The Elaborate Courtship Behavior of Stenobothrus clavatusWillemse, 1979 (Acrididae: Gomphocerinae)*

Authors: Ostrowski, Tim Daniel, Sradnick, Jan, Stumpner, Andreas, and Elsner, Norbert

Source: Journal of Orthoptera Research, 18(2) : 171-182

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.018.0206

Journal of Orthoptera Research, December 30, 2009,18(2): 171-182

The elaborate courtship behavior of Stenobothrus clavatus Willemse, 1979 (Acrididae: Gomphocerinae)*

Submitted July 23, accepted September 15, 2009

Tim Daniel Ostrowski, Jan Sradnick, Andreas Stumpner and Norbert Elsner

Abteilung Neurobiologie, Johann-Friedrich-Blumenbach-Institut, Berliner Str. 28. D-37073 Göttingen.
Email: tostrow@gwdg.de; jsradni@gwdg.de; astumpn@gwdg.de; nelsner@gwdg.de

*This publication is dedicated to Dr. Fer Willemse, an inspiring authority of Greek Orthoptera. He discovered, among many other species, *Stenobothrus clavatus*.

Abstract

The elaborate courtship behavior of the gomphocerine grasshopper *Stenobothrus clavatus*, endemic to a few mountains in Greece, incorporates acoustic signalling and visual display elements to prime the conspecific female. The courtship song, produced by rubbing hind legs against an elytral vein, can be divided into four consecutive phases. The basic movements of phases I, II and IV consist of simple up and interrupted downstrokes, with sound produced during the downstroke only. In contrast, phase III is characterized by a fast sound-producing elevation of the femora, a kick of the tibiae and other visual display elements, such as a fast raising of the antennae with their dark spatulate tips during each movement cycle. The latter is strongly pronounced and therefore a characteristic feature of this species.

The stridulatory file of each hind leg consists of two parts. The proximal part bears a double row of little pegs, whereas the pegs in the distal part are regularly aligned in a single row. The proximal part of the stridulatory file is incorporated in sound production only during phase III. However, frequency spectra from different sound elements produced during phase III were similar. Nevertheless, differences are found between phase I/II and phase III/IV, which are ascribed to variations in contact pressure of the stridulatory file against the forewing, rather than to different portions of the stridulatory file being involved.

Key words

grasshopper, *Stenobothrus clavatus*, acoustic communication, courtship behavior, complex song, visual display

Introduction

Acoustic signalling plays a crucial role for intraspecific communication in several taxa of Orthoptera (Ewing 1984). In short-horned grasshoppers (Acridoidea), species belonging to the subfamily Gomphocerinae are particularly well known for the highly elaborate courtship songs of the males (Faber 1929, 1953; Jacobs 1953; Elsner 1974; Helversen 1986; Vedenina & Helversen 2009). Sounds are produced by rubbing the inner side of the hind legs against the sclerotized radial vein of the forewings. In addition, a few species use wing stridulation for sound production (Koppers 1977, Elsner & Wasser 1995). The song differences between species mostly relate to temporal patterns (*e.g.*, Helversen & Helversen 1975a, 1981; Elsner & Popov 1978; Ragge & Reynolds 1998). Differences in song spectra also exist, but the contribution to species discrimination remains unclear (Meyer & Elsner 1996, 1997; Vedenina *et al.* 2007). The signals of males and preferences of conspecific females co-evolved and differ strongly between closely related species (Helversen & Helversen 1975a, 1975b, 1981, 1994, 1997; Ragge & Reynolds 1998). Correspondingly, these songs are considered to form a powerful reproductive barrier (Perdeck 1958, Kriegbaum 1989, Butlin & Ritchie 1991, Stumpner & Helversen 1994). Nevertheless, hybridization is possible in the lab and has been found to occur in nature (Faber 1953, Vedenina & Helversen 2003, Saldamando *et al.* 2005, Gottsberger & Mayer 2007).

Although sound is the basic element of the male courtship used for sexual stimulation of the female, in some species it is additionally assisted by visual displays. These can comprise movements of antennae, palpi, the head or even the whole body (Faber 1953, Jacobs 1953, Elsner 1968, Otte 1972, Helversen 1986, Ragge & Reynolds 1998). Eye-catching coloration and/or structural peculiarities of the body parts participating in these movements mostly go along with the visual displays (Loher & Huber 1966, Otte 1972, Elsner & Wasser 1995). Such displays seem to have evolved from relatively simple courtships — *e.g.*, in the *Chorthippus albomarginatus* group (Helversen 1986, Vedenina & Helversen 2009) visual displays most likely developed under the influence of strong sexual selection (*e.g.*, Helversen & Helversen 1994). As a result, in some species fantastic behavioral sequences have arisen, with a variety of temporal patterns in the songs and with acrobatic movements. Studying such complex courtships may help to gain insights into mechanisms driving the evolution of pair-forming behavior. This evolution also led to striking differences in behavior in morphologically relatively similar species (best seen in the morphological similarity of females).

We describe the extraordinary courtship behavior of the gomphocerine grasshopper *Stenobothrus clavatus* Willemse, 1979, which combines many acoustic and visual elements and therefore represents a model case for an extremely elaborate courtship display: among all *Stenobothrus* species known, *S. clavatus* has the most complex courtship display (Berger 2008). Moreover, we have reason to assume that hybridization occurs in the field with another *Stenobothrus* species, despite drastic differences in the courtship (Sradnick, Klöpfel, Elsner, forthcoming) — similar to the hybridization observed between members of the *C. albomarginatus* group (Vedenina & Helversen 2003). This might indicate that such elaborate displays may have the potential of awakening interest in related species which do not produce such elements, as for instance the attractiveness of certain song elements of the Tungara frog for female frogs of related species (Ryan *et al.* 1990). A thorough understanding of all elements in the courtship of *S. clavatus* therefore, is also a necessary prerequisite for investigating potential reasons for hybridization of this species in nature.

Methods

Specimens and their distribution.—*S. clavatus* was first discovered by F. Willemse on the Southern massif of Mt Tomaros in northwest Greece (*ca* 20 km southwest of Ioannina) at an altitude between 1300 and 1800 m above sea level. Further populations have recently been found on the northern massif of Mt Tomaros and on Mt Xerovuni *ca* 25 km southeast of Ioannina.

The present study is based on *ca* 75 specimens collected on both mountains. The behavior was observed in the field and in the laboratory. Recordings of sound and stridulatory movements were carried out indoors, either in an apartment near Mt Tomaros or in the Göttingen laboratory. The grasshoppers were kept in small cages (12.5×12×15.5 cm³) and fed with grass of the genus *Festuca*.

Recording of song, leg movements and visual displays.—During recordings, all specimens were placed on a round and fully rotatable heating plate. The temperature varied between 35 and 41 °C. The stridulatory movements of the hind legs were recorded with two opto-electronic cameras designed by Helversen & Elsner (1977): a small piece of light-reflecting foil was attached to the distal end of each hind femur. A light spot sent through the camera's optics illuminated the foil and generated voltage in a photo sensor linearly correlated to the position of the light spot on the hind leg. Stridulatory sounds were recorded with a piezo microphone connected to a flexible rod. All data were digitally stored on a computer via a data-acquisition card (National Instruments) with the software Lab-View7 (National Instruments) and visualized later with DIADEM 9.1 (National Instruments). Three movement recordings (N=3 specimens, n=10-65 data points for each individual) out of over 50 were analyzed in detail for this study, unless indicated otherwise.

Frequency spectra were measured at a distance of 5 cm dorsal of the singing individual (N=3) with a microphone (Brüel & Kjaer 4133) in an anechoic chamber. The signals were amplified (Brüel & Kjaer Measuring amplifier 2610; RMS fast) and filtered (Krohn-Hite filter 3550; 1 kHz high-pass filter). Data were stored on a Pioneer DAT-recorder (D-C88, 96 kHz sampling system) and digitized with a Hewlett Packard input module (type: 35642 B) and the software HP-Analyser (HP 3566A/67A). For evaluation, a gliding average was made over seven subsequent data points (corresponding to 770 Hz).

Movements of the antennae and hind legs were filmed (exemplarily for one male) with a digital camera (EX-F1, Casio) at 300 frames per second. The video was post-processed with Avidemux 2.4.4 (Free Software Foundation, Inc.) and IrfanView 4.23 (Irfan Skiljan). ImageJ 1.41o (National Institutes of Health) was used for the angle measurements.

Fig. 1. Male of *S. clavatus* (×3). Note the spatulate and darkened tips of the antennae. See Plates.

Morphometric measurements of the stridulatory files.—For morphometric analysis of the stridulatory files of *S. clavatus*, isolated hind legs of 10 males were photographed with a video camera (INTAS JVC KY-F32) connected to a stereo-microscope (Wild M 420). The teeth on the hind leg (stridulatory file) were counted from the pictures.

A computer program (TPSdig2) was used for precise measurements of the length of the stridulatory file. This program translates pixels from the digitized photos into millimeters.

A high-resolution picture of the stridulatory file was taken with a scanning electron microscope (LEO 438VP) and the controlling software LEO-32 (v.02.03). For this purpose the hind leg was dehydrated with HMDS (hexamethyldisilazan, Merck Schuchardt OHG). After a drying phase of one hour, the preparation was coated with gold in a 0.5 mbar argon atmosphere to assure conductivity.

Results

Calling song.—In the absence of a conspecific female, male *S. clavatus* (Fig. 1) produce a calling song during which the hind legs are moved up and down in a constant rhythm and sounds are produced during downstrokes only (Fig. 2). The overall hind-leg movement

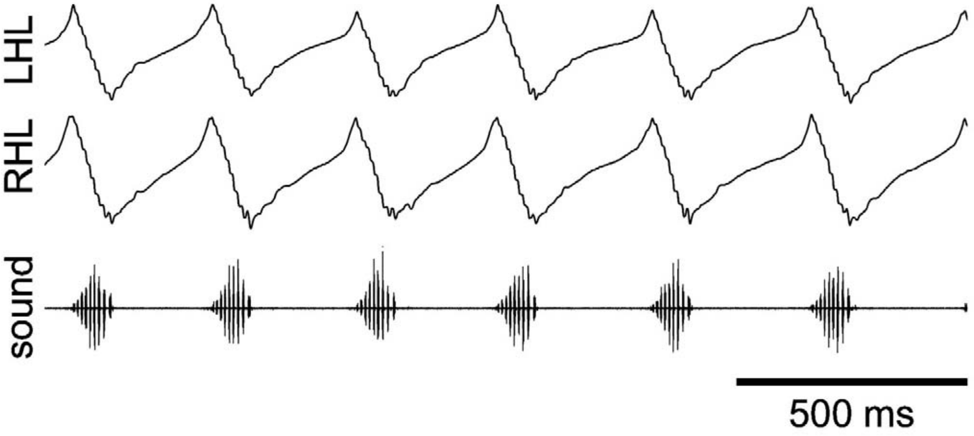

Fig. 2. Calling song. Movement recordings of both hind legs (LHL: left hind leg; RHL: right hind leg) and corresponding oscillogram of the sound.

Table 1. Summary of all measurements of hind leg movement in all four phases of the courtship and in the calling song. N = number of specimens, n = number of data points per specimen.

	Phase I		Phase II		Phase III		Phase IV		Calling song	
overall duration	up to 15 min. (and more)		10-20 s (and more)		2-20 s		2-10 s		1 s to 1 min. (and more)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
single mov. cycle (ms)	258.1	±32.0	106.4	±4.0	496.8	±26.7	282.4	±28.3	264.7	±14.8
upstroke (ms)	191.1	±29.8	55.7	±1.4	158.8	±11.7	207.1	±23.3	189.7	±13.7
downstroke (ms)	67.0	±4.4	50.8	±2.7	338.1	±28.2	75.4	±6.7	75.0	±6.1
	(N=3, n=44-60)		(N=3, n=41-57)		(N=3, n=22-65)		(N=3, n=9-10)		(N=3, n=10-12)	
phase shift (ms)	2.1	±0.3	4.0	±0.9	8.3	±1.9	5.3	±0.9	6.0	±1.0
phase relation (φ)	0.006	±0.001	0.032	±0.010	0.015	±0.004	0.017	±0.003	0.023	±0.002
	(N=3, n=19)		(N=3, n=5-19)		(N=3, n=13-19)		(N=3, n=13-19)		(N=3, n=8-18)	
					first part (N=3, n=24-29)					
rate modulations (1/s)	–		–		90.7	±2.4	113.3	±4.8	109.3	±7.7
					third part (N=6, n=20-41)		(N=3, n=14-22)		(N=3, n=17-25)	
					111.2	±3.1				

cycle is nearly identical with one phase of the courtship song (phase IV - see below). Each sequence (continuous group of movement cycles) can last from a few seconds to more than a minute. A single movement cycle takes on average 265 ms (Table 1), with markedly longer upstrokes than downstrokes. Sound is only produced during the downstroke where clear pauses in the hind leg movement are observable. This stepwise downstroke produces staccato-like sound pulses with a relatively constant repetition rate of 109 [1/s] (Table 1), with first increasing, then decreasing, amplitude. The sound amplitude increases during *ca* 15 (and more) movement cycles at the beginning of a sequence. The hind leg movements are nearly synchronous (phase shift at the upper turning point φ = 0.02, Table1). Sometimes, males start with courtship song in the presence of a conspecific female, but during phase I (see below) switch to the calling song.

Overview of the acoustic and the mating behavior of S. clavatus.—In the presence of the female, an extensive courtship display with acoustic and visual elements is performed. The courtship is divided into four consecutive phases (Fig. 3) and starts with simple hind-leg strokes of low amplitude (phase I). In phase II the movement amplitude is further lowered, resulting in a corresponding lowering of sound amplitude. The duration of phase II is usually very short (in comparison to phase I) and the males quickly pass on to phase III. Phase III is introduced by a slight lateral swinging of the male body in front of the female at the end of phase II. During phase III further optical display elements are added, like raising of the femora and kicking of the tibiae and a slow lowering and rapid lifting of the antennae with their dark spatulate tips (Fig. 1). Sounds of very different amplitude are emitted during different stages of the leg movements. Usually, a copulatory approach follows phase III. If the female rejects the male by defensive kicks, a prolongation of the song with phase IV takes place. The overall leg movements and the sounds that are produced during phase IV are similar to those of the calling song.

The courtship behavior of *S. clavatus* is detailed in what follows. The variability of the courtship will be treated in a separate section. Measured values of the hind leg movements in the courtship song and the calling song are summarized in Table 1.

Courtship behavior of male *S. clavatus*

Phase I.—As typical for many species of the genus *Stenobothrus* (see Berger 2008) the overall duration of the initial phase I is very variable and can last from a few seconds up to 15 min (and more). This phase is characterized by small-amplitude up and downstrokes

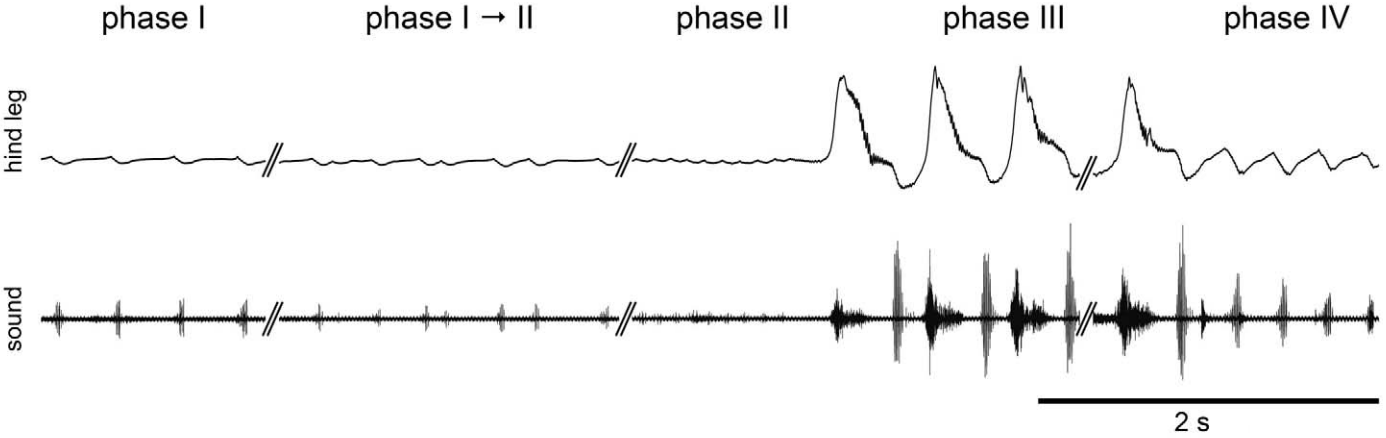

Fig. 3. Subsequent elements from a complete courtship sequence. Movement recordings of the right hind leg of one male (upper trace; up and down in leg movement corresponds to high and low in trace position) with corresponding oscillogram of the sound (lower trace). The maximum movement amplitude is approximately 11 mm; all movements are shown with identical amplification.

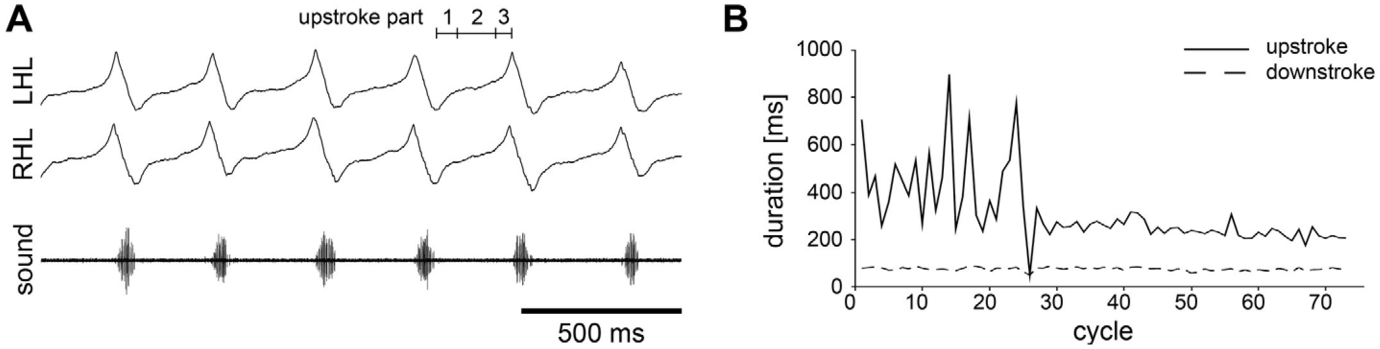

Fig. 4. Phase I of the courtship song. **A**. Movement recordings of both hind legs with annotations to the subdividing parts of the upstroke (LHL: left hind leg; RHL: right hind leg) and corresponding oscillogram of the sound. **B**. Duration of up/downstrokes of single movement cycles from the first movement in phase I onward. Note the large variability of the upstroke duration of the first 27 cycles and the abrupt transition to stable durations from there on.

of the femur. In the major part of phase I these movements follow each other without interruptions. Sound is produced during the downward movement only.

A single movement cycle (upstroke plus downstroke) has a mean duration of 258 ms (Fig. 4A, Table 1). The duration of the upstroke is highly variable in the beginning of phase I (Fig. 4B; beginning of phase I until 27th cycle) and can be divided into three consecutive parts, interestingly resembling the stridulatory movements of the grasshopper *Omocestus viridulus* (Elsner 1974). A fast initial raising of the legs ("part 1") is often followed by a prolonged second part, where the legs can take a resting position. The third part of the upstroke is the fastest part of the movement. The larger portion of phase I however, is characterized by a more constant duration of single-movement cycles, when the second part of the upstroke almost disappears and the complete upstroke lasts, on average, for 191 ms. The downstroke, in contrast, has a relatively constant duration of 67 ms throughout the whole phase (Table 1). During the whole downstroke a 'gappy' sound is produced with first increasing and then decreasing amplitudes. The single sound pulses, as well as the pauses originating from short interruptions of the movement, have much more variable durations and periods than in the otherwise similar sound produced during the calling song. The hind leg movements in phase I and all other phases are nearly synchronous (phase shift $\varphi < 0.04$, Table 1).

Phase II.—After a more or less short transition, phase II (Fig. 5) of the courtship song follows, which lasts 10 to 20 s (or sometimes more) and contains uninterruptedly-adjoined up and downstrokes. A single movement cycle takes about 106 ms and the upstrokes and downstrokes are of nearly equal duration (Table 1). The movement amplitudes are only half of those in phase I (see Fig. 3). The sound produced is similar to that in phase I and only occurs during the downstroke. The overall sound intensity however, is much lower than in phase I and the sound can hardly be picked out of the noise level. Phase II ends with a slight lateral swinging of the body, signalling the beginning of phase III.

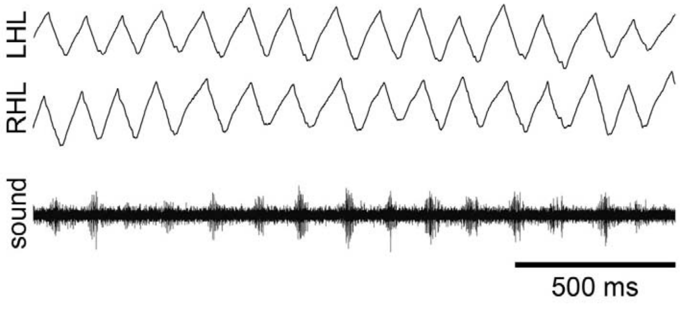

Fig. 5. Phase II of the courtship song. Movement recordings of both hind legs (LHL: left hind leg; RHL: right hind leg) and corresponding oscillogram of the sound. Since the sound here is very soft, the background noise appears relatively high.

Phase III.—Phase III lasts for 2-20 s and follows phase II with no obvious transitional elements in the hind leg movements. The femora are raised abruptly to a position approximately 90° to the body's length axis. The amplitude of the hind leg movement is *ca* 15 times higher than in phase I and II (Fig. 3). These large movements are accompanied by conspicuous antennal movements (see below).

Each leg movement cycle has an approximate duration of 500 ms (Fig. 6, Table 1). It starts with a movement lasting for 159 ms, where the hind legs are raised in a smooth sound-producing upstroke. The sound is an irregular, uninterrupted noise, slowly increasing in amplitude. The downstroke lasts twice as long as the upstroke (Table 1) and is rather complex. It produces the loudest sounds during the whole courtship and is divided into three parts. After some irregular movements, the first part exhibits a fast regular modulation in movement, with a rate of *ca* 91 movements per sec. (Table 1). During these movements nearly uninterrupted sound of slowly decreasing amplitude is produced. Correspondingly, the amplitude of the vibratory movement is highest at the beginning and attenuates to the end of part one, until the modulation is very small in amplitude; this is continued during part two, without however producing detectable sound.

The third part of the downstroke resembles a new type of movement, where the hind legs are moved downward decelerating slowly. Clear pauses in the hind leg movements are observable giving the impression of a stepwise downstroke in the movement recordings (inset "a" in Fig. 6). During this part very loud sounds are produced with each step. The sound pulses (9.5 ± 1.2; N=6, n=5) are staccato-like, adjoined with a mean repetition rate of *ca* 111 [1/s] (Table 1). The sound amplitude symmetrically, first increases and then decreases, during one complete pulse series. Remarkably, the sound pulses of high intensity are produced via leg movements of relatively small amplitude. At the lower turning point of the femur a second, mostly soundless, vibratory movement is visible in some individuals before the next upstroke follows.

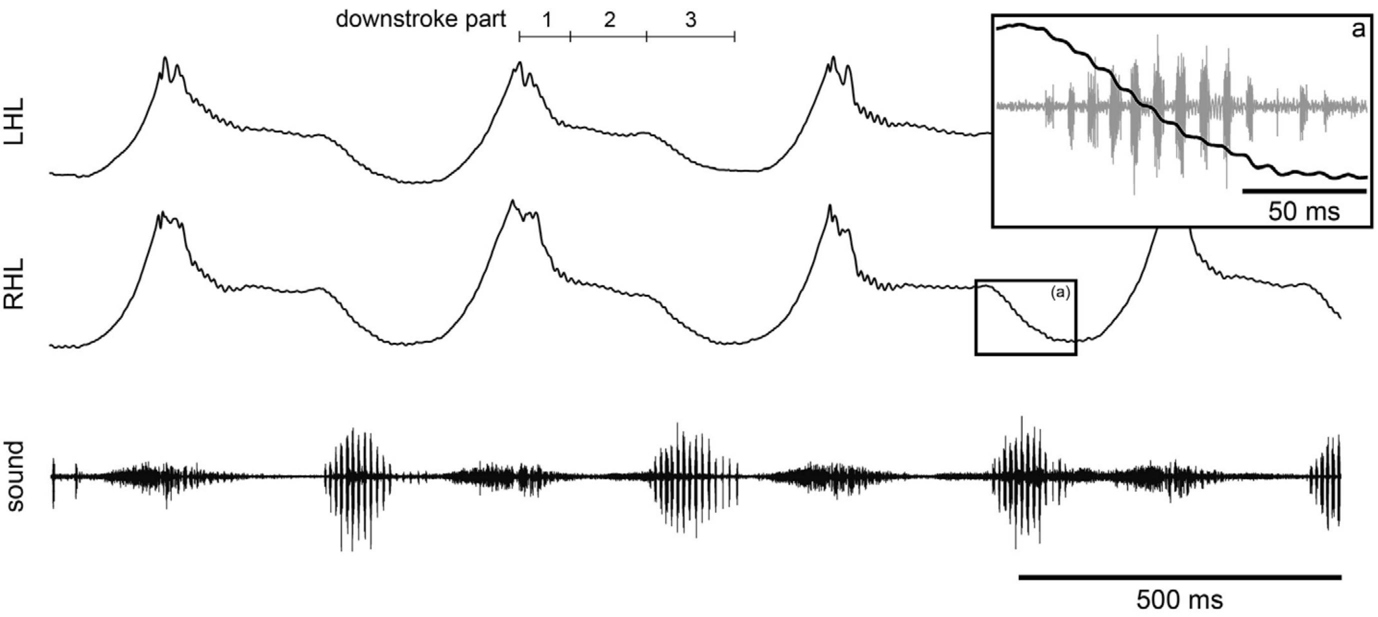

Fig. 6. Phase III of the courtship song. Movement recordings of both hind legs with annotations to the subdividing parts of the downstroke (LHL: left hind leg; RHL: right hind leg) and corresponding oscillogram of the sound. Inset a) Magnified view on the third part of the downstroke with corresponding sound.

Visual display during phase III.—In addition to the sounds that are produced during phase III *S. clavatus* males show elaborate movements to attract the female's visual attention (Fig. 7). One has also to mention that the tip of the femur and base of the tibia are dark brown, contrasting with the remaining hind leg. In virtually all cases of phase III courtship the males are oriented straight on or slightly obliquely toward the head of the courted female. The movements include a fast raising of the femora, kicks of the tibiae and a fast lifting of the antennae. In Fig. 7 we present data of the positions of these appendages relative to the body in this highly stereotyped visual display, exemplarily for one male. At the beginning of the third phase the male's body posture exhibits an antenna angle relative to the body's long axis of 60° (the following details on angles always refer to the body's long axis, except for the details on tibia positions).

For adequate judgement of the extent of the display movements and their potential effect on the female, it is necessary to know details of antennal morphology. The mean length of the antenna is 7.6 ± 0.7 mm (N=7). The last nine antennal segments are darkened and broadened. The third-last segment (mostly) is the broadest, with a mean width of 0.75 ± 0.06 mm (N=55). This, compared to the first flagellomere (mean width: 0.29 ± 0.02 mm, N=55), gives a ratio of 2.6 for the width difference.

In a typical movement cycle in phase III (Fig. 7) the femora are smoothly raised from about 45° to a maximum deflection of *ca* 90°. Relatively low sound amplitudes are emitted by this upward movement. Synchronously the antennae are moved downwards to an angle of -15° to -20° at an approximate speed of 320° per second. Immediately after this relatively slow movement, a fast upstroke (4700°/sec.) of the antennae with their conspicuous dark broadened tips and an extremely fast kick of the orange-red colored tibiae (12500°/sec.) occur. As a result, the antennae take a position of about 80° to the body's long axis and the tibiae are fully extended. The rapid upward movement of the antenna has a duration of *ca* 20 ms, whereas the duration of the kick of the tibiae is 14 ms. The kicking extension of the tibia develops strong forces on the femur position and deflects the femur approximately 10° downwards (Fig. 7, "dip" at the highest position of the femur movement). Subsequently the tibiae are adducted again to the femur and not unusually, the tibiae are shortly extended a second time, though not as high as during the first kick.

During the first two parts of the downstroke of the femora the antennae are slowly moved downwards (110°/s) to a deflection angle of about 45°. With the beginning of the third part of the downstroke of the leg, the antennae appear to initiate the downward movement (320°/s) of the following cycle. Thus during the antennae's downward movement to approximately -20° take place, the third part of the femur's downstroke producing the loudest sounds, the soundless vibratory movements at the lower turning point and the upstroke of the following cycle.

Phase IV.—If the male had no success in mounting the female, in most cases courtship is prolonged with phase IV (Fig. 8) which is in general very similar to the calling song. Phase IV has an overall duration of two to 10 s. The amplitude of hind leg movements is about the same as found in the third part of the downstroke in phase III. A single movement cycle lasts *ca* 282 ms, whereby the upstroke takes 2.5 times as long as the downstroke (Table 1). The upstroke is highly variable in length and may also incorporate a resting position of the hind legs as seen in Phase I. Sound is only produced during the downstroke: a stepwise downwards movement with clear pauses produces staccato-like sound pulses in a similar rate (*ca* 113 [1/s], Table 1) as that observed in the last part of the downstroke in phase III and also in the calling song. The sound amplitude rises over 6 to 8 sound pulses and falls rapidly over two to three pulses. At the end of phase IV a whole courtship sequence has been completed and the male might start with phase I of a new sequence or with producing the calling song after a variable pause.

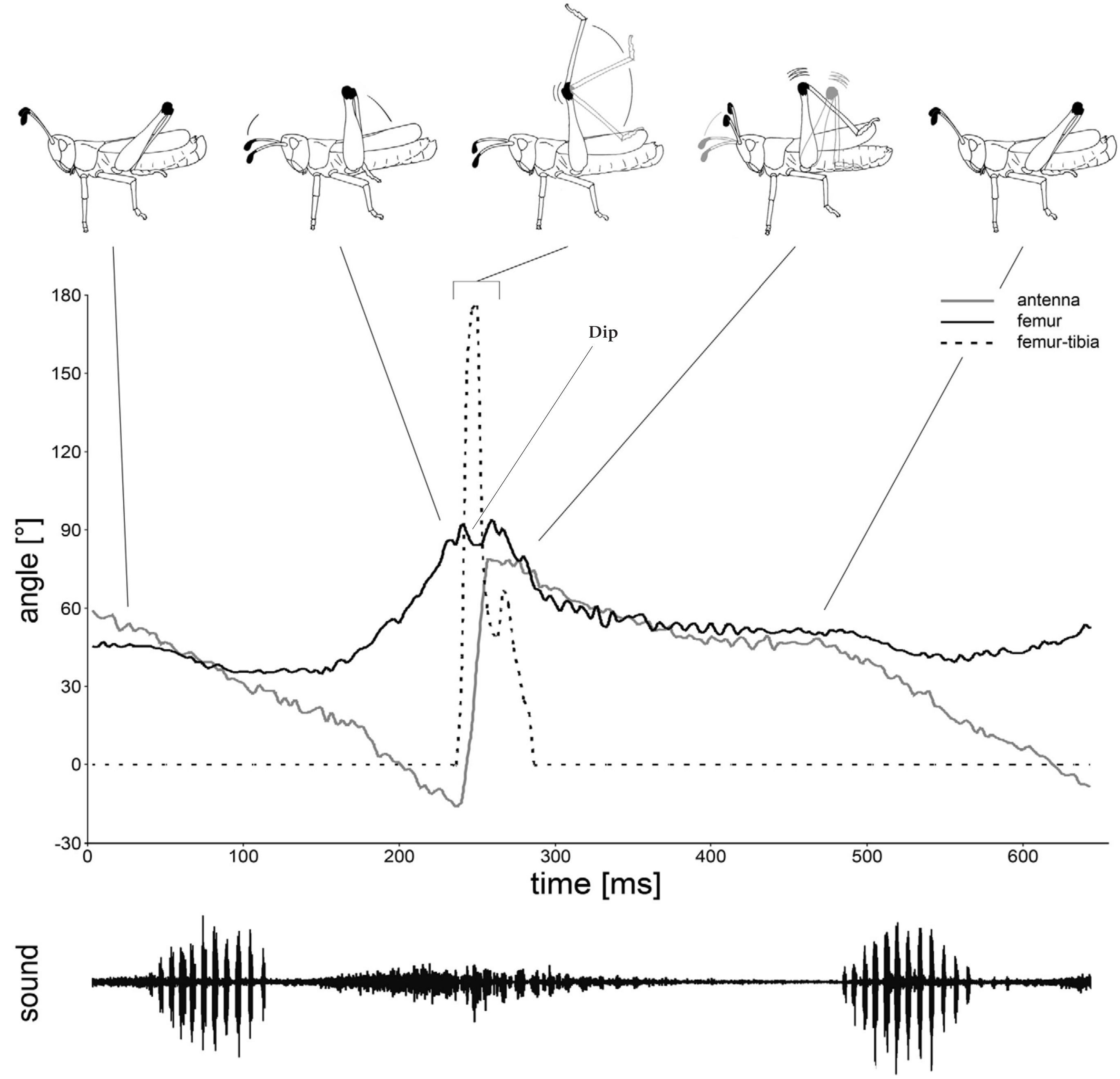

Fig. 7. Movements of the antenna and hind leg during phase III. **Top**: Schematics of a *S. clavatus* male at different moments during one cycle of a phase III movement. **Middle**: Angles of antenna and hind femur relative to the body's length axis and the angle of hind tibia to hind femur during phase III. **Bottom**: Oscillogram representing the sound typically produced during these movements (the sound was not recorded simultaneously with the angle measurements).

Variability of the courtship of S. clavatus.—As shown above, *S. clavatus* males exhibit an elaborate courtship behavior which can be subdivided into four consecutive phases. The progression, duration and pattern of each of these phases underlie intra- as well as interindividual variations. Whereas the overall duration of phase II to IV is more or less constant (Table 1), the duration of phase I may vary considerably from a few seconds up to 15 min. and more. But also the order of the single phases can vary. In some cases, phase III can directly follow phase I by omitting the complete phase II or else phase IV is inserted between the second and the third phase. Phase IV is completely missing when a successful copulation occurs, but may also be missing when no copulation has taken place.

Whereas the movement pattern of the second and fourth phase is highly stereotyped, the movement patterns of the other two phases can vary. Especially at the beginning of phase I, a considerable variation of movement is found. Pauses of varying duration can be inserted in the movement of the upstroke. This sometimes leads to an interruption for many seconds of the whole courtship. The visual display elements in phase III may be reduced in a way that the antennae are held downwards and the upstroke of the legs may be completely lacking.

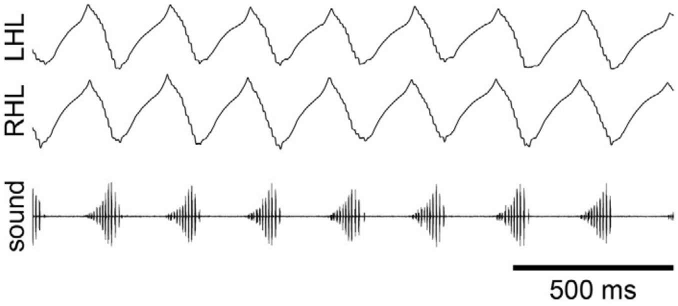

Fig. 8. Phase IV of the courtship song. Movement recordings of both hind legs (LHL: left hind leg; RHL: right hind leg) and corresponding oscillogram of the sound.

Stridulatory organs.—In order to discuss frequency spectra of the male song (next paragraph) it is necessary to have detailed knowledge of the stridulatory organ. The inner side of each hind femur bears an array of little teeth – the stridulatory file. As in all gomphocerine species, the file is scraped against the radial vein of the forewings.

The hind legs of 10 *S. clavatus* males were examined here. The stridulatory file consists of 172.3 ± 17.5 teeth with a mean length of 4.9 ± 0.3 mm. Due to a heterogeneous arrangement of the teeth, the file can be subdivided into two parts (Fig. 9). The first (proximal) part of the stridulatory file has a mean length of 1.6 ± 0.2 mm with 63 ± 11.7 teeth. The most proximal section (0.4 ± 0.1 mm) comprises 10.0 ± 3.7 teeth that are loosely strung together (density: 25.5 ± 3.8 per mm), whereas the adjacent teeth are situated closer to each other. This closer arrangement results in a higher tooth density of 42.2 ± 4.9 teeth per mm. The second (distal) part forms nearly two thirds of the stridulatory file with a length of 3.2 ± 0.4 mm and a mean tooth count of 109.3 ± 13.4. It is characterized by a highly regular alignment in a single row, with a density of about 36.4 ± 2.0 teeth per mm. The end of the stridulatory file (most distal section of the second part; mean length: 0.5 ± 0.2 mm), is comprised of similar characteristics as the proximal section of the first part. Here, 10.7 ± 3.5 teeth are loosely strung together (density: 20.0 ± 3.9 per mm).

Frequency spectra of the male's song.—As is typical for most singing grasshopper species, *S. clavatus* produces a relatively broad-band song. The frequency spectra of the sound produced during each phase are compared in Fig. 10A (N=3; except phase II with N=2). Since the sound pressure differs greatly among single phases (see Fig. 3) only relative amplitudes are displayed in Fig. 10. Phase I and II exhibit nearly the same spectra with two prominent peaks. One peak is between 10 and 13 kHz and the other in the ultra sonic region between 27 and 34 kHz. A third minor peak lies at 4 to 5 kHz.

In contrast, phase III and IV only comprise one major peak between 20 and 27 kHz and one very small peak between 5 and 8 kHz. Surprisingly, phase III and IV even show a minimum in their frequency spectra between 10 and 13 kHz, where phase I and II exhibit a major peak, although in all phases identical parts of the stridulatory file (distal part of the stridulatory file with its highly regular alignment of teeth, Fig. 9) are used. Phase III is the only part where additionally, the hind legs are raised up to a position of 90 degrees to the body's long axis and where the proximal part of the stridulatory file (with its displaced tooth arrangement; see Fig. 9) is involved in sound production. A detailed comparison of the frequency spectra during upstroke and downstroke in phase III is shown in Fig. 10B. No obvious variation in spectra is found when different parts of the stridulatory file are used.

Discussion

The elaborate courtship behavior of male *S. clavatus* described in the present study contains several potentially important elements for species recognition, mate attraction and mate choice. The complexity of the temporal structure of stridulatory movements and the resulting sounds, the differences in frequency spectra emitted in the respective courtship phases and the diversification of optical display elements, makes *S. clavatus* a model case for an extremely elaborate courtship behavior (see also Otte 1972, Helversen 1986).

In the following, questions of the origin and evolution of elaborate courtship, in other species but especially in *S. clavatus*, will be discussed. Further, the importance of visual display elements for recognition by females and the systematic position of *S. clavatus* will be addressed.

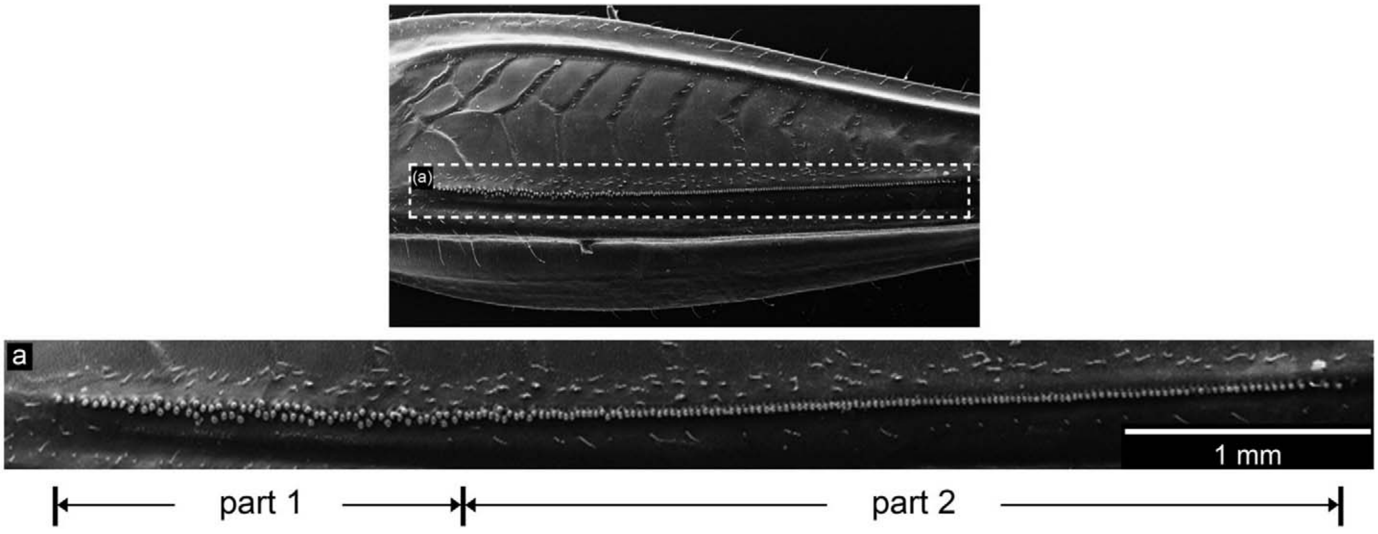

Fig. 9. Scanning electron micrograph of the inner side of the hind leg of a *S. clavatus* male. a) Magnified view of the stridulatory file.

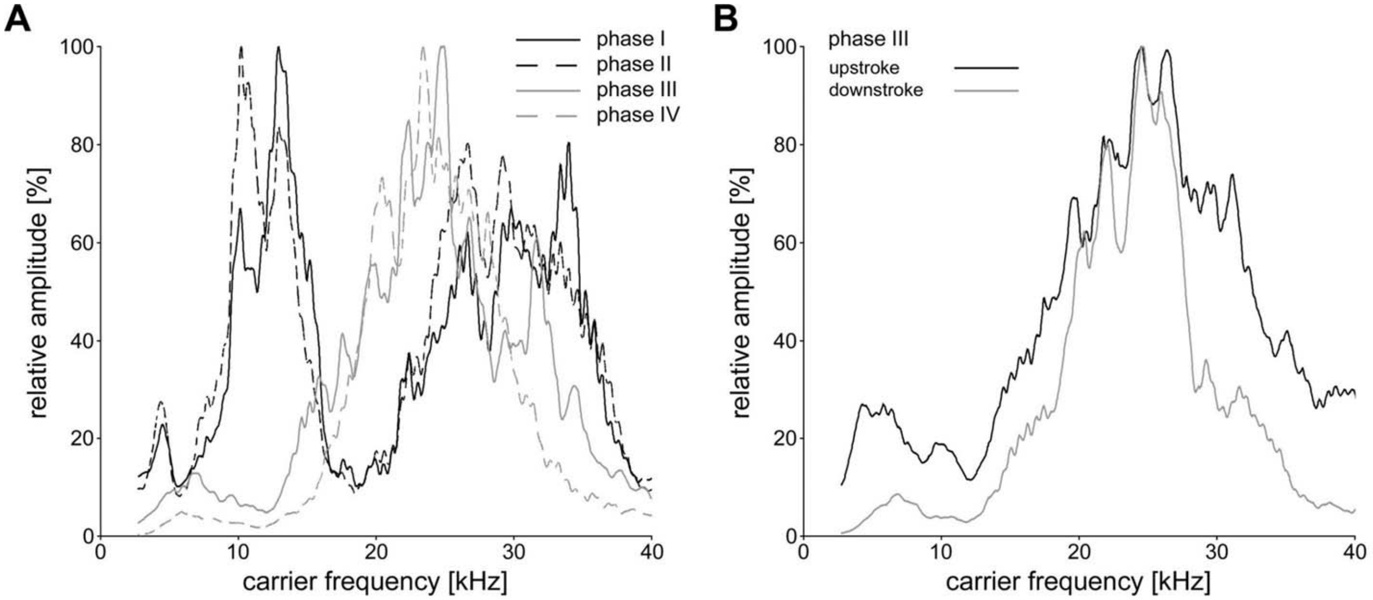

Fig. 10. Frequency spectra of the sound produced during various parts of the male's courtship song (gliding average). **A.** Frequency spectra of all four phases. **B**. Frequency spectra from the sound produced during upstroke and downstroke in phase III.

The courtship of S. clavatus and driving forces for the evolution of elaborate songs.—Differentiation of closely related species and effective premating isolation mechanisms in gomphocerine grasshoppers often are much more obvious in their songs than in ecological or morphological characteristics (Faber 1929, 1953; Jacobs 1953; Perdeck 1958; Otte 1970). Therefore, males and females of different species or subspecies are often able to cross-mate (Alexander & Otte 1967; Helversen & Helversen 1975a, 1975b; Butlin & Hewitt 1985; Vedenina & Helversen 2003; Gottsberger & Mayer 2007).

Temporal patterns of songs are not only decisive for species recognition, but may also be targets of sexual selection (*e.g.*, Helversen & Helversen 1994). Sexual selection in particular might lead to a fast evolution and differentiation of songs and other signals (Otte 1972; Helversen & Helversen 1983, 1994; Helversen *et al.* 2004; Vedenina & Helversen 2009). This is the case in many species of the genus *Chorthippus* Fieber, 1852 where calling songs (mainly used in long distance communication) exhibit great diversity, whereas the courtship song produced in front of a female is not specifically elaborated (aside from some striking exceptions in the *Chorthippus albomarginatus*-group; Faber 1953, Vedenina & Helversen 2009).

In other genera, such as *Stenobothrus* Fischer, 1853, calling songs are fairly simply structured, but the courtship song comprises greater complexity (reviewed in Berger 2008). The various courtship elements found in the behavior of *S. clavatus* can all be found in a same or similar expression in other species, such as simple and interrupted leg movements, leading to either ongoing or pulsed sounds (*e.g.*, in the songs of the *Chorthippus dorsatus* group, Stumpner & Helversen 1994), kicking movements with full extension of the hind tibiae (*e.g.*, in some songs of the *C. albomarginatus* group, Vedenina & Helversen 2009, or in several *Stenobothrus* species, Berger 2008), lateral swinging of the body (*e.g.*, in *Myrmeleotettix maculatus*, Bull 1979) or various movements with antennae (*e.g.*, in *Gomphocerippus rufus*, *M. maculatus*, or *Syrbula*-species, Jacobs 1953, Otte 1972).

The combination of such elements, however, is species specific, even though it appears that during evolution an increasing complexity in courtship in several clades may lead to a combination of similar elements: *Chorthippus oschei*, for example, shows various leg movements of differing pattern and differing amplitude during courtship singing, kicking of hind tibiae and movements of the antennae reminiscent of those of *S. clavatus* (Helversen 1986). There is no doubt that these complex courtships in *C. oschei*, Helversen, 1986 and *S. clavatus*, have evolved independently in evolution (Berger 2008, Vedenina & Helversen 2009).

Complex courtship behavior might serve the function of minimizing the chance for an accidental hybridization, accepting thereby high energetic costs, potential attraction of conspecific males and perhaps attraction of predators (Otte 1972, 1977; Bull 1979; Helversen & Helversen 1994). The often long-lasting courtship sequences also make it likely that females, which upon first contact with the males are unwilling to mate, may be more likely to accept copulation at the end of such a sequence ("primed", *e.g.*, Otte 1972; for a potential physiological mechanism see *e.g.*, Heinrich *et al.* 2001). This factor promotes long courtship behavior in males, at the same time giving the females the chance for extensive sexual selection. This may explain why in different groups (*Chorthippus*, *Stenobothrus*) very similar courtship elements have evolved independently (*cf.* Helversen 1986, Berger 2008).

Visual elements, such as movements of the antennae and hind legs in phase III of *S. clavatus* courtship, likely increase sensory arousal in the "passively observing" female and may reduce the time of courtship needed until a copulation is accepted by her (Elsner 1974). There are observations supporting this (*e.g.*, Otte 1972, Bull 1979), however, to our knowledge, hard data are not available. If the courted female in *S. clavatus* shows a fully receptive state, courtship is often shortened by omitting phase II and copulatory attempts are observed relatively soon after contact of male and female (pers. obs.). As soon as the female signals full receptiveness, there is no further need for the male to invest in courtship behavior.

The observed large variability in duration of the different phases has also been found among species of the *C. albomarginatus*-group (Helversen 1986). The causes for this variability may be motivation and vitality of the male, but in particular an effect of sexual selection and the behavior of the courted female, while the principal patterns produced, potentially serving for species recognition, are rather constant (*e.g.*, Helversen & Helversen 1994).

Surprisingly, in the courtship of *S. clavatus* not only temporal song patterns and visual elements but also frequency spectra of the song elements add to the complexity. The differences in frequency spectra between the first two and the last two phases in the courtship apparently are due to a variation in contact pressure of the stridulatory file against the medial radial vein of the forewings. Physiological support for this speculation is missing so far. It may be underlining the escalation of the behavior, that just with switching from phase II to phase III with the highest complexity in sound and movements, here also the frequency spectrum is changed. It remains unknown whether females actually do discriminate between the different song spectra. The physiological properties of the ear, however, can be expected to clearly pick up these differences (*e.g.*, Römer & Marquart 1984, Stumpner & Ronacher 1991).

Simple courtship movements may originate from ritualized noncommunicative behaviors such as defence or locomotion (Jacobs 1953, Otte 1970, Ragge & Reynolds 1998). Ordinary sound-producing up and downstrokes of the femur, like those found in the calling song or phase I and II of *S. clavatus*, might have been derived from graded repelling movements when touched by a different individual (Otte 1970). Kicking of the hind tibiae originates from primary defence movements, since it can be elicited in all kinds of singing and nonsinging grasshoppers. The extremely rapid extension of the tibia in phase III of *S. clavatus* most likely derives from this defensive kicking. Oscillations superimposed on the downstroke, which are found in phase III of *S. clavatus*, might derive from the motor pattern of the wing beat (Elsner 1974, Elsner & Popov 1978). Purely visual signals, such as the strokes of the antennae, also might have their origin in noncommunicative movements like disturbance behavior (Willey & Willey 1969).

The swinging movement of the whole body of *S. clavatus* as seen shortly before phase III can be an exaggerated form of scanning movements also known as "peering" (Jacobs 1953, Wallace 1959, Loher & Chandrashekaran 1970). Peering is believed to be used by insects to obtain correct visual perception of sizes and distances (Eriksson 1980). Males of *S. clavatus* might use peering to determine the distance to the courted female and a ritualization of this movement could have been incorporated into the courtship as is the case in several other gomphocerine grasshoppers (see above and Elsner 1968, Elsner & Popov 1978). Highly complex courtship behaviors therefore, result from a combination of these simple movements.

Comparative ethological aspects: visual display elements.—During the third phase of the courtship song of *S. clavatus*, very conspicuous visual display elements are incorporated. These elements comprise strokes of the antennae with their dark spatulate tips, a synchronous upstroke of the bright red-colored tibiae and the slight swinging of the whole body. These visual elements only occur in direct adjacency to a female. Sound producing movements of the femur (*e.g.*, upstroke in phase I) with its dark colored femur-tibia joint (found in most *Stenobothrus*-species), might serve as well as a visual signal for the courted female.

There have been some reports about other species from various genera which also exhibit visual display elements accompanied by intense contrast enhancement of body parts. Modifications of antenna morphology and/or contrast enhancement are found for example in *Gomphocerippus rufus* (Elsner 1968, 1974), the *Chorthippus albomarginatus*-group (Helversen 1986), *Myrmeleotettix maculatus* (Jacobs 1953, Bull 1979) and *Syrbula admirabilis* (Otte 1972). Each of these species shows an elaborate courtship, during which the antennae are thrown to the back. In some of these species the movements of the antennae are also accompanied by an upstroke of the femora and additionally of the tibiae. To what extent these movements are recognized by females and affect their behavior is unknown, and one may wonder to what degree these fast movements could be resolved at all.

Considerations of visual display perception by female S. clavatus.—Numerous studies concerning vision and perception of moving objects of grasshoppers have been published in the past (*e.g.*, Jahn & Crescitelli 1938, Wallace 1958, Tunstall & Horridge 1967, Rowell 1971). The most effective stimuli probably are abrupt movements of small contrasting targets anywhere in the visual field (Rowell 1971). Such stimuli evoke intensity changes of illumination over a unit area of the retina, depending on the current level of receptor adaptation (Palka 1967, Rowell & O'Shea 1976). The edges of a moving contrasting object therefore trigger a phasic "On-Off-response" in the movement detector (MD) system, whereas the size and the duration of the stimulus are of secondary importance (Rowell & O'Shea 1976, Rind & Simmons 1992). The antennae of *G. rufus* for example, exhibit distinct features of contrast enhancement, where the slightly broadened and darkened apices of the antennae are accentuated by a white tip. This extreme of contrast ensures a discrimination of the moving antennae against the environment for the perceiving female. In *S. clavatus* the antennae are broadened to an extreme extent (Fig. 1; similar in *Myrmeleotettix antennatus*). Their dark coloration (without a white tip as in *G. rufus*) presumably also reinforces contrast enhancement to the environment, since the natural habitat of *S. clavatus* consists of sparse vegetation and scattered light grey limestone debris.

Looming objects increase the neuronal response until the object reaches a critical dimension. Further enlargement leads to a suppression of the response (Rowell *et al.* 1977). The best responses were measured for single moving edges subtending 15° at the compound eye (Simmons & Rind 1992). In *S. clavatus* a distance of approximately 7 to 8 mm of the broadened apices (length: 2mm) from the female's eye, would evoke the best response, referring to the data known. This calculated distance was indeed observed during the experiments performed in this study.

The detection of motion is independent of direction (Palka 1967), but objects increasing in size are more effective than those decreasing in size (Rind & Simmons 1992). The relatively slow downward movements of the antennae of *S. clavatus* exhibit characteristics of a looming object. During this movement the tips of the antennae come closer to the female's eye by about one antenna length (7.6 mm). This corresponds to an increase of *ca* 11° visual angle at the closest distance of 7 mm, where presumably best responses are evoked. The closer the male sits in front of a female, the greater the increase of visual angle and hence the greater the response of the movement detector system (Rind & Simmons 1992).

The average angular speed of the antennae's apices perceived by the female's eye is *ca* 110° per second during the whole downstroke at a distance of 7 mm. The movement range covers about 45° (within 400 ms) of the female visual field (entire visual field: 180°; Rowell *et al.* 1977). The fast upward movement of the antennae has a speed of *ca* 2250°/s in the movement range of 45° (within 20 ms, Fig. 7). This calculated speed seems much too fast to evoke a perceptible response, since best responses to point-object movements in front of the visual field of the compound eye were measured at an angular velocity of 100-120°/s for receptors (as it is the case for the slow downward movement of the antennae) and up to 200°/s in second order neurons (Srinivasan & Bernard 1975, Juusola & French 1997). Velocities above 1000°/s revealed the smallest response. Furthermore, the apices of the antennae move away from the female's eye during the upstroke, which reduces the neuronal response additionally.

The upstroke of the hind leg in phase III (Fig. 7) has an approximate speed of 550°/s. This might still be detectable by the female, and the dark color of the knees, contrasting with the remainder of the leg, may enhance this movement. However, the rapid upstroke of the bright red-colored tibiae at 12500°/s (175° in 14 ms, Fig. 7), is 2.6 times faster than the upward movement of the antennae (4700°/s). This implies a movement too fast to be noticed by the female.

On the other hand, the contrast-rich coloration (black – white) of the hind tibia and tarsus in several species of the *C. albomarginatus* group (*e.g.*, *C. lacustris*) might indicate these serve as a signal for the females during a courtship element including a rapid upstroke, comparable to that of *S. clavatus* (Helversen 1986, Vedenina & Helversen 2009). One would assume that this movement, despite its speed, is also noticed by the female. On the other hand, there are short pauses or very slow movements *e.g.*, with extended tibiae for several hundred ms (Helversen 1986), which might be the time when the female actually perceives these signals.

The bright red coloration of *S. clavatus's* hind legs, which is so obvious to the human observer, might not be seen as readily by the grasshopper, since it's visual spectral range probably lies between 320 and 570 nm (Bennett *et al.* 1967, Vishnevskaya *et al.* 1986, Briscoe & Chittka 2001). Whether the slight swinging movement of the body at the beginning of Phase III might serve a visual function is not clear. It might do so, since it is performed very slowly and in close distance to the female eye. On the other hand it might only be a scanning movement (Jacobs 1953, Wallace 1959, Loher & Chandrashekaran 1970) to determine the correct distance to the female for most effective performance of the optical display elements which follow.

Systematic position of S. clavatus.—The taxon *Stenobothrus* comprises at least 25 species in Europe, Asia and northern Africa (see Berger 2008). Relationships within this taxon apparently are hard to establish with morphological or molecular methods alone. No phylogenetic tree has been published yet. For phylogenetic reconstructions Berger (2008) used a combination of morphological and behavioral traits, such as the calling or courtship song. Among others, the division into a *Stenobothrus eurasius* group and a *S. rubicundulus* group is very well supported, and is mainly based on the differences of the songs and their production.

Both groups comprise species which show an elaborate courtship behavior, partly also with visual signals (antennae and tibiae upstrokes), though not as elaborate as in *S. clavatus*. The *S. rubicundulus*-group includes *S. clavatus*, *S. werneri*, *S. rubicundulus* and *S. cotticus*. Only the first two species mentioned show a similar optical display (which we called "Phase III" in the case of *S. clavatus*) but the other phases of *S. werneri* do not differ very much from each other. *S. werneri* doesn't possess broadened antennal tips like *S. clavatus*, but uses antenna strokes during courtship (Berger 2008). *S. clavatus* therefore exhibits the most diverse and spectacular courtship of these groups. Given the drastic behavioral differences, it is a complete enigma that hybridization between *S. rubicundulus* and *S. clavatus* has recently been detected in the field (by Helmut Kriegbaum†) and is now studied in detail (Sradnick, Klöpfel, Elsner, in prep.). Whether this might come about because the complex courtship of *S. clavatus* with its spectacular visual elements is also attractive to some *S. rubicundulus* females, remains to be investigated.

Acknowledgements

We especially thank Dr. Heribert Gras and Andrea Wirmer for valuable discussions about optics in grasshoppers. We also thank Prof. Dr. Reinhold Hustert for providing us with a high speed camera and Ralf Schünemann for the invaluable help in programming the Lab-View software. Dirk Berger helped on various stages with discussions about *Stenobothrus* in general and the evolution of songs. We further thank three anonymous referees and the editor for valuable comments on the manuscript.

References

Alexander R.D., Otte D. 1967. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Museum of Zoology University of Michigan 133: 1-62.

Bennett R.R., Tunstall J., Horridge G.A. 1967. Spectral sensitivity of single retinula cells of the locust. Journal of Comparative Physiology A 55: 195-206.

Berger D. 2008. The evolution of complex courtship songs in the genus *Stenobothrus* Fischer, 1853 (Orthoptera, Caelifera, Gomphocerinae). Ph.D. Thesis, University of Erlangen-Nuernberg, Germany.

Briscoe A., Chittka L. 2001. The evolution of color vision in insects. Annual Review of Entomology 46: 471-510.

Bull C.M. 1979. The Function of complexity in the courtship of the grasshopper *Myrmeleotettix maculatus*. Behaviour 69: 201-216.

Butlin R.K., Hewitt G.M. 1985. A hybrid zone between *Chorthippus parallelus parallelus* and *C. p. erythropus* (Orthoptera: Acrididae): behavioural characters. Biological Journal Linnean Society 26: 287-299.

Butlin R.K., Ritchie M.G. 1991. Variation in female mate preferences across a grasshopper hybrid zone. Journal of Evolutionary Biology 4: 227-240.

Elsner N. 1968. Die neuromuskulären Grundlagen des Werbeverhaltens der Roten Keulenheuschrecke *Gomphocerippus rufus* L. Journal of Comparative Physiology A 60: 308-350.

Elsner N. 1974. Neuroethology of sound production in gomphocerine grasshoppers (Orthoptera, Acrididae). I. Song pattern and stridulatory movements. Journal of Comparative Physiology A 88: 67-102.

Elsner N., Popov A.V. 1978. Neuroethology of acoustic communication. Advances in Insect Physiology 13: 229-355.

Elsner N., Wasser G. 1995. Leg and wing stridulation in various populations of the gomphocerine grasshopper *Stenobothrus rubicundus* (Germar 1817). I. Sound patterns and singing movements. Zoology 98: 179-190.

Eriksson E.S. 1980. Movement parallax and distance perception in the grasshopper *Phanlacridium vittatum* (Sjostedt). Journal of Experimental Biology 86: 337-341.

Ewing A.W. 1984. Acoustic signals in insect sexual behaviour, pp. 223-240. In: Lewis T. (Ed.) Insect Communication. 12th Symposium of the Royal Entomological Society of London. Academic Press, London.

Faber A. 1929. Die Lautäußerungen der Orthopteren (Lauterzeugung, Lautabwandlung und deren biologische Bedeutung sowie Tonapparat der Gradflügler). Vergleichende Untersuchungen I. Zeitschrift für Morphologie und Ökologie der Tiere A 13: 745-803.

Faber A. 1953. Laut- und Gebärdensprache bei Insekten: Orthoptera (Geradflügler). Mitteilung aus dem Staatlichen Museum für Naturkunde in Stuttgart, 287 pp.

Fischer LH 1853. *Orthoptera Europaea. Accedunt tabulae lapidibus incisae XVIII, quarum ultima coloribus partim illustrata*. G. Engelmann. Leibzig, 454 pp.

Gottsberger B., Mayer F. 2007. Behavioral sterility of hybrid males in acoustically communicating grasshoppers (Acrididae, Gomphocerinae). Journal of Comparative Physiology A 193: 703-714.

Heinrich R., Wenzel B., Elsner N. 2001. A role for muscarinic excitation: control of specific singing behavior by activation of the adenylate cyclase pathway in the brain of grasshoppers. Proceedings National Academy of Sciences 98: 9919-9923.

Helversen D. von, Balakrishnan R., Helversen O. von, 2004. Acoustic communication in a duetting grasshopper: receiver response variability, male strategies and signal design. Animal Behaviour 68: 131-144.

Helversen D. von, Helversen O. von, 1975a. Verhaltensgenetische Untersuchungen am akustischen Kommunikationssystem der Feldheuschrecken (Orthoptera, Acrididae). I: Der Gesang von Artbastarden zwischen *Chorthippus biguttulus* und *Ch. mollis.* Journal of Comparative Physiology A 104: 273-299.

Helversen D. von, Helversen O. von, 1975b. Verhaltensgenetische Untersuchungen am akustischen Kommunikationssystem der Feldheuschrecken (Orthoptera, Acrididae). II: Das Lautschema von Artbastarden zwischen *Chorthippus biguttulus* und *Ch. mollis*. Journal of Comparative Physiology A 104: 300-323.

Helversen D. von, Helversen O. von, 1981. Korrespondenz zwischen Gesang und auslösendem Schema bei Feldheuschrecken. Nova Acta Leopoldina N.F. 54: 449-462.

Helversen D. von, Helversen O. von, 1983. Species recognition and acoustic localization in acridid grasshoppers: a behavioural approach, pp. 95-107. In: Huber F., Markl H. (Eds) Neuroethology and Behavioural Physiology. Springer, Berlin Heidelberg.

Helversen D. von, Helversen O. von, 1997. Recognition of sex in the acoustic communication of the grasshopper *Chorthippus biguttulus* (Orthoptera, Acrididae). Journal of Comparative Physiology A 180: 373-386.

Helversen O. von, 1986. Gesang und Balz bei Feldheuschrecken der *Chorthippus albomarginatus*-Gruppe (Orthoptera: Acrididae) Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 113: 319-342.

Helversen O. von, Elsner N. 1977. The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. Journal of Comparative Physiology A 122: 53-64.

Helversen O. von, Helversen D. von, 1994. Forces driving co-evolution of song and song recognition in grasshoppers. Fortschritte der Zoologie 39: 253-284.

Jacobs W. 1953. Verhaltensbiologische Studien an Feldheuschrecken. Beiheft 1 Zeitschrift für Tierpsychologie: 1-228.

Jahn T.L., Crescitelli F. 1938. The electrical response of the grasshopper eye under conditions of light and dark adaptation. Journal of Cellular and Comparative Physiology 12: 39-55.

Juusola M., French A.S. 1997. Visual acuity for moving objects in first- and second-order neurons of the fly compound eye. Journal of Neurophysiology 77: 1487-1495.

Koppers S. 1977. Die neuromuskulären Grundlagen des Gesangs der Feldheuschrecke *Stauroderus scalaris*. Diploma Thesis, University of Köln, Germany.

Kriegbaum H. 1989. Female choice in the grasshopper *Chorthippus biguttulus*. Mating success is related to song characteristics of the male. Naturwissenschaften 76: 81-82.

Loher W., Chandrashekaran M.K. 1970. Acoustical and sexual behavior in the grasshopper *Chimarocephala pacifica* (Oedipodinae). Entomologia Experimentalis et Applicata 13: 71-84.

Loher W., Huber F. 1966. Nervous and endocrine control of sexual behavior in a grasshopper (*Gomphocerus rufus* L., Acridinae). Symposia of the Society for Experimental Biology 20: 381-400.

Meyer J., Elsner N. 1996. How well are frequency sensitivities of grasshopper ears tuned to species-specific song spectra? Journal of Experimental Biology 199: 1631-1642.

Meyer J., Elsner N. 1997. Can spectral cues contribute to species separation in closely related grasshoppers? Journal of Comparative Physiology A 180: 171-180.

Otte D. 1970. A comparative study of communicative behavior in grasshoppers. Miscellaneous Publications Museum of Michigan 141: 1-168.

Otte D. 1972. Simple versus elaborate behaviour in grasshoppers. An analysis of communication in the genus *Syrbula*. Behaviour 17: 291-322.

Otte D 1977. Communication in Orthoptera, pp. 334-361. In: Sebeok T.A. [Ed.] How Animals Communicate. Indiana University Press, Bloomington.

Palka J. 1967. An inhibitory process influencing visual responses of a fibre in the ventral nerve cord of locusts. Journal of Insect Physiology 13: 235-248.

Perdeck A.C. 1958. The isolating value of specific song patterns in two sibling species of grasshopper (*Chorthippus brunneus* and *Chorthippus biguttulus*). Behaviour 12: 1-75.

Ragge D.R., Reynolds W.J. 1998. The Songs of the Grasshoppers and Crickets of Western Europe. Natural History Museum, London.

Rind F.C., Simmons P.J. 1992. Orthopteran DCMD neuron: a re-evaluation of responses to moving objects. I. Selective responses to approaching objects. Journal of Neurophysiology 68: 1654-1666.

Römer H., Marquart V. 1984. Morphology and physiology of auditory interneurons in the metathoracic ganglion of the locust. Journal of Comparative Physiology 155: 249-262.

Rowell C.H.F. 1971. The orthopteran descending movement detector (DMD) neurones: a characterisation and review. Journal of Comparative Physiology A 73: 167-194.

Rowell C.H.F., O'Shea M. 1976. The neuronal basis of a sensory analyser, the acridid movement detector system. I. Effects of simple incremental and decremental stimuli in light and dark-adapted animals. Journal of Experimental Biology 65: 273-288.

Rowell C.H.F., O'Shea M., Williams J.L. 1977. The neuronal basis of a sensory analyser, the acridid movement detector system. IV. The preference for small field stimuli. Journal of Experimental Biology 68: 157-185.

Ryan M.J., Fox J.H., Wilczynski W., Rand A.S. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343: 66-68.

Saldamando C.I., Miyaguchi S., Tatsuta H., Kishino H., Bridle J.R., Butlin R.K. 2005. Inheritance of song and stridulatory peg number divergence between *Chorthippus brunneus* and *C. jacobsi*, two naturally hybridizing grasshopper species (Orthoptera: Acrididae). Journal Evolutionary Biology 18: 703-712.

Simmons P.J., Rind F.C .1992. Orthopteran DCMD neuron: a re-evaluation of responses to moving objects. II. Critical cues for detecting approaching objects. Journal of Neurophysiology 68: 1667-1682.

Srinivasan M.V., Bernard G.D. 1975. The effect of motion on visual acuity of the compound eye: a theoretical analysis. Vision Research 15: 515-25.

Stumpner A., Helversen O. von. 1994. Song production and song recognition in a group of sibling grasshopper species (*Chorthippus dorsatus, Ch. dichrous* and *Ch. loratus*: Orthoptera, Acrididae). Bioacoustics 6: 1-23.

Stumpner A., Ronacher B. 1991. Auditory interneurons in the metathoracic ganglion of the grasshopper *Chorthippus biguttulus*. I. Morphological and physiological characterization. Journal of Experimental Biology 158: 391-410.

Tunstall J. Horridge G.A. 1967. Electrophysiological investigation of the optics of the locust retina. Journal of Comparative Physiology A 55: 167-182.

Vedenina V.Yu, Helversen O. von, 2003. Complex courtship in a bimodal grasshopper hybrid zone. Behavioural Ecology and Sociobiology 54: 44-54.

Vedenina V.Yu, Helversen O. von, 2009. A re-examination of the taxonomy of the *Chorthippus albomarginatus* group in Europe on the basis of song and morphology (Orthoptera: Acrididae). Tijdschrift voor Entomologie 152: 65-98.

Vedenina V.Yu, Panyutin A.K., Helversen O. von, 2007. The unusual inheritance pattern of the courtship songs in closely related grasshopper species of the *Chorthippus albomarginatus*-group (Orthoptera: Gomphocerinae). Journal of Evolutionary Biology 20: 260-277.

Vishnevskaya T.M., Cherkasov A.D., Shura-Bura T.M. 1986. Spectral sensitivity of photoreceptors in the compound eye of the locust. Neurophysiology 18: 69-76.

Wallace G.K. 1958. Some experiments on form perception in the nymphs of the Desert Locust, *Schistocerca gregaria* Forskal. Journal of Experimental Biology 35: 765-775.

Wallace G.K. 1959. Visual scanning in the Desert Locust *Schistocerca gregaria* Forskal. Journal of Experimental Biology 36: 512-525.

Willemse F. 1979. *Stenobothrus (Stenobothrodes) clavatus* spec. nov. from Greece (Orthoptera, Acrididae). Entomology Ber. Amsterdam 39: 154-157.

Willey R.B., Willey R.L. 1969. Visual and acoustical social displays by the grasshopper *Arphia conspersa* (Orthoptera: Acrididae). Psyche 76: 280-305.