

**Analysis of the courtship of *Myrmeleotettix antennatus* (Fieber, 1853) –
with general remarks on multimodal courtship behaviour
in gomphocerine grasshoppers**

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Abstract

Gomphocerine grasshoppers are known to produce species-specific songs by a femoral-tegmina mechanism. Male songs are considered to play a crucial role as interspecific hybridization barrier between species since male songs are discriminated by conspecific females according to their preferences towards distinct song structures and temporal patterns. During own comprehensive studies about grasshopper songs it became evident that calling and courtship songs play different roles in the mating systems in different grasshopper species. Whereas in many species calling and courtship songs resemble each other widely (e.g. most *Chorthippus* species), in others highly complex courtship songs evolved containing acoustical and visual elements. That leads to the assumption that different mating systems within Gomphocerinae and even more in caeliferan grasshoppers exist. About the diversity of mating systems in short horned grasshoppers not much is known yet. In this study we describe the multimodal courtship behaviour of *Myrmeleotettix antennatus*. The courtship repertoire contains three acoustical elements and three visual displays in which the antennae, the palps and the body are involved. On the basis of the obtained information we discuss functions of different elements in comparison to published information on elaborate courtship grasshopper species. At the end we make some theoretical considerations about the phylogenetic origin of calling and courtship songs in Gomphocerinae.

Zusammenfassung

Feldheuschrecken innerhalb der Gomphocerinae produzieren artspezifische Gesänge mit Hilfe eines femoral-tegmina Mechanismus. Den Gesängen der Männchen wird eine bedeutende Rolle als zwischenartliche Hybridisationsbarriere zugesprochen, da die Weibchen die akustischen Signale der Männchen entsprechend ihrer Präferenzen bezüglich zeitlicher und struktureller Parameter diskriminieren. Eigene umfassende Untersuchungen an Heuschreckengesängen gaben Hinweise, dass Spontan- und Balzgesänge bei verschiedenen Heuschreckenarten unterschiedliche Bedeutung im Paarungssystem zukommt. Während sich bei vielen Arten (z.B. den meisten *Chorthippus*-Arten) die Spontan- und Balzgesänge kaum unterscheiden, sind bei anderen hochkomplexe Balzgesänge entstanden, die akustische und visuelle Elemente enthalten. Dies lässt vermuten, dass verschiedene Paarungssysteme innerhalb der Gomphocerinen und erst recht innerhalb der Caeliferen existieren. Über die Vielfalt von Paarungssystemen bei Feldheuschrecken ist nicht viel bekannt. In der vorliegenden Studie be-

schreiben wir detailliert das multimodale Balzverhalten von *Myrmeleotettix antennatus*. Die Balz dieser Art enthält drei Gesangselemente sowie drei visuelle Komponenten in welche die Antennen, die Palpen und der Körper integriert sind. Die Funktion verschiedener Elemente wird im Vergleich zu publizierten Daten über komplex balzende Feldheuschrecken diskutiert. Am Ende stellen wir theoretische Überlegungen über den phylogenetischen Ursprung von Spontan- und Balzgesang bei gomphocerinen Feldheuschrecken an.

Introduction

The most important factor in reproductive isolation in gomphocerine grasshoppers compared to mechanical or chemical factors is by far the acoustic communication. The radiation of the subfamily Gomphocerinae could mainly be triggered by the evolution of new acoustical signals (MAYER et al. in press). In contrast to other Acrididae the genital morphology in gomphocerine grasshoppers is not distinctive, and pheromones play only a role in very close sexual contact (OTTE 1970, UVAROV 1977, HELLER 2006). The two most important types of acoustic signals are the spontaneous calling songs and the mating songs. Many taxonomical studies concentrated on calling songs (RAGGE & REYNOLDS 1984, 1988, RAGGE 1986, 1987a,b, GARCIA et al. 1987, CLEMENTE et al. 1989, 1990a,b, RAGGE et al. 1990, SCHMIDT 1990, and others), whereas the courtship songs were not analyzed into detail, although many thorough descriptions of courtship have been published (e.g. FABER 1929, 1932, 1953, JACOBS 1953, OTTE 1970, RAGGE & REYNOLDS 1998). Courtship can be quite complex often including various optical components in addition to acoustic signalling. In species with very complex courtship the calling songs are often simple and not further developed (HELVERSEN 1986, BERGER 2008) and thus, the usefulness of song analysis to infer phylogenetic relationships was questioned (RAGGE 1986, 1987a, REYNOLDS 1986, 1988, RAGGE & REYNOLDS 1998, GARCIA et al. 2003).

Due to the possibility to record in synchrony songs and the underlying hind leg movements by an optical-electronical device (HELVERSEN & ELSNER 1977) it is possible to comparatively study behaviour of closely related species and to analyze phylogeny (HELVERSEN 1986, 1989, WAEBER 1989, GOTTSBERGER & MAYER 2007, BERGER 2008). Analyses of video recordings extend the possibilities to systematically compare movements of other body parts besides hind legs (ATORF 2007, ELSNER 1968, ELSNER & HUBER 1969, RIEDE 1983, BERGER 2008). Comparative analyses of courtship behaviour of species of different taxonomical level allow making an inference on the respective functions of elements within complex behavioural repertoires. Certain song elements, sequences or combinations, even not being homologous seem to have similar functions in courtship display. Here we describe and analyze in detail the complete courtship of *Myrmeleotettix antennatus* by sound, leg movements and video recordings. Furthermore we will compare the courtship of *M. antennatus* with other caeliferan grasshopper species and we will discuss functional and theoretical considerations of the origin of acoustical and optical display in grasshoppers.

Material and methods

Grasshoppers were collected, during a field trip, in a dry sandy steppe southwest of Nové Zámky (Slovakia, east of Nesvady, N 47°55'26.7", E 018°09'34.2", and an altitude of 104 m a.s.l.) in August 2008. Animals were brought alive to the Departments of Zoology of the Universities of Erlangen (Germany) and Vienna (Austria) to record them under controlled laboratory conditions. The songs and the song producing leg movements were recorded using an opto-electronic device (HELVENSEN & ELSNER 1977). A total of 43 recordings containing 48 courtship sequences of 4 males were recorded. Songs were recorded with a 1/2" condenser microphone (G.R.A.S. Type 40AF) equipped with G.R.A.S. 26AP preamplifier. Signals were amplified by a Brüel and Kjær measuring amplifier (Type 2608). Song and leg movement signals were A/D-converted by a custom-build DSP card with sample rates of 125 kHz (leg movements) and 250 kHz (sound). Temporal parameters of the songs and the underlying leg movement patterns were measured, using custom-designed software (W. Schulze) developed in Lab View 7 (National Instruments, Austin, TX, USA) and Turbolab 4.0 (Stemmer software). Analyses and song terminology follows GOTTSBERGER (2007) and BERGER (2008).

In addition, video recordings were made to illustrate the visual courtship components. These videos were made using a Sony Digital Handycam DCR-VX1000E and a Panasonic HDC-SX5. Videos were imported and digitalized with Adobe Premiere Pro CS3 (Adobe 1991-2007) and with iMovie HD 6.0.3. (Apple Computer, Inc. 1999-2006). Analyses of video recordings were made with still frames and with the programs GraphClick 2.9. (Arizona Software, 2006) and ImageJ 1.41 (<http://rsb.info.nih.gov/ij>). Drawings were made from single frames of the video recordings using indian ink pencils of different diameters (Staedtler Mars GmbH & Co. KG, Germany).

Results

Myrmeleotettix antennatus males perform a multimodal courtship display, consisting of acoustical and visual components, when the physical contact to a female is established. We found three acoustical elements and three visual elements, which are arranged in a distinct order (Figs. 1-3).

Priming phase (song element 1)

The courtship was always preluded by series of very gentle pulses which were produced by very low amplitude leg movements, i.e. leg dithering of approximately 1 mm range (element 1; Fig. 1B). One leg was pulled down abruptly and lifted slowly. Each down stroke emitted a single pulse. There was no strict regularity in the coordination in pulse production. Usually legs alternated in producing one pulse, but some times subsequent pulses were produced by the same leg (Fig. 1B). The pulses were of such a low intensity that they were nearly not audible to human ear. Pulses were produced in intervals of approximately 220 ms (Tab. 1). The male usually started to produce pulses more irregularly when it started to court; later they became regular during progress of courting.

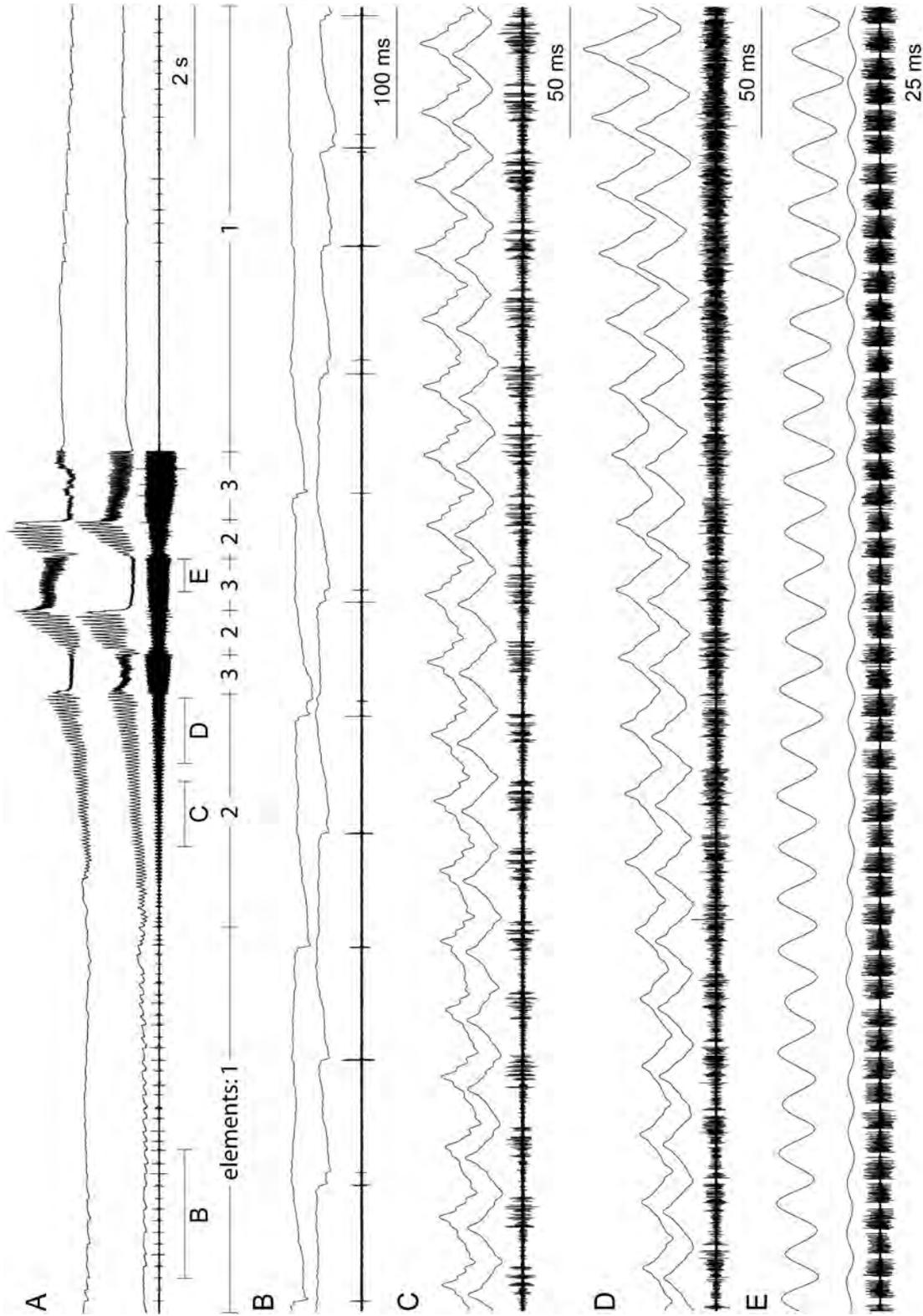


Fig. 1: Oscillograms of the courtship song of a *Myrmeleotettix antennatus* male: **A**: Overview over a whole courtship sequence comprising three acoustical elements (elements 1 to 3 are illustrated in **A**) and **B-E**: Indicated song parts. The lowest trace in each set of recordings is the oscillogram of the sound, above the stridulatory movement patterns of the right (middle trace) and left (top trace) hind legs are shown (recording temperature $\sim 27^{\circ}\text{C}$).

Tab. 1:

Temporal courtship song patterns of *Myrmeleotettix antennatus*. The calculations are based on the analysis of a total of 43 recordings containing 48 courtship sequences of four different males, which were recorded under controlled temperature conditions

element measured	element 1		element 2-3 complex		element 2								element 3				
	pulse period		duration		number per element-2-3-complex	duration of the first element 2	per element-2-3-complex	duration of subsequent element-2 per element-2-3-complex	syllable period	phase shift of the leg movements	ϕ	number per element-2-3-complex	duration	period and frequency of leg vibrations	period and frequency of emitted pulses		
	[ms]	[s]	[s]	[s]	[s]	[s]	[s]	[s]	[ms]	[ms]		[s]	[ms]	[ms]	[ms]	[Hz]	[Hz]
mean	219.8	7.48	2.98	3.72	2.98	0.62	48.5	8.4	62.1	2.94	0.85	18.8	53.2	9.6	104.2		
standard deviation (SD)	93.5	1.06	0.48	0.78	0.14	3.0	1.7	11.9		0.52	0.27	2.6		1.3			
median	205.9	7.35	3	3.72	0.61	48.8	8.3	61.7		3	0.81	18.6		9.4			
min	16.4	5.44	2	2.42	0.07	37.8	0.4	10		2	0.44	11.2		5.1			
max	1812.0	10.64	4	5.96	1.27	64.1	23.6	121.8		4	2.06	31.8		17.4			
n	1757	48	48	48	96	2310	2362	2263		48	140	3724		5562			
N	6	48	48	48	48	48	48	48		48	48	29		29			

n number of measured characters

N number of measured courtship sequences

ϕ phase shift in arc

This might explain the observed high standard deviation (Tab. 1). In the early state of courtship such pulse series can be performed for several minutes until the male switched to produce further elements. Later in courtship, element 1 alternated with the subsequent element complex.

At the beginning of courtship – during element 1 production – the male sat face to face towards the female and presented the clubbed antennae pointed to the front in an angle of about 160° to the body axis (Fig. 2A). The body was held in parallel to the ground (24° between femur and body axis) but was moved slightly from side to side. Palps performed slow opening and closing movements. The hind legs were kept in a degree of 40° to the body length axis and the tarsi were adducted to the tibiae of the singing legs, never having contact to the ground.

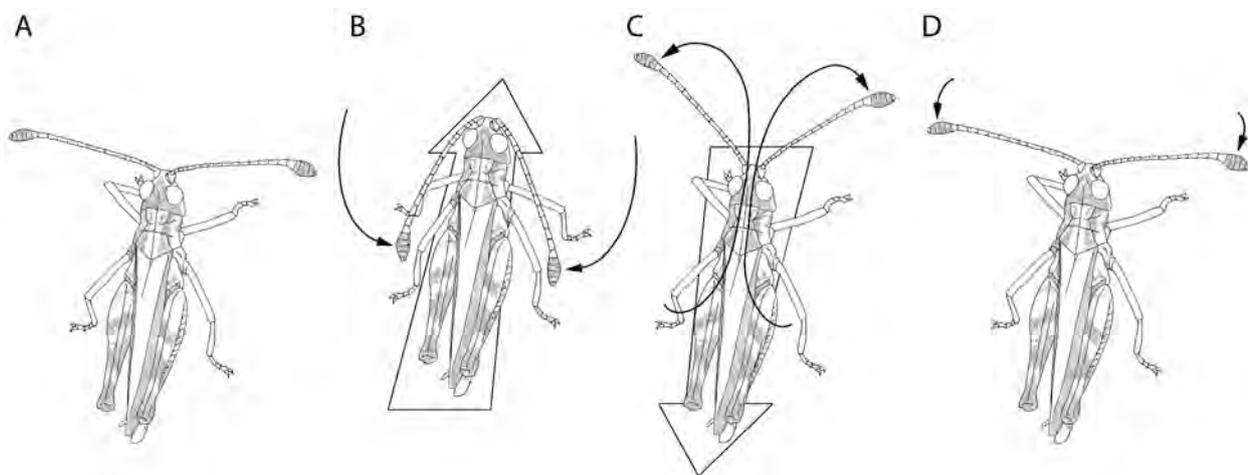


Fig. 2: Illustration of the visual courtship display of a *Myrmeleotettix antennatus* male. **A:** Initial position during element 1. The male is sitting close to the female, presenting its antennae by keeping them apart of the head. Thereby, the male performs body waving side wards around his body axis. **B:** During element 2 production, the clubbed and contrasting coloured antennae are simultaneously and slowly moved back describing a side wards circle. In doing so, the male stretches its body towards the female (arrow). During this phase the excited male moves its palps (not shown). **C:** At the end of each element B the antennae are stroked over the head, i.e. towards the female. Simultaneously, the body is moved back reaching initial position (arrow). **D:** Immediately after the quick forward stroke the antennae are moved apart of the head. After a short pause the male continues courting starting with element 1.

Rhythmic phase (song element 2)

Element 1 led immediately to an element complex, of 7.48 s mean total duration (SD 1.06 s) in which elements 2 and 3 alternated usually three times (rarely 2 or 4 times; Fig. 1; Tab. 1). In element 2 the legs were moved up and down syndromously by a phase shift of 62° . The amplitude of the main leg movement cycles increased consistently and reached its highest deflection at the end of element 2. The first element 2 in the whole element 2-3 complex was highly significant longer than the subsequent ones in all 4 males (Tab. 1; Mann-Whitney U-test male 1 $U= 0.0$, $Z= 2.71$; $p\geq 0.0066$; male 2 $U= 0.0$, $Z= 6.05$; $p\geq 0.00001$; male 3 $U= 0.0$, $Z= 5.20$; $p\geq 0.00001$; in male 4 not enough data were obtained to do sta-

tistic analyses but oscillogram analyses of the songs of male 4 were in line with results of the other males). During down stroke in this first leg movement cycle the legs were stopped several times until they reached the lower turning point (Fig. 1C). These down stroke steps emitted clear pulses divided by clear pauses, whereas the phase shifted straight up stroke emitted a noise of increasing intensity. Later in the first element 2 and during all subsequent second elements of each complex the legs were moved up and down without any stops (Fig. 1D), whereas the frequency and phase shift in which the legs are moved up and down remained constant (compare Fig. 1C and D; Tab. 1). The resulting sound in this part of element 2 was a constant noise. The sound pressure level increased continuously during element 2 (Fig. 1A).

During element 2 with rising excitation antennae were gradually moved along the side and backwards in a semicircle until reaching an angle of 180° to body axis with the tip of antennae pointing to the back of the animal (Fig. 2B; Fig. 3A). This rhythmic phase was accompanied by a continuous uplifting of the body (until more than 30° Fig. 3B) – thereby, the male often bent towards the female standing on its four fore legs (Fig. 2B) – and a very intensively up- and down movement of the flashy white maxillary and labial palps was performed resulting in a rapid fluctuation of angles between 30° up to 80° (Fig. 3C).

Excitation phase (song element 3)

At the end of element 2 cycle, one leg was pulled down in its initial position, whereas the contra lateral leg started to perform high frequent vibrations without lowering its position in a frequency of approximately 50 Hz (Fig. 1E; Tab. 1). This was the song element 3. The ipsi lateral leg was moved in the same manner in antidromic coordination, low position and in very low amplitude. The emitted sounds were series of homogeneous pulses in a frequency of approximately 100 Hz, caused by the precisely antidromic moving of the legs and the fact that both turning points of the legs – the upper and the lower one – do not emit any sound. Interestingly, the “higher” vibrating leg alternated between subsequent elements 3 in each courtship sequence (Fig. 1A) (and regularly in following courtship sequences; data not shown).

Exactly in the moment when a *M. antennatus* male changed from element 2 to 3, it threw the antennae in an extremely rapid movement of less than 4 ms to the front (Fig. 2C; Fig. 3A). During the throwing of the antennae the body was moved backwards into the initial position. After this convulsive reaction antennae were moved to sides again (Fig. 2D). The body, which had reached the highest upright position, an angle of 30° to ground, shortly after the throw of the antennae, was abruptly lifted down again (Fig. 3B). In this phase the palps were nearly not moved anymore (Fig. 3C).

After performing several courtship sequences, using vibrations of element 3, the males stroked their legs several times into the air in irregular intervals and tried to mount the female to copulate. If the female rejected the copulation attempt the male usually started courting again.

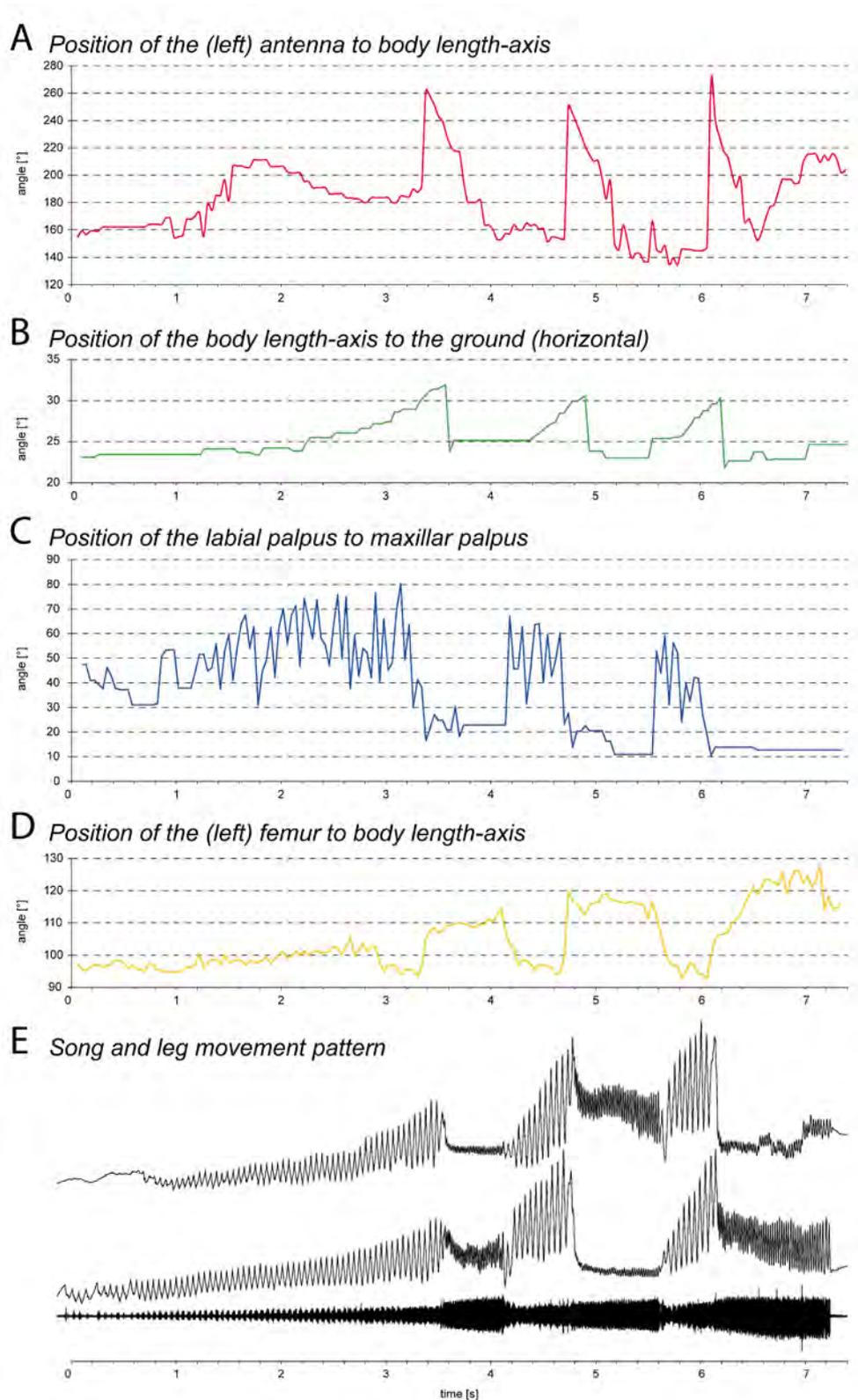


Fig. 3: Visual courtship components aligned with acoustic elements performed by males of *Myrmeleotettix antennatus* during courtship. **A**: Angle between tip of left antenna to body length-axis. **B**: Angle between body length-axis to the ground. **C**: Angle between left labial and maxillary palps. **D**: Angle between left femur to body length-axis. **E**: Oscillogram of the song and sound producing leg movement patterns of element-2-3-complex. Representation of the oscillograms and recording temperature as in Fig. 1.

Repetition of rhythmic and excitation phases

When antennae reached the side position again, like at the end of priming phase, the rhythmic phase begun anew, with gradual uplifting of body and moving of antennae to the back. Palps were again moved heavily up and down. Element 2 was performed as before with songs being more gentle, until again in a sudden movement antennae were thrown in direction of female. Rhythmic and excitation phases were in 77% of all analysed sequences performed three times (Fig. 1A; Fig. 3E). This element triplet alternated with element 1 several times until a copulation attempt by the male followed.

Discussion

Courtship behaviour of *Myrmeleotettix antennatus*

1) Song

Courtship behaviour of *Myrmeleotettix antennatus* males consists of complex and multimodal displays that are composed of acoustic and visual elements. Thereby, different body parts are involved in signalling. Three acoustical and three visual elements shape the courtship behaviour of *M. antennatus*. The acoustical units were always produced in a strict order and were extensively repeated before a copulation attempt of the male followed. The gentle element 1, consisting of low amplitude acoustic signals – a series of pulses –, alternated with the louder element-2-3-complex. Such alternation of gentle and louder parts is quite common in multi-component acoustic signals in Gomphocerinae and seems to play an important role in courtship behaviour (FABER 1953, JACOBS 1953, ELSNER 1968, ELSNER & HUBER 1969, OTTE 1972a, HELVERSEN 1986, RAGGE & REYNOLDS 1998, BERGER 2008). Complex courtship repertoires are often preluded by low intensity parts which are produced extensively in the early stage of courting until the male switches to produce further elements (FABER 1953, JACOBS 1953, ELSNER 1974a, 1975, RAGGE & REYNOLDS 1998, BERGER 2008). We observed that the locomotion activity of the females was reduced, when the male produces element 1 close to the female. That indicates that element 1 acts to bring the female in the stage of *passive acceptance* (LOHER & HUBER 1964), whereas further song elements likely act in the meaning of *active attraction* sensu RIEDE (1983). The latter ones, namely element 2 and 3 are signals of elaborate complexity and higher intensity in contrast to element 1. The first element 2 of each element-2-3-complex is particularly longer than subsequent ones. At the beginning the legs are moved straight upwards whereas they are stopped several times during downward stroking. In this part the song contains a clear syllable structure, consisting of intensity modulated rustling noise during a phase shifted up stroke and pulses during the synchronised down stroke stops of the legs. This syllable structure is widespread within gomphocerine grasshoppers (ELSNER & POPOV 1978, HELVERSEN & HELVERSEN 1994, RAGGE & REYNOLDS 1998, BERGER 2008). It is assumed to represent a plesiomorphic syllable pattern of complex singing genera, e.g. *Chorthippus*, *Stenobothrus* and *Omocestus* (BERGER 2008, MAYER et al. in press) to which *Myrmeleotettix* is closely related to (CLEMENTE et al. 1989, 1990b, MAYER et al. in press). As behavioural and neurophysiological observations reveal, the complex leg movement patterns likely resulted from the activity

of two neuronal pattern generators. Whereas the main leg movements are assigned to unifunctional pleuro-thoracal muscles acting in e.g. locomotion, the superimposed down stroke steps or high frequent leg vibrations are likely the result of the activity of muscles which act bifunctional in both, movement of the hind legs and the wings (WILSON 1962, ELSNER 1974a,b, 1975, 1983). Later during element 2 the legs are straight stroked up and down in the same intervals as before, probably by the lack of activity of the flight oscillator. In contrast, in element 3 legs are moved in low amplitude and at high frequency, i.e. probably by the activity of exclusively the neural flight oscillator. This alternating failure of neuronal pattern generators within one song was never observed in Gomphocerinae until now. In conclusion, we assume that the first syllables during element 2 (Figure 1C) – which combine the two upper mentioned rhythms – are ancestral song elements within the element-2-3-complex of *M. antennatus*, even if all other parts (Figure 1C, E) are produced by more simple leg movement patterns, resulting in more simple structured sound. Furthermore, syllables of the first part of element 2 are the main part of the calling song in this species (FABER 1953, SAVITSKY 2005). The song of *M. antennatus* contains ancestral song elements which are lacking in other species of this genus. The songs of *M. maculatus* and *M. pallidus* for example are composed mainly of acoustical elements produced by simple up and down movements and high frequent vibrations of the hind legs (RAGGE & REYNOLDS 1998, SAVITSKY 2005, ATORF 2007). In this regard, *M. antennatus* represent a link in the evolution of new song patterns in this genus. Beside of this there are big differences between the species not only by morphology and song, but especially in the visual courtship displays between *Myrmeleotettix*-species. Unfortunately, SAVITSKY (2005) did not mention the conspicuous visual displays in his work.

2) Visual components

The visual repertoire of *M. antennatus* during courtship is very complex and differentiated, but with nearly no variation in performance between the observed individual males. Therefore the complex movements of different parts of body are ritualized and repeated stereotypically in a highly species-specific manner. The different elements, i.e. body rocking, palp flapping, and antenna stroking, probably originated from other behavioural contexts and have later been ritualized during courtship (OTTE 1970).

The first peculiar non-acoustic behaviour elements during courtship are side to side movements of the body during element 1 production. This behaviour was observed exclusively during the priming phase whereas during all other courtship phases it was lacking. Side to side body movements during courtship were observed frequently in different courtship phases of various grasshopper species (compare FABER 1953, JACOBS 1953, OTTE 1970). In some species, e.g. in *Stenobothrus fischeri* where conspicuous side to side shaking is produced during excitation phase this behaviour must be regarded as attraction behaviour in *S. fischeri* (*active attraction* after RIEDE 1983, 1986), since in this phase the legs which contain contrasting knee coloration are wide-angled moved (BERGER 2008). In *Myrmeleotettix antennatus* the function of body rocking is not that clear. The gentle accentuated priming phase, as the initial part of courtship, is thought

to be acting to decrease the locomotor activity of the female (*passive acceptance* after LOHER & HUBER 1964). Since the legs of *M. antennatus* do not exhibit contrasting colouration and the legs are moved in only small deflection, the function of body side to side movements in *M. antennatus* is clearly different to similar movements of other gomphocerine grasshopper species. On one hand, body rocking in this species could be regarded as movements acting in visual scanning, i.e. the process of orientating to objects – here the female – in the visual field (KENNEDY 1945, FABER 1936, 1953, WALLACE 1958, 1959) to be sensitive for smallest females reactions. Such fixation movements are common in grasshoppers and likely resemble the origin of body rocking movements incorporated in courtship. Under consideration of the position of the antenna during priming phase (Fig. 2A) a second function of body rocking could be the presentation of the clubbed and contrasting coloured antennae towards the female. Comparable behaviour was observed in *Gomphocerippus rufus*, where the male displays its antennae passively by shaking the head during the priming phase of courtship (FABER 1953, JACOBS 1953, ELSNER 1968).

The palps of Acrididae function as mechano- and chemoreceptors and play an important role in food finding and selection (FRINGS & FRINGS 1949). During feeding and testing of food, the palps make irregular flicking movement as well as extensive rapid vibrations, which are known as palpation. Palpation increases the amount of sensory input reaching the central nervous system and it was suggested that palpation maintains a continuous flow of information to the central nervous system (BLANEY & DUCKETT 1975). Beside the central function palpation plays in feeding, it seems that movement of palps can also play an important role during courtship (FABER 1953, OTTE 1970). Possibly female sex pheromones are sensed through the sensilla which are concentrated on the tips of maxillary and labial palps. Whereas the role of the palps for feeding and physiological processes thereby is well studied especially concerning pest species (HASKEL & MORDUE 1969, HASKEL & SCHOONHOVEN 1969, BLANEY & CHAPMAN 1970, BLANEY et al. 1971, BERNAYS et al. 1972, BLANEY 1974, IGNELL et al. 2001 and references therein), about the role of palps in sexual behaviour not much is known yet (ATORF 2007).

Males of *M. antennatus* move the palps heavily during element 2 in the rhythmic phase. Simultaneously they move the body and head towards the females (Fig. 2B). Additionally palps in *M. antennatus* are pure white, therefore contrasting to the dark head, so that movement gets quite conspicuous. It is well conceivable that the colour-contrast creates an extra visual stimulus. This white coloration of palps is also found in other grasshopper species, like e.g. *Omocestus rufipes*, and was hypothesized to be a strong optical signal, although this species does not move palps during courtship (ATORF 2007). Hence female pheromones could be sensed easily and olfactory communication is hypothesized to have evolved prior to acoustic communication (OTTE 1970), the phylogenetic older function of palpation during courtship is probably the perception of con-specific odours. The use of contrasting coloured palps for visual courtship stimulus likely evolved later. Rhythmic movements of palps during courtship are found also in many other species e.g. like in *Calliptamus italicus*, *Podisma pedestris*, *Gomphocerippus*

rufus, *Aeropus sibiricus* (FABER 1953), in *Syrbula admirabilis* and *S. fuscovittata* (OTTE 1972a), and in *Tylotropidius speciosus* (Eypreocnemidinae; LAUB-DROST 1959). Although the function of palp movement is not known yet, we assume that the original function during feeding was modified into a ritualized movement playing an important role in courtship.

The most conspicuous visual element of *M. antennatus* is the movement of the antennae during courtship. The antennae, which primarily function as sense organs in grasshoppers get very eye-catching because they are clubbed, have curved tips, show conspicuous colour contrast to the rest of the antennae, and are furthermore moved fast. Throwing of antennae is a common element in different genera of visual displaying gomphocerine grasshoppers and occurs in e.g. *Stenobothrus*, *Gomphocerippus*, *Gomphocerus*, *Syrbula*, and *Chorthippus* species (FABER 1953, JACOBS 1953, ELSNER 1968, 1974a, ELSNER & HUBER 1969, OTTE 1970, HELVERSEN 1986, WAEBER 1989, BERGER 2008), but also in species of other subfamilies, like in *Taramassus* (Eypreocnemidinae; LEVY & BUTLIN 1994). But whereas in *M. antennatus* the antennae are slowly moved to the side to suddenly be thrown to the front, in most other species antennae are suddenly thrown from the front side- or backwards over the head like e.g. in *Myrmeleotettix maculatus*, *Stenobothrus eurasius* and *Gomphocerippus sibiricus* (FABER 1953, JACOBS 1953, BULL 1979, WAEBER 1989, ATORF 2007, BERGER 2008). In most Gomphocerine the visual display of antennae stroking is usually accompanied by leg stroking where the femora and often also the tibiae are thrown in the air (FABER 1953, JACOBS 1953, BULL 1979, HELVERSEN 1986, WAEBER 1989, RAGGE & REYNOLDS 1998, ATORF 2007, BERGER 2008, MAYER et al. in press). These optical displays are typically supported by darkened hind knees. In contrast, in *Myrmeleotettix antennatus* no leg strokes could be observed during courtship and contrasting knee colouration is not expressed. Antennae stroking in general is supposed to be originated from disturbance reactions (WILLEY & WILLEY 1969) that could be frequently observed when animals were disturbed or touched by other animals or the experimenter. In this case the animals raise the antennae into the opposite side of the disturbing interference. Clear differences in morphological modifications of the antennae in various taxa, as e.g. Gomphocerinae *Syrbula* (OTTE 1972a), *Gomphocerus* (JACOBS 1953, ELSNER 1974a), the *Chorthippus albomarginatus*-group (HELVERSEN 1986, VEDENINA & HELVERSEN 2003), *Myrmeleotettix* (BULL 1979), *Gomphocerippus* (JACOBS 1953, ELSNER 1968, ELSNER & HUBER 1969), Oedipodinae (LAUB-DROST 1959, FABER 1936, 1953, JACOBS 1953, WILLEY & WILLEY 1969, OTTE 1972b), Eypreocnemidinae (LEVY & BUTLIN 1994), and others, indicate that distinct movements of the antennae became independently involved in communication in several lineages of short horned grasshoppers and seem to be more widespread than it was supposed by OTTE (1970). In all studied species with modified antennae, the antennae are incorporated in courtship (ATORF 2007). Thereby, morphological modifications reach from filiform-prolonged-bended, clubbed, and flattened-broadened. Also not conspicuously modified antennae are used for signalling (FABER 1953, OTTE 1972a, WILLEY AND WILLEY 1969). Therefore the distribution of optical signals of the antennae, as by other body parts too, in grasshoppers are largely unknown.

Theoretical considerations on the origin of divergent song types in Gomphocerinae

Gomphocerine grasshoppers have a complex bidirectional communication system. They produce songs by rubbing a row of stridulatory pegs on the inner side of their hind legs against a sclerotised edge on the fore wing (SIEBOLD 1844, YERSIN 1854, LANDOIS 1867, GRABER 1872, FABER 1929, 1953, JACOBS 1953, ELSNER 1974a, HELVERSEN & ELSNER 1977, ELSNER & POPOV 1978, and others), and different male song types are produced in different behavioural contexts (summarised in e.g. HUBER 1956, ALEXANDER 1957, 1967, FRINGS & FRINGS 1958, INGRISCH & KÖHLER 1998). The calling and courtship songs serve exclusively for intra-specific communication and are under high pressure of sexual selection.

About the variety of communication systems in grasshoppers not much is known (GREENFIELD 1997). Also the functions of different courtship elements in complex courtship repertoires in gomphocerine species often remain unclear. In the first part of this paper we described and discussed the extraordinary courtship repertoire of *Myrmeleotettix antennatus* and tried to explain the functions of the different visual and acoustic elements which are produced by the males of this species during courtship. The reasons why different song types have evolved in grasshoppers is discussed in e.g. BERGER (2008). Another question that arises is the phylogenetic origin of calling and courtship songs in Gomphocerinae.

Calling songs are produced by males spontaneously and in irregular intervals without having physical contact to female, i.e. long distance signals. They are mostly short and stereotyped signals which are answered acoustically by receptive con-specific females (JACOBS 1949a,b). Thereby, females discriminate strictly according to distinct song structures and temporal parameters of male songs (HELVERSEN 1972, HELVERSEN & HELVERSEN 1975, 1983, 1994, 1997, BUTLIN & RITCHIE 1991, ERÍKSSON 1993, 1994, CHARALAMBOUS et al. 1994, HELVERSEN et al. 2004, BRIDLE et al. 2006, GOTTSBERGER 2007, GOTTSBERGER & MAYER 2007). The main functions of the calling songs are species recognition and mate localisation. The exchange of songs between the sexes ("anaphony" FABER 1932, WEIH 1950, "allelphony" FABER 1953), allows the male to locate and find the mating partner phonotactically.

When the physical contact to a female is established the male changes its behaviour and produces courtship songs, i.e. short distance communication signals. The courtship songs comprise two major functions, serving to species identification and bringing the female from a semi-receptive into a fully receptive state so that she permits copulation (FRINGS & FRINGS 1958, BULL 1979, OTTE 1970, ELSNER 1974a, EWING 1984 etc.).

Since courtship songs often comprise calling song parts (FABER 1932, 1953, JACOBS 1953, BERGER 2008, this paper discussion part one), calling song could be regarded as the ancestral song type from which the courtship song descended. Further, the fact that in many species the calling song and courtship songs widely resemble each other could support this idea. On the other hand, it is very unlikely that the basis of the effective sender receiver system of gomphocerine grass-

hoppers can be found in long distance signals. That leads us to the following theoretical considerations.

In general, the occurrence of an orthopteran species and thus the aggregation of the sexes in a habitat are mainly influenced by extrinsic factors, as e.g. macro- and microclimatic conditions, topography and land use (FABER 1932, KALTENBACH 1970, KÖHLER 1990, DETZEL 1998, INGRISCH & KÖHLER 1998, SCHLUMPRECHT & WAEBER 2003). Within an appropriate environment the number of individuals of a species should be high enough to be able to register con-specific signals. Even calling songs, which have the function of long distance signals, are only effective in a limited range of about several metres (MINCKLEY & GREENFIELD 1995, MINCKLEY et al. 1995).

Ancestral songs in Gomphocerinae likely were short one-element-signals and are assumed to have originated from signals without communication function, as e.g. defence reactions (OTTE 1970). Such primitive vocalisations are also produced in the presence of con-specifics by other grasshoppers with simple songs, as e.g., oedipodids which do not produce acoustical long range signals but perform simple acoustical signals in the presence of a mate (*Acrotylus*: BLONDHEIM & SHULOV 1972, *Oedipoda*: FABER 1936, 1953, JACOBS, 1953, OTTE 1970, LAUB-DROST 1959, *Sphingonotus*: GARCIA et al. 2001). It is very conceivable that the origin of the complex acoustic communication system in gomphocerine grasshoppers was a simple short range signal which could be recognised as species-specific signal by con-specifics, firstly within and later outside of the visual range. This signal was likely universally used for defence and species recognition. Whether it worked in female stimulation remains unclear. The function sharing into 1st species recognition, 2nd mate location and 3rd sexual stimulation and the differentiation in different song types (calling and courtship song) out of the ubiquitously used ancestral signal must have been caused by the evolutive pressure of sexual and natural selection. In general, calling songs are usually short and intense, whereas courtship songs or repertoires are longer and gentler. The combination of song duration and intensity is probably a result of the conflict of the biological and physical requirements of the sender-receiver system and the avoidance of predators and competitive con-specific males (BURK 1982, ROBERTS et al. 2007). Calling or courtship songs reached different complexity levels in different Gomphocerinae lineages. Whereas, in some taxa calling and courtship songs resemble widely each other, differing only in duration and intensity, in several lineages extraordinary complex courtship repertoires evolved (FABER 1929, 1932, 1953, JACOBS 1953, VAUPEL 1956, ELSNER 1968, ELSNER & HUBER 1969, OTTE 1970, 1972a,b , BULL 1979, RIEDE 1983, 1986, HELVERSEN 1986, WAEBER 1989, RAGGE & REYNOLDS 1998, BERGER 2008, this study). The question which of the two song types calling or courtship song, is the phylogenetic older one remains open. The actual calling song resembles more the ancestral multifunction song by its simple structure than the courtship song. In contrast, it seems to be more likely that signals of a sender became functional as a species-specific communication signal in presence of a receiver. In this case an ancestral short distance signal represents the origin of all further communication signals of Gomphocerinae.

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