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Stable and Variable Parameters in Courtship Songs of Grasshoppers of the Subfamily Gomphocerinae (Orthoptera, Acrididae)

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Abstract—The courtship behavior of seven grasshopper species of the subfamily Gomphocerinae from different localities of Russia, Ukraine and Greece was described. Not only the sounds but also the corresponding stridulatory movements of the hind legs and visual display accompanying the courtship song were analyzed. Comparison of the degree of variation in different courtship parameters showed that the most stable traits were the syllable and pulse periods. The potential role of stable and variable traits in the grasshopper courtship songs is discussed.

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Acoustic communication is the principal way of finding individuals of the opposite sex in grasshoppers of the subfamily Gomphocerinae. Numerous behavioral and electrophysiological studies carried out during the last three decades have shown that for recognition of conspecific signals, different species of Gomphocerinae mostly use the temporal parameters of the signal, such as the duration of acoustic phrases, the frequency and duration of pulses in a phrase, the syllable envelope characterizing the relative intensity of different pulses, etc. (Zhantiev, 1981; Helversen and Helversen, 1983, 1994; Ronacher and Stumpner, 1988; Vedenina and Zhantiev, 1990; Stumpner et al., 1991; Stumpner and Helversen, 1994; Balakrishnan et al., 2001). The calling song, emitted by a single male to attract a female, should be highly antijamming, i.e., it should contain a set of characters which would be reliably detected against the noise background and differentiated from the signals of other orthopteran species. Sympatric species of grasshoppers have been shown to be segregated by the so-called acoustic niches: the calling song of each species is characterized by a specific complex of acoustic parameters, whereas the ranges of variation of these complexes do not overlap in simultaneously singing species (Bukhvalova and Zhantiev, 1993; Bukhvalova, 2006; Tishechkin and Bukhvalova, 2009). The most stable characters of the calling song are the repetition period and the envelope of the syllable, and also the general pattern of the signal.

Each individual has to recognize a conspecific individual of the opposite sex and also to estimate its "quality" (Andersson, 1994). Since the number of males ready for mating always exceeds the number of receptive females, the problem of choosing the better mate confronts the females (Kriegbaum, 1989; Helversen and Helversen, 1994). However, the relative stability and low intraspecific variation of calling songs in Orthoptera offer little opportunity for females to select the "best" male. From a distance, the females may only prefer those males that produce the most loud and stable songs (Zhantiev, 1981). A different situation is observed when the male starts emitting the courtship song in the direct proximity of the female. The courtship behavior in different species of Gomphocerinae may include not only acoustic but also vibrational, visual, chemical, and mechanical signals. Some parameters of such a polymodal signal may be more stable and may serve for recognition of conspecific individuals, whereas other parameters, showing a higher level of variation, may be used for evaluation of the mate quality (Vedenina, 2005).

Under the conditions of high population density which is often observed in grasshoppers, individuals of different sexes may meet each other by chance

(Kriegbaum, 1989; Kriegbaum and Helversen, 1992). In case of such an encounter, the male touches the female with its antennae and, if the female appears to be conspecific, starts the courtship without emitting the calling song. Thus, it would be important to find out which parameters of the courtship song are more stable and therefore serve for recognition of the conspecific male, and which are more variable and may therefore serve for assessment of its individual qualities. The variability of the courtship songs in Gomphocerinae has been little studied. V.Yu. Savitsky described in detail the courtship songs of different grasshopper species and measured their parameters but did not estimate the degree of their variation (Savitsky, 2000, 2002, 2005; Savitsky and Pekarev, 2007).

In the recent decades, the calling songs started to be actively used for taxonomic purposes. The attention of researchers was focused on the most stable parameters, such as the repetition period and the envelope of the syllable (e.g., see Bukhvalova, 1993; Vedenina and Bukhvalova, 2001; Tishechkin, 2008; Willemse et al., 2009). In our opinion, the stable parameters of the courtship songs can be no less useful in the taxonomy of grasshoppers. They may be particularly helpful when dealing with groups of species that emit similar calling songs but highly different courtship songs, such as the genus *Stenobothrus* (Elsner and Wasser, 1995; Berger, 2008) or the *Chorthippus albomarginatus* species group (Vedenina and Helversen, 2003, 2009).

This paper contains new data on the variation of courtship songs of seven species of grasshoppers recorded in different geographic localities of Russia, Ukraine, and Greece. Our analysis included not only the sounds but also the stridulatory movements of the legs, which allowed us to classify the signals more reliably and to measure their temporal parameters more precisely. It is known that the hind legs of most grasshopper species move with a certain phase shift during stridulation. This shift may vary with time; moreover, the leg movement pattern itself may also vary (Elsner, 1974). The phase shift may conceal the individual pulses composing the syllable or obscure the gaps between the syllables. We also analyzed the display movements of males associated with courtship, which could provide additional visual signals. The degree of variation of the different parameters of the courtship song was compared with the variation of the most stable parameter of the calling song, namely the syllable repetition period.

MATERIALS AND METHODS

The material was collected in different geographic localities of Russia, Ukraine, and Greece, from 2004 to 2012 (Table 1). The captured grasshoppers were kept in cages measuring 60 × 40 × 30 cm. The signals were recorded in the laboratory at temperatures 30–35°C. To record the courtship songs, the male was placed near the female. The stridulatory movements of the legs were recorded with an opto-electronic device implementing the method developed by the German researchers (Helversen and Elsner, 1977; Hedwig, 2000). Pieces of reflecting foil were glued onto the outer distal lobes of the male's hind femora. A piece of reflecting foil was glued to the distal part of each hind leg femur of a male and two opto-electronic cameras were focused on the illuminated reflecting dots. Each camera was equipped with a position-sensitive photodiode that converted the upward and downward movements of the hind legs into voltage signals. The songs were recorded using a Brüel & Kjær 4191 microphone with the frequency range 3 Hz–40 kHz. These signals were A/D converted with a custom-built PC card. The sampling frequency was 100 kHz for songs and 2 kHz for leg movements. The temporal parameters of the signals were measured using Turbolab 4.0 (Bressner Technology, Germany) and CoolEdit (Syntrillium, US) software. Each parameter was measured 10 times in each signal where it was possible. The signal parameters were statistically analyzed using the Excel and Statistica software. In addition, the courtship behavior was recorded with a Sony DCR-TRV 355E video camera, and the video recordings were analyzed using Adobe Premiere and Virtual Dub software.

RESULTS

The temporal parameters of grasshopper signals were described using the terminology accepted in a number of earlier publications (Zhantiev, 1981; Savitsky, 2000, 2002, 2005; Berger, 2008; Vedenina and Helversen, 2009; Vedenina and Mugue, 2011). The sound generated by a single shift of the hind femur in one direction is referred to as a *pulse*; the complete cycle of up-and-down movement of the femur results in a *syllable* which may consist of several pulses; the syllables are grouped into *phrases*. A phrase may consist of a sequence of identical syllables or of several sequences of syllables of different types; in the latter case, each sequence of similar syllables is referred to as an *element*.

Table 1. The species studied, collection localities, and the number of individuals and signals recorded

Species	Collection localities	Number of males studied (signals recorded)
Myrmeleotettix maculatus (Thunberg, 1815)	Ukraine, Nikolayev Prov., 20 km SE of Pervomaisk. 47°58.2′N, 31°05.8′E	1 (4)
	Russia, Kostroma Prov., 30 km SW of Manturovo. 58°08.17′N, 44°19.2′E	4 (9)
	Ukraine, Cherkassy Prov., 17 km S of Kanev. 49°35.6′N, 31°29.5′E	1 (3)
Myrmeleotettix antennatus (Fieber, 1853)	Ukraine, Kherson Prov., Kinburn Spit. 46°25′N, 32°02.3′E	2 (5)
	Russia, Saratov Prov., 29 km SW of Krasnyi Kut. 50°43.4′N, 46°46.2′E	2 (9)
Stenobothrus lineatus (Panzer, 1796)	Russia, Saratov. 51°34′N, 45°54′E	2 (7)
	Ukraine, Khmelnitsky Prov., 28 km N of Kamyanets-Podilsky. 48°55.3′N, 26°28.3′E	2 (7)
	Greece, Epirus, Ioannina, env. of Métsovon. 39°49′N, 21°08′E	2 (5)
Stenobothrus nigromaculatus (Herrich-Schäffer, 1840)	Ukraine, Nikolayev Prov., 20 km SE of Pervomaisk. 47°58.2′N, 31°05.8′E	2 (10)
	Russia, Saratov. 51°32.4′N, 45°59′E	4 (14)
	Ukraine, Vinnitsa Prov., 16 km NW of Mogilev-Podilsky. 48°30.7′N, 27°38′E	2 (3)
	Russia, Orenburg Prov., 58 km SE of Sorochinsk. 52°01.4′N, 53°42′E	1 (3)
Stenobothrus fischeri (Eversmann, 1848)	Russia, Saratov. 51°34′N, 45°54′E	1 (7)
	Greece, Epirus, Ioannina, env. of Métsovon. 39°49′N, 21°08′E	1 (6)
	Greece, Epirus, Ioannina, Timphy Mts, 5 km NW of Monodendrion. 39°54′N, 20°43′E	1 (1)
	Greece, Macedonia, Drama, Phalacron Mts. 41°17′N, 24°03′E	2 (5)
Gomphocerippus rufus (Linnaeus, 1758)	Ukraine, Poltava Prov., 9 km N of Shishaki. 49°56.7′N, 34°0.6′E	4 (7)
	Russia, Samara Prov., 29 km W of Togliatti. 53°30.5′N, 49°56.9′E	3 (8)
Chorthippus biguttulus (Linnaeus, 1758)	Russia, Kaliningrad Prov., env. of Svetlogorsk. 54°56.1′N, 20°08.5′E	2 (10)
	Russia, Kostroma Prov., 30 km SW of Manturovo. 58°08.2′N, 44°19.2′E	3 (14)
	Russia, Samara Prov., 29 km W of Togliatti. 53°30.5′N, 49°56.9′E	3 (9)
	Russia, Orenburg Prov., 58 km SE of Sorochinsk. 52°01.4′N, 53°42′E	3 (3)
	Russia, env. of Orenburg, glades along the Ural River. 51°44.4′N, 55°20.7′E	1 (2)

Table 2. Parameters of the courtship song of *Chorthippus biguttulus*

Parameters of the signal	Kaliningrad Prov.	Kostroma Prov.	Samara Prov.	Orenburg Prov.	Environs of Orenburg
Period of element A, s	2.9	1.9	4.08	–	3.5
	1.4–4	0.81–3.7	3.6–4.5		2.5–4.9
	0.34	0.48	0.10		0.24
Duration of element A, s	2.04	1.47	2.24	–	2.08
	0.665–3.64	0.489–2.75	1.65–2.85		1.20–4.04
	0.53	0.46	0.22		0.52
Period of syllables in element A, s	0.057	0.067	0.060	–	0.058
	0.052–0.07	0.055–0.148	0.042–0.093		0.041–0.091
	0.04	0.20	0.13		0.27
Interval between elements A and B, s	2.94	1.5	2.15	–	–
	1.7–3.5	1.19–2.72	1.89–2.36		
	0.24	0.31	0.09		
Duration of element B, s	0.845	1.02	0.834	–	–
	0.585–2.3	0.56–2.24	0.55–1.45		
	0.53	0.53	0.34		
Period of syllables in element B, s	0.066	0.070	0.058	–	–
	0.051–0.073	0.038–0.09	0.039–0.08		
	0.06	0.16	0.14		
Period of syllables in the calling song, s	–	0.059	–	0.063	–
		0.053–0.071		0.048–0.076	
		0.12		0.12	

Note: The mean value, range, and coefficient of variation are given for each parameter.

The courtship songs are described below not in the taxonomic order but according to increasing the number of the song elements.

Chorthippus biguttulus

The courtship song of *Ch. biguttulus* was slightly different from the calling song (e.g., see Bukhvalova, 1993; Helversen and Helversen, 1994; Ragge and Reynolds, 1998). Its main element (A) was almost identical to the calling song, and consisted of syllables 1.5–2.2 s long repeated with a period of 1.9–4.1 s (Table 2). The amplitude of syllables in element A increased gradually, reaching its maximum approximately in the middle third of the element (Fig. 1). Each syllable of element A may be subdivided into one high-amplitude pulse and several pulses with lower amplitude (Figs. 1*g*, 1*h*). The high-amplitude pulse was generated by almost simultaneous downward movements of both hind legs but the two or three subsequent up-and-down movements occurred with a phase shift. Therefore, only the high-amplitude pulse may be distinguishable within the syllable (Fig. 1*g*). Element A was sometimes followed, with an interval of 1.5–3 s, by a considerably less loud element B, which could be recorded only in some signals and not in all the males (Fig. 1*c*). During the generation of element B the legs were kept in an almost vertical position (Figs. 1*a*, 1*b*) but the pattern of the syllables was similar to that of element A.

The most stable parameters of the courtship song were the syllable period in both elements, even though the coefficients of variation of these parameters were greater than that of the syllable period in the calling song (Table 2). The period and duration of element A and the duration of element B appeared to be the most variable.

Gomphocerippus rufus

The courtship behavior of *G. rufus* started with movements of the head and palps from side to side and

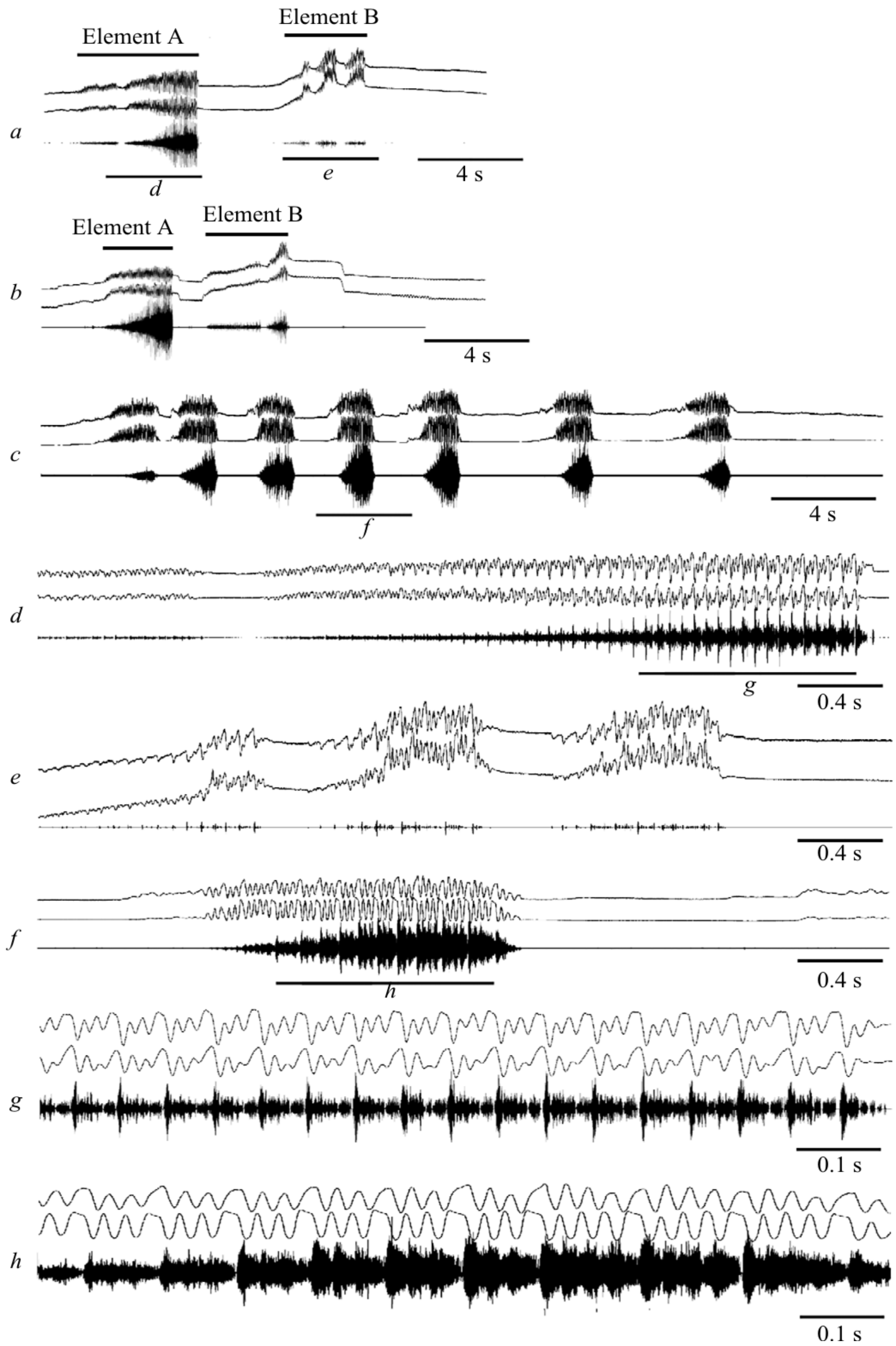

Fig. 1. Oscillograms of courtship songs of *Chorthippus biguttulus* from Kaliningrad Province (*a*), Kostroma Province (*b*), and the environs of Orenburg (*c*). Oscillograms *a* and *b* show elements A and B; oscillogram *c* shows only the repeated element A. Fragments of oscillograms *a* and *c* are shown in *d*–*h* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale.

irregular low-amplitude movements of the legs generated a very soft song (Fig. 2). These were followed by an abrupt stroke of the antennae and hind legs, the movement of the legs generating a single high-amplitude pulse (Fig. 2*c*). The male sometimes emitted several such pulses with a period of about 1 s and then

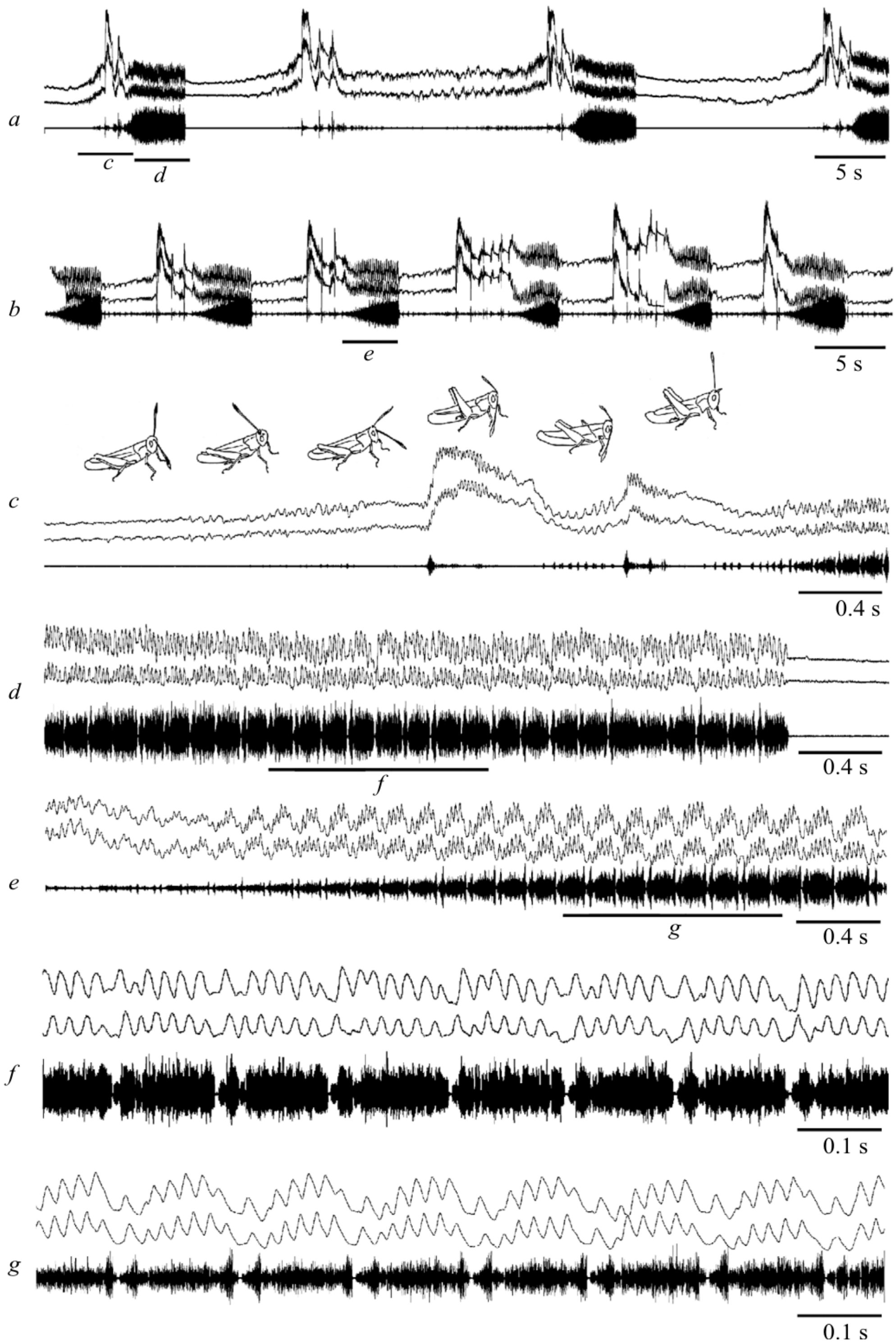

Fig. 2. Oscillograms of courtship songs of *Gomphocerippus rufus* from Poltava Province (*a*) and Samara Province (*b*). Fragments of oscillograms *a* and *b* are shown in *c–g* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. The drawings show the position of the hind legs and antennae at different moments of courtship corresponding to fragment *c*.

emitted a phrase with gradually increasing amplitude of syllables which was almost identical to the calling song (Vedenina and Zhantiev, 1990; Ragge and Reynolds, 1998). The only difference was the fact that during the courtship song, stridulation was accompanied by slow movements of the antennae. Each syllable in the phrase started with a synchronous up-and-down leg-movement generated a more or less distinct pulse. However, the subsequent four or five strokes occurred with an increasing phase shift (Figs. 2*f*, 2*g*), producing a noise-like signal in which individual pulses could be hardly distinguished. The envelope of the syllable was variable; for example, the oscillograms of the songs of some males revealed a high-amplitude pulse not only at the beginning but also at the end of the syllable (Fig. 2*g*).

The most stable parameter of the courtship song was the period of the syllables (Table 3). Other parameters, such as the period and duration of the phrase, and also the period and number of the display leg movements, were more variable.

Stenobothrus lineatus

The courtship behavior of *S. lineatus* started with alternating low-amplitude movements of the two legs producing low-amplitude pulses (element A, Figs. 3*a*, 3*b*). After some time, the legs started to move synchronously but the temporal parameters of the song remained the same. Element A could be produced for a long time, sometimes for tens of minutes; then the male suddenly switched to element B which was very similar to the calling song (Vedenina and Zhantiev, 1990; Ragge and Reynolds, 1998). Its legs started to move very slowly (0.7–0.8 ms), with a gradually increasing amplitude. Contrary to what was observed during element A, the leg movements during element B always displayed a small phase shift (Fig. 3*d*). The downward movement of the legs was sometimes interrupted by a short and abrupt stroke with a simultaneous swing of the antennae. Such display movements were performed several times during element B. The latter was abruptly replaced by element C, during which the amplitude of leg movements strongly decreased while their frequency increased (Fig. 3*e*). Element C was emitted for 10–15 s and was followed by element B. These two elements could be emitted in turn for a considerably long time.

The period of syllables in element B proved to be the most stable parameter, comparable to that of syllables in the calling song (Table 4). The periods of syllables in the other two elements were more variable; the duration of elements B and C and the number of display movements of the antennae were also characterized by a higher level of variation.

Table 3. Parameters of the courtship song of *Gomphocerippus rufus*

Parameters of the signal	Ukraine	Russia
Period of the phrase, s	16.99	9.39
	9.2–32	5.46–11.1
	0.47	0.13
Duration of the phrase, s	3.39	3.05
	2.6–4.55	1.97–4.11
	0.18	0.20
Period of elements, s	0.136	0.136
	0.116–0.185	0.135–0.156
	0.13	0.05
Period of display movements of the legs, s	0.930	1.098
	0.343–1.535	0.765–2.972
	0.27	0.31
Number of display movements of the legs during the phrase	2.60	2.62
	1.0–4.0	1.0–4.0
	0.26	0.31

Note: see Table 2.

Myrmeleotettix antennatus

The courtship song of *M. antennatus* started with low-amplitude leg movements performed at rates of 4–6 Hz. The resulting short pulses were described as element A (Figs. 4*a*, 4*b*). This element was often emitted for a long time (up to several minutes), making it difficult to obtain the complete record. Element A was followed by the main phrase in which we distinguished two elements, B and C. Of these, element B resembled the first part of the calling song, and element C, its second part (Savitsky, 2005). In the courtship song, these elements were sometimes repeated in turn two or three times. Element B was produced by simple movements of the legs with a small phase shift (Figs. 4*c*–4*f*). Individual pulses could be discerned in the syllables only at the beginning of the element; then they were obscured and even the boundaries of the noise-like syllables became indistinct. On completion of element B, the male performed a characteristic swing of the antennae from the backward position (Berger and Gottsberger, 2010). Element C was always generated by low-amplitude vibrations of only one leg at a rate of 60–70 Hz, the consecutive elements being produced in turn by the right and left leg

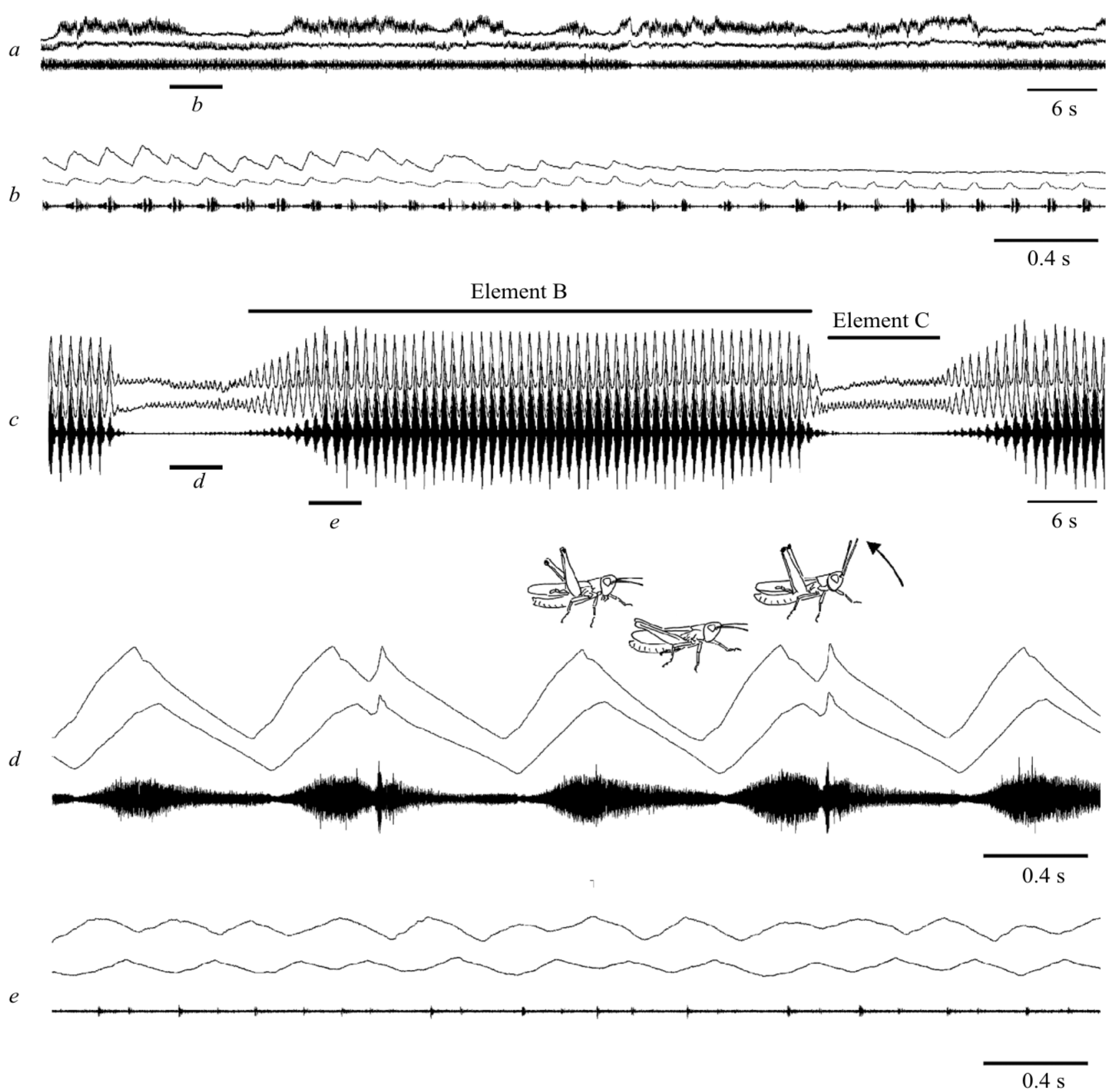

Fig. 3. Oscillograms of courtship songs of *Stenobothrus lineatus* from Saratov. Oscillograms *a* and *b* show element A; oscillograms *c–e* show elements B and C. Fragments of oscillograms *a* and *c* are shown in *b* and *d–e*, respectively, at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. The drawings show the position of the hind legs and antennae at different moments of courtship corresponding to fragment *e*.

(Figs. 4*c*, 4*e*, 4*f*). The movement of the leg in any direction produced a pulse, the intervals between the pulses being easily discernible in the oscillogram. The phrase always ended with element C. The rate of leg vibration often decreased at the end of the phrase; since this decrease was abrupt rather than gradual, element C could be subdivided into elements C1 and C2 (Fig. 4*c*).

The most stable parameters in the courtship song of *M. antennatus* were the periods of syllables in element B and of double pulses in element C (Table 5). Other parameters proved to be much more variable.

Myrmeleotettix maculatus

The courtship song of *M. maculatus* started with alternating syllables resembling those of the calling song

Table 4. Parameters of the courtship song of *Stenobothrus lineatus*

Parameters of the signal	Saratov	Saratov Prov.	Ukraine	Greece
Duration of element B, s	43.3	41.4	34.6	32.5
		33–49.6	17–43.7	25.3–43.8
		0.28	0.21	0.30
Duration of element C, s	15.9	10.2	10.0	
			8.36–11.8	
			0.11	
Number of display movements of the legs and antennae during element B	2.5	2	1.6	2.7
	2–3		0–3	2–3
	0.28		0.56	0.22
Period of syllables in element A, s	0.126	–	–	0.119
	0.089–0.15			0.112–0.132
	0.15			0.05
Period of syllables in element B, s	0.759	0.827	0.751	0.824
	0.733–0.794	0.818–0.841	0.654–0.835	0.8–0.951
	0.02	0.01	0.07	0.03
Period of syllables in element C, s	0.333	0.354	0.394	0.225
	0.256–0.376	0.305–0.395	0.278–0.625	0.132–0.341
	0.13	0.09	0.19	0.33
Period of syllables in the calling song, s	0.793	–	–	0.996
	0.779–0.802			0.978–1
	0.01			0.01

Note: see Table 2.

(Bukhvalova and Vedenina, 1998; Savitsky, 2005; Vedenina and Mugue, 2011). They were referred to as element A. However, unlike those of the calling song, the syllables of element A were low and usually alternated with short single or double pulses (Figs. 5*d*, 5*e*). The next element (B) started abruptly with a powerful stroke of the hind legs and was accompanied by a characteristic swing of the antennae. This was followed by high-amplitude syllables consisting of two parts. At the beginning of the syllable (element B1), the legs worked in phase opposition and vibrated with higher amplitude and rate, whereas in the second part of the syllable (element B2) the rate and amplitude of the leg movements were lower (Figs. 5*f*, 5*h*). As a result, the first part of the syllable was noise-like whereas the second part revealed double pulses in the oscillogram. The envelope of the syllables varied (Figs. 5*f*, 5*h*). These syllables were gradually transformed into syllables of type A. The third element of the courtship song, namely element C, also started abruptly with a characteristic swing of the legs and antennae which was followed by syllables with a lower amplitude and a higher rate, different from those of element B (Fig. 5g). Element C was accompanied by low-amplitude vibrations of the whole body and lateral movements of the head. Then the whole cycle was repeated.

The most stable parameters of the courtship song of *M. maculatus* were the periods of syllables in all the three elements, and also the period of leg movements during element B (Table 6). Their variation was comparable to that of the period of syllables in the calling song. Other parameters of the courtship song were characterized by higher variation.

Stenobothrus nigromaculatus

The courtship song of *S. nigromaculatus* started with alternating elements A and B (Fig. 6). Element A was a sequence of low-amplitude pulses repeated at a rate of 6–8 Hz. Element B resembled the calling song (Vedenina and Bukhvalova, 2001; Vedenina and Mugue, 2011) and consisted of pulses repeated

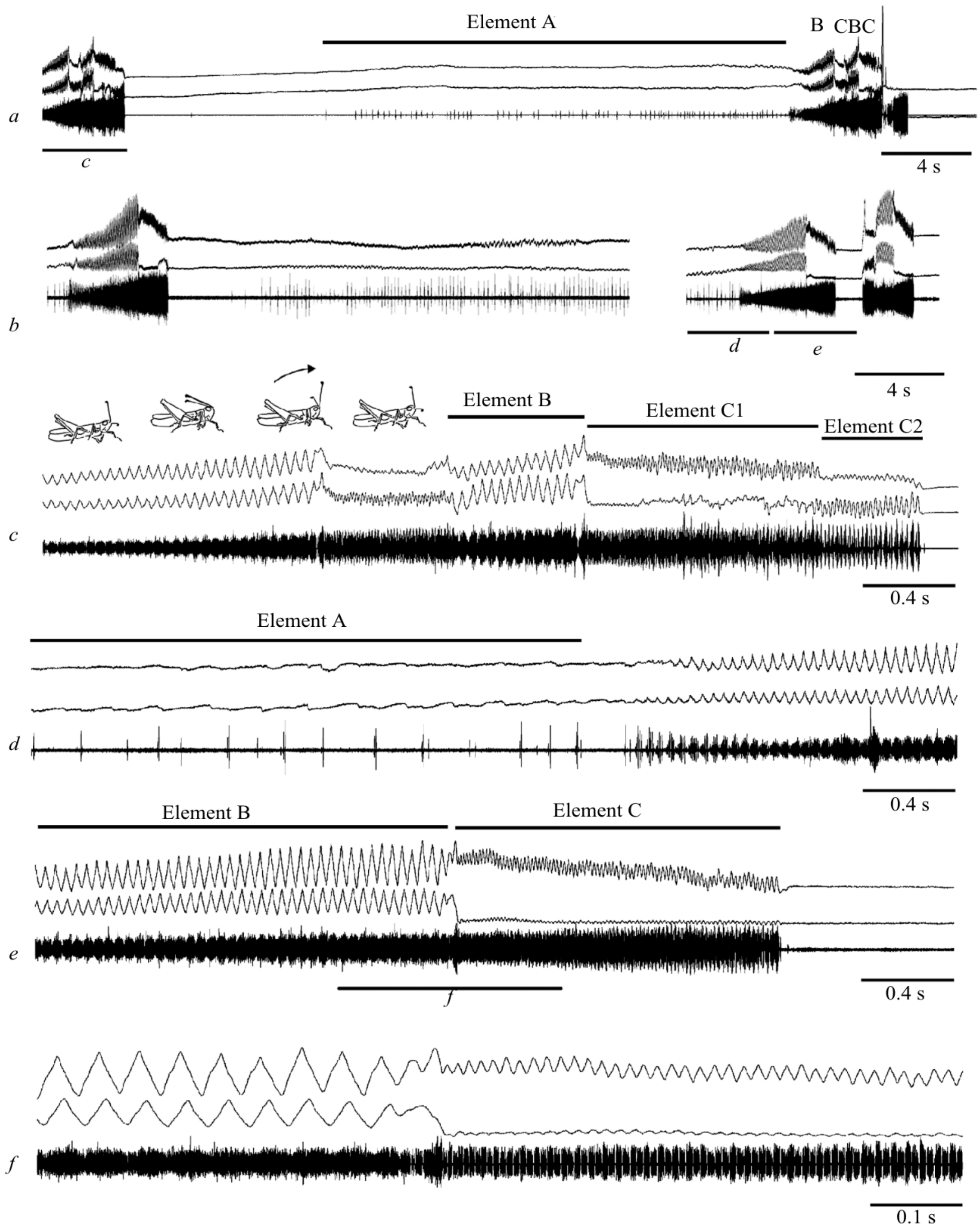

Fig. 4. Oscillograms of courtship songs of *Myrmeleotettix antennatus* from Kherson Province (*a*) and Saratov Province (*b*). Fragments of oscillograms *a* and *b* are shown in *c–f* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. A, B, and C are elements of the signal. The drawings show the position of the hind legs and antennae at different moments of courtship corresponding to fragment *c*.

at a rate of 100–125 Hz and a gradually increasing amplitude (Fig. 6*c*). A series of several alternating elements A and B was followed by the complex element C: the male abruptly moved its hind legs upward and oscillated them quickly in phase opposition; then the legs were moved downward and started vibrating synchronously with a lower rate (Fig. 6*d*). This sequence was followed by an element resembling element B, which was designated as element C1. Then the legs again moved abruptly upward but worked synchronously, without a period of asynchronous oscillation (Fig. 6*e*). As a result, series of more frequent pulses (element C1) alternated with series of less frequent pulses (element C2) 3–8 times, after which elements A and B were again emitted in turn.

The most stable parameters of the courtship song of *S. nigromaculatus* in all the geographic localities were the period of pulses in element B and the periods of syllables and pulses in element C (Table 7). Their variation was comparable to that of the period of pulses in the calling song. The other measured parameters showed a greater degree of variation which also varied between the populations.

Stenobothrus fischeri

The courtship song of *S. fischeri* always started with a sequence of low-amplitude pulses (element A) produced by low-amplitude movements of the legs at a rate of 3.5–11 Hz (Fig. 7). These were followed by the main phrase comprising several elements. Element B resembled the calling song (Savitsky and Pekarev, 2007; Vedenina and Mugue, 2011) and was generated by relatively simple leg movements at a rate of 11–14 Hz. The loudest pulses were produced during a stepwise downward movement of the femora. In the signal of the male from Saratov, the syllable structure in the middle third of this element changed in such a way that the loudest pulses corresponded to the upward movements of the femora (element B2, Fig. 7*g*). It is interesting that the pattern of leg movements recorded by the opto-electronic device did not change. Element B2 was almost completely absent in the signals of males from Greece; two syllables of the B2 type could be discerned at the end of element B in the signals of one male only (Fig. 7*c*). Element C, usually emitted after element B, was generated by high-amplitude leg movements at a rate of 3.8–5 Hz and accompanied by rapid strokes of the tibiae and lateral movements of the body (Figs. 7*c*, 7*f*). The series of distinct pulses were mostly produced by stepwise downward movements of the femora. Element D, immediately following element C, consisted of alternating series of 2–3 pulses and was produced by simple leg movements at a rate of 3–9 Hz. Then element A and the main phrase were repeated. The number of elements in the main phrase varied in different males. For example, element B was absent in the signals of two males from Greece, whereas the male from Saratov almost never produced element D.

Table 5. Parameters of the courtship song of *Myrmeleotettix antennatus*

Parameters of the signal	Ukraine	Russia
Duration of the main phrase, s	4.4	4.9
	1.4–5.5	2.5–6.6
	0.30	0.28
Duration of element B, s	1.3	2.7
	0.4–2.6	0.7–3.8
	0.69	0.49
Duration of element C, s	0.972	1.2
	0.5–2.02	0.6–1.6
	0.41	0.26
Period of pulses in element A, s	0.239	0.171
	0.090–0.771	0.096–0.226
	0.60	0.21
Period of syllables in element B, ms	41	44
	34–46	39–49
	0.05	0.04
Period of double pulses in element C1, ms	14	16
	12–16	14–17
	0.09	0.05
Period of double pulses in element C2, ms	19	20
	14–24	18–21
	0.12	0.07

Note: see Table 2.

The most variable parameters were the duration of elements C and D, and the most stable ones were the periods of syllables in elements B and C (Table 8). The variation of the most stable parameters of the courtship song was comparable to that of the calling song.

DISCUSSION

Comparison of the variability of the temporal parameters of courtship songs of seven species of grasshoppers of the subfamily Gomphocerinae showed that the most stable parameters in all the species studied

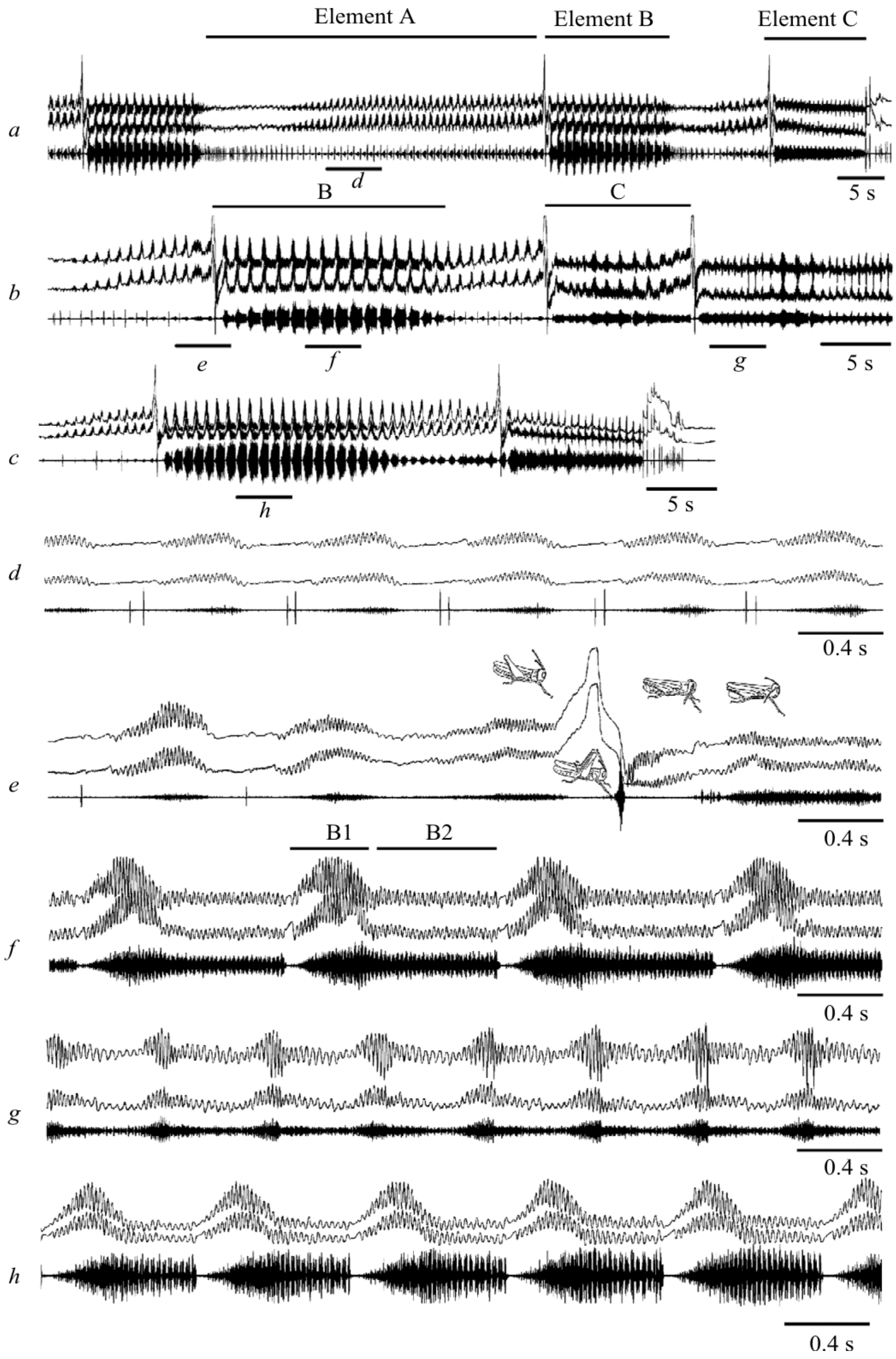

Fig. 5. Oscillograms of courtship songs of *Myrmeleotettix maculatus* from Cherkassy Province (*a*), Nikolayev Province (*b*), and Kostroma Province (*c*). Fragments of oscillograms *a–c* are shown in *d–h* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. A, B, and C are elements of the signal. The drawings show the position of the hind legs and antennae at different moments of courtship corresponding to fragment *e*.

were syllable and pulse periods. The pattern of leg movements during a syllable was also relatively stable even though the syllable envelope revealed a certain degree of variation. Such parameters as the number of syllables in a phrase, the duration and period of a phrase, and the duration and number of different elements were highly variable. The periods of visual signals (display movements) also varied but the patterns of the signals themselves proved to be quite stereotypic. A certain similarity can be observed between the courtship and calling songs. In the calling song, the period of syllables is also one of the most stable parameters which can be regarded as a species-specific character (Bukhvalova and Zhantiev, 1993; Bukhvalova, 2006; Tishechkin and Bukhvalova, 2009). As mentioned above, individuals of different sex may meet by chance under the conditions of a high population density, and the male may start to court without producing the calling song. Thus, the female sometimes has to recognize the conspecific male not before but already in the process of courtship. Therefore, the similarity of stable parameters in the different types of signals of the same species appears to be quite logical.

Our analysis showed that the elements of the song accompanied by display movements of the legs, antennae, head, etc. were the most variable. For example, element B was present in the signals of some males of *Ch. biguttulus* but absent in the signals of others (Fig. 1). This element was accompanied by raising of the hind legs, which likely provided an additional visual cue for the female. The period and number of high-amplitude leg strokes during generation of short pulses in *G. rufus* varied greatly even within one signal (Fig. 2). The duration of element C in *S. fischeri*, during which the male turned from side to side and swung its tibiae, was also highly variable, and the element itself was generated irregularly (Fig. 7*b*). The variability of these parameters indicates that they may be used for evaluation of the individual qualities of the male. According to one of the sexual selection theories, namely the “good genes” theory (Hamilton and Zuk, 1982; Zahavi, 1987), a certain character may be attractive because it serves as an indicator of a fit male with good genes. For example, the song with a greater duration or intensity of one of the elements as compared to average appears to be more attractive for the females. One of the possible explanations of this phenomenon is that such a signal has greater metabolic costs and therefore demonstrates a high “quality” of the male emitting it (Stupmner and Helversen, 1994; Gerhardt and Huber, 2002). The song accompanied by display movements of different body parts, such as antennae or legs, will be also more “expensive” in terms of energy and may therefore serve as an indicator of a strong and healthy mate (Vedenina and Helversen, 2003, 2009).

Table 6. Parameters of the courtship song of *Myrmeleotettix maculatus*

Parameters of the signal	Nikolayev Prov.	Cherkassy Prov.	Kostroma
Number of syllables in element A	28.5 10–47 0.92	29.7 23–38 0.26	30.1 10–55 0.57
Period of movements of the legs and antennae, s	23.6	25.9 24.5–27.3 0.08	19.8 14.5–30 0.31
Number of syllables in element B	14 12.0–16.0 0.20	14.8 14–15 0.03	20.4 18–25 0.12
Duration of element C, s	–	10.1	9.2 6.8–12.02 0.18
Period of syllables in element A, s	0.772 0.668–0.862 0.08	0.756 0.721–0.781 0.02	0.581 0.480–0.652 0.06
Period of syllables in element B, s	1.02 0.867–1.077 0.07	0.877 0.825–0.972 0.04	0.764 0.661–0.798 0.04
Period of syllables in element C, s	0.492 0.46–0.537 0.06	0.476 0.456–0.50 0.03	0.430 0.379–0.498 0.07
Period of leg movements during element B1, ms	16 15–17 0.04	16 15–17 0.05	18 15–21 0.08
Period of leg movements during element B2, ms	20 19–21 0.03	23 21–26 0.05	24 21–29 0.09
Period of syllables in the calling song, ms	781 643–859 0.06	–	609 563–642 0.03

Note: see Table 2.

It is essential that the period of high-amplitude syllables and pulses was found to be stable not only in the element of the courtship song resembling the calling song, but also in other elements characteristic only of the courtship song. Therefore, analysis of the courtship songs can be used for taxonomic purposes. Such analysis is necessary when dealing with some species groups with similar calling songs, for example, *S. rubicundus*, *S. eurasius* or *Ch. albomarginatus* (Elsner and Wasser, 1995; Berger, 2008; Vedenina

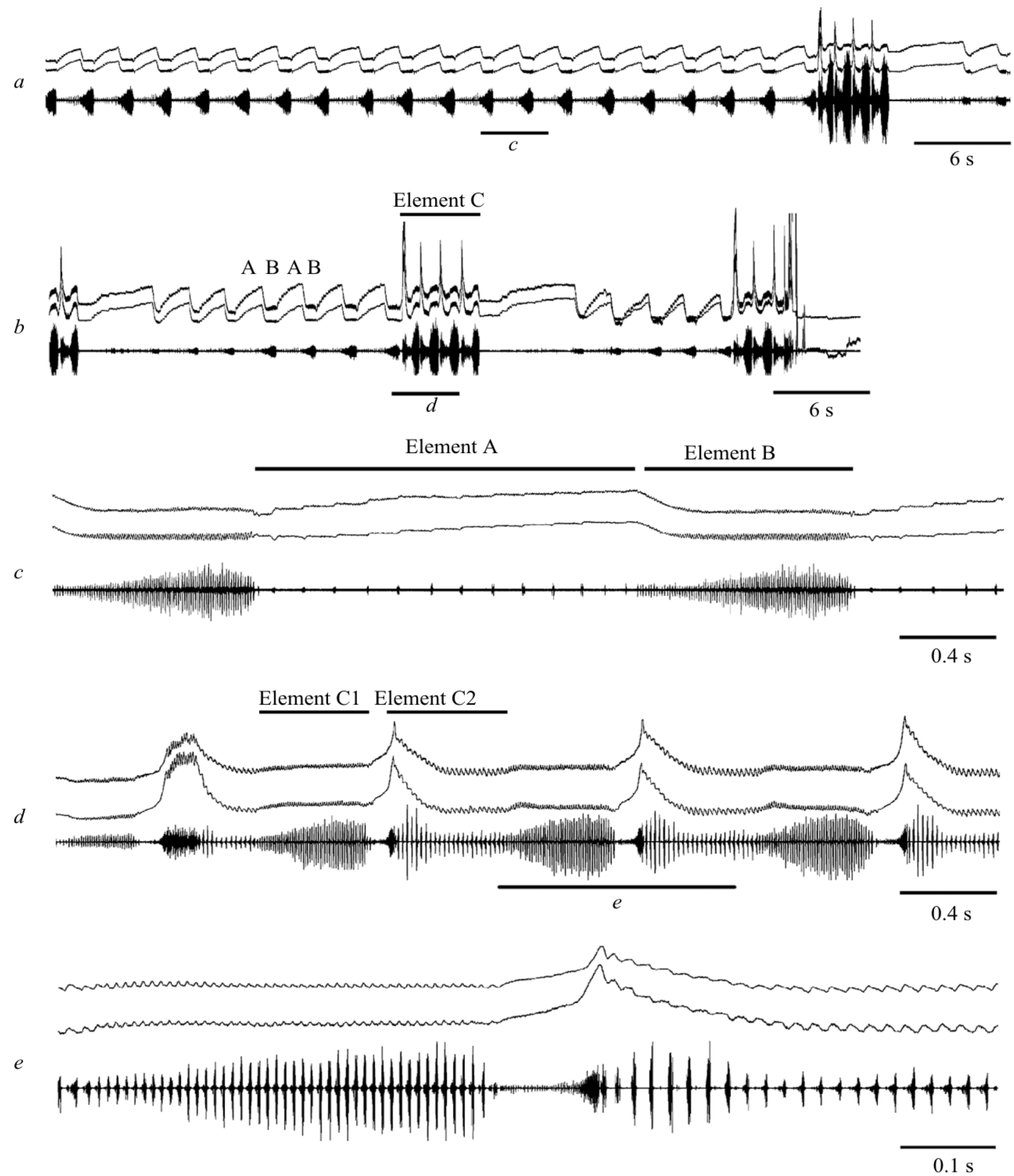

Fig. 6. Oscillograms of courtship songs of *Stenobothrus nigromaculatus* from Nikolayev Province. Fragments of oscillograms *a* and *b* are shown in *c–e* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. A, B, and C are elements of the signal.

and Helversen, 2009). Moreover, since the courtship song is more strongly affected by sexual selection than the calling song (Vedenina, 2005), the process of speciation may start with divergence in the courtship songs. We may therefore assume that interpopulation differences should be more pronounced in the courtship songs than in the calling ones, but this assumption remains to be tested in the future research.

Table 7. Parameters of the courtship song of *Stenobothrus nigromaculatus*

Parameters of the signal	Vinnitsa Prov.	Nikolayev Prov.	Saratov	Orenburg Prov.
Period of pulses in element A, s	–	0.119	0.154	–
		0.095–0.184	0.123–0.263	
		0.14	0.21	
Period of element B, s	2.95	2.41	2.09	2.39
	2.3–3.68	1.44–6.87	1.19–3.14	1.95–2.90
	0.13	0.34	0.24	0.09
Duration of element B, s	1.095	0.823	0.696	0.993
	0.851–1.513	0.501–1.043	0.387–1.21	0.78–1.17
	0.20	0.14	0.27	0.12
Number of syllables in element C, s	8.33	4.25	5.88	3.5
	6.0–13.0	3.0–5.0	4.0–8.0	3.0–4.0
	0.48	0.17	0.18	0.16
Period of syllables in element C, s	1.17	1.15	1.02	1.33
	1.048–1.35	1.022–1.333	0.848–1.178	1.24–1.43
	0.07	0.07	0.08	0.05
Period of pulses in element B, ms	10	8	9	10
	8.0–12.0	8.0–9.0	8.0–10.0	9.0–12.0
	0.13	0.06	0.06	0.10
Period of pulses in element C1, ms	10	9	9	11
	9.0–11.0	8.0–10.0	8.0–10.0	8.0–13.0
	0.06	0.02	0.05	0.11
Period of pulses in element C2, ms	20	17	19	24
	17–21	16–19	16–21	18–27
	0.06	0.04	0.06	0.07
Period of pulses in calling song, ms	–	–	9	–
			8.0–10.0	
			0.05	

Note: see Table 2.

One should also emphasize the significance of technical parameters of the acoustic equipment for adequate analysis of the courtship songs. Even though the spectra of the grasshopper songs generally have broadband frequency ranges, these ranges extend considerably into the ultrasonic part of the spectrum (Vedenina and Zhantiev, 1990; Meyer and Elsner, 1996) which cannot be recorded by common equipment. Moreover, different elements of the courtship song may have their maxima in different frequency ranges (Vedenina et al., 2007; Ostrowski et al., 2009). The amplitude ratio of different elements of the signal may be distorted if the upper boundary of the recorded frequency range does not exceed 12.5 kHz (as in older models of portable recorders and common microphones) or even 22 kHz (as in newer models). For example, if the maximum energy of a certain element lies at 25–30 kHz (Meyer and Elsner, 1996; Vedenina et al., 2007; Ostrowski et al., 2009), the amplitude of that element in the oscillogram will be relatively small. Comparison of our recordings of the courtship song of *M. antennatus* (Fig. 4) and similar recordings published by Savitsky (2005) reveals differences in the relative amplitude of elements B and C. In the recordings of V.Yu. Savitsky, the amplitude of element C is almost 3 times as great as that of element B, whereas in our material the two values are comparable. This fact clearly indicates that the upper fre-

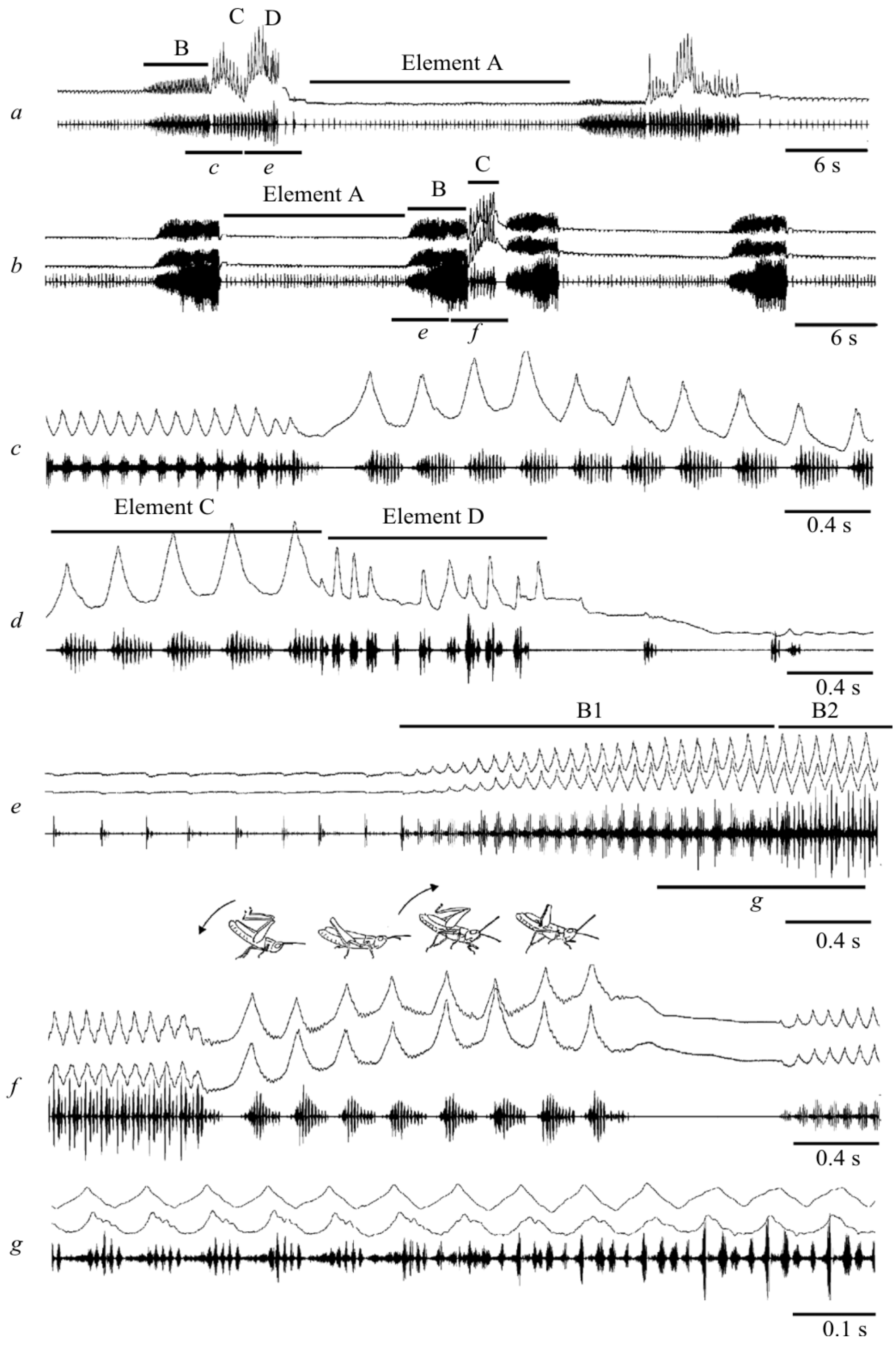

Fig. 7. Oscillograms of courtship songs of *Stenobothrus fischeri* from Greece (*a*) and Saratov (*b*). Fragments of oscillograms *a* and *b* are shown in *c*–*g* at a higher speed. Trajectories of movements of the hind legs are shown above each oscillogram on the same time scale. The drawings show the position of the hind legs at different moments of courtship corresponding to fragment *f*.

quency boundary of the equipment used by V.Yu. Savitsky was too low.

Our study has revealed an interesting trend which may be characteristic not only of grasshoppers of the subfamily Gomphocerinae but also of other orthopterans. The parameters corresponding to the lowest levels of the rhythmic pattern of the signal are usually the most stable. On the contrary, the parameters corre-

Table 8. Parameters of the courtship song of *Stenobothrus fischeri*

Parameters of the signal	Russia	Greece, biotope 1	Greece, biotope 2	Greece, biotope 3
Repetition period of the phrase, s	18.1	23.8	33.1	38.8
	14.7–28.6	21.6–26.2		34.1–43.5
	0.21	0.06		0.17
Duration of element B1, s	1.7			5.1
	0.98–2.2			4.7–5.4
	0.13			0.05
Duration of element B2, s	2.5			0.2
	0.97–3.5			
	0.31			
Duration of element C, s	3.3	4.6	2.3	3.98
	1.95–5.2	2.7–5.7	1.5–3.2	2.3–6.8
	0.51	0.20	0.33	0.37
Duration of element D, s	0.2	1.7	1.7	1.6
		0.87–2.6	1.3–2.1	1.02–2.6
		0.50	0.33	0.35
Period of pulses in element A, s	0.257	0.285	0.300	0.328
	0.223–0.326	0.162–0.479	0.261–0.334	0.271–0.382
	0.09	0.28	0.08	0.09
Period of syllables in element B1, ms	71	–	–	86
	62–82			81–98
	0.07			0.06
Period of syllables in element B2, ms	74	–	–	–
	69–81			
	0.05			
Period of syllables in element C, s	0.223	0.189	0.202	0.261
	0.182–0.269	0.163–0.224	0.187–0.212	0.220–0.307
	0.09	0.08	0.04	0.10
Period of syllables in element D, ms	–	72	58	102
		58–112	46–68	69–193
		0.18	0.11	0.35
Period of syllables in the calling song, ms	72	–	88	–
	66–76		82–98	
	0.03		0.04	

Note: see Table 2.

sponding to the higher rhythmic levels show a higher level of variation. In our opinion, this fact may have a physiological explanation. The species-specific stridulatory pattern is generated by interneurons of the third thoracic ganglion which, in their turn, are controlled by command neurons in the brain (Ronacher, 1989; Hedwig, 1992, 1994). Each type of command neurons triggers the generation of only one type of stridulatory pattern (Hedwig and Heinrich, 1997). Experiments with pharmacological stimulation of the brain command neurons in several grasshopper species showed that even in acute experiments the patterns produced in the nervous system were very stable and almost identical to those of the intact insects. At the same time, the duration of phrases and the number of elements in the signal varied greatly depending on the site and level of stimulation (Vedenina et al., 2001; Heinrich et al., 2001, 2012). It was also shown that "decisions" on the timing, type, and intensity of stridulation were made in a specific area of the brain, the central complex, which also received multimodal sensory information from the various sense organs. Besides, it was demonstrated that the activity of the command neurons may be modulated by neurons of the corpora allata via their terminals ending in the central brain areas (Heinrich et al., 2012). Thus, the higher rhythmic levels of the signal are regulated by a complex neural network localized in different ganglia of the central nervous system and may be modulated depending on the activation of different sensory inputs and the hormonal status of the insect, whereas the pattern of an individual syllable is almost completely determined by the activity of several neurons in one thoracic ganglion. The simplest pacemakers are known to be highly reliable and stable. Considering the structural similarity of the nervous system in different representatives of Orthoptera, we may assume that the same trend exists in representatives of Ensifera.

It should be noted that many elements of the courtship behavior of the studied species are similar, even though the species belong to different genera and even different tribes. Synchronous and asynchronous movements of the legs alternate in all the courtship songs despite the great diversity of the stridulatory patterns. On the one hand, such alternation can often be observed in the calling songs as well, resulting in alternation of acoustic patterns with different pulse repetition rates. On the other hand, these movements may serve as the additional visual signals for the female. If the male's legs move in antiphase, the visible rate of their movements is doubled. Swings of antennae can be observed in *S. lineatus*, *M. maculatus*, *M. antennatus* (tribe Stenobothrini), and *G. rufus* (tribe Gomphocerini). Abrupt high-amplitude upward movements of the legs can be observed in *M. maculatus*, *S. fischeri*, *S. nigromaculatus*, and *G. rufus*. Males of *M. maculatus* and *G. rufus* move their heads from side to side in a highly specific manner at certain moments of courtship. These data indicate that different elements of the courtship behavior evolved independently and convergently in the course of evolution (Vedenina and Mugue, 2011).

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