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A description of the song of *Isophya modesta modesta* (Frivaldszky 1867) with notes on its relationship to *I. modesta rossica* Bey-Bienko, 1954

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Abstract

Acoustic signals used during the pair-forming behavior of *Isophya modesta modesta* are described for the first time. Specimens from Hungary, Rumania and the Ukraine have been studied. The male calling song of *I. m. modesta* is composed of single syllables. Each syllable consists of a shorter main impulse-series (120 to 240 ms) and a longer terminal impulse-series (200 to 2500 ms), separated from each other by a silent interval of 4 to 9 s. Uniquely in *I. m. modesta*, females can produce 2 response songs during 1 syllable of the male: after the male's main impulse-series, and most frequently, after the terminal impulse-series. Playback experiments revealed that the second female response song is related to the end of the male's terminal impulse-series. *I. m. modesta* and *I. m. rossica* were formerly regarded as two different species only subtle morphological differences being known between the 2 taxa. But as the male calling songs are apparently identical, and with the present state of our knowledge, it is reasonable to treat "*I. rossica*" as a subspecies of *I. modesta*. The only remarkable difference in the pair-forming acoustic communication of the 2 subspecies is the different timing of female response song, indicating that the 2 taxa have diverged from each other to a certain degree.

Keywords:

Orthoptera, acoustic signals, male-female duet, oscillogram, taxonomy

Introduction

Sound production is widespread among orthopteran insects and is often the most conspicuous element of their behavior. Generally its main function is to transmit information between males and females during their pair-forming behavior. Typically males stridulate spontaneously and females decide which male to approach or respond to on the basis of their songs. Male song may convey several kinds of information to the females, such as species identity (e.g., Perdeck 1985, Bailey & Robinson 1971, Eiriksson 1993, Doblér *et al.* 1994, Tauber & Pener 2000), body size (Latimer 1981a, Simmons 1988, Brown *et al.* 1996), age (Stiedl *et al.* 1981, Ritchie *et al.* 1995), condition (Wagner & Hoback 1999, Scheuber *et al.* 2003) and location (e.g., Bailey & Thomson 1977). Acoustic signals are also used during competitive male-male interactions (Latimer & Scharal 1986, Greenfield & Minckey 1993). Furthermore, some studies reported interspecific acoustic competition between sympatric bush-cricket species (Latimer 1981b, Greenfield 1988). A number of predator and some parasitoid species are known to trace their orthopteran prey or host on the basis of its song (Walker 1964, Walker & Wineriter 1991, Zuk *et al.* 1995, Bailey & Haythornthwaite 1998, Lehmann & Heller 1998). From these examples it can be

seen that the acoustic communication of Orthoptera is not only a conspicuous phenomenon, but also a very important element of the behavior of these insects, and thus our knowledge of their songs constitutes a fundamental part of their natural history.

Isophya is the second most species-rich genus of Tettigonioidae in Europe (after the closely related genus *Poecilimon*, which is the most species rich; for details see Heller *et al.* 1998). All of them are slowly moving brachypterous insects with rather similar morphology (Harz 1969, Naskrecki 2003). The high degree of morphological uniformity often makes their taxonomy problematic and the identification of specimens is generally difficult. To solve these problems is not only a matter of descriptive zoology, but it is practically important, either because many of them have been recorded as agricultural pests (see Heller *et al.* 1998), or because recently several species have become rare and locally endangered (e.g., Nagy 1981, Varga *et al.* 1990).

Similarly to other phaneropterid genera, in *Isophya* pair-formation is usually achieved by acoustic duetting between males and females (Zhantiev & Dubrovin 1977, Heller & Helversen 1986, Heller 1990, Orci *et al.* 2001). In contrast to morphology, the amplitude modulation of male calling songs and the timing of female response are rather diverse and strictly species-specific in this genus. The male calling songs have been described in the majority of the European species (Heller 1988) and in several cases the female response was also studied, but there are still some species for which we know nothing about their acoustic communication. One of those species has been *Isophya modesta* (Frivaldszky 1867).

The type locality of the nominotypical subspecies of this species is in western Rumania (Mehadia) (Frivaldszky 1867). The range of this subspecies extends from the northeast part of the Balkan Peninsula across Transylvania and Dobruza until at least the Podolian tableland (Harz 1969). The western and northernmost border of its distribution is constituted as small, isolated Hungarian populations (Nagy 1981, Nagy & Rácz 1996). Our knowledge of the eastern limit of its range is rather uncertain because morphologically it is very similar to *Isophya modesta rossica* Bey-Bienko 1954, a subspecies described from the surroundings of Kupjansk (situated at the southern feet of the middle-Russian tableland, eastern Ukraine) which has been regarded as a different species up to now (Bei-Bienko 1954). The species' similarity was recognized by Harz (1969) and Kis (1960) and mentioned as a problem which needs further investigation. We think that our descriptive study of the song of *I. m. modesta* offers new results clarifying the relationship of the 2 taxa.

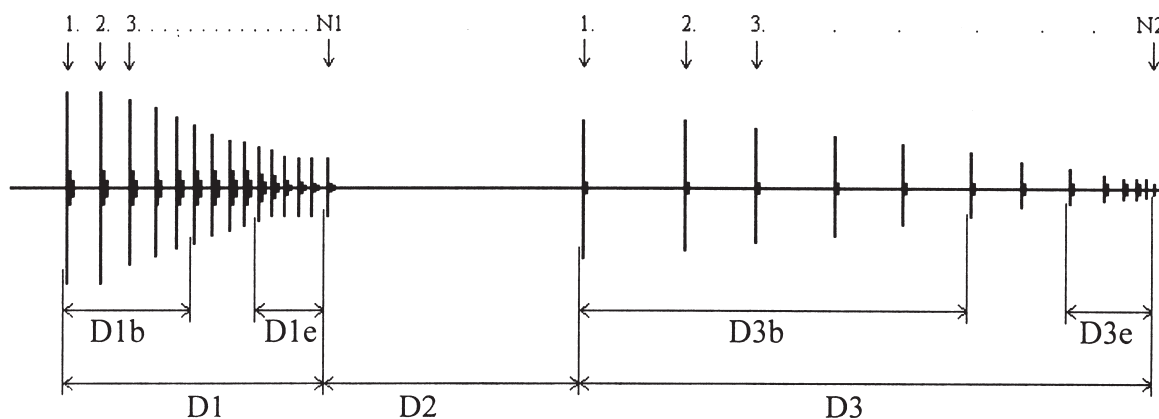


Fig. 1. Schematic drawing showing oscillographic pattern of a syllable of the male calling song of *I. modesta* and measurements of the song characteristics examined in this study.

Materials

We have analyzed the calling songs of 15 males and the response songs of 3 females of *I. m. modesta*. The examined specimens were collected from the following regions of Hungary and Rumania: 7 males and 3 females from the Mecsek Mountains [southern western Hungary; lat 46°03'N, long 18°16'E], 2 males from the Mátra Mountains [northern eastern Hungary; lat 47°56'N, long 19°53'E], 6 males from the Central Transylvanian Mountain Range [W Rumania; lat 46°29'N, long 23°34'E]. Songs of 8 males from the Ukraine (Kanev Forest Reserve, near Kiev; lat 49°44'N, long 31°30'E) were also examined. (The subspecific identity of the Ukrainian males is uncertain because we could not examine the female response song in that population, but on the basis of the shape of their cerci they belong to *I. m. modesta*.)

Methods

Sound recording and playback.—Sound recordings were made using a Sony TCD-D8 DAT recorder connected to a Monacor ECM 920 condenser microphone or a Pettersson D240X ultrasound detector (using its time expansion function [$\times 10$], frequency range 10 to 120 kHz, sampling rate 307 kilosamples/s [kss]) and a Racal Store 4D instrumentation tape recorder with microphones Brüel & Kjaer 4133 and 4135, as well as a SONY WM3 cassette recorder with a Uher microphone (M 645). Recordings were transferred to a PC equipped with a Sek`d Sienna sound card. Sound analyses were carried out using the software Cool Edit Pro. Wing movements were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988). Air temperature varied between 18.5 and 27 °C during the recordings (see Table 1 and the captions of Table 2, 3).

To elicit the response song of females and to study its timing we played back original and manipulated male calling songs from the above-mentioned PC through an ALTEC LANSING ACS22 speaker. The original syllable from which the playback signals were made was recorded by the Sony TCD-D8 DAT recorder and therefore contained the frequency components of the song only below 24 kHz. Females were placed on a bunch of plants positioned at a distance of 80 to 100 cm from the speaker. One original and 5 manipulated syllable types were played back in random order. The original syllable contained a terminal impulse-series of a duration of 1384 ms (type1). The manipulated syllables were made from that original one by cutting off or duplicating some impulses in the middle part of the terminal impulse-series, thus lengthening [1666 ms (type2), 1951 ms (type3), 2614 ms (type4)] or shortening [600 ms (type5)] the terminal impulse series, but leaving unaltered all the other properties of the syllable. Furthermore we created a syllable type [type6] in which the final part of the terminal impulse series was deleted; this type therefore was short and its impulse repetition slow at the end of the terminal impulse-series (in comparison to the typically high impulse-repetition rate observable at the end of the terminal-impulse series [Fig. 2]).

Song terminology.—Song terminology follows Ragge & Reynolds (1998). We used the following set of terms for description of the song:

Calling song: spontaneous song produced by an isolated male.

Syllable: the song produced by one opening-closing movement cycle of the tegmina.

Hemisyllable: the song produced during the opening movement (opening hemisyllable) or during the closing movement (closing hemisyllable) of the tegmina.

Table 1. Data for the circumstances of the recordings from which the oscillograms in Fig. 2 have been made. (Abbreviations: KGH – Klaus-Gerhard Heller, BN – Barnabás Nagy, KMO – Kirill Mark Orci, GSZ – Gergely Szövényi).

Specimen collected from	Collected by	Recorded by	Date recorded	Air temperature	oscillogram
Torockó Mountain Range (Rumania)	BN	KMO	9 VII 2000	23.7 °C	Fig. 2/A
Mátra Mountains (Hungary)	BN	KMO	2 VII 2000	25.2 °C	Fig. 2/B
Mecsek Mountains (Hungary)	GSZ&OKM	KMO	28 VI 2000	22.9 °C	Fig. 2/C
Kanev Forest Reserve (Ukraine)	KGH	KGH	18-23 VI 1996	25 °C	Fig. 2/D
Kanev Forest Reserve (Ukraine)	KGH	KGH	18-23 VI 1996	24 °C	Fig. 2/E

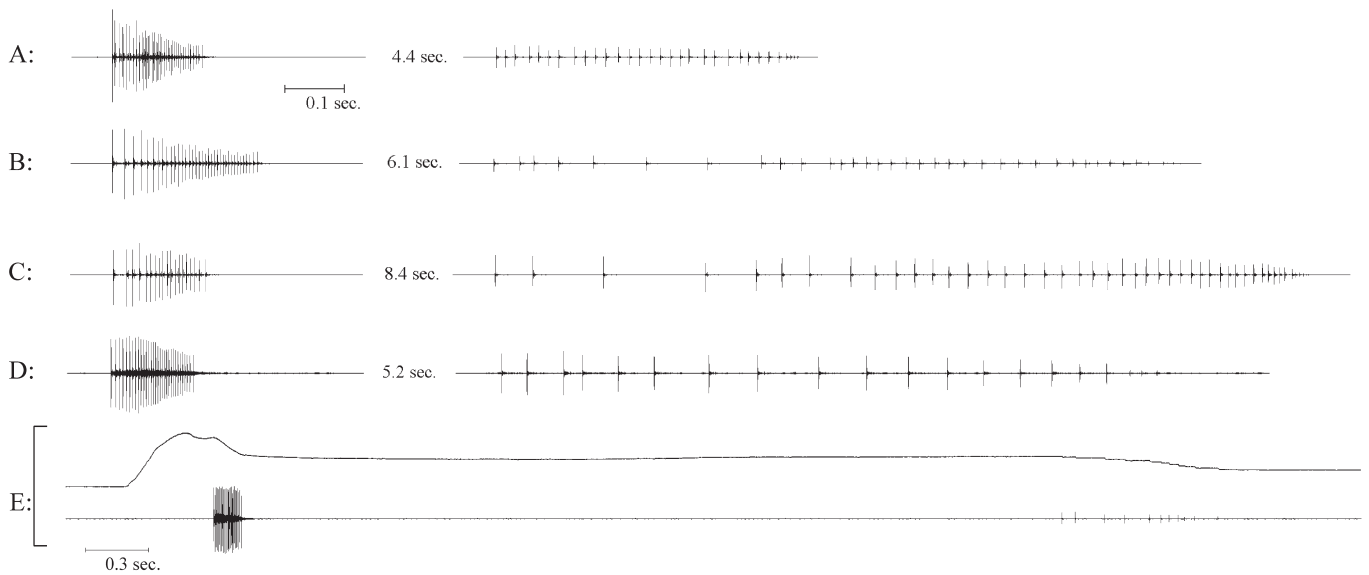


Fig. 2. Oscillograms of male calling song of *Isophya m. modesta*: A, B, C, D, one-trace oscillograms of main and terminal impulse series of single syllables (time scale as shown in A is the same in B, C, D; for data on the recordings and specimens see Table 1); E, two-traced oscillogram of a syllable, note the different time scale (upper line: tegmen movement, lower line: sound waveform).

Impulse: a simple undivided transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file).

Click: an isolated distinct impulse.

Song characters.—The songs of orthopteran insects are generally amplitude-modulated signals. Most bushcricket and grasshopper species produce wide-band carrier waves, thus spectral properties of the song are less species-specific than rhythmic characters, and do not change significantly within one syllable. Therefore we concentrated mainly on examining and describing the rhythmic features of the song of *I. m. modesta*. The following characters were measured (Fig. 1): duration of the main impulse series (D1), the time elapsed during the production of the first 5 and last 5 impulses of the main impulse-series (D1b and D1e, respectively), number of impulses in the main impulse series (N1), duration of the interval between the main and terminal impulse series (D2), duration of the terminal impulse series (D3), the time elapsed during production of the first 5 and last 5 impulses of the terminal impulse series (D3b and D3e, respectively), number of impulses in the terminal impulse series (N2), and the length of the delay of female response (RD).

Results

Songs from the Carpathian Basin (Hungary, Rumania [Transylvania]).—The male calling song of *I. m. modesta* is composed of single syllables, which are repeated rather slowly (2 to 3 syllables per min [this and all the following data were measured between 19 to 27 °C]). Each syllable consists of a shorter main impulse series (120 to 240 ms) and a longer terminal impulse series (200 to 2500 ms), which are separated from each other by a silent interval of 4 to 9 s (Figs 2/A-C). The peak amplitude of the impulses generally decreases during both series. In the main impulse series the number of impulses varied between 20 and 50, and the impulse repetition rate was high and nearly constant or increasing (D1b/D1e varied between 1.4 and 2.3, $n=15$). The terminal impulse-series contained 10 to 50 impulses. At the beginning of that series impulse repeti-

tion is generally so slow that each impulse can be heard as distinct clicks (5 to 50 impulses/sec, $\bar{x} = 13.9$ impulses/sec), but gradually impulse repetition rate increases and amplitude decreases so that the end of the series sounds as a quiet purr (28 to 240 impulses/sec, $\bar{x} = 68.5$ impulses/sec).

We found significant negative correlation between the number of impulses in the main (N1) and terminal impulse series (N2): $r = -0.7443$, $p = 0.001$, $n = 15$ (Pearson product-moment correlation). The duration of the main (D1) and terminal (D3) impulse series as well as that of the interval between them (D2) showed significant correlation with the ambient air temperature (Fig. 3), and can be characterized by the following regression equations: $D1 = -12.02 * T + 466.60$, $r = -0.843$, $p < 0.000$, $n = 15$; $D2 = -498.2 * T + 18695$, $r = -0.773$, $p = 0.001$, $n = 15$; $D3 = -174.9 * T + 5075.8$, $r = -0.7843$, $p = 0.001$, $n = 15$, (T is the ambient air temperature in °C). Descriptive statistics of the measured rhythmic song characters can be seen in Table 2.

Most intensive frequency components of the carrier wave are between 10 to 40 kHz with 2 intensity-peaks (a more intense about 13 to 21 kHz and a less intense between 27 to 35 kHz) in the main impulse series and generally 1 intensity peak (between 12 to 19 kHz) in the terminal impulse series (Fig. 4/A, B) (sometimes a second intensity peak around 30 to 35 kHz is also observable in the terminal impulse series).

Wings are moved so slowly during the production of syllables that the main elements of their movement can be observed by the unaided human eye. Immediately before the beginning of the syllable the wings are opened silently and then the main impulse series is produced during the partial closing movement of the wings. After that, wings are held halfway between their most opened and totally closed position, producing no sound (interseries interval). Then the closing movement continues, producing the terminal impulse series until the wings reach their closed resting position. This kind of movement pattern can be seen in the case of a specimen collected from the Ukraine (Fig. 2E).

Responsive females communicate with males by emitting short response songs in reply to the male calling song (Fig. 5). During

Table 2. Descriptive statistics for examined characters (see Fig. 1 for abbreviations) of male calling song of *I. m. modesta*; specimens from Transylvania (W Rumania) and Hungary (durations given in ms; recordings made at 19 to 27 °C).

Character	abbrev.	n	\bar{x}	Min.	Max.	$s_{\bar{x}}$
Duration of main impulse series	D1	15	181.1	128.4	239	41.67
Duration of first 5 impulse periods in main impulse series	D1b	15	46.2	25.2	79	16.38
Duration of last 5 impulse periods in main impulse series	D1e	15	26.2	16	45	8.95
Number of impulses in main impulse series	N1	15	35.3	21.6	45.6	7.80
Duration of interval between main and terminal impulse series	D2	15	6860.7	3739.4	10969.25	1882.76
Duration of terminal impulse series	D3	15	920.9	216.4	2187.4	651.54
Duration of first 5 impulse periods in terminal impulse series	D3b	15	359.0	102.4	974	278.93
Duration of last 5 impulse periods in terminal impulse series	D3e	15	73.0	20.8	179.2	37.42
Number of impulses in terminal impulse series	N2	15	25.8	11.6	44	10.84

Table 3. Descriptive statistics for examined characters (see Fig. 1 for abbreviations) of male calling song of *I. modesta*; specimens from the Ukraine (durations given in ms; recordings made at 18.5 to 25 °C).

Character	abbrev.	n	Mean	Min.	Max.	Std.Dev.
Duration of main impulse series	D1	8	157.2	92	266	67.14
Duration of first 5 impulse-periods in main impulse series	D1b	8	46.3	21	77	24.92
Duration of last 5 impulse periods in main impulse series	D1e	8	38.9	25	74.8	17.32
Number of impulses in main impulse series	N1	8	22.3	16	29.3	5.70
Duration of interval between main and terminal impulse series	D2	8	5669.4	4150	9483.2	2224.84
Duration of terminal impulse series	D3	8	1025.8	431.7	2306.75	655.57
Duration of first 5 impulse periods in terminal impulse series	D3b	8	514.7	237	730.8	180.91
Duration of last 5 impulse periods in terminal impulse series	D3e	8	206.2	85.8	390.3	120.78
Number of impulses in terminal impulse series	N2	8	16.8	7.7	33	10.35

that acoustic duetting, both males and females try to approach each other. The female response song is a short impulse series composed of a few impulses (number of impulses varied 1 to 14) with variable impulse repetition pattern. Generally the impulse series begins with 1 or 2 loud impulses which is/are followed by a group of some quiet impulses. The duration of the whole response song varied 1 to 120 ms. Sometimes the first response song was followed by a second one after an interval of 300 to 500 ms (this can be seen after the main impulse series of the male in Fig. 5A, and after the terminal pulse series of the male in Fig. 5D). This second response song consisted of 2 or 3 loud impulses.

Generally females emit their response after the terminal impulse-series of the male song. In the examined 3 females the response delay varied between 102 and 215 ms ($\bar{x} = 163$). But sometimes they responded after the main impulse series (in this case with a longer response delay of 463 to 708 ms [$\bar{x} = 578$]) or after both impulse series of the male (Fig. 5A). During the playback trials the length of female response delay was rather similar in the case of the male song types 1, 2, 3, and 4 (Fig. 5B-E), suggesting that females use the end of the terminal impulse series of the male song to time their response. However an increased response delay was observable when females responded to the song types 5 and 6 (Figs 5F,G).

The song of some Ukrainian specimens.—In the Ukrainian specimens the rhythmic pattern of the male calling songs was principally the same as that of the Hungarian and Transylvanian *I. m. modesta* males: they produced single syllables composed of a main impulse-series (90 to 270 ms) and a terminal impulse series (430 to 2300

ms), separated by a silent interval of 4 to 8 s (Fig. 2D,E). All the examined characters overlapped widely regarding the 2 populations (compare Tables 2, 3). However, the number of impulses in the main impulse series and the number of impulses in the whole syllable were significantly higher in the specimens from the Carpathian Basin than in the Ukrainian ones (t-tests for independent samples, $p < 0.001$ in both cases). The temperature dependence of D1, D2 and D3 can be described as $D1 = -14.07 * T + 463.28$, $r = -0.8309$, $p = 0.011$; $D2 = -474.5 * T + 15989$, $r = -0.8454$, $p = 0.008$; $D3 = -152.1 * T + 4334.8$, $r = -0.92$, $p = 0.001$ (symbols are the same as described above). These regression equations are quite similar to those obtained for the Hungarian-Transylvanian males (Fig. 3). Spectral properties of the song are very similar to those of the Hungarian and Transylvanian males (see Fig. 4C, D).

Stridulatory files.—In the examined Hungarian and Transylvanian males the length of stridulatory file varied between 3.1 and 3.65 mm ($\bar{x} = 3.39$, $n = 11$), and contained 124 to 143 stridulatory pegs ($\bar{x} = 134$, $n = 11$). The size of stridulatory pegs increased while their density decreased gradually towards the proximal end of the file (Figs 6A, B). We could examine the stridulatory file of only one Ukrainian male: it was 3.2 mm long and contained 127 pegs. The arrangement pattern of the stridulatory pegs was similar to that described above for the Hungarian-Transylvanian males (Fig. 6C).

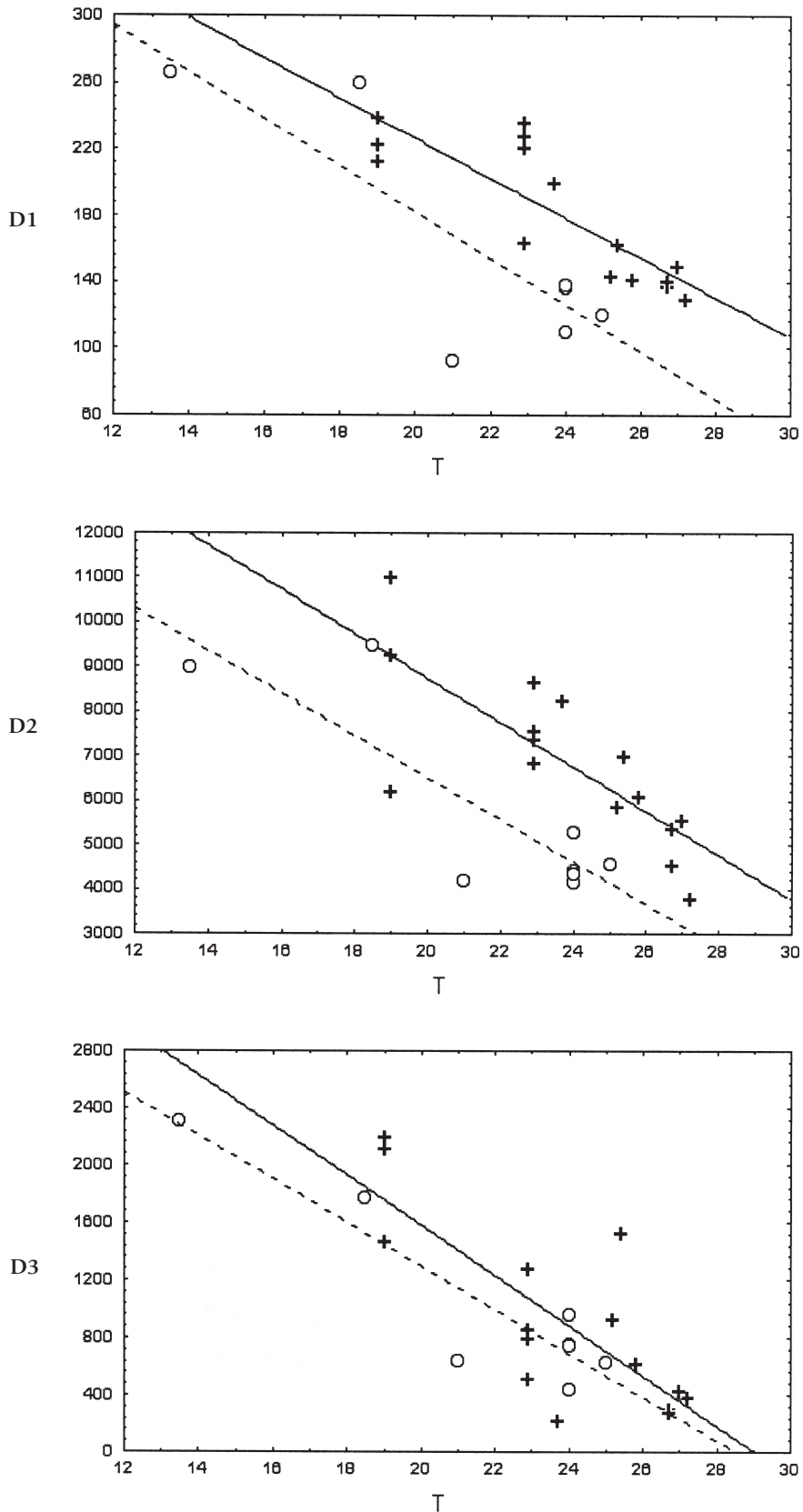


Fig. 3. Temperature dependence of D1, duration of main impulse series; of D2, duration of interval between main and terminal impulse series; of D3, duration of the terminal impulse series. For regression equations and correlation coefficients see text.

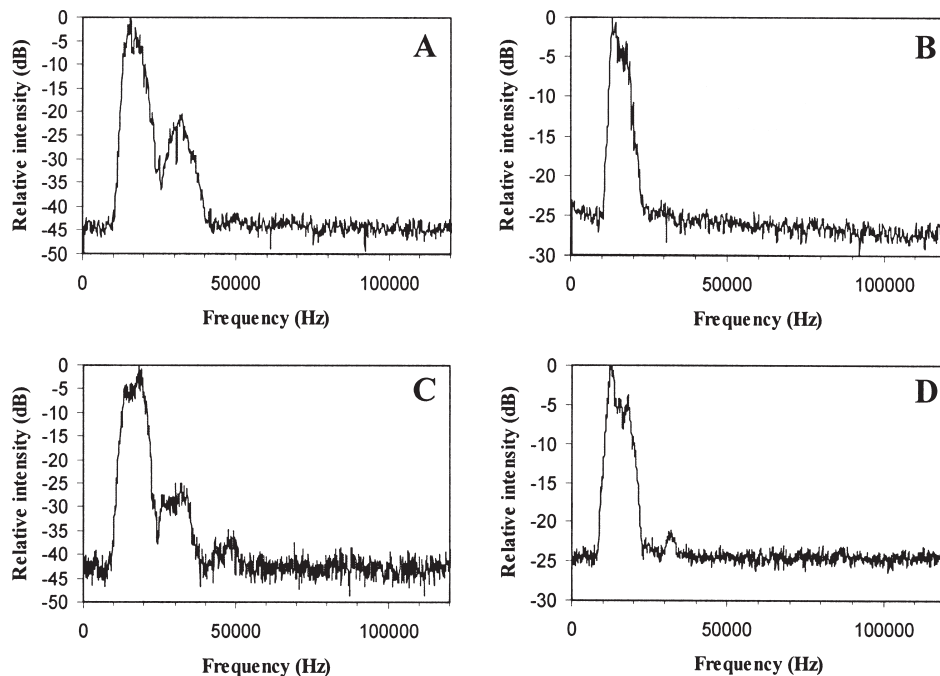


Fig. 4. Power spectra of male calling song of *I. modesta* (FFT size 4096; window function: Blackmann-Harris). A, spectrum of a main impulse series (a male from SW Hungary); B, spectrum of a terminal impulse series (same specimen as in A); C, spectrum of a main impulse series (a male from the Ukraine); D, spectrum of a terminal impulse series (same specimen as in C).

Discussion

Regarding its basic structure – a main impulse series and a terminal impulse series separated from each other by a silent interval – the male calling song of *I. m. modesta* is similar to that of *I. m. rossica*, *I. brunneri* Retowski 1888, *I. speciosa* Frivaldszky 1867, *I. amplipennis* Brunner v. Wattenwyl 1878 and *I. costata* Brunner v. Wattenwyl 1878 (Heller 1988). However in the last 4 species the silent interval between the two impulse series is much shorter (around 2 s or less) than in *I. m. modesta* and *I. m. rossica* (4 to 7 s). Moreover in *I. brunneri* the terminal impulse series is very short, containing only a few impulses; in *I. speciosa* and *I. amplipennis* the terminal impulse series is rather dense and divided into 2 parts, contrary to the long and continuous terminal impulse series of *I. m. modesta* and *I. m. rossica*; in *I. costata* the terminal impulse series follows very quickly the main impulse series, so that the silent interval is reduced to only 150 to 400 ms and impulse repetition fluctuates containing impulse groups of 1 to 5 impulses. The only taxon for which the male calling song seems to be very similar to that of *I. m. modesta* is *I. m. rossica*. Regarding *I. m. rossica* we refer to the oscillogram published by Zhantiev & Dubrovin (1977) showing the calling song of a male collected near the type locality of the subspecies.

The female response song of *I. m. modesta* showed a rather variable impulse-repetition pattern, but its timing – in relation to the male song – is strictly defined and specific, just as in the other phaneropterid species where males and females find each other by acoustic duetting (Robinson 1980, Heller & Helversen 1986, Dobler *et al.* 1994). Uniquely in *I. m. modesta*, females can produce 2 response songs during one syllable of the male: after the male's main impulse series and after the terminal impulse series. Presently

it seems that the only important difference between the acoustic communication of *I. m. modesta* and *I. m. rossica* is the timing of the female response: in *I. m. rossica* it is emitted during the initial part of the terminal impulse series (after the first few impulses of that series) (Zhantiev & Korsunovskaya 1986). In *I. m. modesta* our results suggest that the female response after the terminal impulse series is related to the end of the male's terminal impulse series. This finding coincides with Zhantiev & Korsunovskaya's (1986) results on *I. taurica* Brunner v. Wattenwyl 1878 and *I. stepposa* Bey-Bienko, 1954. They found that the female response is related to the end of the male's main impulse-series (which is called an impulse in their terminology), in contrast to *Leptophyes albovittata* (Kollar 1833), where it is related to the beginning of the male syllable. Generally the female response is related to a conspicuous element of the male song, but in *I. m. modesta* the terminal impulse-series shows a gradual decrescendo, without any conspicuous element at its end. Moreover our results show, that the final, high impulse-density part of the terminal impulse-series is not even necessary to elicit female response (Fig. 5G). So presently it is not clear what kind of mechanism(s) help(s) females to recognize the end of the male song in their "noisy" natural environment.

Our results on the acoustic signals of *I. m. modesta* show – in accordance with the morphological similarity – that this taxon and *I. m. rossica* are very closely related to each other. At the same time subtle morphological differences and the different timing of the female response indicate that the two taxa have diverged from each other to a certain degree. Intraspecific morphological variability is rather high in some of the species of this genus (see *I. modestior* Brunner v. Wattenwyl 1882 or *I. kraussii* Brunner v. Wattenwyl 1878

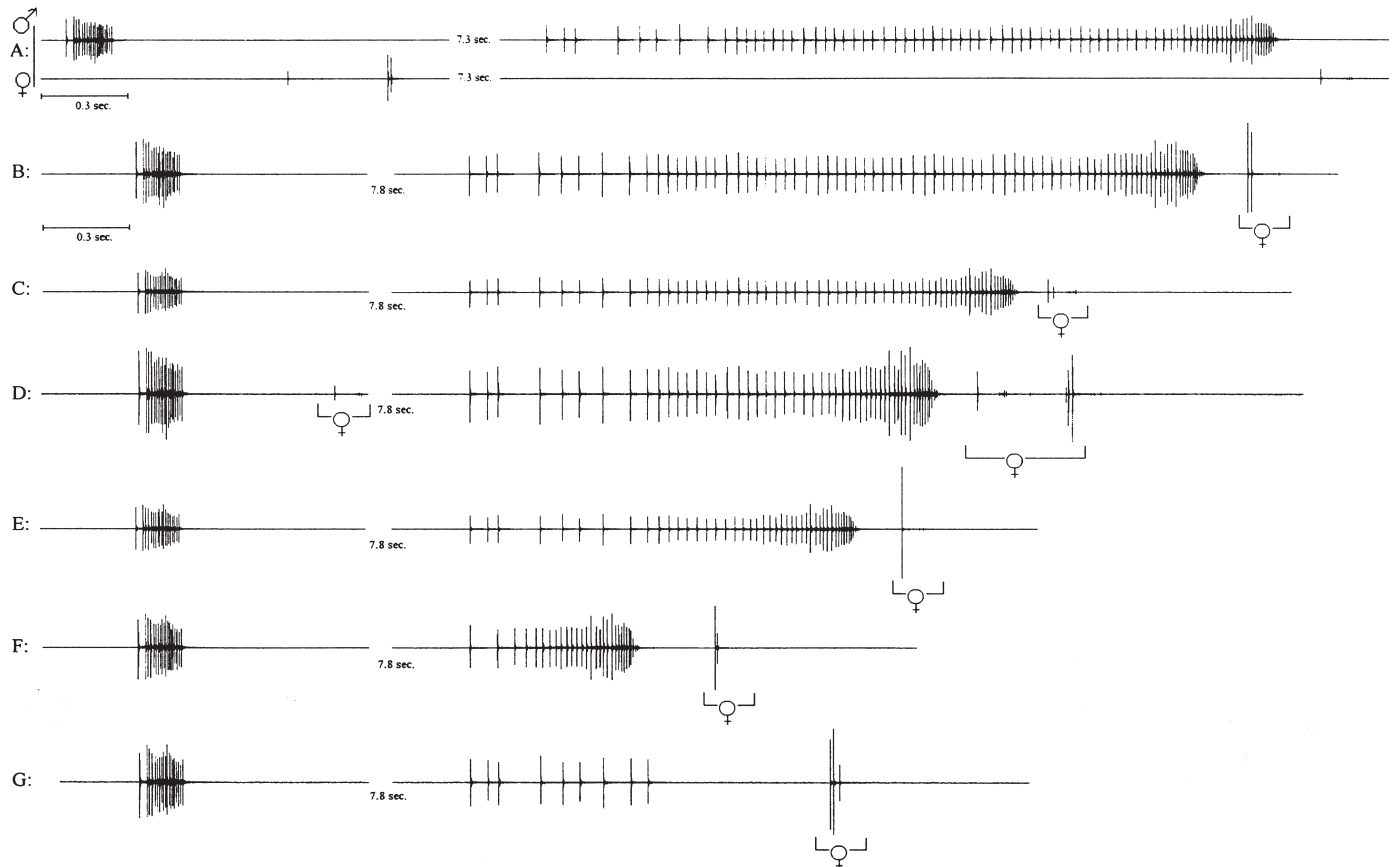


Fig. 5. Oscillograms showing male-female duet of *Isophya m. modesta*: A, a two-traced oscillogram; B, C, D, E, F, G, one-traced oscillograms showing female response songs given in reply to playback of manipulated male songs: type I (B), type II (C), type III (D), type IV (E), type V (F), type VI (G).

in Heller *et al.* 2004), and it is unlikely that the difference in the timing of female response could maintain reproductive isolation, because not only the males but also the females, actively approach the opposite sex by phonotaxis in both taxa. Therefore the presently known differences between *I. m. modesta* and *I. m. rossica* are not enough for us to believe that they belong to different evolutionary lineages, separated by inherent reproductive isolation. So we think it is most reasonable to treat "*Isophya rossica*" (a taxon formerly regarded as specifically distinct) as a subspecies of *I. modesta*.

Our study characterizes the oscillographic pattern of the acoustic signals of *I. m. modesta* and presents basic data on rhythmic parameters, but this is only the first step toward the understanding of the function and information content of those signals. We do not know which parameters play a key role in the species recognition and mate choice of the females and males in this species. What is the function of the 2 main elements of the male's syllable? Why does the female response delay differ in the case of main impulse series and terminal impulse series? We think that the difference in the timing of the female response is not enough to maintain reproductive isolation between the 2 subspecies; however a certain degree of assortative mating may result from this if the males have definite preferences against the timing of the female response. An experimental study to examine that question would be interesting, especially because in Orthoptera we do not know of any study on the geographic variability of female sexual signals and the possible role of that variability in speciation.

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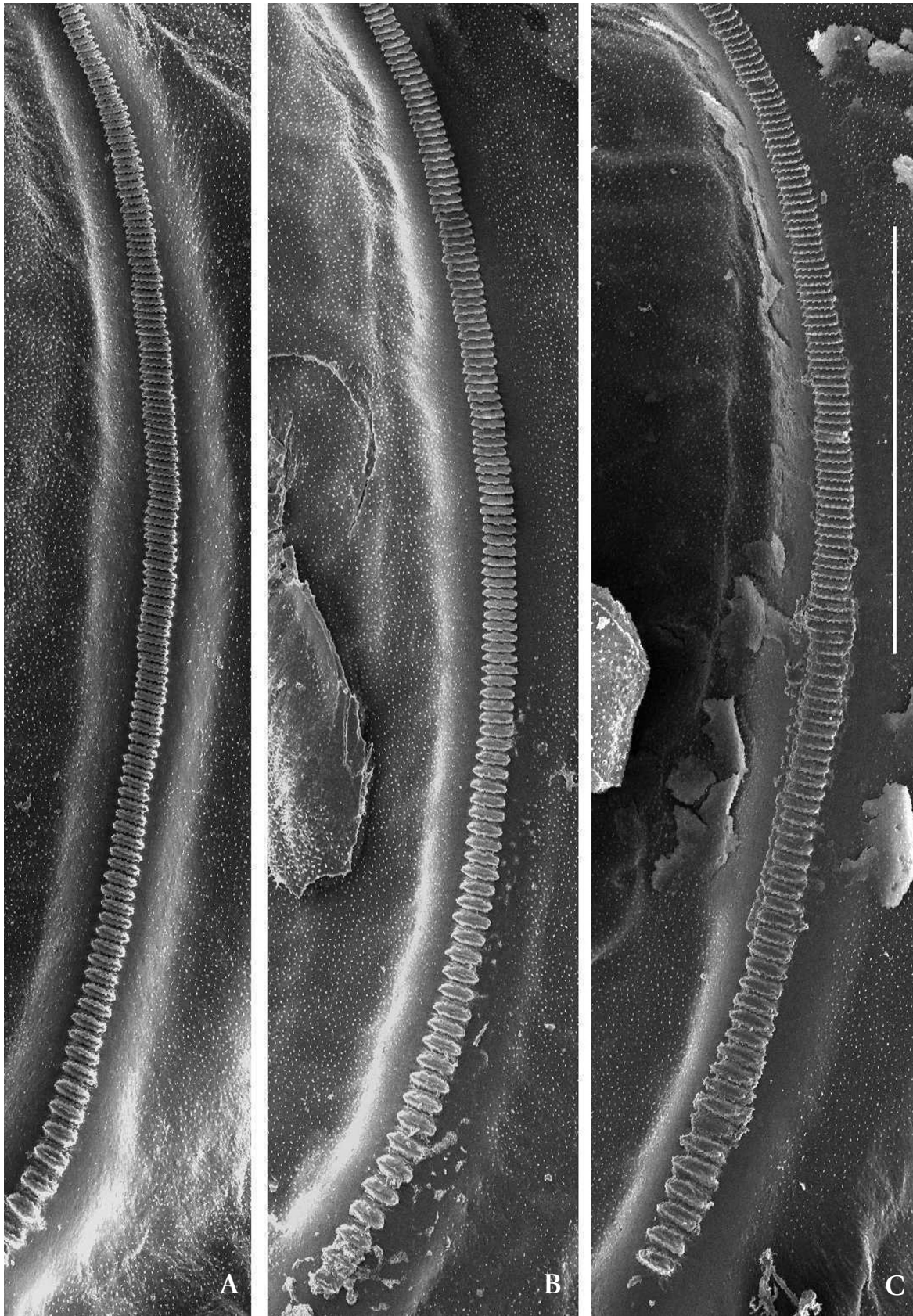


Fig. 6. Stridulatory files of *Isophya m. modesta*: A, specimen from SW Hungary (Mecsek Mountains); B, specimen from W Rumania (Trockó Mountains); C, specimen from the Ukraine (Kanev Forest Reserve, near Kiev). Scale bar 1 mm, the same for all photos.

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