHz: 8°: -14 dB, 15°: -27 dB, Lars Petterson, Wretgränd 9D, S-75322 Uppsala, Sweden), linked to a Sony TC-D5M cassette recorder. The ultrasound detector, when used on "time-expansion mode", stores 0.7-s sections of song in memory using a sampling frequency of 350 kHz. Thus, all time and frequency characteristics of the song were adequately preserved and expanded in time by a factor of 10 before being recorded on cassette. The microphone of the ultrasound detector was placed in the middle of the vegetation layer surrounding the male's singing perch (where females were often found) and pointed towards the singing male during recording. Each sample was taken in the middle of a song bout. Recordings were made at distances of 0.5–13.0 m from the singing male, but most in the range 1–4 m. The first recording was made at 0.5 m from the male and then the distance increased at intervals until the song could no longer be detected by the ultrasound detector. The recording levels of the ultrasound detector and the tape recorder were kept constant for all recordings from a single male, allowing sound pressures to be compared at different distances.

Three to 8 measurements were taken from each male depending on the time available until the male changed position or stopped singing. We measured the elevation of the male's singing perch above the ground and estimated the mean height of the vegetation surrounding the perch.

Analysis of song recordings. The time-expanded signals were analysed on Uniscan 4500 sonograph to determine the relative sound pressure levels of each frequency band at different distances from the male. The closing (higher-intensity) phases of three pulses were chosen at random from the recorded song sections. As the different frequencies are not at peak at exactly the same time, two samples were taken from different places in each pulse, one where the fundamental frequency was at a peak and one where the first harmonic was at a peak. As there is variation between males in the power spectra of their songs, the sound pressure was estimated in a frequency range around the mean of each frequency band. These frequency ranges were taken to be 7.2–13.6 kHz for the fundamental, 15.2–24.8 kHz for the 1st harmonic and 24.8–37.6 kHz for the 2nd harmonic. The relative sound pressures (1–100 dB) of successive 160-Hz intervals within each frequency range were measured and converted to absolute sound pressure before averaging the values for each frequency band. The noise level (environmental noise and noise added by the instruments) was estimated in sections between pulses and the mean noise level at each frequency range subtracted from the average signal pressure at each band. The resulting measures of sound pressure were then reconverted to the decibel scale.

Calculation of excess attenuation. The inverse square law describes how sound energy spreads with distance due to spherical expansion. Inverse square attenuation, ISA (dB), for a given distance, d_i , from the source is given by:

$$\text{ISA} = 20 \log(d_i/0.5) \quad (1)$$

where 0.5 m was the closest distance at which the mean sound pressure level, $I_{0.5}$ (dB), of the signal was measured.

The excess attenuation is defined as the difference between the measured attenuation of the signal at a certain distance and the attenuation expected due to spherical expansion alone (Marten and Marler 1977). Thus, the excess attenuation of the signal, δ_i , at each distance d_i from the source can be estimated as:

$$\delta_i = I_{0.5} - I_i - 20 \log(d_i/0.5) \quad (2)$$

where I_i (dB) is the measured sound pressure of the signal at distance d_i .

The slope of the regression of δ_i on d_i , denoted by E , is the coefficient of excess attenuation, an estimate of mean excess attenuation of the signal per unit distance from the source, i.e.

$$\delta_i = E(d_i - 0.5) \quad (3)$$

It is an oversimplification to assume that excess attenuation increases linearly with distance (Michelsen 1985), but for the purpose of this study it seems justified. The fit to the data points was reasonably good, and no indication of general under- or overestimation of the excess attenuation could be observed.

The total attenuation of the signal at distance d_i from the source [$I_{0.5} - I_i$ (dB)] can now be defined as:

$$I_{0.5} - I_i = 20 \log(d_i/0.5) + E d_i \quad (4)$$

Calculation of female hearing range. An estimate of the peak sound pressure level of the dominant frequency measured from an independent sample of singing males (≈ 94 dB at 50 cm above the wings) was used to calibrate all sound recordings analysed on the Uniscan. The lowest SPL at which a song can be heard by a female *T. viridissima* [I_h (dB)] has been estimated as approximately 30 dB over the frequency range 10–30 kHz (Rheinlaender and Römer 1986).

To estimate the female hearing range, we substitute I_h for I_i in Eq. (4) and solved for d_i by iteration. Separate estimates of the female hearing range were made for each male at each of the three frequency bands. For each frequency band, the female hearing range was then plotted against the elevation of the male signaller in relation to the top of the vegetation surrounding his singing perch.

Results

Spatial dispersion of singing males

On 4 out of 5 days singing males were highly clumped within the habitat as a whole. However, within clumps consisting of more than 5 individuals, males were regularly spaced (Table 1). The dispersion pattern of males in the habitat on 1 of the 5 census days is shown in Fig. 2.

Analysing male dispersion in relation to the height of vegetation reveals that 69% of all males ($n=197$) were observed singing on vegetation 1–3 m above ground, although this vegetation covered only 14% of the entire habitat. The remaining males were distributed fairly equally between the lowest layer of vegetation (16% of all males within an area comprising 67% of the study site) and taller bushes and trees (15% of all males in an area comprising 15% of the study site). These results show that males are not randomly distributed between vegetation of different heights ($\chi^2 = 384.0$, 2 df, $P < 0.0001$); they appear to show a strong preference for vegetation of intermediate height and avoid

Table 1. Analysis of male dispersion in the habitat on 5 days during 1987. *N* denotes the number of calling males, *R* the Clark and Evans (1954) dispersion parameter, *A* the area in m²; * $P < 0.05$, ** $P < 0.01$

Date	Whole habitat (<i>A</i> = 18000 m ²)			Within clumps			
	<i>N</i>	<i>R</i>	Dispersion	<i>N</i>	<i>A</i>	<i>R</i>	Dispersion
8/9	55	0.709**	Clumped	18	1380	1.294*	Spaced
				8	270	1.980**	Spaced
9/9	54	0.434**	Clumped	11	392	1.340*	Spaced
				7	299	1.399*	Spaced
12/9	29	0.569**	Clumped	10	275	2.136**	Spaced
				6	221	1.757**	Spaced
23/9	35	0.755**	Clumped	8	920	1.539**	Spaced
				11	1701	1.521**	Spaced
2/10	11	0.763	Random	—	—	—	—



Fig. 2. Diagrammatic representation of the study site at Dagnasjön showing different layers of vegetation and positions of singing males on 1 of the 5 census days

singing from the lowest vegetation consisting mainly of thick sedge and reed beds.

The distribution of nearest-neighbour distances in each vegetation layer is shown in Fig. 3. The observed mean nearest-neighbour distances are longest for the lowest layer of vegetation and shortest for the highest layer. Thus, males tend to aggregate in places that afford them the possibility of broadcasting their songs from positions above the surrounding vegetation.

Males separated by distances of < 2 m were invariably involved in physical or acoustical interactions (alternating exchanges of short trills). Within each vegetation type, the proportion of males involved in such interactions was 14% in the lowest layer of vegetation, 13% in the intermediate layer and 54% in the tallest layer of vegetation. The incidence of interaction is thus significantly higher when males are singing from the tallest vegetation ($\chi^2 = 22.7$, $df = 2$, $P < 0.001$).

The vertical distribution of singing males in each vegetation type is shown in Fig. 4. In the lowest level of vegetation, males cluster close to the tops of the plants, approximately 1 m above ground. When singing on taller plants (1–3 m), males cluster around a strong mode 0.25–0.5 m above the surrounding vegetation, and when singing in trees (> 3 m tall) they cluster at around 1.5 m above the surrounding vegetation (on average 2.5 m

above ground level). Thus, in all but the lowest layer of vegetation in the habitat, males were never found singing at the maximum elevation possible.

Excess attenuation

The coefficient of excess attenuation (*E*) of male song increases with frequency but decreases markedly with the elevation of the male above the surrounding vegetation (Fig. 5). Excess attenuation of the fundamental frequency ranges from a maximum of about 4 dB/m when the male is singing in the midst of thick grass to 0.1 dB/m when the male is elevated above the surrounding vegetation. The corresponding decrease in *E* with increasing elevation is 6–0.3 dB/m for the 1st harmonic and 13–0.7 dB/m for the 2nd harmonic. For all frequency ranges, *E* decreases most rapidly as the male moves up from the middle of the vegetation to about 1 m above the surrounding vegetation; thereafter, there is a negligible decrease in *E* with increasing elevation. The fairly constant excess attenuation at higher elevations seems to be a consequence of the fact that the signal passes from the male to the microphone almost entirely through the air when the male is elevated more than 1 m above the surrounding vegetation; thus, attenuation of the sig-

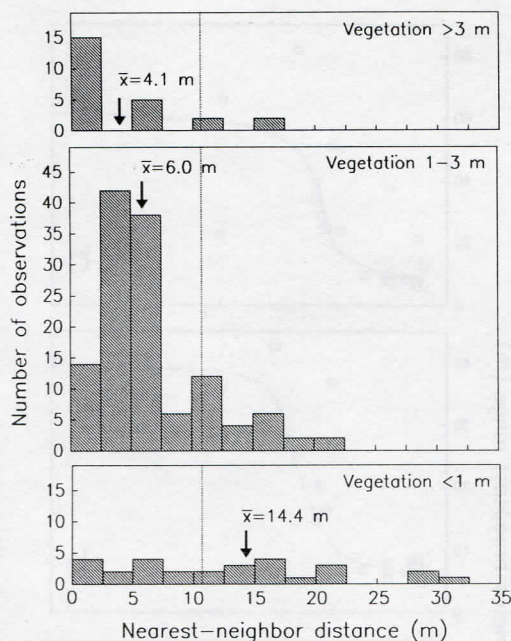


Fig. 3. Distribution of nearest-neighbour distances in each of the three main layers of vegetation. Overall mean is 6.8 m. Dotted line shows expected mean nearest-neighbour distance (10.7 m) assuming random dispersion of males

nal due to absorption by vegetation and the ground is at a minimum.

Female hearing range

Female hearing range changes in concert with changes in the coefficient of excess attenuation at different heights in the vegetation (Fig. 6). For the fundamental frequency, a singing male may increase his broadcast range from about 8 m to 60 m (i.e. 7.5 times) as it moves up from the midst of the vegetation to 1 m above it. For the 1st and 2nd harmonics of the song, the corresponding increase in broadcast range is 6–38 m (6.3 times) and 4–14 m (3.5 times), respectively. As expected, the broadcast range for a given elevation of the singing male is greatest for the lowest frequency components of the song: these frequencies suffer less excess attenuation due to absorption and scattering by the ground, vegetation and air.

Discussion

Song propagation in the habitat

One important aspect of the habitat in relation to sound propagation is the nature of the vegetation surrounding

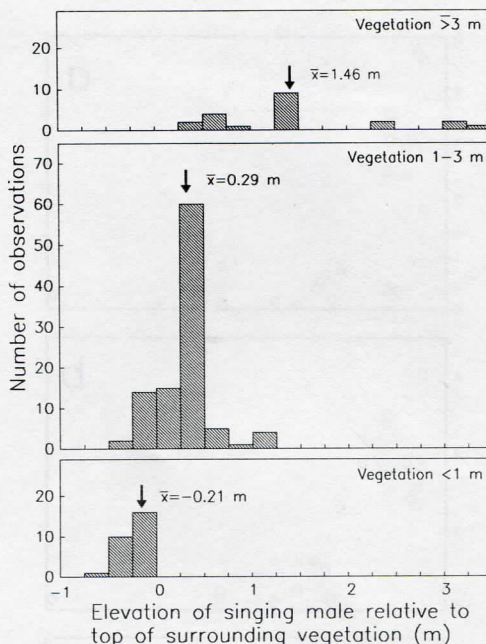


Fig. 4. Distribution of heights of singing males in each of the three main layers of vegetation. Overall mean is 0.36 m above the surrounding vegetation

the signaller. Moreover, propagation of sound through vegetation is highly frequency-dependent. Excess attenuation is much more severe for higher frequencies (e.g., Keuper et al. 1986; Römer and Bailey 1986). Excess attenuation is also strongly influenced by the elevation of the source and receiver above ground and their respective positions in the vegetation layer (e.g., Paul and Walker 1979).

Our estimates of excess attenuation for males singing at different heights in the vegetation support these general expectations and show good quantitative agreement with the results of other workers. For example, Keuper and Kühne (1983) estimated that the excess attenuation of pure sinusoidal tones travelling through tall, dense grass increases with frequency by a factor of about 0.1 dB/m per kHz. They found that the excess attenuation of a 30-kHz tone varied from 5 dB/m through loose grass to 15 dB/m through dense grass. These values correspond closely to our own estimates of the coefficient of excess attenuation for the 30-kHz component of *T. viridissima* song, which vary within the range 3.5–13.7 dB/m when insects were singing in the lowest layer of vegetation (singing male at -0.3 m with respect to the top of the plants).

The considerable variation in our field measurements of excess attenuation for males at the same elevation was to be expected (see Fig. 5). This variation may have been caused by many factors, such as a slight variation

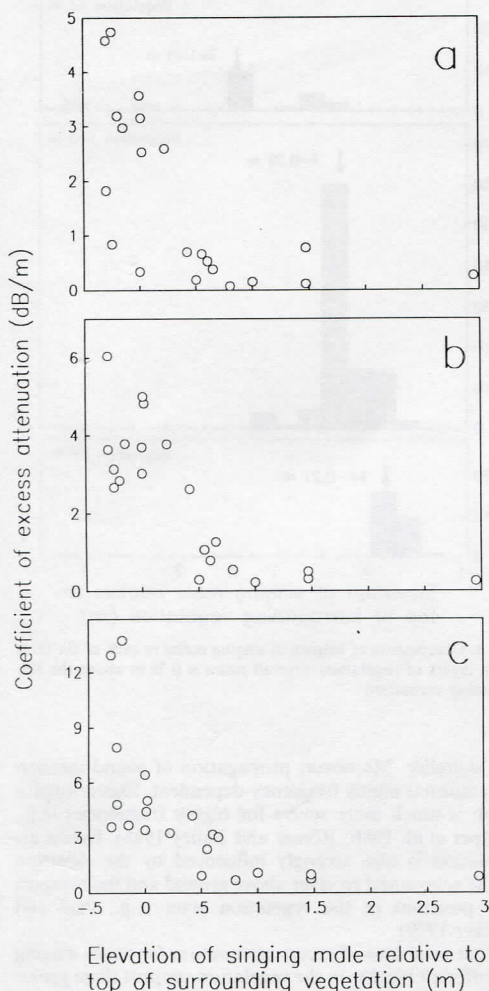


Fig. 5a-c. Coefficient of excess attenuation (E) for males singing at different heights relative to the surrounding vegetation: (a) dominant frequency band, ~10 kHz; (b) 1st harmonic, ~20 kHz; (c) 2nd harmonic, ~30 kHz

in air temperature and humidity, and differences in the density of the vegetation surrounding the male that were not possible to control for in our study. Also, because sound emission by a male *T. viridissima* is directional, a small change in male posture can cause large differences in sound pressure at a given distance, even if the male remains at the same elevation (Keuper et al. 1988).

Our estimates of female hearing range indicate that a female can expect to detect the fundamental frequency components of male song over a maximum distance of about 60 m when the male is elevated >1 m above the lowest layer of vegetation, or over a distance of about

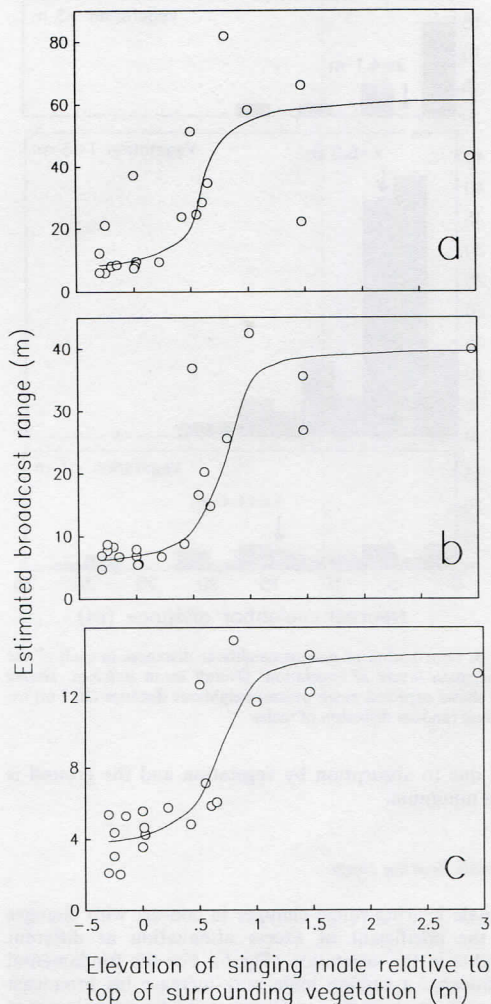


Fig. 6a-c. Estimated broadcast range of (a) dominant frequency, (b) 1st harmonic and (c) 2nd harmonic. The detection range is estimated assuming an auditory threshold of 30 dB

20 m when the male sings from the top of the lowest vegetation layer. Rheinlaender and Römer (1986) measured the maximum hearing distance of *T. viridissima* to be 40–50 m in a grassland habitat and about 20 m in denser bushland. Although their technique of estimating hearing range differed from ours (they broadcast synthetic *T. viridissima* song through a loudspeaker and used identified auditory nerve cells in the female as “biological microphones”), there is good agreement between our studies.

A few workers have estimated the hearing range of other orthopterans in their natural habitats. These esti-

mates vary very much, depending on such factors as the frequencies utilized by the species, characteristics of the habitat and the position of the signaller and receiver relative to the ground and the vegetation. The general trend, however, fits our results very well. Assuming an initial sound pressure level of about 90 dB (at 50 cm) and a detection threshold of around 30 dB, frequencies of around 10 kHz have broadcast ranges between 10–15 m, frequencies around 30 kHz range between 2–15 m, and 20 kHz components travel intermediate distances (Thiele and Bailey 1980; Keuper and Kühne 1983; Keuper et al. 1986; Römer and Bailey 1986).

An important question concerns the biological significance of our estimates of female hearing range. Several studies suggest that it is important not only that the peak sound pressure level of the song exceed the threshold for detection by females, but also that the harmonic content of the song be preserved to elicit an appropriate behavioural response, i.e. phonotaxis. In two-choice tests, female crickets (*Teleogryllus commodus*) show a clear preference for songs with harmonics (Latimer and Lewis 1986). A similar preference for songs with a preserved harmonic structure has been shown in female bushcrickets, *Tettigonia cantans* (Latimer and Sippel 1987). The presence of unattenuated high-frequency components in the song may be critical for localization of the signaller once the song has been detected by the female. Females seem to move towards the closest male they can hear (Arak et al. 1990), and the presence of high frequencies in the song is probably important to estimate distance (Bailey and Yeoh 1988). Recordings from the central nervous system of *T. viridissima* show optimal directional sensitivity to a pure tone of 20 kHz, and coding of directional information improves as the intensity of this stimulus increases (Rheinlander and Römer 1980). Thus, both the absolute intensity and the harmonic content of the song appear to be important for localization in this species.

Behavioural adaptations of singing males

Our results show that males prefer microhabitats that allow them to broadcast their songs from perches elevated above the surrounding layer of dense vegetation. Males aggregate in patches of taller vegetation, but within such patches maintain regular interindividual distances by physical and acoustical interactions with their neighbours (see also Brush et al. 1985; Schatral et al. 1985). The acoustic cues males use to maintain spacing probably include the relative harmonic content of songs as well as the absolute intensity (Keuper et al. 1986; Latimer and Lewis 1986; Römer and Bailey 1986; Römer 1987; Simmons 1988). In this study the mean interindividual distance was approximately 6 m. Songs broadcast over this distance propagate with their harmonic structure largely preserved (see Fig. 6), providing other males and receptive females with unambiguous directional information about the position of the signaller. We suggest, therefore, that this pattern of spacing allows males to maximize the broadcast range of their songs

in the habitat as a whole while maintaining a minimum distance free from competitors within which prospective mates can accurately localize them.

The vertical distribution of males is more difficult to explain in terms of signalling strategy. Males can increase their broadcast range by moving up to 1 m above the surrounding vegetation; thereafter, there is very little extra increase in broadcast range with increasing elevation (Fig. 6). It might be predicted, therefore, that males should sing from positions at least 1 m above the surrounding vegetation. However, our data are inconsistent with this prediction: in the favoured microhabitats, males clustered at heights of only 0.25–0.5 m above the surrounding vegetation, even though there was ample opportunity to sing from taller plants.

A possible explanation for this discrepancy is that males experience greater costs when singing at higher elevations. One such cost could be an increased risk of predation when singing in an exposed position near the top of a plant stem. Although we never observed predation at our study site, singing males were very wary when approached and showed rapid escape responses by diving into cover. Presumably this behaviour has been selected for as an evolutionary response to predation.

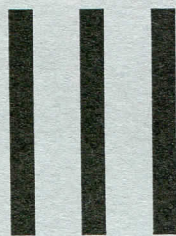
Another cost may result from increased aggression directed at males singing from higher positions. This suggestion is supported by our data which show a significantly higher frequency of aggressive interactions as elevation increases (see also Dadour and Bailey 1985). Males singing from elevated positions provide a stimulus which is more attractive to females and therefore constitute a greater "threat" to rivals who are competing for the same females. The high frequency of challenges directed at such males might therefore make it unprofitable to sing from such positions. Not only do repeated aggressive interactions involve a risk of injury (personal observations), they also cause the singing behaviour to be interrupted, resulting in a reduction in total broadcasting time. The vertical spacing of males may, therefore, reflect a compromise between maximizing broadcast range and minimizing the cost of aggressive interactions.

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ABSTRACT

The behaviour of the grasshopper *Omocestus viridulus* was studied in the field and in the laboratory. In the field males and females were individually marked and their position recorded on a grid system of the size, depending on the behaviour of males was monitored, and in the laboratory the courtship sequence was studied. The number of individuals in the area was estimated. There were around 120 individuals of each sex, 400 m² or 0.25 m². The males moved frequently, on average 24.1 cm/min, in walking, jumping or flying, and the same individual might be found all over the area during the observation. The sex ratio was 1.0 male to 1.0 female. The females also moved, but were less active than the males.

SINGING AND ASSOCIATED BEHAVIOUR IN THE GRASSHOPPER *OMOCESTUS VIRIDULUS*

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ABSTRACT

The behaviour of the grasshopper Omocestus viridulus was studied in the field and in the laboratory. In the field both males and females were individually marked and their position plotted on a grid system of the area, secondly the behaviour of males was monitored, and in the laboratory the courtship sequence was studied. The number of animals in the area was estimated. There were around 150 individuals of each sex in 400 m^2 or $0.38/\text{m}^2$. The males moved frequently, on average 24.1 cm/min , by walking, jumping or flying, and the same individual male could be found all over the area during the observation. Thus, the males did not stay on any exclusive area. Females also moved, but were more stationary than males. The song rate was highest in the middle of the day, and solar radiation was more important than air temperature in controlling male singing. The average duration of all songs was 18.91 s ($\text{SD} = 6.91$, $N = 607$) and the average mean song duration for individual males was 19.34 s ($\text{SD} = 5.61$, $N = 191$). There was however considerable variation in duration of songs produced by a single male. When intervals between songs were short males produced shorter songs. The males were sometimes found interacting with other males. These interactions did not include physical fighting, but associated with male-male interactions was a special type of song, termed rivalry song. If a female stridulated the male went to her directly but often males also courted females that did not stridulate. When the male found a female he engaged in, sometimes prolonged, courtship which was characterized by different song types given in a sequence. The courtship usually followed the same pattern. First the male approached the female emitting special clicks followed by a courtship song, sometimes repeated several times, and then jumped on the female, accompanied by yet another song type. The duration of courtship was more influenced by air temperature than by solar radiation. The male mate location strategy appears to be a mixture of searching and singing and the system is characterized by high mobility and large variation in the songs.

INTRODUCTION

The mating system of gomphocrine grasshoppers is characterized by the use of song in all phases of the mate finding behaviour. They differ from many other orthopteran insects since females not only respond with phonotaxis but also stridulate and thus signal their position to males (Jacobs 1953; Haskell 1958).

The song is produced by rubbing pegs on the hind legs against veins in the wings. A song is a train of pulses, and each pulse corresponds to a complete movement of the legs (Haskell 1957; Elsner 1974; Skovmand and Pedersen 1978, 1983). The males use many different song types. The most common is the calling song which the male uses when he is alone to call for females (Ragge 1986). Another is the rivalry song predominantly used when the male is close to another male (Jacobs 1953; Haskell 1957), but most song types are used in the close range courtship (Otte 1972; Bull 1979; Riede 1986).

The calling song is highly species specific (Ragge 1986), and females react selectively to male songs (Perdeck 1958; von Helversen and von Helversen 1975). Many different parameters of songs have been identified. Females either prefer intermediate values of the character close to the mean of natural songs (Butlin et al. 1985; Butlin and Hewitt 1988; Eiríksson in press a), or they prefer longer or more songs (Eiríksson in press b).

Males and females usually find each other by alternating between song and phonotaxis. Males sing the calling song and receptive females approach the male by phonotaxis and respond with a stridulation of their own (Skovmand and Pedersen 1978). When the male hears a female respond he goes to her directly (personal observation). The males can also find females by direct searching (Butlin and Hewitt 1986) and song may not be equally important in finding a female in all species (Ritchie et al. 1990). When a male has found a female he engages in a prolonged courtship that ends in copulation. Stridulation is not necessary for copulation in all species, whereas in others it invariably precedes copulation (Blondheim 1990).

The common green grasshopper, *O. viridulus*, is widely distributed over northern and central Europe and extends into southern Europe (Ragge 1965; Willemse 1984). It is usually found in dry fields adjacent to wet areas. The behaviour is in many ways typical for gomphocerine grasshoppers. In this study the singing and associated behaviour of males is described, such as movement, interactions and courtship.

METHODS

Field observations were performed at Uppsakulle, an ancient viking burial mound close to Tovetorp, a field station belonging to Stockholm University, approximately 90 km south of Stockholm. A 20 x 20 m working area was marked in a protected area around the mound. The area was divided into 2 x 2 m squares by small poles at the corners of the squares. All observations were performed within that area on sunny days in July and August, between 0700 and 2000 hours.

The study was conducted in three years (1987-1989). Males and females were captured and marked and their position plotted on different days. The behaviour of individual males was monitored. Furthermore, a few males and females were taken into the laboratory to look into the courtship sequence.

Density estimates

The grasshoppers were marked individually with a unique colour code on the thorax. A total of 275 grasshoppers, 160 males and 115 females, were marked on 11 days over a period of 16 days. The number of grasshoppers, recaptured at least once, was 157, 96 males and 61 females (Fig 1).

The number of males and females in the observation area was estimated in two ways. The total number of animals can be estimated by the ratio of marked animals and the number found compared to the number marked before (capture-recapture method, e.g. Krebs 1978). This method was used in seven days. This was always done on two consecutive days to minimize the effect of immigration-emigration and mortality.

The second method was based on the assumption that the probability of finding all animals is equal. How often different animals are found should then fit a Poisson distribution. This makes it possible to calculate how many animals were not found and thus estimate the total number of animals in the area.

Long time movement

The positions, where a grasshopper was located, was plotted on the grid system of the area. The central position of the animals was calculated as the average of the x and y coordinates for all captures.

The distance furthest away from the central position is an indication of the size of the area covered by an individual, and was used to compare the movement of the sexes.

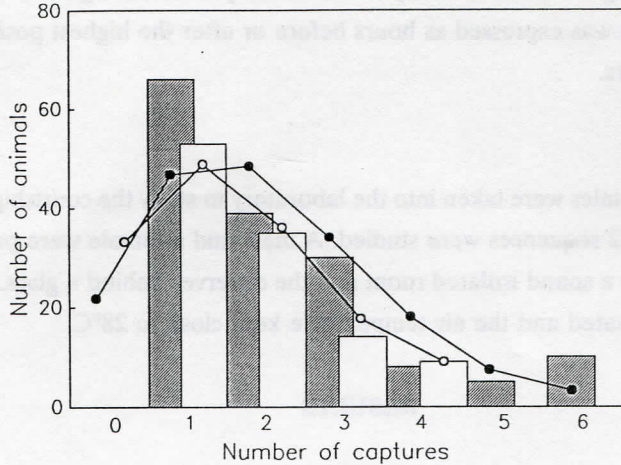


Figure 1. The number of times an animal was recaptured. Shaded columns = Males. Unshaded columns = Females. The circles and lines show the fitted Poisson distribution and the estimated number of animals not found.

Monitoring male behaviour

The number of monitored males was 313, and the following aspects of their behaviour was described. The calling songs were counted, and the duration of each song and the interval between songs was timed. The movement patterns were categorized into walk, jump and fly, the distance they moved was estimated in each case, and the number of jumps and flies counted. The duration of male-male interactions was estimated and the number of rivalry songs was counted. If the male got engaged in close range courtship with a female the pair was observed until it separated and the behaviour described.

The observation was terminated after 10 min except in three cases. If the male had been singing and was still sitting, the observer waited until he moved to get an estimate of number of songs in a song bout. If the male was engaged in interaction with other males or if the male was courting a female, the total time was measured. The male was sometimes lost before the 10 min observation period ended, most often when it jumped or flew away a few meters or when it walked deeper down in the vegetation.

Temperature was measured in the grass after each observation period ended. It was noted if the sun was hidden behind occasional clouds for part of the period. The solar radiation changes with time of day since the sun position is highest in the middle of day. This change was expressed as hours before or after the highest position of the sun at ca 1300 hours.

Courtship sequence

Males and females were taken into the laboratory to study the courtship sequence more closely, and 42 sequences were studied. A male and a female were put together into a small cage in a sound isolated room and the observer behind a glass. The room was brightly illuminated and the air temperature kept close to 28°C.

RESULTS

Density estimates

The number of animals in the area estimated with the capture-recapture method was 145 (SE = 35, N = 6; 0.36/m²) for females, and 134 (SE = 12, N = 7; 0.34/m²) for males.

The estimated numbers from the Poisson distribution were 144 females (0.36/m²) and 177 males (0.44/m² Fig. 1). In the case of females the distribution observed is not significantly different from the Poisson distribution, but the difference is significant in the case of males ($\chi^2 = 11.13$, df = 3, P = 0.76, and $\chi^2 = 27.68$, df = 5, P < 0.001, respectively).

Long time movement

Males and females were evenly distributed all over the observation area. Males were very mobile (Fig 2), but females were more stationary (Fig. 3). For males the average maximum distance from the central position was 4.94 m (SD = 3.36, N = 96) and for females 3.57 m (SD = 2.64, N = 61). The difference between the means was 1.37 m (t = 2.7, P = 0.007).

Movement

The males alternated between sitting still, grooming or eating, singing and moving, but occasionally they engaged in interactions with other males and close range courtship with females. If the sun was not shining the male usually stayed in the same

spot and moved very little. When the sun started to shine the males usually either moved or started to sing.

When the males started to move they either walked, jumped or flew. The average distance moved was 24.1 cm/min (SD = 37.5, N = 236), and this distance was not found to change significantly during the day (Anova $F = 0.907$, $p = 0.54$, N-classes = 13, N-males = 236).

The interval between songs when the male moved was on average larger than when they were sitting in the same spot, but there does not seem to be a difference between intervals they spent only walking or when they jumped or flew as well (Fig. 4).

Singing

When the male was going to sing he usually perched on a straw slightly above the ground, but he often moved up and down the straw before he started to sing. The male sometimes sunbathed, i.e. he lowered one of the hind legs, laid on the side and exposed the wing to the sun. The wings of males are darker than the rest of the body which should result in more absorption of solar radiation.

The males sang on average 0.31 songs per minute (SD = 0.41, N = 274). The song rate was highest in the middle of the day and lower both in the morning and the evening (Fig. 5). The influence on song rate of three variables, cloudiness, position of the sun, and temperature, was tested with a stepwise multiple regression. Two variables entered the model, cloudiness and sun position (Table I). Temperature did not explain significantly more of the variation, but temperature is obviously dependent on radiation.

Individual songs varied in duration from 3.7 s to 49.4 s with an average of 18.91 (SD = 6.91, N = 607, Fig. 6), and the average duration of mean song duration from individual males was 19.34 (SD = 5.61, N = 191).

After a male finished a song he could stay in the same spot and sing another song or move. The males sang 1 to 9 songs before they moved, but the majority of males sang only one song in the same spot. The distance moved and number of songs was correlated ($r_s = 0.4386$, N = 236, $P < 0.001$). There was a positive relationship between the intervals between songs and the duration of next song (Fig 7).

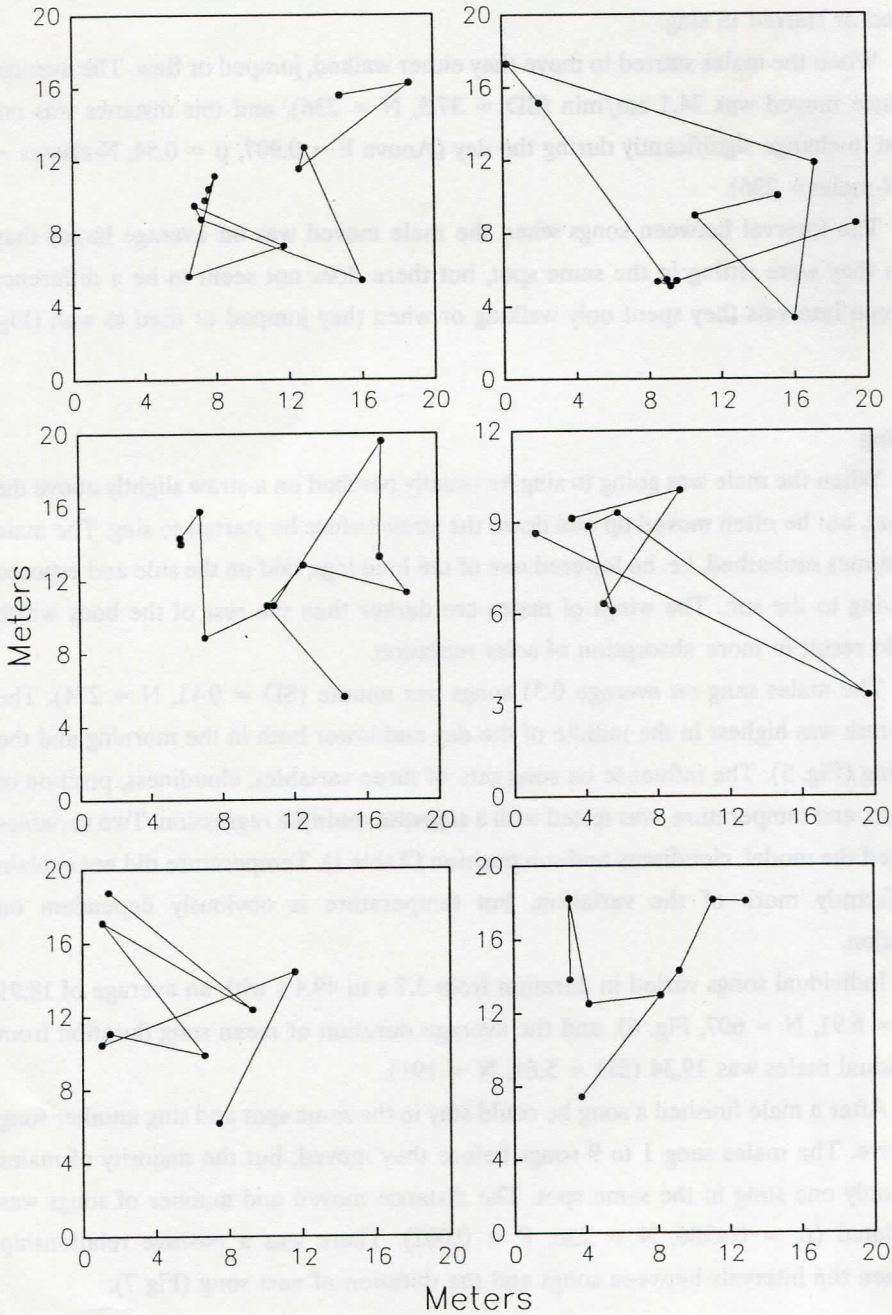


Figure 2. The movements of six males in the observation area during the same time. The lines combine the positions in time.

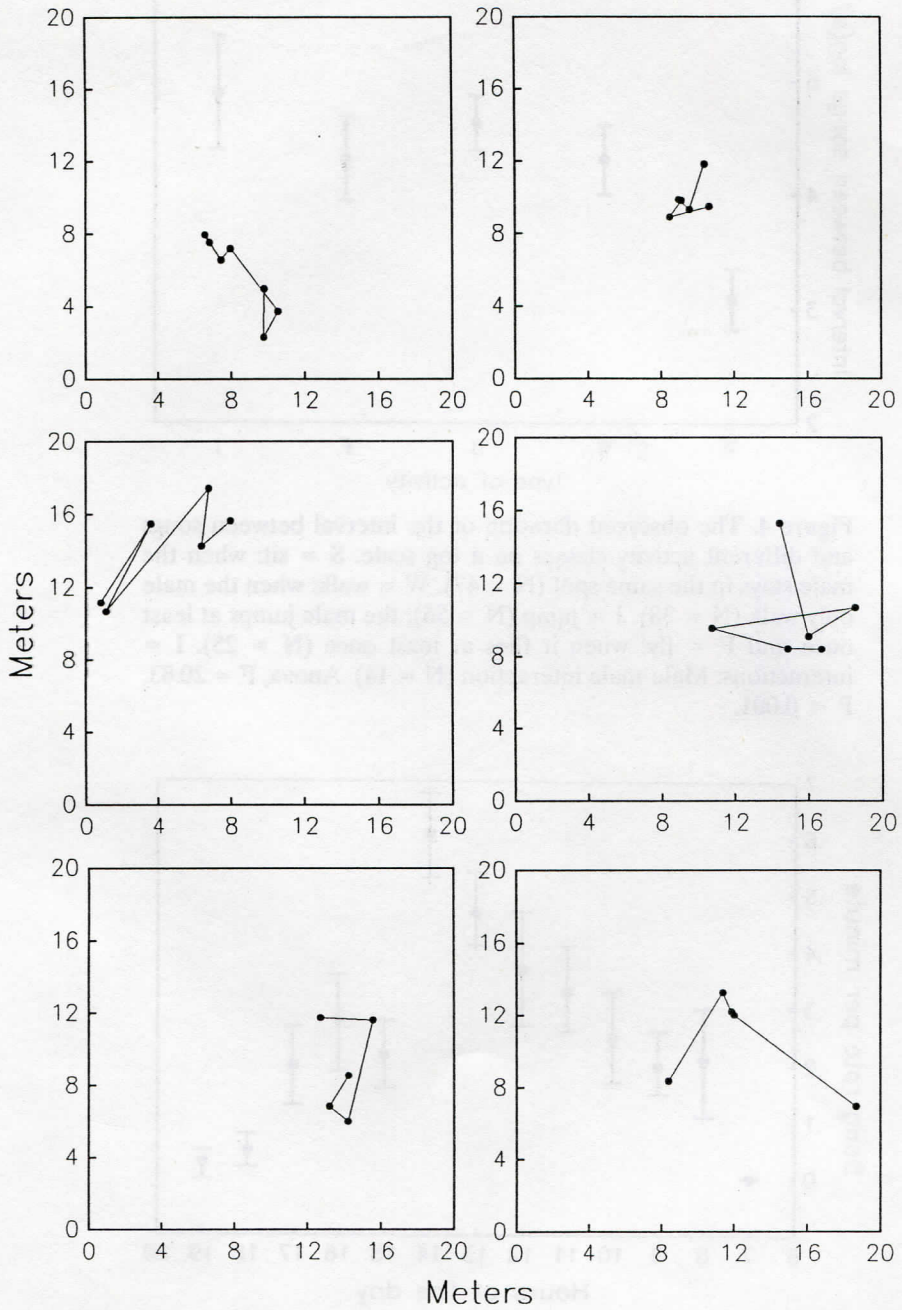


Figure 3. The movements of six females in the observation area during the same time. The lines combine the positions in time.

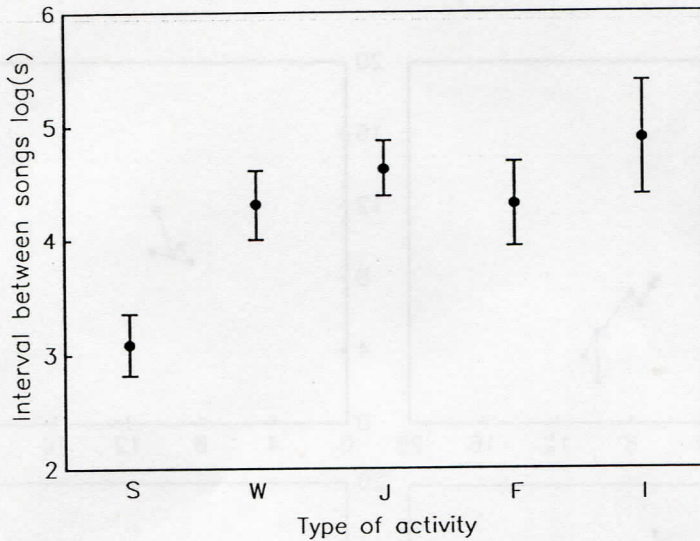


Figure 4. The observed duration of the interval between songs and different activity classes on a log scale. S = sit: when the male stays in the same spot ($N = 47$). W = walk: when the male only walk ($N = 38$). J = jump ($N = 56$): the male jumps at least once and F = fly: when it flies at least once ($N = 25$). I = interactions: Male-male interaction ($N = 14$). Anova, $F = 20.83$, $P < 0.001$.

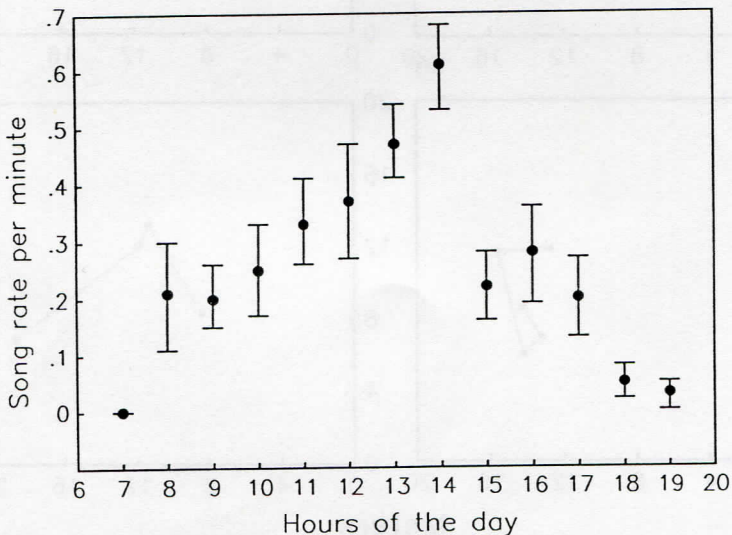


Figure 5. The mean song rate per minute at different times of the day and SE ($F = 3.58$, $P = 0.0001$, $N = 274$).

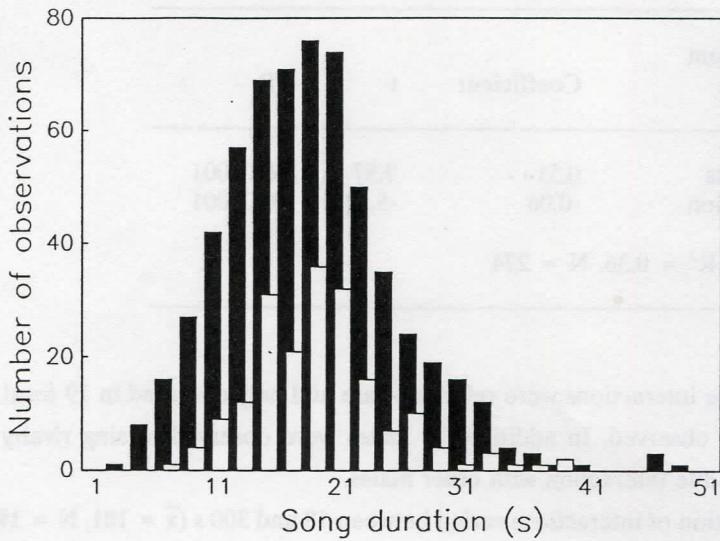


Figure 6. The distribution of song durations. Shaded columns: individual songs. Unshaded columns: The mean duration of songs from individual male. Songs = 607, males = 191.

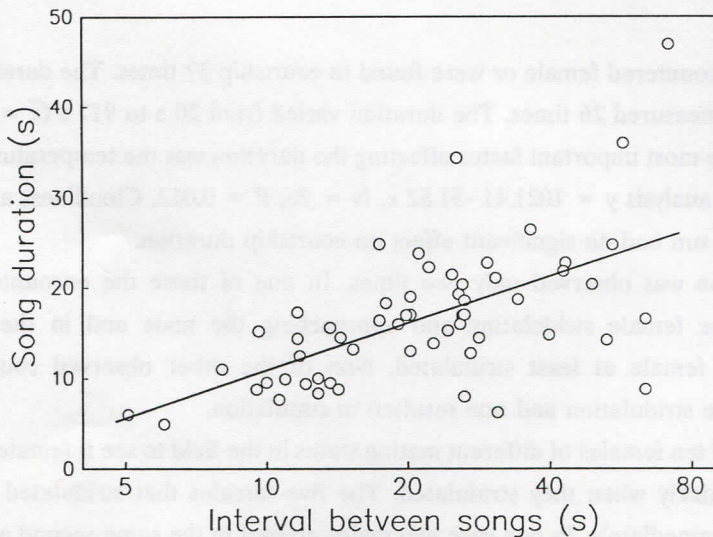


Figure 7. The relationship between the mean interval of each male from last song and the mean song duration. The fitted regression line $\ln(y) = 1.309 + 0.458 \ln(x)$, $N = 58$, $P < 0.001$.

TABLE I. Stepwise multiple regression analysis of male song rate.

Independent variable	Coefficient	t	P
Cloudiness	0.51	7.57	0.00001
Sun position	-0.06	-5.54	0.00001
Adjusted $R^2 = 0.36$, $N = 274$			

Interaction

Male-male interactions were relatively rare and only observed in 19 focal males out of the 313 observed. In addition, 11 males were observed to sing rivalry songs without any visible interaction with other males.

The duration of interactions varied between 18 and 300 s ($\bar{x} = 101$, $N = 19$). The average number of rivalry songs in an interaction was 8.78. The number of rivalry songs and the duration of interaction was positively correlated ($r_s = 0.616$, $N = 33$, $P = 0.005$).

Courtship

Males encountered female or were found in courtship 37 times. The duration of courtship was measured 26 times. The duration varied from 20 s to 917 s ($\bar{x} = 215$ s, $SD = 209$). The most important factor affecting the duration was the temperature (Fig 8). Regression analysis $y = 1021.41 - 31.82 x$, $N = 26$, $P = 0.012$. Cloudiness and the position of the sun had no significant effect on courtship duration.

Copulation was observed only two times. In one of those the encounter was initiated by the female stridulating and approaching the male and in the other encounter the female at least stridulated. Non of the other observed courtships included female stridulation and non resulted in copulation.

I released ten females of different mating status in the field to see if females were found more quickly when they stridulated. The five females that stridulated where found almost immediately. In one case two males arrived in the same second and the male that came first copulated. I observed five females that did not stridulate for one

hour. Two of the females were not found within the observation hour, but three were found within 10-40 min.

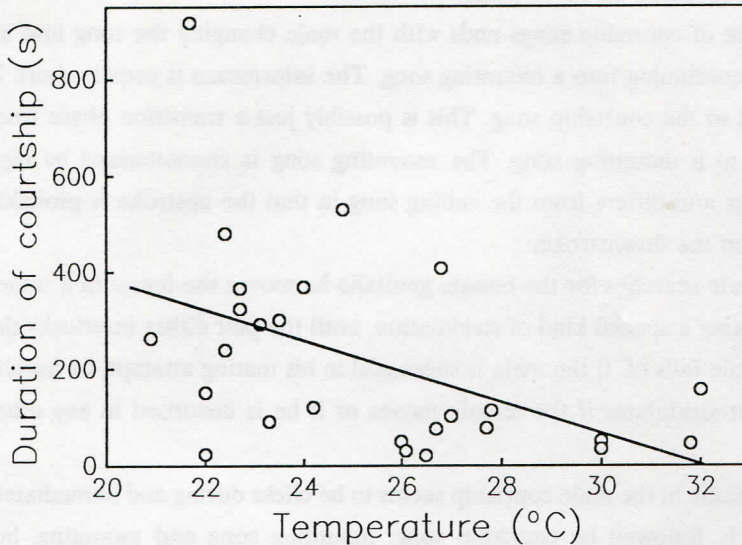


Figure 8. The relationship between the duration of courtship and the temperature. The fitted regression line is: $y = 1021.41 - 310.82x$, $N = 26$, $P = 0.012$.

The courtship sequence

In the laboratory all courtship followed a basic theme. After a male found a female a typical sequence was as follows: The male walks slowly towards the female and produces sharp "clicks" at the same time. If the female does not move away, the male stops approximately 1 cm from the female, usually in a lateral position (see also Riede and Huber 1979), and starts a courtship song. At the end of the courtship song the male begins a short "intermezzo", followed by a loud "mounting song" and finally attempts to copulate.

The clicks are not made as other stridulations, but by flicking the tibiae up and backwards, striking the wings with the terminal spines at the base of the tibia. Often both legs are kicked together, but sometimes they are moved one at a time, changing haphazardly from one side to the other. The number of clicks in a string varies, but are most often between 2 and 8.

The courtship song has the same structure as the calling song. The calling song is usually between 10 and 25 s, whereas the courtship song typically lasts between 20 and 80 s (Eiríksson in press a). Usually the male produced only one courtship song, but the song could be repeated up to 11 times.

The sequence of courtship songs ends with the male changing the song into an "intermezzo" and continuing into a mounting song. The intermezzo is usually short. It is quiet compared to the courtship song. This is possibly just a transition phase from a courtship song to a mounting song. The mounting song is characterized by high position of the legs and differs from the calling song in that the upstroke is probably more effective than the downstroke.

While the male searches for the female genitalia he moves the femur in a rather irregular way, making a special kind of stridulation, until the pair either interlocks the genitalia or the male falls of. If the male is successful in his mating attempt, he usually remains silent, but stridulates if the female moves or if he is disturbed in any other way.

The basic theme in the male courtship seems to be clicks during and immediately after the approach, followed by courtship song, mounting song and mounting, but deviations are found in almost every part of the sequence. However, the males never began a sequence with a mounting song (always observed to precede mounting), and the special kind of stridulation was always made when locking the genitalia.

The time from the first click to copulation attempt varied greatly, from less than a minute to half an hour. Every element of the sequence could be repeated several times, before changing to another song type, or the male could alternate between clicks and courtship songs before producing mounting song. The only real danger of the male losing contact with the female was during the mounting song or the mounting attempt, since the female frequently jumped away during this phase.

DISCUSSION

The number of males and females in the observation area was estimated to be around 150 ($0.32/\text{m}^2$) for each sex. Males were very mobile and apparently not restricted to any part of the area since individual males were found all over the observation area, but females were more stationary.

The mean song duration (Fig. 6) was in the same range as reported earlier (Jacobs 1950, 1953; Weih 1951; Ragge 1965, 1986). Duration is one of the song

parameters that differs highly between species (Ragge 1986). If the song duration serves the purpose of species recognition, a small variation in duration would be expected. There was however a very large variation in the duration of songs, and it has been shown that the duration per se is not important in this species but rather the total amount of singing (Eiríksson in press b). This variation is partly caused by a change in the male singing strategy since males sing on average shorter songs at higher densities (Eiríksson in press c).

Interaction between males were not physical and males have never been observed to fight, but interactions are characterized by the rivalry song. These songs are usually much shorter than calling songs. They could be part of the spacing system (Young 1971), but they could also serve the same function as calling songs (Eiríksson in press c).

When a male heard a stridulating female he went to her directly and engaged in courtship. The male however also approached females that had not responded with stridulation. Stridulating females are more easy to find, but maybe more importantly, those females are more likely to copulate. Males are not secure of mating even if they find a female. The receptiveness of females change with time and females are more likely to stridulate as their receptivity increases (Haskell 1960; Hartmann and Loher 1974). Female response stridulation is rarely observed in the field (Ragge 1955), probably because such females are found very quickly by males.

The males seemed to change their behaviour according to the weather. Temperature is known to affect the behaviour of grasshoppers (Skovmand and Pedersen 1983; Bauer and von Helversen 1987). Body temperatures of insects generally fluctuate in response to the amount of incoming solar radiation. The grasshoppers do regulate the effect of radiation by exposing them selves differently to the sun and sunbathe (Joern 1981), and it is not necessary the air temperature that is most important.

The mate locating behaviour of males appears to be a mixture of searching and singing and the system is characterized by high mobility. In the middle of the day when the conditions were most favorable the male sang most. Later in the day when the sun radiation decreases they stopped singing but continued moving.

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IV

**FEMALE PREFERENCE
FOR SPECIFIC PULSE DURATION OF MALE SONGS
IN THE GRASSHOPPER *OMOCESTUS VIRIDULUS***

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ABSTRACT

The preference of female Omocestus viridulus for synthetic male songs of different pulse duration was estimated in two experiments. In the first, the probability of the female responding with stridulation was measured during presentation of a randomized series of songs of different pulse duration. The second experiment measured phonotaxis of stridulating females towards loudspeakers in two-choice playbacks of songs of different pulse duration. In both experiments the females preferred songs with an intermediate pulse duration of 70-80 ms, which coincided with the mean for natural songs of 76 ms. The results indicate the presence of stabilizing selection on pulse duration through female preference, and suggest that this song parameter may be important for species recognition.

INTRODUCTION

The acoustic communication systems of many animals, especially birds, frogs and insects, have been successfully used to study different aspects of sexual selection (see Searcy & Andersson 1986 for a review). Orthopteran insects have become increasingly popular in this field of research, as males and females of most orthopteran species readily respond to playback of song, permitting experimental investigations of song function (see Otte 1977; Ewing 1989 for reviews).

Pulse or chirp repetition rate often codes for species identity (e.g. Bailey & Robinson 1971; Pollac & Hoy 1979; Doherty & Hoy 1985). In grasshoppers the most important characters of the song for correct species recognition are the pulse (syllable) repetition rate (*Chorthippus* spp: Perdeck 1958; *Chorthippus brunneus*: Butlin et al. 1985), the frequency characteristic of a pulse (*Omocestus viridulus*: Skovmand & Pedersen 1978), the duration of the low or high intensity phase within the pulse, or the ratio between the two phases (*C. biguttulus*: von Helversen 1972). Information in the song about the quality of the individual is less well understood, but may be contained in the temporal structure of the song, as well as in spectral parameters, intensity and song rate (e.g. Latimer & Schatral 1986; Bailey et al. 1990).

Grasshoppers of the subfamily Gomphocerinae differ from most other orthopterans in the behavioural response of females to male songs (e.g. Riede 1987). Females not only show phonotaxis to singing males, but also respond with a stridulation of their own. The establishment of pairs in gomphocerine grasshoppers usually involves stridulation by solitary males and the approach of sexually receptive females, or the alternation of male and female songs followed by both sexes approaching one another (e.g. Jacobs 1953; Haskell 1958). Females respond to male songs in a regular manner. The first response detected is an alert posture which is usually followed by orientation. Then the female usually runs or jumps in the direction of the sound and stridulates (see also Skovmand & Pedersen 1978). The whole sequence is usually repeated several times.

In this study I estimated female preference of the grasshopper, *O. viridulus*, for songs of different pulse duration. In one experiment the female stridulatory response and in another female phonotaxis to loudspeakers were used as criteria of choice. Two experiments were performed since it is difficult to estimate both types of responses in the same setup. Males were recorded under the same experimental conditions as

females, and the observed preference of females is compared with the natural variation in pulse duration of recorded male songs.

METHODS

Song recording and playback

The computer facilities of the Linguistic Department of the University of Stockholm were used to analyse pulse structure and also to synthesize artificial sound. Simulations of male song were made on the basis of a sample of natural songs recorded in the field at Tovetorp (Fig. 1a), with the help of descriptions in Elsner (1974), Skovmand & Pedersen (1978, 1983) and Kutsch & Schiolten (1979).

The synthetic pulse was made of broad-band electronically generated fricative sound (Fig. 1b). Each pulse was divided into two phases: high intensity and low intensity. The duration of the two phases changed with pulse duration, but the ratio of the two phases was kept constant at 72:28 (low intensity phase: high intensity phase) with respect to the total duration of the pulse. The high intensity phase reached maximum intensity after one-third of its duration and was kept at maximum for the remaining two-thirds. The low intensity phase had a carrier frequency around 4 kHz. At the start of the high intensity phase, a high frequency element with a carrier frequency around 16 kHz was introduced, and both frequency elements were kept to the end of the pulse. The high intensity phase was therefore bimodal in frequency.

The normal calling song of *O. viridulus* males usually lasts 10 - 25 s (Ragge 1986) ($\bar{x} \pm SD = 16.7 \pm 7.57$, $N = 58$, personal observation). The synthetic pulse of seven different durations (60, 70, 80, 90, 100, 120 and 150 ms) was repeated continuously at constant amplitude, to create a standard 15-s song and transferred to a tape (Revox A700 tape recorder, tape speed 19 cm/s).

I collected *O. viridulus* near Tovetorp, a field station of Stockholm University, situated 90 km southwest of Stockholm. Males were collected from the field as adults and kept for a few days in the laboratory until their songs were recorded. All females used in the experiments were collected as nymphs in the field and reared to imagines in the laboratory. They were kept as virgins until tested. A female was used once in the analysis, but if she did not stridulate, and thus was not receptive, she was retested after a few days.

Experiments and recordings took place in a sound-attenuated room at Tovetorp. Recordings were made from a control room, separated from the experimental room

by a window. The experimental room was brightly illuminated with two 400 W light bulbs and the air temperature was kept close to 28°C.

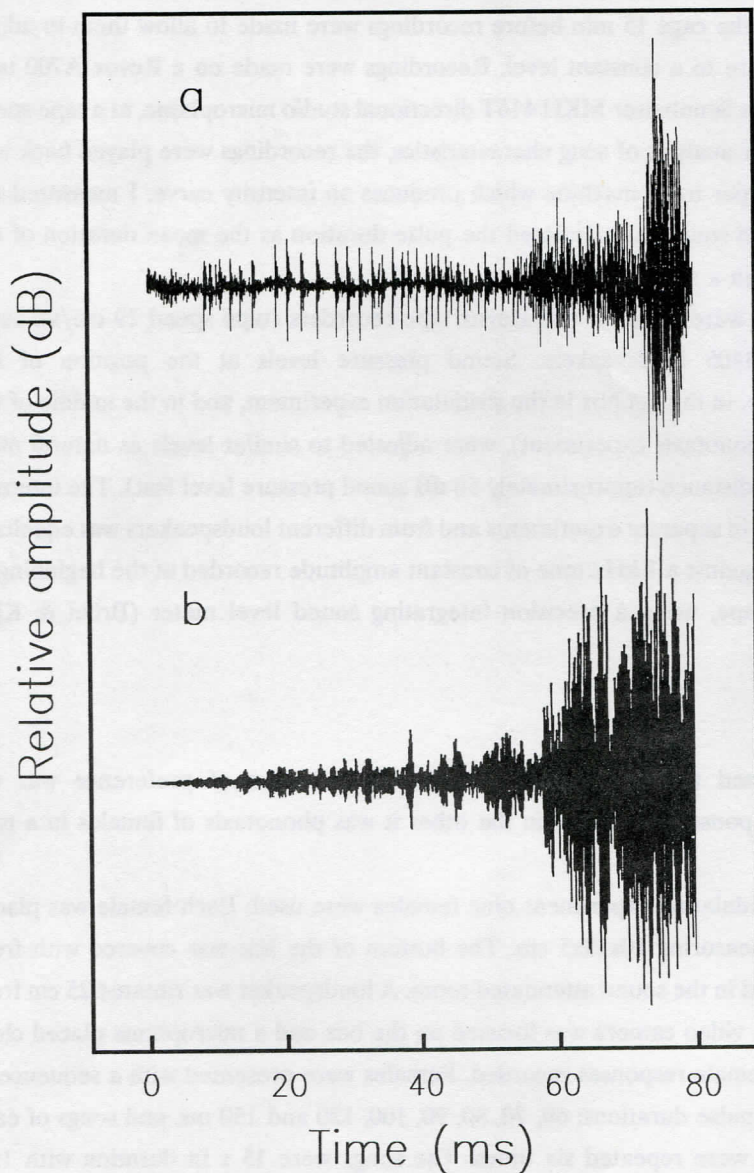


Figure 1. The pulse structure of the song of male Omocestus viridulus. a) Pulse taken from natural song. b) Synthetic pulse.

I recorded 169 male courtship songs, from 24 individuals, 1 - 17 songs per male, by confining each male with a female in a cage of light, soft net, measuring 10x10x10 cm, 10 cm beneath a microphone and 4 m from two 400 W light bulbs. The males were placed in the cage 15 min before recordings were made to allow them to adjust their temperature to a constant level. Recordings were made on a Revox A700 tape recorder, using a Sennheiser MKH 416T directional studio microphone, at a tape speed of 38 cm/s. For analysis of song characteristics, the recordings were played back into a Mingograf paper trace machine which produces an intensity curve. I measured the duration of each song and calculated the pulse duration as the mean duration of the last 100 pulses in a song.

Playbacks were done on two Revox tape recorders (tape speed 19 cm/s), using Siare TWZ 53405 loudspeakers. Sound pressure levels at the position of the grasshopper (i.e. in the net box in the stridulation experiment, and in the middle of the arena in the phonotaxis experiment), were adjusted to similar levels as natural male songs at 50 cm distance (approximately 50 dB sound pressure level fast). The intensity of the playback in separate experiments and from different loudspeakers was equalized by calibrating against a 1 kHz tone of constant amplitude recorded at the beginning of the playback tape, using a precision integrating sound level meter (Brüel & Kjær Model 2221)

Procedure

I performed two experiments. In one the criterion of preference was the stridulatory response of females; in the other it was phonotaxis of females in a two-choice test.

In the stridulation experiment nine females were used. Each female was placed in a net box measuring 10x15x5 cm. The bottom of the box was covered with fresh grass and placed in the sound attenuated room. A loudspeaker was situated 25 cm from the net box. A video camera was focused on the box and a microphone placed close to it, and the female responses recorded. Females were presented with a sequence of songs of seven pulse durations: 60, 70, 80, 90, 100, 120 and 150 ms, and songs of each pulse duration were repeated six times. The songs were 15 s in duration with 15 s silence between consecutive songs. Two minutes of silence followed the presentation of songs of each pulse duration before songs of other pulse duration were presented. The order of presentation of different songs was randomized.

For the phonotactic experiment, a circular arena of diameter 200 cm was constructed, bounded by a vertical wall, 40 cm high, lined with synthetic foam. The arena floor was covered with earth and cut grass which was renewed frequently. Care was taken to have fresh grass evenly distributed in the arena to eliminate directional bias caused by searching for food. A conspicuous orange string was used to divide the arena floor into 16 equal sectors, and concentric circles of radius 20, 40, 60, 80 and 100 cm divided each sector into five sections (see Morris et al. 1975 for a similar setup). The loudspeakers were placed at the borderline of two sectors at opposite sides of the arena.

Eight different choice experiments were performed on 105 females. In each experiment the females could choose between songs of two different pulse durations, played at the same time on a random schedule, by stridulating and moving towards one of the loudspeakers. The choices were 40/80, 60/70, 60/80, 70/80, 70/90, 70/150, 80/90 and 80/120 ms (see Fig. 2. for the natural distribution of pulse duration).

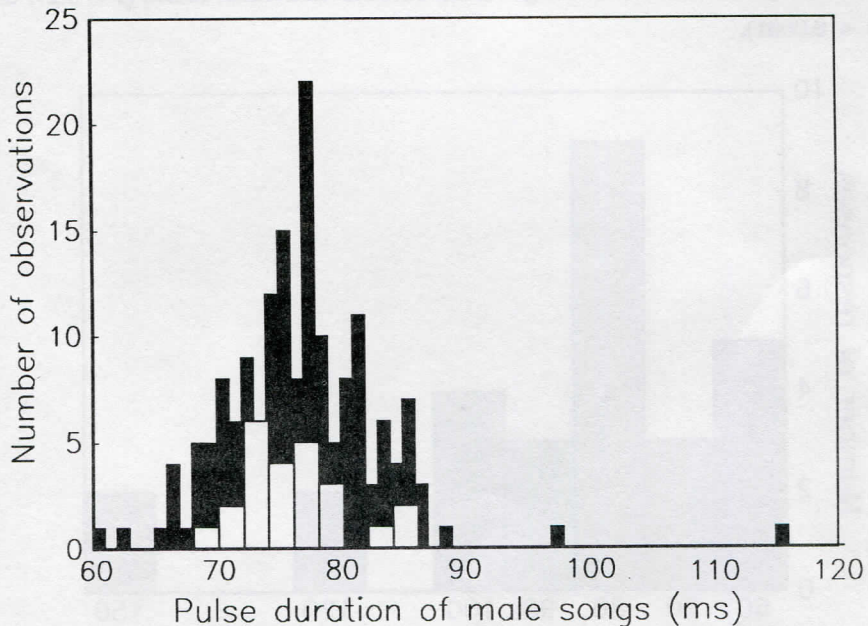


Figure 2. Distribution of the pulse duration of individual songs from all males (■) and of the mean pulse duration for individual males (□).

The females were placed in a small net box, in the middle of the arena. The cover of the box could be removed by pulling a string from the control room, and the females thus released. The females were allowed 15 min to settle down in the box and adjust to room temperature. Then the cover was removed, the tape recorders were started and songs of different pulse duration played from each loudspeaker. The experiment was monitored for 15 min, or until the females had left the arena. The route of the grasshopper was plotted on a drawing of the arena. The movement is defined as a positive response when the grasshopper stridulated and moved at least 40 cm into a quartile of the arena containing a loudspeaker, and stayed there to the end of the experiment or left the arena in that quartile.

RESULTS

Song analysis

The mean duration of courtship song was 55.93 s ($SD = 30.8$, $N = 169$). The mean pulse duration (Fig. 2) was 76.03 ms ($SD = 4.23$, N of songs = 169, N of males = 24). The pulse duration of songs varied between individual males ($F = 5.27$, $df = 23$, $p < 0.0001$).

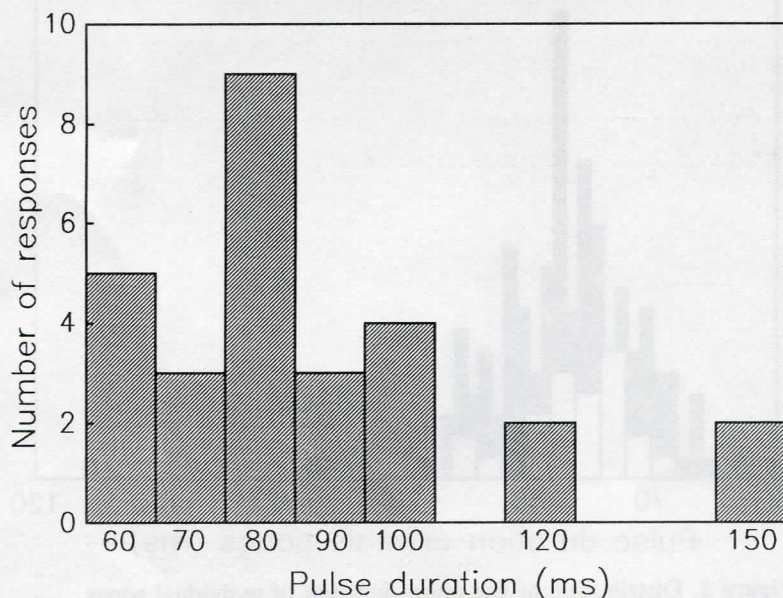


Figure 3. Number of female stridulatory responses to presentations of series of male songs of different pulse duration.

Stridulation experiment

Females responded with their own stridulation to songs of all pulse durations presented. All the females responded to the 80 ms pulse duration. There were two responses to pulse durations of 120 and 150 ms, and between three and five responses to other alternatives (Fig. 3). Friedman two-way analysis by ranks revealed significant variation in the probability of females responding with respect to pulse duration (test statistic = 18.9, $N = 9$, $p < 0.004$). Post-hoc pairwise comparisons between the response to 80 ms and any of the other alternatives showed a significant difference when compared to 70 or 90 ms ($p = 0.036$) and 120 or 150 ms ($p = 0.022$).

Phonotaxis experiment

In all five of the tests in which the difference between the playback songs was 20 ms or more, songs with a pulse duration of 70 or 80 ms were preferred over other alternatives (Table I). When the difference was 10 ms, there was no significant difference in female response.

TABLE I. Number of females that stridulated and moved towards one of the loudspeakers playing songs of different pulse duration in a series of two choice tests.

Pulse 1/pulse 2	Δ	Preference	p^*	N
40/80	40	0/8	0.0078	9
60/70	10	3/8	0.2265	17
60/80	20	2/13	0.0074	21
70/80	10	1/5	0.2187	10
70/90	20	6/0	0.0312	11
70/150	80	13/2	0.0041	18
80/90	10	3/1	-	7
80/120	40	8/0	0.0078	12

Pulse 1/pulse 2: the pulse duration in ms of the alternative songs. Δ : the difference between the pulse alternatives. Preference: number of females that moved towards the song with the respective pulse duration. p^* : Two tailed binomial test. N: number of females used.

The probability of a phonotactic response occurring after the female had stridulated was not equal in the different experiments. The proportion of females that stridulated but did not move out of the centre of the arena increased as the ratio between the pulse durations of the song alternatives decreased (Fig. 4).

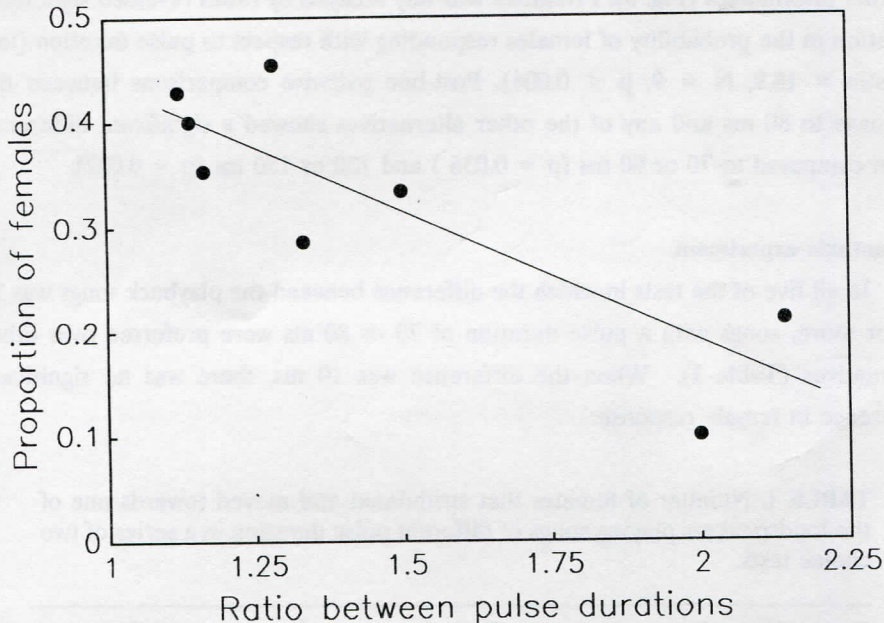


Figure 4. The proportion of females that stridulated in an experiment but did not move to a loudspeaker quartile versus the ratio between pulse durations of songs played, and the fitted regression line ($P < 0.0066$).

DISCUSSION

The females responded to songs of all pulse durations, but there was a significant difference in the probability of stridulatory response to the different song types (Fig. 3). The observed peak response was to pulses of 80 ms duration, where all the females tested responded. In the phonotaxis experiment, the females also preferred the songs with a pulse duration of 70-80 ms (Table I).

As the two alternative songs played in the phonotaxis experiment became more similar, an increasing proportion of females failed to choose one of the two loudspeakers even though they stridulated freely (Fig. 4). This could be due to loss of

information that is necessary for orientation when the songs became too similar (see Ronacher et al. 1986), and therefore a possible consequence of the experimental situation, or it could be that there was a motivational conflict about which way to move and therefore no net movement. Stridulation and phonotaxis are not necessarily elicited by the same song parameters, as pattern recognition and directional analysis are two processes operating in parallel in the grasshopper's central nervous system (von Helversen 1984; von Helversen & von Helversen 1987).

In this study I maintained constant ratio between the low and high intensity phases of the pulse, and thus kept the total amount of energy in all songs constant, eliminating the possibility that females are simply choosing between songs on the basis of energy content. However, the durations of the low and high intensity phases change with pulse duration and the preference for a particular song could depend on the trade-off between these two parameters (e. g. Doherty & Hoy 1985). The parameter of importance could therefore be differences in the duration of either the low or the high intensity phase as in *C. biguttulus* (von Helversen & von Helversen 1981). Using the proportions of the two phases in the pulse could also make the recognition independent of temperature (von Helversen & von Helversen 1987), as the pulse duration of males changes with temperature (Skovmand & Pedersen 1983).

A courtship song is a version of the advertisement song that the male sings during close range courtship with the female. Where the normal advertisement song usually ranges from 10 to 25 s (Jacobs 1953; Ragge 1986), the mean duration of the courtship song is 55.9 s (SD = 30.8). In other respects the two songs are very similar. The mean pulse duration of recorded courtship songs (Fig. 2) was 76.03 ms coinciding with the observed preference of females for songs of 70 or 80 ms pulse durations. Pulse duration varies between individual males, indicating that it is potentially subject to selection.

Characters associated with species recognition are expected to be under stabilizing selection (Falconer 1981). In a study on *C. brunneus* (Butlin et al. 1985), males with intermediate pulse duration were most successful in mating with females, but it was not clear if selection was due to female preference or male-male interactions. The results of this study show that selection on pulse duration could be caused by female behaviour alone as the difference in female behaviour with respect to pulse duration could cause a difference in male mating success.

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V

ABSTRACT

Male grasshoppers of the genus *Omocestus* have a highly specific division of the calling song. Two playback experiments were conducted to investigate how females in this genus respond to different male songs. Females responded more readily to songs with longer durations than to songs with shorter durations. There was, however, a threshold duration below which females did not respond. Females did not necessarily respond to songs with longer durations than to songs with shorter durations. A number of the females responded to songs with longer durations than to songs with shorter durations. These results suggest that the duration of individual songs is not important per se in eliciting female response, and that a male needs to sing with a certain duration in order to elicit a response. However, in order to maximize the effect of his song, he must also sing in a way to increase the overlap with female response, and increase the probability of eliciting the female response.

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ABSTRACT.

Male grasshoppers of the genus Omocestus have a highly species specific duration of the calling song. Two playback experiments were conducted to investigate how variation in song duration affected female response. Females responded more readily and with longer stridulations to longer male songs. There was, however, a diminishing return in the female response so a male will gain less and less by singing longer songs. Repetition of short songs, in order to give the same total duration as a long song, gave similar or even more intense response. Females did not necessarily wait for a male song to finish before responding themselves with stridulation. A majority of the females had already started to respond when a long song ended. However, the females spent more time moving, probably towards the singing male, as a response to longer songs. These results suggest that the duration of individual songs is not important per se in evoking female response, and that a male seems to gain most female response by singing as much as possible. However, in order to maximize the efficiency of his singing, he must also time his songs to decrease the overlap with female response singing, and increase the probability of hearing the female response.

INTRODUCTION

Many Orthopteran insects produce elaborate songs during intra-specific communication. It was demonstrated early in experiments on crickets (*Gryllus campestris*; Regen 1914), that females are attracted to the sound of conspecific males. Several parameters of the song have been shown to be important in evoking a reaction in females (von Helversen & von Helversen 1987), for example, pulse structure (e.g. Acrididae: von Helversen & von Helversen 1983), pulse or song repetition rate (e.g. Gryllidae: Walker 1957; Hill et al. 1972; Pollack & Hoy 1979; Acrididae: Butlin et al. 1985), frequency and harmonic content of the song (e.g. Gryllotalpa: Ulagaraj & Walker 1975; Gryllidae: Latimer & Lewis 1986), and calling bout duration (Gryllidae: Hedrick 1986).

The calling song of grasshoppers is highly species specific (Ragge 1986). The calling song of different species can be distinguished by quantitative variation in three characters; pulse (syllable) repetition rate, song (echeme) duration and song repetition rate. Characters that differ between species might be important for species identification. If song duration is one such important character, and several species with shorter and longer songs were involved, females would be expected to show a preference for songs of intermediate duration (see Butlin et al. 1985) as a result of stabilizing sexual selection (Falconer 1981). With only two species involved, character displacement might be the result (Littlejohn 1981), and females should prefer extremely short or long songs. However, if song duration is not used for species identification, and total magnitude of song is more important than the duration of individual songs, the females would also prefer long songs, but a similar stimulation effect would be expected by repeating short songs.

Unlike most other orthopterans, female grasshoppers of the subfamily gomphocerinae are not only attracted to a singing male, but also respond with a song of their own. The male is not stationary but moves frequently between song bouts. Both males and females move towards each other after hearing the song (Jacobs 1950; Jacobs 1953; Haskell 1958). Several authors have used the stridulatory response of female grasshoppers to estimate the stimulus value of different characters of male songs (von Helversen 1972, 1984; von Helversen & von Helversen 1975, 1981; Skovmand & Pedersen 1978, 1983; Charalambous 1990; but see Butlin & Hewit 1986).

Here I examine the importance of song duration in the grasshopper *Omocestus viridulus*. The long calling song of this species, usually 10 - 25 s, makes it suitable for experimental manipulation of the song duration. *O. viridulus* has a sister species *O.*

rufipes, which has a very similar singing system. The main difference seems to be that the song duration of O. rufipes is about half that of O. viridulus and the songs have shorter pulses (Ragge 1986, pers. obs.). Both species were found at the collection site, so the problem of recognizing the species is a very real one for Omocestus females.

The pulse duration of song affects female preference in O. viridulus (Eiríksson in press) and here I tested experimentally if O. viridulus females preferred songs of certain duration by performing two playback experiments. The duration of individual songs was varied in one experiment, and both the duration and number of songs was varied in the other. The duration of individual songs does not seem to be important for species identification as females prefer longer total durations of singing. Several short songs can stimulate the female as much as one long. The males seem to distribute their singing to stimulate females but also hear the female response.

METHODS

O. viridulus females were collected in the vicinity of Tovetorp, a research station of Stockholm University, situated 90 km southwest of Stockholm, Sweden. All females were collected as nymphs, reared to imagoes, and kept as virgins until they were used in the experiments. Experimental females were chosen at random from the stock, when they were less than three weeks old, and each was used once in the different experiments. Since this study concerns how different durations of male song affect female stridulatory response, a female was included in the analysis if she responded in at least one of the trials. Females that respond with stridulation are said to be in the state of active copulatory readiness (Hartmann & Loher 1974).

The song is produced by rubbing pegs on the hind legs against the wings. A complete movement of the legs corresponds to one pulse, and a song is a repetition of pulses (see Elsner 1974; Skovmand & Pedersen 1978, 1983, Ragge 1986 for description of song). The calling song of O. viridulus lasts from 10 to 25 s with a mean duration of 14 to 19 s (Jacobs 1950; Weih 1951; Jacobs 1953; Ragge 1986; $\bar{x} = 16.67$ s, $SD = 7.59$, $N = 58$, pers. obs.). The females prefer songs with a pulse duration around 80 ms under same conditions as used here (Eiríksson in press, see also Skovmand and Pedersen 1983).

The computer installation of the Linguistics Department of Stockholm University was used to manipulate the duration of male songs. Recorded song from an O. viridulus male was transferred to the computer. A pulse, 80 ms in duration, was chosen,

and electronically cut out of the song. The cut out pulse was repeated different numbers of times to make songs of varying durations. The complete songs were transferred from the computer to a Revox A700 tape recorder at a tape speed of 38 cm/s. To each tape was added a 1 kHz tone of constant amplitude to make it possible to adjust the intensity of songs in different trials more carefully.

Experiments took place in a sound-attenuated room at Tovetorp research station. Recording equipment and the observer were situated in a control room separated from the experimental room by a window. The room was brightly illuminated with a 400 watt light bulb. The air temperature was kept close to 28°C. The temperature of the females was probably somewhat higher than the room temperature, due to direct absorption of incident radiation from the lights.

Playback was done with a Revox A700 tape recorder at a tape speed of 38 cm/s, using a Siare TWZ 53405 loudspeaker. Sound intensity was measured with a Brüel & Kjær type 2221 precision integrating sound level meter. The loudspeaker was placed 100 cm from the net box containing a female and the sound intensity set to 50 dB re. 20 µPa at the site of the grasshopper. The mean behavioral threshold of females is 45 dB at 28°C (Skovmand & Pedersen 1983).

During a test a female was placed in a box measuring 10x12x5 cm made of soft highly transparent net. The bottom of the box was covered with fresh grass to provide food for the female and the box placed in the sound attenuated room. The female was placed in the box 1 h before the trial and the box kept at 28°C to allow the female to adjust to the temperature and get used to the box. The box was placed in the experimental room 15 min before the trial. The equipment were adjusted and started and the female left undisturbed for at least 5 min before the playback started. All trials were monitored for 10 min from the start of the playback.

Each female was tested with the different trials of each experiment on the same day, but left to rest 1.5 h between trials to minimize the risk of influence from the last performance. The different trials were done in random order.

The experiments were monitored with a video camera (Canon VM-E1) and a microphone. The time when the female started to walk and the start and end of each song were measured from the videotape, using a clock displayed on the video monitor, to the accuracy of 1/10 of a second. The stridulatory movements of the hind legs were used when measuring female singing rather than the recorded sound, as the movement could be timed more accurately. From this measurement the total female singing time

was calculated, but also the latency from the start of the playback to the first response song, and the time interval between the female started walking until she responded with a song.

In Experiment 1, 20 females were presented with a single song each trial. Five trials were performed with songs of varying duration: 3.75, 7.5, 15, 30 and 60 s.

In Experiment 2, songs of three different durations: 3.75, 15 and 60 s, were played to 23 females. The 60 s song was played only once, but the shorter songs were repeated so that the total duration of song was the same (i.e. 60 s) in each trial. The song was repeated after a silence 7 times longer than the song. Thus after a 3.75 s song came a silence of 26.25 s, the song was repeated 16 times and there were 7.5 min from the start of the first song to the start of the last. Similarly a 15 s song was followed by a silence of 1 min 45 s, the song was repeated 4 times and there were 6 min from the start of the first song to the start of the last.

RESULTS

A typical female response sequence started with an alert posture which was followed by the female turning in the direction of the loudspeaker and then walking or jumping in that direction. After this manoeuvre a female usually responded with a stridulation. The female stridulatory response is similar to the male normal calling song, but it is usually much quieter. The female then alternated between short bursts of stridulation, and walking until she stopped (see also Skovmand & Pedersen 1978). There was considerable variation in the response pattern. Sometimes the female started to sing right away and did not move, and sometimes she moved for a long time before responding with a stridulation.

In experiment 1, 60% of the females answered to 3.75 s, 75% to 7.5 s, 90% to 15 s, 95% to 30 s and 100% to 60 s. The total duration of female singing increased as the duration of the song increased. The correlation coefficient between female singing duration and log song duration is positive in 18 out of 20 females (two tailed binomial test, $P < 0.001$, $N = 20$). With increasing song duration it appears to be a diminishing return in terms of female stridulatory response (Fig 1).

In experiment 2, all of the females responded to 15 s songs, but 87% to 3.75 s songs and 95.7% to the 60 s song. Female response duration differed between treatments (Fig. 1). The response to 16 repetition of 3.75 s songs was at a similar level

as the response to a single 60 s song, but the response to four 15 s songs increased to a higher level (Friedman analysis of variance, $P = 0.038$).

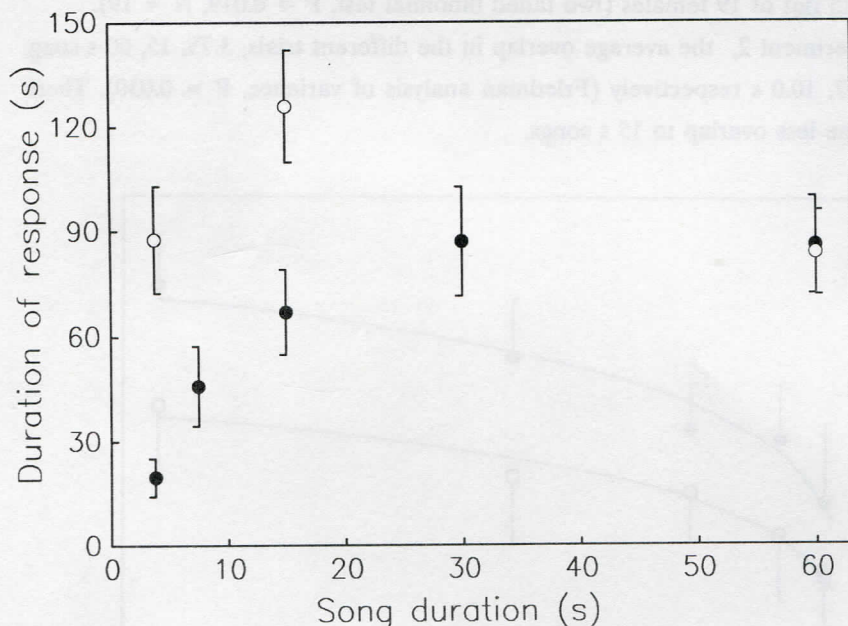


Figure 1. The mean total duration of female stridulatory response. Closed circles: when only one song was played. Open circles: when short songs were repeated to give the total duration of 60 s. Vertical bars show the standard error.

The response to a 60 s song was measured in both experiments with very similar results (Fig. 1). It is therefore possible to compare the response to each song duration in the two experiments. The duration of stridulatory response to the 3.75 and 15 s song increased markedly when they were repeated (Mann-Whitney, $P < 0.001$, $N_1 = 23$, $N_2 = 20$ and $P = 0.0137$, $N_1 = 23$, $N_2 = 20$, respectively, Fig. 1).

The time from the start of the playback until the female responded with stridulation varied considerably. The females did not necessarily wait for the playback to end before they started to stridulate themselves. There was therefore sometimes a considerable overlap between the female response stridulation and the playback song. Sometimes whole songs of the female response singing were covered by the playback.

In experiment 1, the mean overlap increased as the song duration increased. There was no overlap in trials with 3.75 s, but in trials with 7.5, 15, 30 and 60 s songs,

the average overlap was 0.040, 0.105, 2.805 and 11.61 s respectively. The correlation coefficient between overlap of individual female response and log song duration is positive in 15 out of 19 females (two tailed binomial test, $P = 0.019$, $N = 19$).

In experiment 2, the average overlap in the different trials, 3.75, 15, 60 s song, was 8.85, 4.7, 10.0 s respectively (Friedman analysis of variance, $P = 0.030$). There appears to be less overlap to 15 s songs.

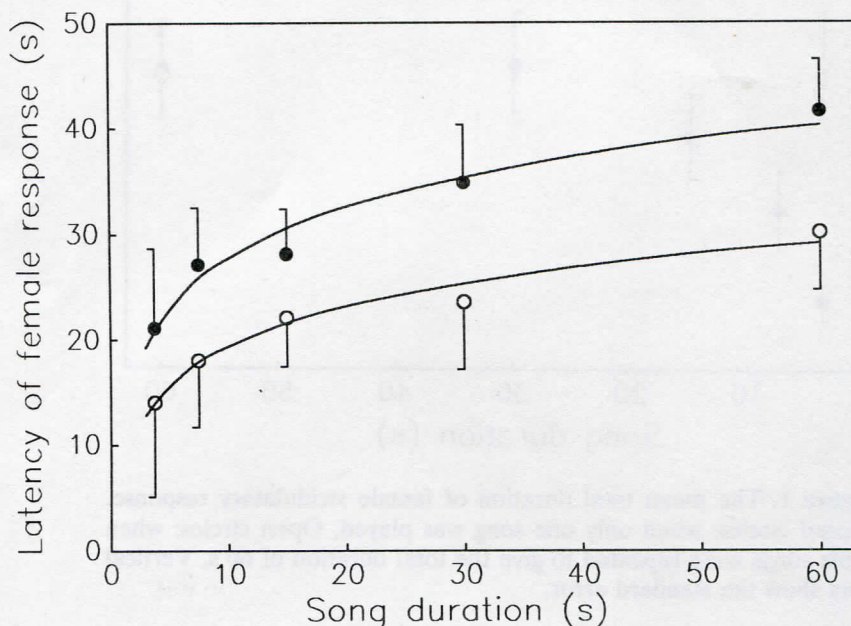


Figure 2. Latency of female response to different durations of male song. Closed circles: The mean time from the start of the playback to first stridulation. Open circles: The mean time after the female started walking until she started to stridulate. The vertical bars show the standard error. The fitted curves were obtained by linear regression of data on log song duration (latency: $y = 11.5 + 7.03 * \ln(x)$; time walking: $y = 6.82 + 5.45 * \ln(x)$).

In experiment 1, the mean latency of the female stridulatory response increased as the duration of the playback increased (Fig. 2). The correlation coefficient between latency and log song duration is positive in 18 out of 19 females (two tailed binomial test, $P < 0.001$). This is probably partly due to the fact that females that failed to respond to the shorter song durations needed longer playback to get aroused. The time

spent moving is a large part of the latency period and that time did also increase as the song got longer (Fig 2). The correlation coefficient is positive in 15 out of 19 females (two tailed binomial test, $P = 0.019$).

DISCUSSION

If the duration of the male calling song is used for species identification it would be expected that females would prefer songs that made the specie's identity most clear. This could take two forms in the case of *O. viridulus*. The female could either prefer an intermediate state of song duration and thus select against males that deviate from the species mean, or the females could prefer long songs, as *O. viridulus* sings longer songs than other species of the genus.

The results show that the magnitude of female response increases as the song duration increases (Fig 1). If the females prefer the mean song duration, it would have been expected that the females responded most strongly to songs close to the mean and less to both very short and very long songs. On the other hand, a preference for the longest song could also separate *O. viridulus* from other species of the genus. This is consistent with the results of experiment 1 (Fig 1), as the response is greater to longer songs. However, if the song duration was important per se, repeating short songs would be expected to produce weaker response than a single preferred song of the same duration. The results of experiment 2 (Fig 1) show that the repetition of a very short song (3.75 s) gives the same magnitude of response as one long song. Thus song duration is not likely to be used for species identification in *O. viridulus*.

Another possibility is that female response is determined solely by the amount of male song per time unit. However, it should be noted that when 15 s songs are repeated to give the total song duration of 60 s the response is greater than the response to one 60 s song. Thus, total amount of song is also insufficient to explain the magnitude of female response. There are probably two reasons for this.

First, there seems to be a diminishing return in the female response as the song gets longer, so the second half of a 60 s song increases the female response very little if at all (Fig 1). When the 15 s songs are repeated, the last song is delivered when it is probable that the female has stopped singing, and then it seems to be easy for a male to stimulate the female to resume her singing.

Second, the females do not hear an equal amount of song. The latency of female stridulatory response increases as the song duration increases (Fig 2), but the females

do not necessarily wait for the male to stop singing, but start to respond with stridulation even when the male is still singing. The majority of the females had started to stridulate before the 60 s song ended. This means that there is sometimes a considerable overlap between male singing and female response. The probability of overlap increases as the song gets longer, as the duration of female response increases very little if at all for long songs. There is evidence that grasshoppers are deaf when singing themselves (Hedwig 1986; Wolf & von Helversen 1986). This would mean that a song delivered after the female has started to sing would not stimulate the female to stridulate any more.

The high response to the repetition of the 15 s song (Fig 1), is probably partly because there is less overlap with female response singing, but also because the timing of delivery is important. The stimulus effect of male singing seems to be determined by the amount of song and how it is distributed in time.

Singing is probably very costly for the male as very little of the energy used to produce sound is transferred to acoustical energy (Kavanagh 1987: Gryllidae and Gryllotalpa). It is therefore important for the male to increase the efficiency of his song in stimulating females. This can be done by decreasing the overlap with female stridulatory response, and delivering the song when it influences females the most. Furthermore, the male needs to hear the female in order to be able to localize her. If the female starts to sing while he is still singing he runs the risk of missing the female response.

The time the female spends moving increases as the song gets longer. It could be of adaptive value for the male to sing longer to give the female more time to move towards him, but this is counteracted by a greater risk of not hearing the female.

It seems reasonable to assume that male song duration of *O. viridulus* is shaped by the female response behaviour. The male tries to maximize the probability of stimulating females by singing as much as possible, but at the same time minimize the overlap with female response by taking a pause when females have started to respond, and resume his singing when the female response has declined and she is again responsive to male song.

The males are usually surrounded by other males. The probability that other males will encounter the female will increase as the female moves for longer time, especially if she starts to stridulate. It is therefore important for the male to hear the female response song as early as possible when there are many males around which

will emphasize the gain by distributing the singing effort in time. The need to listen for competing males would affect the song duration in the same direction (Greenfield 1990), but the relative importance of these two causes in shaping the song needs further investigation.

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VI

**DENSITY DEPENDENT SONG DURATION
IN THE GRASSHOPPER *OMOCESTUS VIRIDULUS***

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ABSTRACT

Although duration of grasshopper song is species specific, there is also considerable variation within species. One possible reason for this is that males are adjusting their singing tactics in relation to the density of competitors. Males are expected to sing shorter songs when other males are nearby to enhance the probability of hearing female response or to listen to other males. To test this hypothesis an experiment was performed by placing different numbers of Omocestus viridulus males in large outdoor cages and monitoring their singing behaviour. The results show that males sing on average shorter calling songs as the number of males increases. It was also found that males compensate for singing shorter songs by singing more songs, so the total time spent singing stays similar at all densities. The scenario is complicated by the singing of very short songs which are mainly, but not exclusively, used in male-male interactions. The probability that males sing rivalry songs increases with the density of males and the number of these songs increases as male-male interactions get longer. The results suggests that part of the variation in the duration of calling songs reported in several field studies is caused by a change in singing tactics at different densities of males. The function of rivalry songs is not clear. These songs may function in the spacing of males or may be an extremely short form of the normal calling song used when other males are very close.

INTRODUCTION

Acoustic communication is widely used in orthopteran insects, and in most species song plays an important part in sexual behaviour. The calling song of the male stimulates the female to respond, either by showing phonotaxis towards the male (Morris et al. 1975; Bailey & Yeoh 1988), or with stridulation that helps the male to locate the female (Haskell 1958; Robinson 1990). The structure of the song often codes species identity (Perdeck 1958; von Helversen & von Helversen 1987; Ritchie 1991), and may signal male quality, as size, to females or to other males (Forrest 1983; Simmons 1988).

A calling male faces the dilemma that while he is attempting to stimulate females he must also take into account competing males. In order to maximize his mating opportunities, the male has to evaluate the situation constantly and change his signalling tactics accordingly (Shaw 1968; Otte & Joern 1975; Greenfield & Shelly 1985; Cade & Cade 1992).

The correlation between male signalling and mating success is a central theme in sexual selection theory (reviewed in Searcy & Andersson 1986), and many research workers have realized that orthopteran insects offer excellent opportunities for carrying out experimental tests of the theory. Most work has been done on crickets (Gryllidae), mole crickets (Gryllotalpidae) and bushcrickets (Tettigonidae) (reviewed in Ewing 1989), but the work on grasshoppers (Acrididae) is increasing (e.g. Skovmand and Pedersen 1978; von Helversen and von Helversen 1981; Butlin et al. 1985; Ritchie 1990).

Grasshoppers of different species differ markedly in the structure of their songs (Ragge and Reynolds 1984; Ragge 1986, 1987). In many cases, there are special songs for the different phases of courtship (Jacobs 1953; Bull 1979). The songs are relatively simple and most can be described by variation in three parameters: pulse (syllable) duration, song (echeme) duration, and song repetition rate. The pulse duration of grasshopper songs has received considerable attention. It has been found to be important in stimulating females to mate, and is thought to code species identity (von Helversen 1972; Butlin et al 1985; Butlin & Hewitt 1987; Eiríksson in press a). Song and song sequence duration have been much less studied than pulse duration despite the fact that they show great variation. The song of different species can vary from a few seconds to several minutes (Ragge 1986, 1987).

In grasshoppers females not only approach calling males, but also signal their position by stridulating in response to the male. This behaviour distinguishes

grasshoppers from most other orthopteran insects (e.g. Gryllotalpidae, Ulagaraj and Walker 1975; Gryllidae, Cade 1980; Tettigonidae, Arak et al. 1990). Thus a grasshopper male has two main options. He can actively search for females (Butlin & Hewitt 1986), or he can stay put, sing the normal calling song and wait for females to respond either with phonotaxis or stridulation (Jacobs 1950, Haskell 1958). The main male strategy used varies among species and is probably correlated with the typical response behaviour of females (Eiríksson in press b). Female stridulation does not seem to be necessary for copulation in some species, but in others it invariably precedes copulation (Blondheim 1990).

The need to listen to the singing of other individuals could influence the duration of male calling songs. Grasshoppers cannot hear stridulations from other individuals while they are singing themselves (Hedwig 1986, Wolf and von Helversen 1986), and females do not necessarily wait for a male to end his song before they start to stridulate (Eiríksson in press b). Therefore, a male must stop singing in order to hear the female and thereby localize her (see also Greenfield 1990).

If there are many competing males around a singing male, he runs the risk that another male hears a responding female and gains the advantage of being the first male to court her (e.g. Otte 1977). Therefore, it would be expected that males sing shorter songs when other males are close by, in order to increase the probability of being the first male to hear the female. Conversely, when the male is alone, the main concern would be to sing long enough to stimulate the female to respond.

Omocestus viridulus is a grasshopper which uses acoustics in all phases of courtship. The behaviour of males in the field is a mixture of searching and singing. The normal calling song is long, between 10 and 25 s (Weih 1951; Jacob 1953; Ragge 1986). A male often sings only one song and then, after waiting a moment, moves to another location, or he may repeat the song a few times before moving. Sometimes the male walks around the singing spot for some time, often creeping under the vegetation, presumably searching for females.

Males not only sing the normal calling song but also sing very short songs. The latter song type is predominantly used when males are close to one another, and has been referred to as rivalry song (Faber 1929; Jacobs 1950; Haskell 1957; Young 1971). The function of rivalry songs is not clear, but it is thought to affect male spacing.

To study the effect of male density on song duration an experiment was performed using *O. viridulus*. Males were placed in large outdoor cages and the singing of males was monitored for different male densities in the cage.

METHODS

Experiments were performed at Tovetorp, a field station of Stockholm University, situated 90 km south of Stockholm. Singing males were collected in a protected area around an ancient viking burial mound close to Tovetorp, and kept in the laboratory for at least one day before they were used in an experiment.

The experiments were performed in large outdoors cages. The cages were made with a wooden frame, 1 m high and covering an area of 2.5 x 2.5 m (6.25 m²). The sides and top of the frames were covered with black, transparent net. Three cages were constructed and put outdoors at ten meter intervals in a field otherwise free of *O. viridulus*. The grass inside the cages was cut short to make the bottom uniform and make it easier to see the grasshoppers. Two of the cages were used in experiments, and the third to acclimatize males to outdoor conditions. The males were taken out of the laboratory in the morning of the experimental day, marked with a unique color code on the thorax, and put in the acclimatization cage until they were needed. All experiments were performed between 1100 and 1500 hours, when singing activity is at a peak in the natural environment.

One to 16 males were removed from the acclimatization cage and put in the two experimental cages. After at least half an hour had passed since transfer from the acclimatization cage, one male in a cage was chosen at random as the focal male and his behaviour monitored for 20 min. The sun sometimes disappeared behind an occasional cloud before the 20 min period had elapsed and those periods are excluded from the observations. If the sun did not shine brightly for at least half the time (10 min), the trial was discarded. All measured rates are expressed as number of events in 10 min.

The normal calling songs of the focal male were counted and the duration of each timed with a stop watch. Interactions with other males were counted and the duration timed. An interaction was defined as the period of time when two males are moving in relation to each other. The rivalry songs of the focal male were also counted. These songs are much shorter than the normal calling song, usually between half a second and

2 seconds, and are therefore difficult to time with a stopwatch. Movement of the focal male was described in terms of distance walked, number of jumps and distance jumped.

Rivalry songs (Fig. 1) are mainly used when males are very close to another. However, males have been observed singing these short songs without being in visual contact with any male, and responding to a singing male more than 50 cm away. A structural difference was used to distinguish between rivalry songs and calling songs. Rivalry songs are relatively constant in amplitude, and are not characterized by the initial rise in volume of the normal calling song. The pulse also sounds different (Jacob 1953), probably because there is less distinction between the intensity of the upstroke and downstroke of the leg (see Skovmand & Pedersen 1978; Elsner 1974 for a description of song structure).

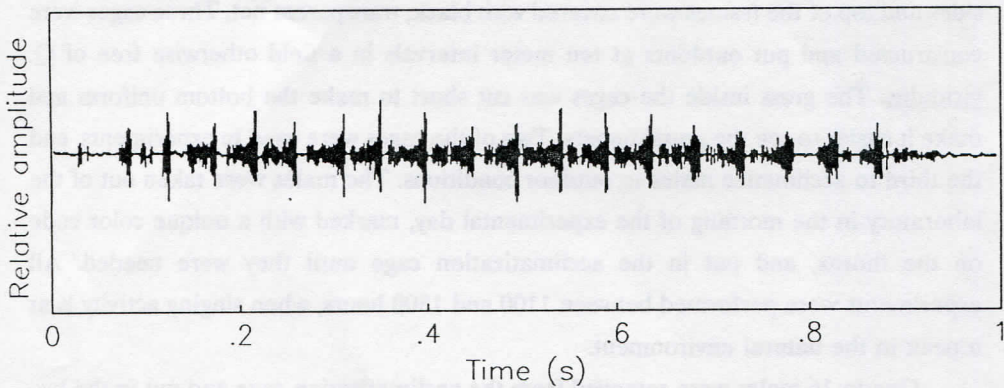


Figure 1. An oscillogram of rivalry song.

Even if it is quite clear in most cases what is a rivalry song and what is a calling song there are long rivalry songs or short calling songs that can be difficult to put into a category. Since the main concern of this study was to test for a decrease in the duration of the calling song with increasing male density, doubtful cases were classified as rivalry songs.

The general level of singing activity in the cage was also measured by counting the number of calling songs and rivalry songs by all the males in the cage. When there were many males in the cage two observers worked together, one to monitor the focal male and the other to record the total singing activity. As the cages were large, sometimes the observer lost sight of the focal male before the trial was completed. In those cases the observations on general singing activity were completed and the

measurements of song duration kept but observations on movement and number of songs of the focal male discarded.

The air temperature in the grass was measured at the end of each trial. Temperature is known to affect the song duration (Skovmand and Pedersen 1983). Although all experiments were performed under very similar conditions, the air temperature varied from 19°C to 27°C between trials ($\bar{x} = 23.04$) but no significant correlation was found between song duration and temperature ($r_s = 0.119$, $P = 0.634$, $N = 29$).

When each trial was completed, the focal male was removed and not used in further experiments, but the remaining males were returned to the acclimatization cage to be used in subsequent experiments.

RESULTS

A total of 44 trials were performed, with 10 different numbers of males in the cage (1, 2, 4, 5, 8, 10, 12, 13, 14 and 16 males). The song duration of the 29 focal males were timed, one to 5 songs from each male. The observed range of song durations was from 7.16 to 30.1 s, and the largest range of a single male from 7.16 to 18.5 s. A linear regression analysis showed that mean song duration decreased as the number of males in the cage increased (Fig. 2).

If the total number of songs produced by all males is used to calculate the number of songs per male the average is 0.904 songs in 10 min ($SD = 0.578$, $N = 44$). A regression of total number of songs per male on number of males in the cage showed that males sang more songs when there were more males in the cage (Fig. 3).

The total time the focal male spent singing was calculated by multiplying the mean song duration and number of songs. The males spent around 5% of the time singing and that proportion did not change with number of males in the cage ($y = 28.0 + 0.381 x$, $P = 0.625$, $N = 29$).

Nine interactions involving the focal male were observed. Excluding trials with only one male in the cage, the number of interactions did not increase significantly as number of males in the cage increased ($r_s = 0.286$, $P = 0.123$, $N = 30$). The duration of interactions varied between 8 and 353 s ($\bar{x} = 152$, $SD = 132$, $N = 9$). The number of other males in the cage did not seem to affect the time spent per interaction ($r_s = -0.272$, $P = 0.441$, $N = 9$), but the sample size is very small.

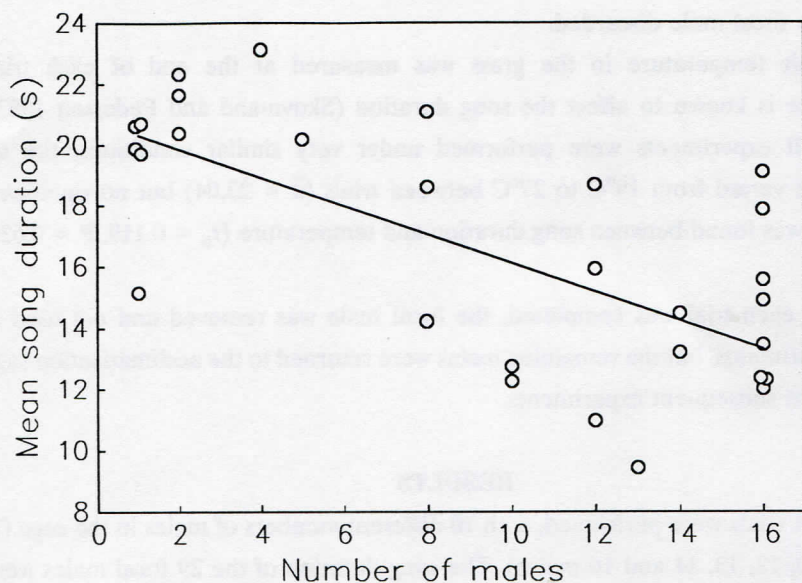


Figure 2. The mean duration of male calling songs with different numbers of males in the cage, and the fitted regression line ($y = 20.8 - 0.444 x$, $P < 0.001$, $N = 29$).

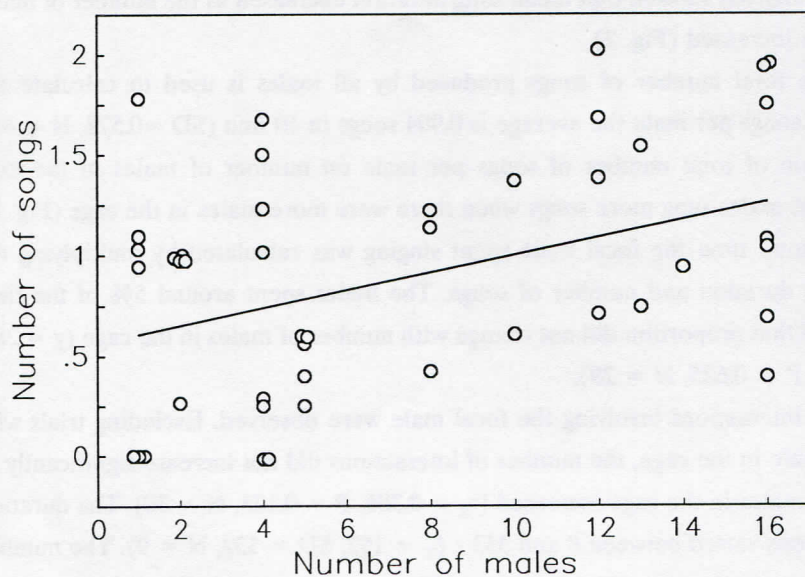


Figure 3. The average number of songs per male in 10 min with different number of males in the cage, and the fitted regression line ($y = 0.607 + 0.041 x$, $P = 0.009$, $N = 44$).

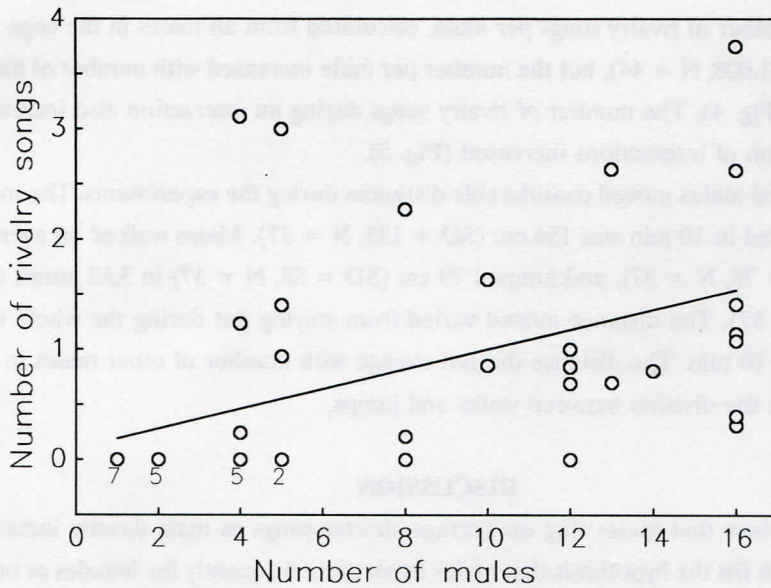


Figure 4. The average number of rivalry songs emitted per male in 10 min with different numbers of males in the cage, and the fitted regression line ($y = 0.0937 + 0.089x$, $P < 0.001$, $N = 44$).

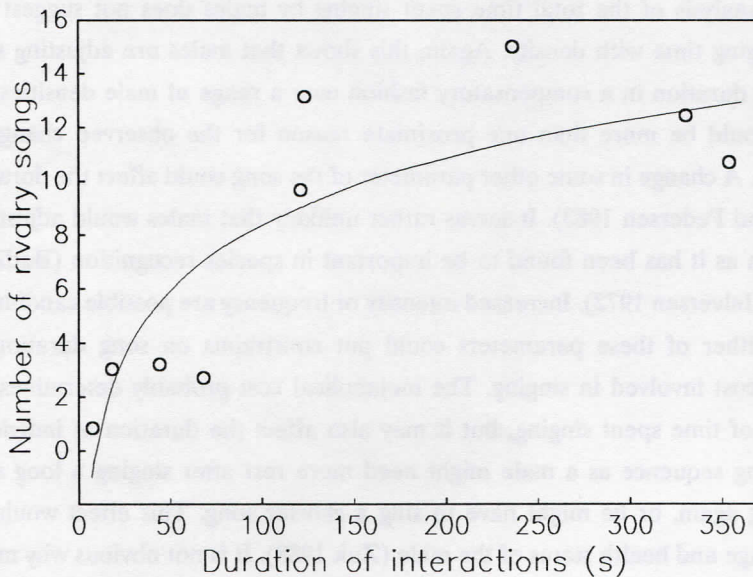


Figure 5. The number of rivalry songs emitted by focal males during an interaction versus duration of interactions, and the fitted regression line ($y = -7.96 + 3.55 \ln(x)$, $P < 0.001$, $N = 9$).

The number of rivalry songs per male, calculated from all males in the cage was 0.758 (SD = 1.008, N = 44), but the number per male increased with number of males in the cage (Fig. 4). The number of rivalry songs during an interaction also increased as the duration of interactions increased (Fig. 5).

The focal males moved considerable distances during the experiments. The mean distance moved in 10 min was 156 cm (SD = 133, N = 37). Males walked on average 77 cm (SD = 78, N = 37), and jumped 79 cm (SD = 88, N = 37) in 3.63 jumps (SD = 4.27, N = 37). The distance moved varied from staying put during the whole trial to 471 cm in 10 min. The distance did not change with number of other males in the cage, nor did the division between walks and jumps.

DISCUSSION

The results show that males sing on average shorter songs as male density increases (Fig. 2), which fits the hypothesis that males listen more frequently for females or other males when there are many competitors around. The overlap with singing of other males probably decreases with song duration, which can enhance the trend. The males seem to compensate for the shorter songs at higher densities by singing more songs (Fig. 3). An analysis of the total time spent singing by males does not suggest any change in singing time with density. Again, this shows that males are adjusting song rate and song duration in a compensatory fashion over a range of male densities.

There could be more than one proximate reason for the observed change in singing tactics. A change in some other parameter of the song could affect the duration (Skovmand and Pedersen 1983). It seems rather unlikely that males would adjust the pulse duration as it has been found to be important in species recognition (Butlin et al. 1985; von Helversen 1972). Increased intensity or frequency are possible candidates. Increase in either of these parameters could put constraints on song duration by affecting the cost involved in singing. The metabolic cost probably determines the total amount of time spent singing, but it may also affect the duration of individual songs in a song sequence as a male might need more rest after singing a long song before singing again, or he might have to sing a shorter song. This effect would be enhanced by age and health status of the male (Zuk 1988). It is not obvious why males should change their singing behaviour in this way. In general the correlation between song parameters needs further investigation.

The duration of calling songs of *O. viridulus* has been measured by many researchers, and the reported values are generally between 10 and 25 s (Jacobs 1950, 1953; Weih 1951; Ragge 1965, 1986). The mean song duration in this study was 16.7 s (SD = 3.92, N = 29), and is in the same range as the reported values.

The regression analysis in Fig. 2 predicts that a solitary male sings a 20.3 s song, which is in upper range of the song durations reported. For 16 males in the cage, which represents a high density, the prediction is a 13.7 s song, which is at the lower end of the reported range. That the results of this experiment are in general agreement with field observations demonstrates that the experimental situation was realistic and suggests that some of the variation in reported song duration arises because the males have been observed at different densities.

The number of songs per male varied a lot in this study (Fig. 3), and this was expected since the number of songs that males in the field sing before changing place varies between one and 9 (pers obs, see also Ragge 1965). The mean number of songs per male in 10 min was rather low in this study (\bar{x} = 0.9, SD = 0.57), and the males spent only around 5% of the time singing. Field measurement of song rate over a range of different densities are largely lacking, although lone males have been observed to sing at a much higher rate (pers. obs.).

Direct searching could be an important part of the mate finding strategy, especially at high densities. Since male movement ought to be a measure of searching, one might expect it to increase as the number of competitors increases. This effect was not found in the present study but that could be because the cages were too small to obtain a realistic measurement of movement or because of small sample sizes and large variation.

Rivalry songs are mainly emitted when a male is very close to another male. The number of rivalry songs in an interaction increases as the interaction gets longer (Fig. 5). The number of rivalry songs also increases with male density (Fig. 4) which points to increased interaction. However, direct observation of male-male interactions did not show that they were more common or longer at higher densities. A possible explanation is that sometimes a male sings these very short songs when he is not close to any other male. This could of course be the beginning of interaction that did not go any further, and therefore was not registered as interaction, or the observer may have failed to see the antagonist. It could also be that males sing rivalry songs as a response

to the songs emitted by other males without engaging in any other form of interactive behaviour or without being in visual contact with another male.

The function of rivalry songs is not clear. It seems likely that rivalry songs are part of the males spacing system (Young 1971) as has been found in other orthopteran insects (e.g. Campbell & Shipp 1979; Schatral et al. 1984), but there is also the possibility that this type of song is an extremely short version of the normal calling song. As these songs are too short to time with a stopwatch their duration in this experiment is not known. Jacobs (1953) found these songs to last from 0.5 to 0.75 s but they can last longer (pers. obs.).

If it is assumed that rivalry song lasts one second the total duration of these short songs would be the same as the values on the y-axis in Fig. 4. If this singing time is added to the total duration of the normal calling song the total time spent singing is still very similar at all densities.

Even if the proportion of time males spend singing does not change, the manner in which they arrange their singing seems to vary according to the situation. When there are many competitors around the male, he sings shorter songs but at a higher rate. Whether this is to listen for female responses or to monitor other males is not revealed by this experiment. Further experiments are needed to evaluate the reasons for the shorter songs at higher densities. The question of whether the rivalry songs emitted when other males are very close are extremely short calling songs also needs further investigation.

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VII

ABSTRACT

Male of the grasshopper *Omocestus viridulus* sing long "calling songs" to attract females to respond. The influence of acoustic competition between males on the duration of their songs was studied in the laboratory by recording two males at different distances from each other and also when they were alone. There is a significant difference in the duration of their songs when they sing alone. This variation in song duration is not directly related to body size, but smaller males seem to sing more than larger males. When a male is singing, another male singing nearby has a significant effect on the duration of his song. The variation in song duration is not directly related to body size, but smaller males seem to sing more than larger males. When a male is singing, another male singing nearby has a significant effect on the duration of his song. The variation in song duration is not directly related to body size, but smaller males seem to sing more than larger males.

ACOUSTIC COMPETITION AND ITS EFFECT ON SONG DURATION IN THE GRASSHOPPER *OMOCESTUS VIRIDULUS*

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ABSTRACT

Males of the grasshopper Omocestus viridulus sing long "calling songs" to stimulate females to respond. The influence of acoustic competition between males on the duration of their songs was studied in the laboratory by recording two males at different distances from each other and also when they were alone. There is variation between males in the duration of their songs when they sing alone. This variation in song duration is not directly related to body size, but smaller males seem to need more time to recover after a song to sing another equally long song. The variation in duration of songs produced by an individual male is also large, which is partly explained by an influence from a rival male. Males sing shorter songs as the distance to a rival male decreases, and the variation in song duration increases as the distance gets shorter. As the time interval from the last song of the rival male decreases a male also sings shorter songs. This time interval has less effect at larger distances. When the rival male is not singing or the distance is great the male sing songs of similar duration as when singing alone. At short distances when short calling songs were expected, another song type appeared. This type has been termed "rivalry song" and has been associated with male-male aggression. I suggest that calling song and rivalry song are just two ends of a song continuum serving the same function. Both stimulate females, but the duration is modified depending on the presence of other males.

INTRODUCTION

Research on acoustic communication in orthopteran insects have until recently focused primarily on species specificity of different male song characters (e.g. Perdeck 1958; von Helversen and von Helversen 1983; Butlin and Hewitt 1985; Ragge et al 1990) and on female preference for characters of conspecific songs (Latimer and Sippel 1987; Ritchie 1990, 1991; Charalambous 1990). However, work on variation in song parameters within populations is increasing (e.g. Walker 1980; Ritchie 1992) and it has been established that there exists considerable variation in both behaviour and song between individuals of the same population (Cade 1975; Schatral and Bailey 1991).

There is also wide variation in the songs sung by a single individual. Some of this variation is caused by environmental factors such as temperature (e.g. Skovmand and Pedersen 1983; Barrientos and Den Hollander 1990) and light conditions (Shaw 1968). Male body size influences certain song parameters, such as intensity (Latimer and Schatral 1986; Schatral 1990), frequency (Gwynne and Bailey 1988), and percent of time spent singing (Arak et al. 1990). Song is also influenced by morphological variation in the sound production apparatus (Latimer and Schatral 1986).

The behaviour of males is also influenced by the presence of other individuals. Density of males has been shown to affect behaviour in orthopteran insects. Most of this work has been carried out on species where males are territorial (Otte and Joern 1975; Greenfield and Shelly 1985) or more or less stationary (Schatral et al. 1984; Cade and Cade 1992). The situation is different in many grasshoppers, where females not only approach singing males but also answer with stridulation of their own (Haskell 1958; Eiríksson in press a,b).

The behavioural repertoire of grasshoppers includes many types of songs that can be distinguished by structural differences and by the behavioural context in which they appear (Jacobs 1953; Otte 1970, 1977). Several different song types are used when the male is courting a female (Bull 1979) but the most common song is the calling song, used to advertize for females.

When males get close to one another a different song type is heard. This song is usually much shorter in duration and sounds qualitatively different from the usual calling song. Although this song has sometimes been categorized as a distinct "rivalry song", and has been associated with male-male interactions (Jacobs 1950, 1953; Ragge 1965). It is however, possible that it is simply a shortened version of the normal calling song used for attracting females when other males are close.

In the grasshopper Omocestus viridulus a male only stays in the same spot for a short time and sings a few songs before he either walks around the spot or moves to a new location, sometimes several meters away, and resumes singing (personal observation). The calling song varies greatly in the field and males sing shorter songs at higher male density (Eiríksson in press c).

There is an increased probability that a female will answer as a male sings longer songs, but the total amount of singing is more important in eliciting female response than the duration of individual songs (Eiríksson in press b). However, there is competition between males not only to stimulate females and elicit female response, but also to be first to hear the female when she responds. The high mobility of grasshopper males means that the number of close males is changing constantly. There is also evidence that grasshoppers are deaf while singing themselves (Hedwig 1986; Wolf and Helversen 1986; see also Römer and Bailey 1990). At higher densities it would therefore be advantageous to sing shorter songs to be able to monitor female response more frequently and also other males (see also Greenfield 1990), but to keep the total singing similar by singing more songs (Eiríksson in press c).

To study how a male song changes in relation to the presence of other males, an experiment was performed in which two males were recorded at different distances from one another. It was found that the males sang on average shorter songs when the rival male was closer, and when the rival male had been singing recently.

METHODS

Grasshoppers were collected as nymphs in a protected area around Uppsakulle, ca 100 km south of Stockholm, Sweden. The males were reared to imagines in the laboratory. Shortly after the final moult the experimental males were chosen at random from available males and put into individual cages and kept there until used in experiments. Males were used in experiments when they had been observed to sing in the holding cages, 1 - 3 weeks after their final molt.

Experiments were performed in a sound isolated room, with the observer and equipment in a control room separated by a window. The males were put into small cages 5 * 5 * 12 cm, covered with black transparent net. The cages were put on a shelf, 10 cm wide and 3 m long, 1 m above the floor in the middle of the room and with 100 w light bulbs suspended 30 cm above the cages. The temperature was kept close to 35°C. The males were recorded on video and the sound also on a tape recorder.

The males were paired at random and put into the experimental room at least 45 min before the experiment started. Recordings started when one of the male started to sing and continued for 45 min. Recordings were made from 30 males in 8 different situations, where the distance between the males was 5, 12, 25, 50, 100, 200, 300 cm and when the male was alone. Sometimes neither of the males started to sing within 45 min and the trial was discarded.

A total of 2079 songs were recorded. The duration of each song was timed to an accuracy of 0.1 s. The time intervals between successive songs emitted by a male and the intervals between a given male's songs and those of the rival male were calculated.

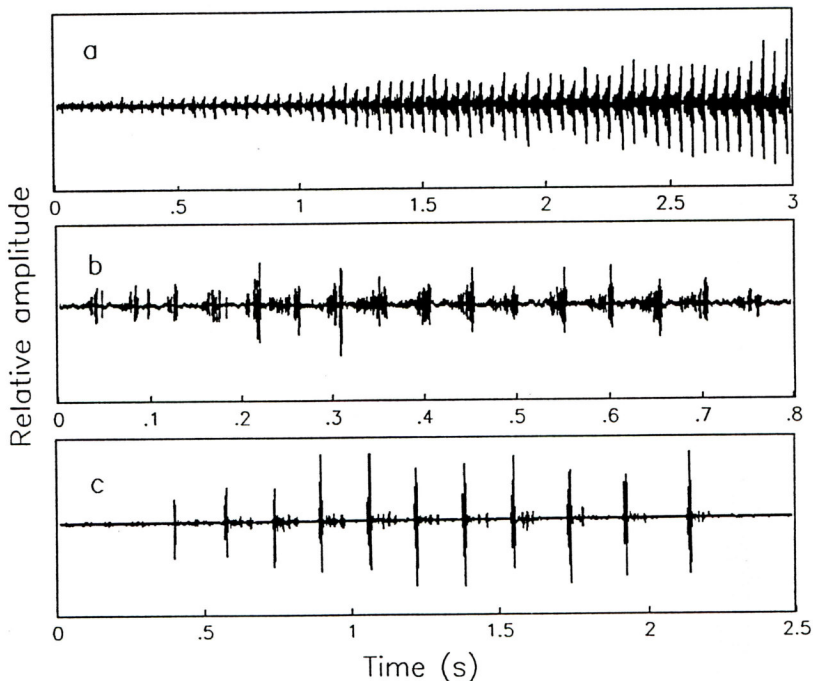


Figure 1. The structure of different song types. a) The first 3 s of a 16 s calling song. b) rivalry song. c) Tick song.

The songs were categorized into three types: calling song, rivalry song and tick song (Fig. 1). The distinction was only based on structural characters of the song and not on the duration. The calling song has a typical rise in volume and large amplitude difference between the upstroke phase and the downstroke phase of the pulse (Fig. 1a). The rivalry song has a more constant volume and less distinction between the phases of the pulse (Fig. 1b). In most cases it is obvious what is a calling song and what is a

rivalry song, but there were a small portion of songs that had the characteristics of both (mean duration 3.15, $N = 71$). These songs were categorized according to the dominant pattern of the song (see also Jacobs 1953; Kutsch 1976; Kutsch and Schiolten 1979).

The morphology of the male can influence his singing. The length of thorax ($\bar{x} = 3.00$ mm, $SD = 0.20$, $N = 30$) was measured as indication of size. The characters of the stridulatory file, length ($\bar{x} = 4.06$ mm, $SD = 0.38$, $N = 30$) and number of pegs ($\bar{x} = 120.9$, $SD = 10.02$, $N = 30$) were measured (for description of the stridulatory file see Pitkin 1976, 1979). The density of pegs ($\bar{x} = 29.01$, $SD = 2.09$) was calculated as number of pegs divided by the length of the stridulatory file (pegs/mm). The number of pegs and the length of the stridulatory file were correlated ($r_s = 0.55$, $N = 30$, $P < 0.003$), but neither of these measures nor the density of pegs were significantly correlated with thorax length.

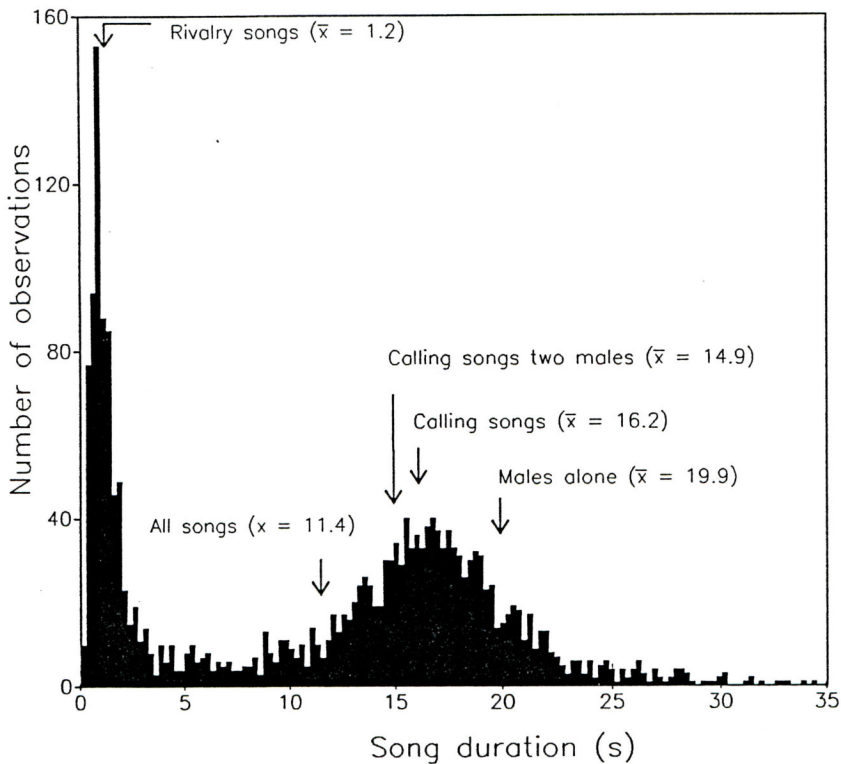


Figure 2. The distributions of durations of all recorded songs ($N = 2015$; tick songs are excluded). Inserted are the means of the different song groups mentioned in the text.

RESULTS

Song duration varied very much and its distribution had a pronounced bimodality (Fig. 2). The two peaks in the figure correspond roughly to the means of rivalry songs and of calling songs. The tick songs (mean duration = 3.86 s, SD = 2.23, N = 64) are excluded from the figure, as they were rare. Tick songs were only recorded 64 times from 22 males in 10 to 63% of the trials with the different distances, with one to three tick songs in each trial. Probability of tick songs did not change significantly with distance ($r_s = 0.33$, $P = 0.38$, $N = 8$).

The most common song emitted by males during the experiment was the calling song (mean duration = 16.16 s, SD = 5.22, $N = 1375$). This is the type of song males sang when they were alone, and then the mean duration was 19.9 s (SD = 4.48, $N = 334$). Although there was considerable variation between individual males (Fig. 3), no significant relationship was found between song duration and male size ($r_s = 0.27$, $P = 0.20$, $N = 24$), nor did max song duration and size correlate ($r_s = 0.14$, $P = 0.45$, $N = 30$). It was also tested if the variation in song duration was related to male size but significant relation was not found ($r_s = -0.05$, $P = 0.82$, $N = 25$).

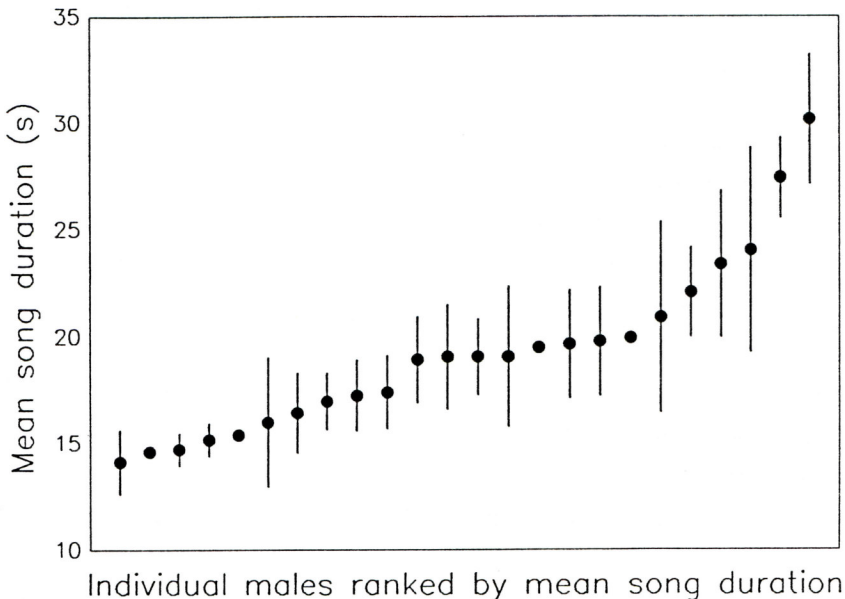


Fig. 3. The average calling song duration \pm SD of individual males when they do not hear other males. The males are ranked according to the mean duration of their songs (Anova, $F = 27.61$, $p < .001$, $N\text{-males} = 24$, $N\text{-songs} = 334$).

Since singing costs energy (Kavanagh 1987), a male might need time to recover after singing before he can start again. Similarly, a male's present song duration might be influenced by his singing activity in the immediate past. Thus, the time since the previous song and the duration of that song might be factors explaining variation in song duration. A natural variable to express this dependance would be the time available for recovery per second of the previous song ($t_{\text{rec}}/t_{\text{prev}}$). However, time per se might have an additional effect, which would be more pronounced for short times.

To investigate this, a multiple regression of individual male song duration on the two variables $t_{\text{rec}}/t_{\text{prev}}$ and $\log(t_{\text{prev}})$ was performed. To study situations where males would be expected to sing long songs (influence of the rival male small), those cases when the male was singing alone or where the rival male was at least 100 cm away were included in the analysis.

For part of the males (13 of 25), the multiple regression turned out to explain significant amount of the variation in song duration (with a positive coefficient for $t_{\text{rec}}/t_{\text{prev}}$ and a negative for t_{rec}). Since this effect of the immediate past is likely to result from limited endurance, one might expect that a small male would be more constrained by his immediate past than a large male. This seems in fact to be the case. There was a significant negative relationship between the size of a male and the coefficient of determination (R^2) of the multiple regression ($r_s = -0.46$, $P = 0.023$, $N = 25$). This means that smaller males are more affected by their previous singing, and implies that smaller males need a longer recovery time.

Similarly, a higher number of pegs on the stridulatory file could also constrain the male. The calculated correlation between density of pegs of the stridulatory file and the R^2 of the multiple regression was positive as expected but not significant ($r_s = 0.28$, $P = 0.16$, $N = 25$).

Part of the variation in the duration of songs from an individual male (Fig. 4) is explained by the distance to the other male (Fig. 5). Calling songs were on average shorter when the males were closer to one another ($r_s = 0.95$, $P = 0.012$, $N = 8$), and variation in song duration also increased as the distance between males decreased ($r_s = -0.91$, $P = 0.017$, $N = 8$).

When the distance between the males was 50 cm or less, rivalry songs appeared (mean duration = 1.18 s, SD = 0.73, $N = 640$). When rivalry songs and calling songs were combined the decrease in song duration became more pronounced, and also the increased variation (Fig. 5).

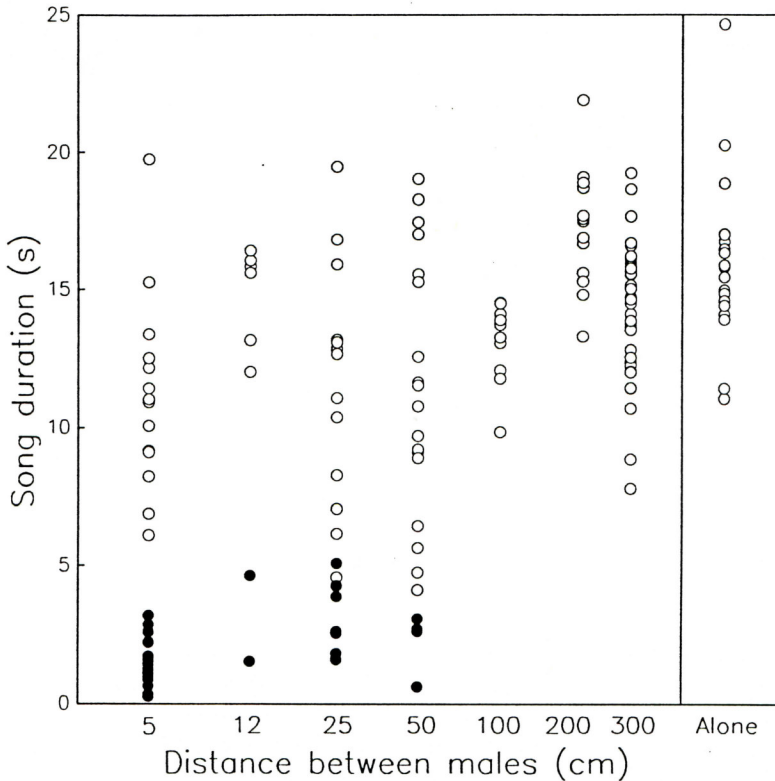


Figure 4. The duration of all songs recorded from one male at different distances. The last row separated by a line represent the male when he does not hear other males. Open circles = calling songs. Filled circles = rivalry songs.

There was large variation in the durations of songs emitted by an individual during a trial (Fig. 6). If the male sang shortly after another close male he was more likely to sing a very short song but as the time interval since the rival male's last song increased, the song duration increased (Fig. 7).

To evaluate the effect of distance on the influence of the rival male song, the regression coefficient of song duration on the time since the rival male's last song was calculated for each male at each distance (as in Fig. 7). The value of this regression coefficient was then plotted against distance between males resulting in a negative slope in 17 out of 18 males (two tailed binomial test, $P < 0.001$). This demonstrates that the interval between the songs of rival males has stronger impact on song duration when rivals are close.

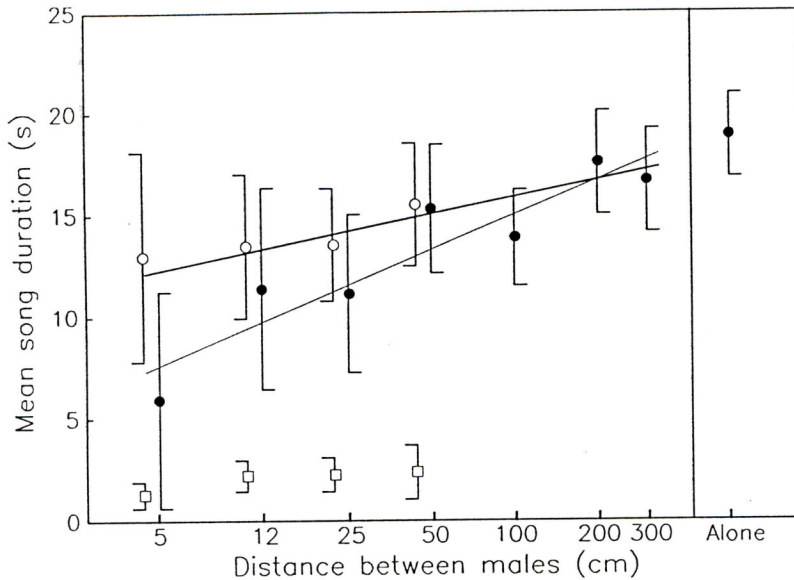


Figure 5. The average song duration and SD of all the males at different distances. Black dots: all songs. White dots: calling songs. Squares: rivalry songs. Tick songs are excluded. The two lines are fitted by regression on calling songs ($y = 10.35 + 1.19 * \log(x)$) and all songs ($y = 3.62 + 2.48 * \log(x)$).

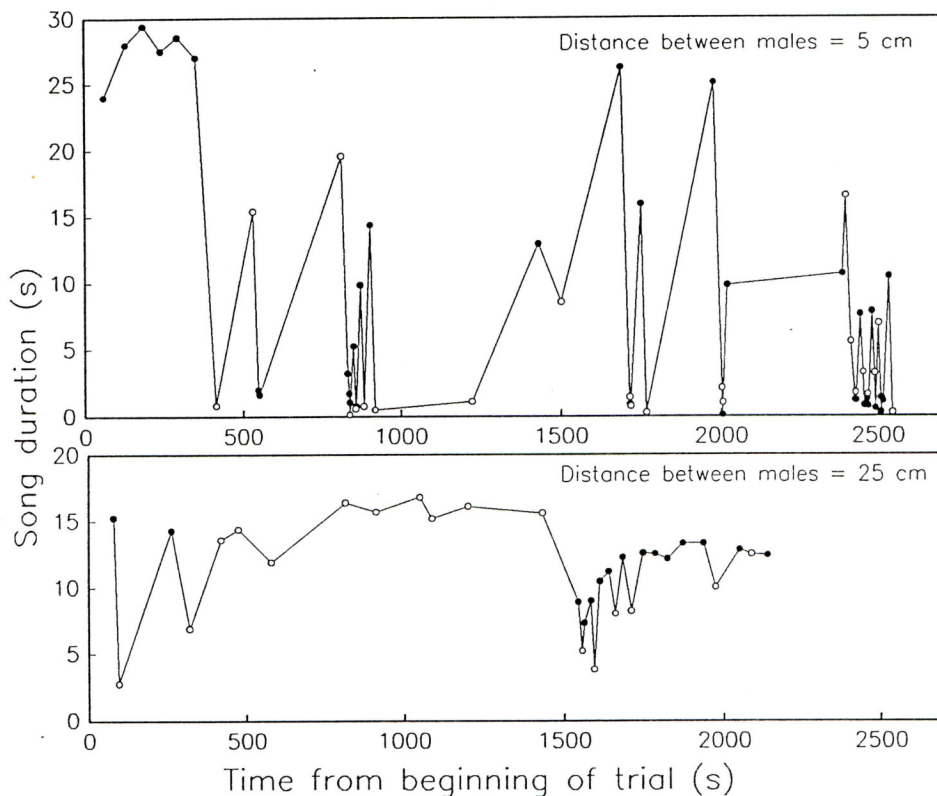
DISCUSSION

The average calling song duration of different males varied between 15 and 30 s (Fig. 3), with an overall average of 16.16 s. These song durations are in agreement with what would be expected from female response pattern (Eiriksson in press b; see also Hedrick 1986). Mean song duration in the field has been measured to be between 10 and 25 s (Jacobs 1950, 1953; Weih 1951; Ragge 1965, 1986; personal observation), so the songs in this experiment are in the same range as other reported values.

The variation in song duration between males does not seem to be influenced directly by body size. However, the singing endurance is affected by male size, as small males seem to need a longer recovery time between songs.

The presence of other males causes a male to sing shorter songs. In the field, the number of close males would be highly variable, as the males move frequently. A male seems to decide the duration of the songs he sings on the basis of the time since he last heard another male (Fig. 7) and how close that male was (Fig. 5). If he does not hear

another male for some time he resumes a song duration similar to the one used when singing alone.



Figur 6. The song duration and time record of singing in two example trials where the distance between the males is a 5 cm and b 25 cm. The different males in each trial are denoted by black and white dots.

When songs get very short there is a change in structural characteristics (Fig. 1). These short songs have been referred to as rivalry songs, but it is unclear what their precise function is. Young (1971) studied rivalry songs in *Chorthippus brunneus* and suggested that these songs are used to establish a dominance hierarchy and to maintain small individual home ranges. *O. viridulus* males have not been observed to fight and have very large home ranges. Individual *O. viridulus* males can move across an area of 20 x 20 m in a very short period (personal observation). It is therefore inconceivable that rivalry songs are associated with maintaining exclusive territories in *O. viridulus*.

This does not mean that the rivalry songs are not important in the short-term spacing of individuals. Note, however, that possible function of rivalry songs does not explain their short duration.

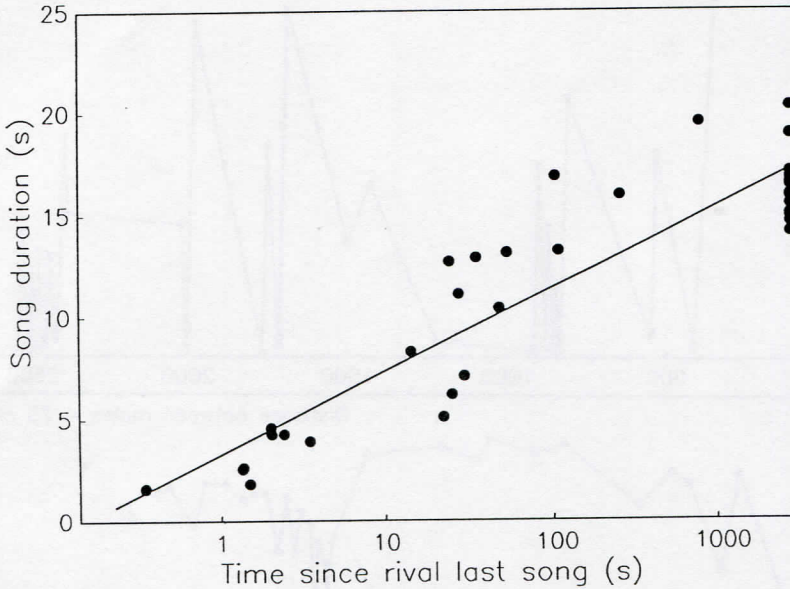


Fig. 7. Example of the relationship between the song duration of a male and the time from the last song of the rival male during one trial. The distance between the males was 25 cm.

There is, however, a form of male competition that could account for the variation in song duration. *O. viridulus* females do not wait for males to stop their singing before they start singing themselves (Eiríksson in press b). When there are other males around, a male would need to cease singing more frequently to increase the chance of being the first to hear the female response. As a consequence, he should reduce the duration of the calling song, and increase the number of songs (Eiríksson in press c). The observed reduction in calling song duration with decreasing distance supports this idea (Fig. 5).

The very short rivalry songs may represent an extreme form of this singing strategy, still intended to stimulate females to answer (see Schatral et al. 1984), whilst at the same time increasing the probability of hearing female response and to monitor nearby males more frequently (Greenfield 1990). This interpretation implies that the rivalry song is not a different song type used for a different function but only a

variation of the normal calling song. The interpretation is supported by the observation that when extremely short calling songs were expected, rivalry songs appeared. The change to short song types with decreasing distance between males can also be interpreted as means of minimizing overlap, thus reducing acoustic interference with the singing of other males.

When other singing males are close the male modifies his songs. His singing behaviour is consistent with monitoring the female stridulatory response and singing of rival males. Thus the observed variation in the song duration in the grasshopper O. viridulus is partly the result of acoustic competition between males.

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