DENSITY DEPENDENT SONG DURATION IN THE GRASSHOPPER OMOCESTUS VIRIDULUS

by

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(With 5 Figures)
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Summary

Although duration of grashopper 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 female 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), molecrickets (Gryllotalpidae) and bushcrickets (Tettigonidae) (reviewed in EWING, 1989), but the work on grasshoppers (Acrididae) is increasing (e.g. SKOV-MAND & PEDERSEN, 1978; VON HELVERSEN & VON HELVERSEN, 1981; BUTLIN et al., 1985; RITCHIE, 1990).

Grasshoppers of different species differ markedly in the structure of their songs (RAGGE & 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 & 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 & HEWIT, 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 & 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; JACOBS, 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 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 is 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 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 outdoor cages. The cages were made with a wooden frame, 1 m high and covering an area of 2.5 × 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 an 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.
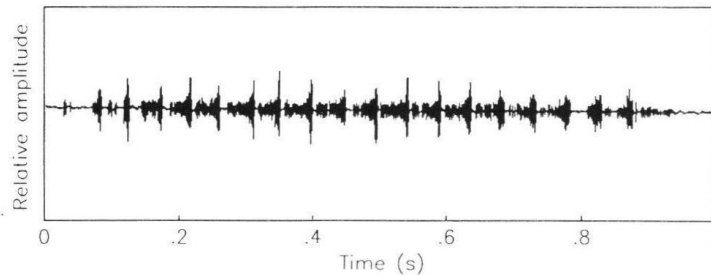

Fig. 1. An oscillogram of rivalry song.

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 one 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 (JACOBS, 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.

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 & PEDERSEN, 1983). Although all experiments were preformed 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.

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
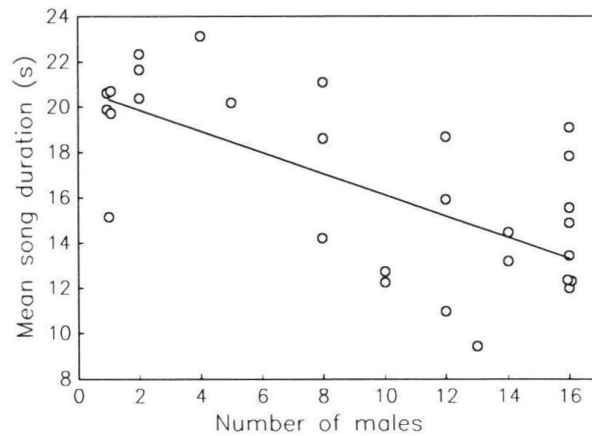
Fig. 2. The mean duration of male calling songs with different numbers of males in the cage, and the fitted regression line (y = 20.8 - 0.444 x, p < 0.0001, N = 29).
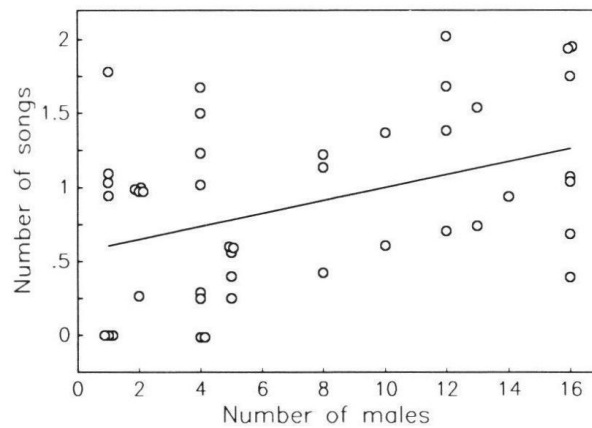

Fig. 3. The average number of songs per male in 10 min with different number of males in the cage, and the fitted regression line (y = 0.607 + 0.041 x, p = 0.0094, N = 44).

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 male in the cage, nor did the division between walks and jumps.
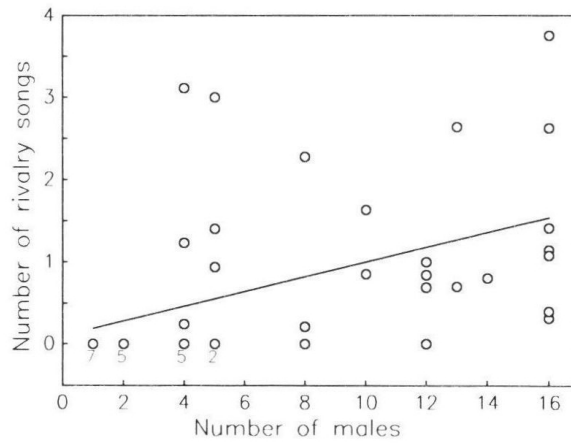
Fig. 4. The average number of rivalry songs emitted per male in 10 min with different numbers of males in the cage, and the fitted regression line ($y = 0.0937 + 0.089\,x$, $p < 0.0011$, $N = 44$).
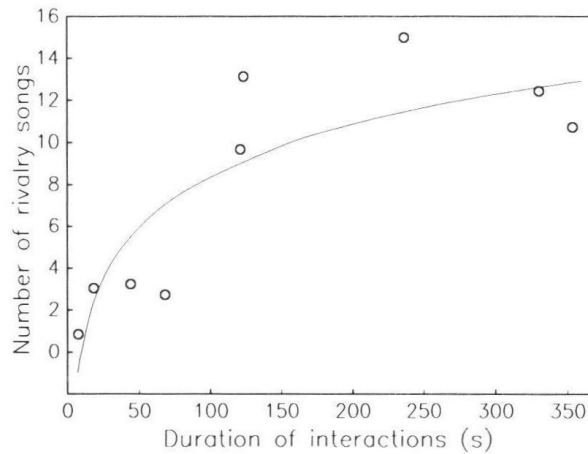

Fig. 5. The number of rivalry songs emitted by focal males during an interaction versus duration of interactions, and the fitted regression line ($y = -7.96 + 3.55\,\ln(x)$, $p = 0.0015$, $N = 9$).

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 shorrter songs at higher density 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 & 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 frequence are possible candidates. Increase in either of these parameters could put constraints on song duration by affecting the cost involved in singing. The metabolical cost probably determines the total amount of time spent singing, but it may also affect 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 ananlysis 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 (x̄ = 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 male 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 to 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 being in visual contact with another male.

The function of rivalry songs is not clear. It seem likely that rivalry songs are part of the males spacing system (YOUNG, 1971) as has been found in other orthoperan 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 extremely short calling songs also needs further investigation.

References

ARAK, A., EIRÍKSSON, TH. & RADESÄTER, T. (1990). The adaptive significance of acoustic spacing in male bushcrickets *Tettigonia viridissima*: a perturbation experiment. — Behav. Ecol. Sociobiol. 26, p. 1-7.

Bailey, W. J. & YEOH, P. B. (1988). Female phonotaxis and frequency discrimination in the bushcricket *Requena verticalis*. — Physiological Entomology 13, p. 363-372.

BLONDHEIM, S. A. (1990). Patterns of reproductive isolation between the sibling grasshopper species *Dociostaurus curvicercus* and *D. jagoi jagoi* (Orthoptera: Acrididae: Gomphocerinae). — Trans. Am. Ent. Soc. 116, p. 1-64.

Bull, C. M. (1979). The function of complexity in the courtship of the grasshopper *Myrmeleotettix maculatus*. — Behaviour 69, p. 201-216.

BUTLIN, R. K. & HEWITT, G. M. (1986). The response of female grasshopper to male song. — Anim. Behav. 34, p. 1896-1899.

—— & —— (1987). The structure of grasshopper song in relation to mating success. — Behaviour 104, 152-161.

——, —— & WEBB, S. F. (1985). Sexual selection for intermediate optimum in *Chorthippus brunneus* (Orthoptera: Acrididae). — Anim. Behav. 33, p. 1281-1292.

CADE, W. (1980). Alternative male reproductive behaviors. — Florida Entomol. 63, p. 30-44.

—— & CADE, E. S. (1992). Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer*. — Anim. Behav. 43, p. 49-56.

CAMPBELL, D. J. & SHIPP, E. (1979). Regulation of spatial pattern in populations of the field cricket *Teleogryllus commodus* (WALKER). — Z. Tierpsychol. 51, p. 260-268.

EIRÍKSSON, Th. (in press a). Female preference for specific pulse duration of male songs in the grasshopper, *Omocestus viridulus*. — Anim. Behav.

—— (in press b). Song duration and female response behaviour in the grasshopper *Omocestus viridulus*. — Anim. Behav.

ELSNER, N. (1974). Neuroethology of sound production in Gomphocerine grasshoppers (Orthoptera: Acrididae). I. Song patterns and stridulatory movements. — J. Comp. Physiol. 88, p. 67-102.

EWING, A. W. (1989). Arthropod bioacoustics: Neurobiology and behaviour. — Edinburgh University Press.

FABER, A. (1929). Die Lautäusserungen der Orthopteren. (Lauterzeugung, Lautabwandlung und deren biologische bedeutung sowie Tonapparatt der Geradflügler) vergleichende Untersuchungen I. — Z. Morphol. und Ökol. der Tiere A, 13, p. 745-803.

FORREST, T. G. (1983). Calling songs and mate choice in mole crickets. — In: Orthopteran mating systems: sexual competition in a diverse group of insects (D. T. GWYNNE & G. K. MORRIS eds). Westview Press, Boulder, Colorado, p. 185-204.

GREENFIELD, M. D. (1990). Evolution of acoustic communication in the genus *Neoconocephalus*: Discontinuous songs, synchrony, and interspecific interactions. — In: The Tettigonidae. Biology, systematics and evolution (W. J. BAILEY & D. C. F. RENTZ, eds). Crawford House Press, Bathurst, p. 71-97.

GREENFIELD, M. D. & SHELLY, T. E. (1985). Alternative mating strategies in a desert grasshopper: evidence of density-dependence. — Anim. Behav. 33, p. 1192-1210.

HASKELL, P. T. (1957). Stridulation and associated behaviour in certain Orthoptera. 1. Analysis of the stridulation of, and behaviour between, males. — Brit. J. Anim. Behav. 5, p. 139-148.

—— (1958). Stridulation and associated behaviour in certain Orthoptera. 2. Stridulation of females and their behaviour with males. — Anim. Behav. 6, p. 27-42.

HEDWIG, B. (1986). On the role in stridulation of plurisegmental interneurons of the acridid grasshopper *Omocestus viridulus* L. II. Anatomy and physiology of ascending and T-shaped interneurons. — J. Comp. Physiol. 158, p. 429-444.

HELVERSEN, D. VON (1972). Gesang des Männchens aund Lautschema des Weibchens bei der Feldheuschrecke *Chorthippus biguttulus* (Orthoptera, Acrididae). — J. Comp. Physiol. 81, p. 381-422.

—— & HELVERSEN, O. VON (1981). Korrespondenz zwischen Gesang und auslösendem Schema bei Feldheuschrecken. — Nova acta Leopold 54, p. 449-462.

HELVERSEN, O. VON & HELVERSEN, D. VON (1987). Innate receiver mechanisms in the acoustic communication of orthopteran insects. — In: Aims and methods in neuro-ethology (D. M. GUTHRIE, ed.). Manchester University Press, p. 105-150.

JACOBS, W. (1950). Vergleichende Verhaltensstudien an Feldheuschrecken. — Z. Tierpsychol. 7, p. 169-216.

—— (1953). Verhaltensbiologische Studien an Feldheuschrecken. — Z. Tierpsychol., Beiheift 1.

MORRIS, G. K., KERR, G. E. & GWYNNE, D. T. (1975). Calling song function in the bog katydid, *Metrioptera sphagnorum* (F. WALKER) (Orthoptera, Tettigoniidae): Female phonotaxis to normal and altered song. — Z. Tierpsychol. 37, p. 502-514.

OTTE, D. (1977). Communication in Orthoptera. — In: How animals communicate (T. A. SEBEOK ed.). Indiana University Press, Bloomington & London, p. 334-361.

—— & JOERN, A. (1975). Insect territoriality and its evolution: population studies of desert grasshoppers on cresote bushes. — J. Anim. Ecol. 44, p. 29-54.

PERDECK, A. C. (1958). The isolating value of specific song patterns in two sibling species of grasshoppers (*Chorthippus brunneus* Thunb. and *C. biguttulus* L.). — Behaviour 12, p. 1-75.

RAGGE, D. R. (1965). Grasshoppers, crickets and cockroaches of the British Isles. — Frederick Warne & Co., London.

—— (1986). The songs of the western European grasshoppers of the genus *Omocestus* in relation to their taxonomy (Orthoptera: arididae). — Bull. Br. Mus. Nat. Hist. (Ent.) 53, p. 213-249.

—— (1987). The songs of the western European grasshoppers of the genus *Stenobothrus* in relation to their taxonomy (Orthoptera: Acrididae). — Bull. Br. Mus. Nat. Hist. (Ent.) 55, p. 393-424.

—— & REYNOLDS, W. J. (1984). The taxonomy of the western European grasshoppers of the genus *Euchorhippus*, with special reference to their songs (Orthoptera: Acrididae). — Bull. Br. Mus. Nat. Hist. (Ent.) 49, p. 103-151.

RITCHIE, M. G. (1990). Are differences in song responsible for assortative mating between subspecies of the grasshopper *Chorthippus parallelus* (Orthoptera: Acrididae)? — Anim. Behav. 39, p. 685-691.

—— (1991). Female preference for 'song races' of *Ephippiger ephippiger* (Orthoptera: Tettigonidae). — Anim. Behav. 42, p. 518-520.

ROBINSON, D. (1990). Acoustic communication between the sexes in bushcrickets. — In: The Tettigonidae. Biology, systematics and evolution (W. J. BAILEY & D. C. F. RENTZ, eds.). Crawford House Press, Bathurst, p. 112-129.

SCHATRAL, A., LATIMER, W. & BROUGHTON, B. (1984). Spatial dispersion and agonistic contacts of male bush crickets in the biotope. — Z. Tierpsychol. 65, 201-214.

SEARCY, W. A. & ANDERSSON, M. (1986). Sexual selection and the evolution of song. — Ann. Rev. Ecol. Syst. 17, p. 507-533.

SHAW, K. C. (1968). An analysis of the phonoresponse of males of the true katydid, *Pterophylla camellifolia* (FABRICIUS) (Orthoptera: Tettigonidae). — Behaviour 31, p. 204-260.

SIMMONS, L. W. (1988). The calling song of the field cricket, *Gryllus bimaculatus* (DE GEER): constraints on transmission and its role in intermale competition and female choice. — Anim. Behav. 36, p. 380-394.

SKOVMAND, O. & PEDERSEN, S. B. (1978). Tooth impact rate in the song of a shorthorned grasshopper: A parameter carrying specific behavioral information. — J. Comp. Physiol. 124, p. 27-36.

—— & —— (1983). Song recognition and song pattern in a shorthorned grasshopper. —J. Comp. Physiol. 153, p. 393-401.

ULAGARAJ, S. M. & WALKER, T. J. (1975). Response of flying mole crickets to three parameters of synthetic songs broadcast outdoors. — Nature 253, p. 530-532.

WEIH, A. S. (1951). Untersuchungen über das Wechselsingen (Anaphonie) und über das angeborene Lautschema einiger Feldheuschrecken. — Z. Tierpsychol. 8, p. 1-41.

WOLF, H. & HELVERSEN, O. VON (1986). 'Switching-off' of an auditory interneuron during stridulation in the acridid grasshopper *Chorthippus biguttulus* L. — J. Comp. Physiol. A, 158, p. 861-871.

YOUNG, A. J. (1971). Studies on the acoustic behaviour of certain Orthoptera. — Anim. Behav. 19, p. 727-743.

ZUK, M. (1988). Parasite load, body size, and age of wild-caught male field crickets (Orthoptera: Gryllidae): effects on sexual selection. — Evolution 42, p. 969-976.