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Sounds of two species of band-winged grasshoppers (Orthoptera: Acrididae: Oedipodinae) from southern Kazakhstan

Сигналы двух видов саранчовых подсемейства Oedipodinae (Orthoptera: Acrididae) из южного Казахстана

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КЛЮЧЕВЫЕ СЛОВА: *Helioscirtus moseri*, *Sphingonotus savignyi*, призывный сигнал, демонстрационный полёт, тональный сигнал.

ABSTRACT. Songs of *Sphingonotus savignyi* and *Helioscirtus moseri* from southern Kazakhstan are described and illustrated by oscillograms and sonograms. In both species, calling song consists of sounds produced by wings during flight display and syllables produced by stridulation immediately after landing. In addition, the male *S. savignyi*, when on the ground, both alone and in the presence of a female, produces a song of different type using stridulation. *S. savignyi* songs include noise and pure-tone syllables; the latter have a regular sine carrier, which is visible on oscillograms at high speed. In one of the studied localities in southern Kazakhstan, *S. savignyi*, *H. moseri*, and *S. obscuratus latissimus* were strictly sympatric. Still, wing crepitation in these species differ either in the syllable repetition period or in the general scheme of the temporal pattern (prolonged single echeme or the sequence of short echemes). Apparently, such differences ensure reliable segregation of acoustic communication channels in these species.

РЕЗЮМЕ. Приведены иллюстрированные осциллограммами и сонограммами описания сигналов *Sphingonotus savignyi* и *Helioscirtus moseri* из Южного Казахстана. У обоих видов призывный сигнал состоит из звуков, издаваемых крыльями во время демонстрационного полёта, и пульсов, продуцируемых при помощи стридуляции сразу после приземления. Кроме того, самец *S. savignyi*, находясь на земле, как в одиночестве, так и в присутствии самки издаёт сигнал другого типа с помощью стридуляции. Сигналы *S. savignyi* включают шумовые и тональные компоненты; последние имеют правильное синусоидальное заполнение, что хорошо видно на осциллограммах при высокой скорости развёртки. В одном из исследованных местонахождений в Южном Казахстане *S. savignyi*, *H. moseri* и *S. obscuratus latissimus* были строго симпатричны. Однако крыловые сигналы этих видов различается либо периодом повторения пульсов, либо общей схемой временного рисунка (продолжительная одиночная серия или последовательность коротких серий). По-видимому, такие различия обеспечивают надёжное разделение каналов акустической коммуникации у этих видов.

Introduction

Most species of band-winged grasshoppers (Orthoptera: Acrididae: Oedipodinae) have bright and contrasting coloration of the hind wings and/or hind legs and may appear to use primarily visual cues during competitive and mating interactions. However, stridulatory sound apparatuses of different types were described in many species of this subfamily, and their structure is used as a taxonomic character [Shumakov, 1963; Benediktov, 2009]. Also, a significant number of Oedipodinae species have some of the longitudinal veins of the hind wings thickened [Bey-Bienko, Mishchenko, 1951], which may indicate that such species produce sounds using their wings during so-called flight displays. Finally, even in taxonomic and faunistic works there are indications that a number of Oedipodinae produce sounds during flight [Bey-Bienko, Mishchenko, 1951; Shumakov, 1963]. All this suggests that members of this subfamily widely use acoustic communication in intraspecific interactions.

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Investigation of the acoustic communication of North American Oedipodinae started in the second half of the 20th century (e.g., Wiley, Wiley [1969]). In the comprehensive work of Otte [1970], sounds and mating behavior of more than 70 of ca 200 species of North American Oedipodinae were described and illustrated by dynamic spectrograms (sonograms). Flight displays were detected in 38 species studied, stridulation during courtship behavior occurs in 59 species. On the other hand, stridulation in stationary solitary males, which is so characteristic of the Gomphocerinae (Orthoptera: Acrididae), was observed in only two species of Oedipodinae.

The Palearctic Oedipodinae are no less diverse; in particular, Bey-Bienko & Mishchenko [1951] list about 120 species for the fauna of Russia, Transcaucasia, Kazakhstan, Turkmenistan, Uzbekistan, Kyrgyzstan, Tajikistan, and adjacent territories. However, information on the sounds and mating behavior of the Palearctic Oedipodinae is much more scarce. Brief descriptions of the flight display sounds of four species of Oedipodinae from Xinjiang Uygur Autonomous Region, China illustrated by oscillograms were published by Xi *et al*. [1992]. Oscillograms of signals (=songs) of the widespread European species, *Psophus stridulus* (Linnaeus, 1758) were presented in Ragge and Reynolds [1998]. Sounds and flight displays of five species of Bryodemini (Orthoptera: Acrididae: Oedipodinae) from Eastern Kazakhstan and Southern Siberia were described by Russian authors [Benediktov, 1998; Savitsky, Lekarev, 2007; Tishechkin, 2010].

In some species, the calling song includes sounds produced by different mechanisms. Singing male of *Hyalorrhipis clausi* (Kittary, 1849) periodically jumps a few centimeters and produces crepitation sounds by wings. Then it begins to alternate syllables produced by wings with syllables produced by stridulation while sitting on the ground [Savitsky, Lekarev, 2007]. Recently, similar mechanism of sound production was described in *Sphingonotus obscuratus latissimus* (Uvarov, 1925). The main part of its signal is produced by wings during flight display, but immediately after landing the male produces several syllables by stridulatory movements of hind legs [Tishechkin, 2022].

Also, many species of Oedipodinae, while sitting on the ground, produce signals by means of tegmino-femoral stridulation and some other mechanisms. However, these signals apparently represent an additional cues and are used only at short distances after visual contact has been established between individuals [García *et al*., 1997, 2001; Husemann, Hochkirch, 2007; Larrosa *et al*., 2007, 2010; Savitsky, Lekarev, 2007; Benediktov, 2009, 2015, 2018]. Only in *Stethophyma grossa* (Linnaeus, 1758) single male produces calling signals for attracting conspecific female; thus, communication system in this species is the same as in Gomphocerinae (Orthoptera: Acrididae) [Ragge, Reynolds, 1998; Savitsky, Lekarev, 2007].

In the present paper, descriptions of sounds of *Sphingonotus savignyi* Saussure, 1884 and *Helioscirtus moseri* Saussure, 1884 (Orthoptera: Acrididae: Oedipodinae) from Southern Kazakhstan, illustrated by oscillograms and sonograms are given. Since the signals of both species are rather peculiar, these data expand our understanding of the acoustic communication of band-winged grasshoppers.

Material and methods

Grasshopper sounds were recorded from freely-moving insects under field conditions by means of Roland R-05 wave/mp3 recorder at the sampling frequency 96 kHz. Oscillograms and sonograms of signals were produced with Cool Edit Pro 2.1 software.

Song terminology is accepted after Ragge and Reynolds [1998]. A **syllable** is a sound produced by one complete up- and downstroke of the hind leg. In this paper, we also use this term for a short discrete sound produced by wings during flight. An **echeme** is a first-order assemblage of syllables. An **echeme-sequence** is a first-order assemblage of echemes. **Repetition period** is a time span from the beginning of one song element (an echeme or a syllable) to the beginning of the next similar element.

Generic attribution of *S. savignyi* is accepted after Cigliano *et al*. [2024].

Specimens studied are deposited in the collection of the Zoological Museum of M.V. Lomonosov Moscow State University.

Results

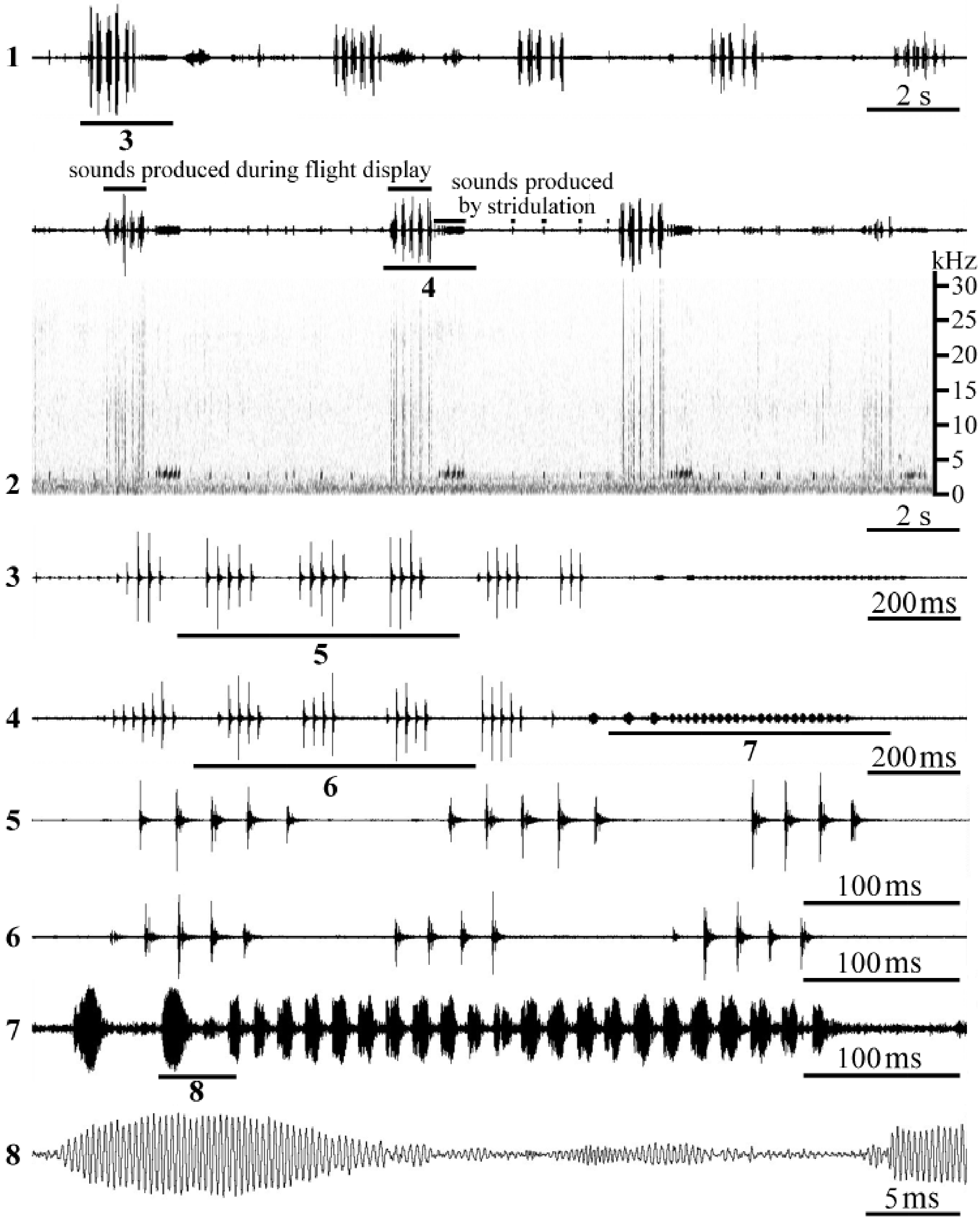
Sphingonotus savignyi Saussure, 1884
Figs 1–15, 22.

MATERIAL. 1. Southern Kazakhstan, ca 30 km north of Almaty, environs of Kara-Oy village, pebble shore of the Kaskelen River, 43.5381° N, 76.8678° E, 22.VI.2024, signals of five males were recorded at 30–35 °C.

2. Southern Kazakhstan, the rocky desert in the Charyn River Valley, ca 20 km north of Chundzha (=Shinzha), 43.7153° N, 79.4175° E, 24.VI.2024, signals of three males were recorded at 40–42 °C.

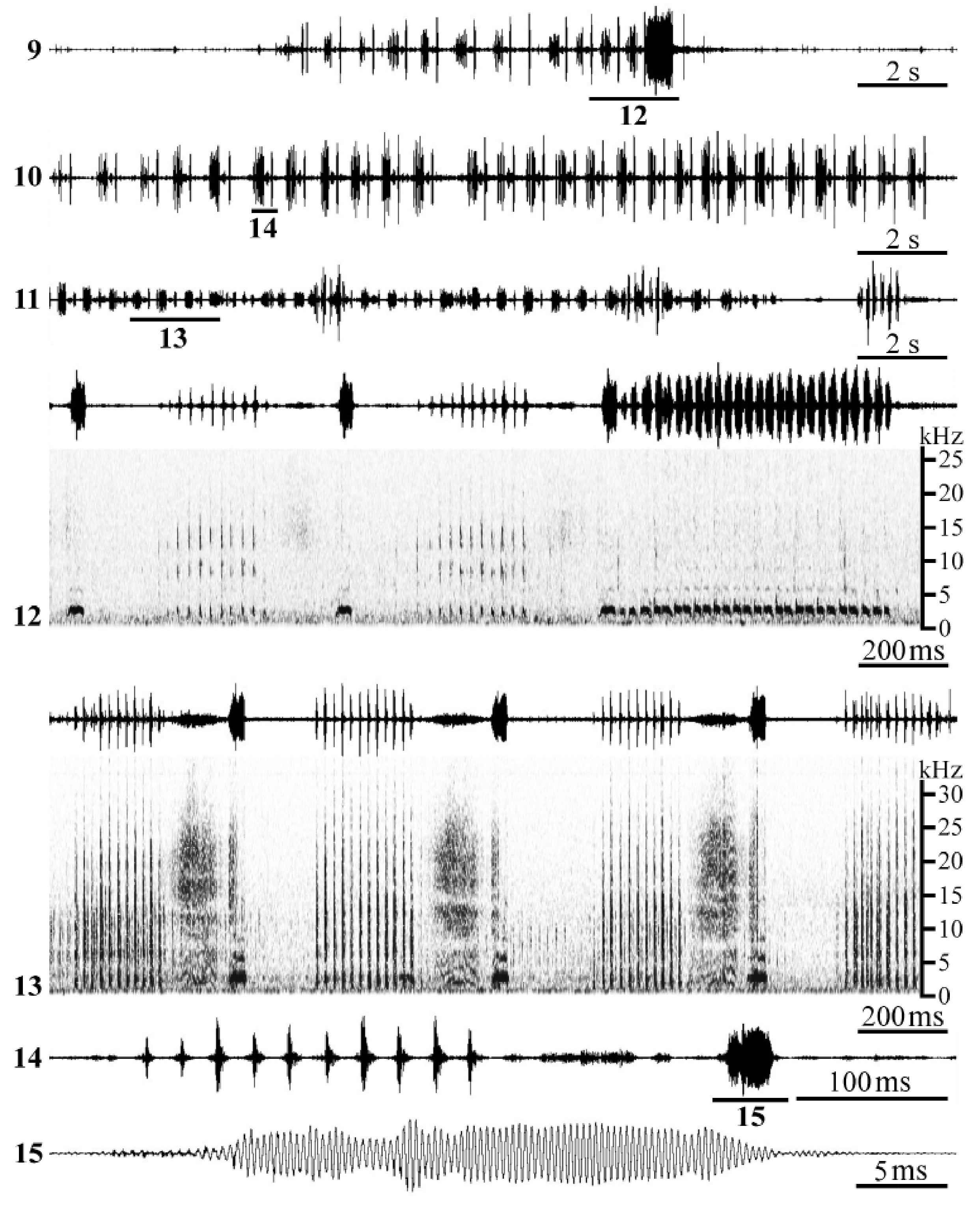
SONGS. Songs of two types were recorded in males of *S. savignyi*.

The song of the first type is an echeme-sequence produced during a flight display and followed by a sequence of syllables produced by stridulatory movements of hind legs immediately after landing (Figs 1–8). The flight display lasts for about 1.0–1.5 s at a height of about 30–40 cm; during the flight the male produces 5–6 echemes including 3–8 (typically, 4–6) syllables each (Figs 1–4). Syllable repetition period averages 19–22 ms, echeme repetition period varies from 150–180 up to 200–300 ms in males from both localities in spite of the air temperature differences during recordings (Figs 5–6). Immediately after landing, the male usually, but not always, produces several pure-tone syllables with a carrier frequency of about 2.7–3.1 kHz; on the oscillograms at high speed it is visible that these syllables have a regular sine carrier (Figs 7–8). To the human ear, this part of the song sounds like bird whistles or cricket pure-tone songs. Typically, the male produces 1–3 syllables separated by gaps of 50–100 ms and followed by an echeme lasting for 350–500 ms and having a syllable repetition period 19–22 ms at 30–35 °C and 15–17 ms at 40–42 °C (Figs 3–4, 7). After that he produces single syllables separated by gaps from



Figs 1–8. *Sphingonotus savignyi*, the male song of the first type. 1, 3–8 — oscillograms; 2 — oscillogram and sonogram at the same speed. Faster oscillograms of the parts of signals indicated as “3–8” are given under the same numbers.

Рис. 1–8. *Sphingonotus savignyi*, сигнал первого типа. 1, 3–8 — осциллограммы; 2 — осциллограмма и сонограмма при одной скорости развёртки. Фрагменты сигналов, помеченные цифрами “3–8”, представлены на осциллограммах под соответствующими номерами.



Figs 9–15. *Sphingonotus savignyi*, the male song of the second type. 9–11, 14–15 — oscillograms; 12–13 — oscillograms and sonograms at the same speed. Faster oscillograms and sonograms of the parts of signals indicated as “12–15” are given under the same numbers.

Рис. 9–15. *Sphingonotus savignyi*, сигнал второго типа. 9–11, 14–15 — осциллограммы; 12–13 — осциллограммы и сонограммы при одной скорости развёртки. Фрагменты сигналов, помеченные цифрами “12–15”, представлены на осциллограммах под соответствующими номерами.

200–300 up to 600–800 ms until he starts the next flight display. Usually, the male performs up to 5–7 flight displays with a period of about 5–6 s (Figs 1–2).

The male produces the song of the second type by stridulation while sitting on the ground. This song is an echeme-sequence lasting up to 20–25 s (Figs 9–11). Echeme repetition period normally averages 500–950 ms, but sometimes increases up to 1.5–2.0 s and more. Each echeme consists of a succession of short click-like noise syllables following each other with a period of 15–21 ms in our recordings, one low-amplitude prolonged noise syllable sometimes almost indistinct on oscillograms, and one pure-tone syllable usually subdivided by amplitude modulations into several partially merged parts (Figs 12–15). The number of click-like syllables per echeme varies in different males from 5–10 up to 25–30; their number apparently decrease when the male starts singing more regularly. The carrier frequency of the pure-tone syllable is 2.5–2.8 kHz i.e. almost the same as in pure-tone syllables in the song of the first type (Figs 12–13). Sometimes, in the end of the song of the second type the male produces the same succession of pure-tone syllables as in the end of the song of the first type (Figs 9, 12). Also, occasionally he starts flight displays during producing the song of the second type (Fig. 11).

The song of the first type can be confidently classified as a calling song produced by single mature male for attracting conspecific female. The song of the second type was registered both in single male (at least no female was visible nearby) and in male courting female. Usually, courting male was sitting a few centimeters near female and singing. If the female attempted to escape, he moved after her, producing songs in the pauses between his movements, and, having overtaken her, sat in front of her head to head (Fig. 22). No attempts of copulation were observed.

REMARKS. Some longitudinal veins of the hind wing in *S. savignyi* are slightly thickened [Bey-Bienko, Mishchenko, 1951: 626], which is typical of species that produce signals during display flight.

The ability of this species to produce sounds in flight was noted by Shumakov [1963: 159]. A verbal description of its song, including the indication that the sounds produced on the ground resemble whistling, is given by Husemann & Hochkirch [2007] but no signal descriptions illustrated by oscillograms are known to us.

Helioscirtus moseri Saussure, 1884
Figs 16–20, 23.

MATERIAL. Southern Kazakhstan, the rocky desert in the Charyn River Valley, ca 20 km north of Chundzha (=Shinzha), 43.7153° N, 79.4175° E, 24.VI.2024, in the same biotope with *S. savignyi*, signals of six males were recorded at 40–42 °C.

SONGS. While singing, the male periodically flies up to a height of about a meter and lands near the takeoff point. Singing males stay in rocky or sandy areas devoid of vegetation (Figs 23–24). The number of males at the studied location was very high, so their songs usually overlapped, forming an unceasing chorus.

The male calling song is an echeme produced during flight display and followed by low-amplitude syllable or, maybe, several merged syllables produced by stridulatory movements of the hind legs immediately after landing (Figs 16–20). Sometimes these syllables are inaudible and, apparently, absent. The song repetition period usually averages 3–5 s and only occasionally reaches 7–9 s. Duration of an echeme produced by wings is about 0.8–1.1 s, syllable repetition period in it is 18–19 ms in our recordings. The gap between the parts of a song produced during the flight and on the ground averages 90–180 ms, duration of the part produced on the ground is 100–240 ms.

REMARKS. Bey-Bienko and Mishchenko [1951: 635] points out that some of the longitudinal veins of the hind wings in species of *Helioscirtus* Saussure, 1884 are thickened, which is typical of species that produce signals in flight. Very brief description of the song of *H. moseri* from Northeastern China illustrated by only one oscillogram was published by Xi *et al*. [1992]. As far as can be judged, the signals of males from Kazakhstan and China are very similar.

Discussion

In the song structure and acoustic behavior, *S. savignyi* differs from most Oedipodinae and, in some characters, even from all other Acrididae.

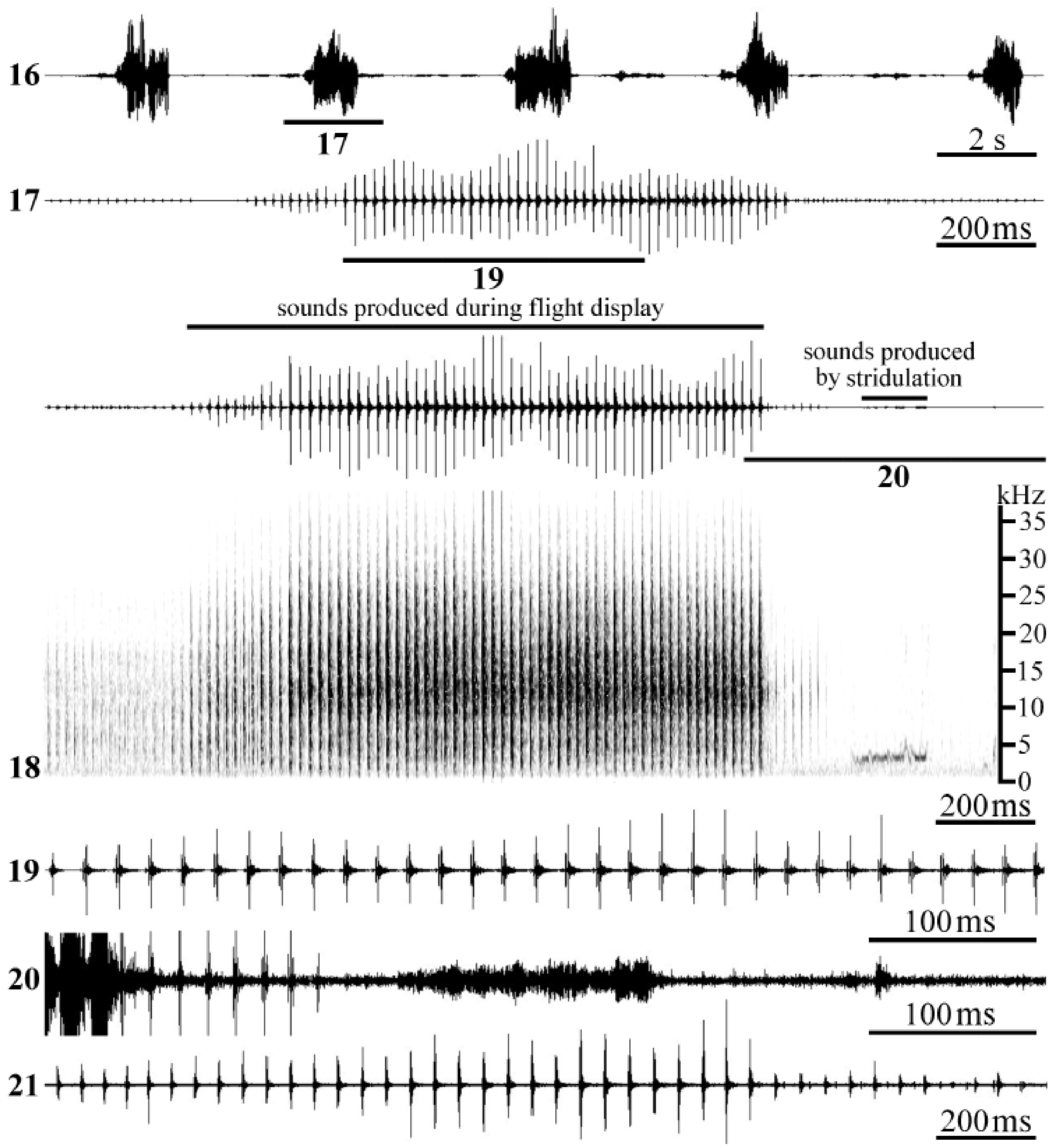
Firstly, songs of both types include both noise and pure-tone syllables. The latter is typical of Grylloidea (Orthoptera) but was not described in Palearctic Acrididae. The exact mechanism of sound-producing in this species was not studied. We can only note that when producing short click-like syllables, the male quickly moves his legs, holding them at an angle of about 30° to the body axis, i.e. almost as in a resting position. When producing a pure-tone syllable, he sharply raises them upwards by about 50–60° from the body axis.

Secondly, the single male can produce the calling song when sitting on the ground. Among Palearctic Oedipodinae, similar acoustic behavior was observed only in *Stethophyma grossa* [Ragge, Reynolds, 1998; Savitsky, Lekarev, 2007] and *S. magister* (Rehn, 1902) (our unpublished data). However, these two species live among dense vegetation in moist habitats, which is completely untypical for Oedipodinae.

The same behavior was described in two North American species associated with open habitats [Otte, 1970]. In one species, *Cibolacris parviceps* (Walker, 1870), males do not crepitate during flight but possess stridulation which may have a female-attracting function [Otte, 1970: 72]. The other species, *Dissosteira carolina* (Linnaeus, 1758), is noted for its hovering flight accompanied by sound producing. At the same time, “sometimes solitary males of *D. carolina* sit in one spot for many minutes and stridulate, presumably to attract sexually responsive females” [Otte, 1970: 47]. *S. savignyi* demonstrates similar behavior, since it also performs flight displays but sometimes stridulate sitting on the ground.

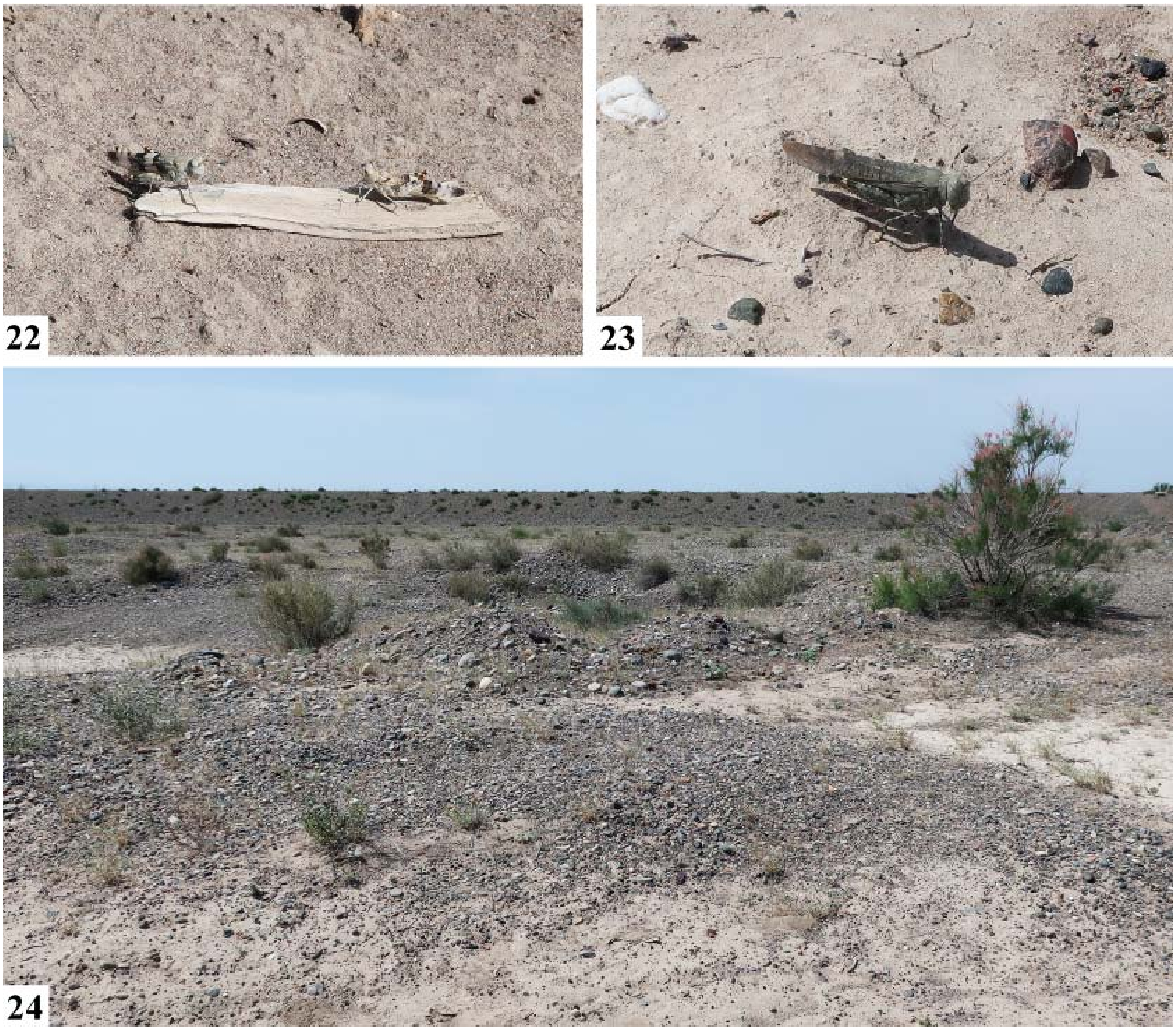
Thirdly, in this species, the song of the first type is a combination of sounds produced by different mechanisms, wing crepitation and stridulation, during two different types of activity, flight display and sitting on the ground, respectively. The same phenomenon is observed in *H. moseri* and was described in *H. clausi* [Savitsky, Lekarev, 2007] and *S. obscuratus latissimus* [Tishechkin, 2022]. Apparently, as we supposed earlier [Tishechkin, 2022], in Oedipodinae this is not a rare case.

In the rocky desert in the lower Charyn River Valley, where our observations were carried out, *S. savignyi*, *H. moseri*, and *S. obscuratus latissimus* are strictly sympatric. Both when singing on the ground and during flight displays, they stay exclusively in open rocky or sandy areas and are acoustically active during the same season and time of day (Figs 22–24). Songs of *H. moseri* and *S. obscuratus latissimus* are similar in the general scheme and are prolonged echemes produced during flight displays and usually followed by one or several low-amplitude syllables produced immediately after landing. Still, in *H. moseri* the syllable repetition period in the echeme averages 18–19 ms, whereas in



Figs 16–21. Calling songs of Oedipodinae. 16–20 — *Helioscirtus moseri*; 21 — *Sphingonotus obscuratus latissimus*. 16–17, 19–21 — oscillograms; 18 — oscillogram and sonogram at the same speed. Faster oscillograms of the parts of signals indicated as “17” and “19–20” are given under the same numbers.

Рис. 16–21. Призывные сигналы Oedipodinae. 16–20 — *Helioscirtus moseri*; 21 — *Sphingonotus obscuratus latissimus*. 16–17, 19–21 — осциллограммы; 18 — осциллограмма и сонограмма при одной скорости развёртки. Фрагменты сигналов, помеченные цифрами “17” и “19–20”, представлены на осциллограммах под соответствующими номерами.



Figs 22–24. 22 — *Sphingonotus savignyi*, male (right) courting a female; 23 — *Helioscirtus moseri*, male after flight display; 24 — southern Kazakhstan, the rocky desert in the Charyn River Valley, the habitat of *S. savignyi*, *H. moseri*, and *S. obscuratus latissimus*.
Рис. 22–24. 22 — *Sphingonotus savignyi*, самец (справа), ухаживающий за самкой; 23 — *Helioscirtus moseri*, самец после демонстрационного полета; 24 — южный Казахстан, каменистая пустыня в долине р. Чарын, местообитание *S. savignyi*, *H. moseri* и *S. obscuratus latissimus*.

S. obscuratus latissimus it is more than twice as long and averages 44–50 ms (cf. Figs 17–18 and 21). In *S. savignyi*, the syllable repetition period averages 19–22 ms i.e. almost the same as in *H. moseri*. However, unlike *S. obscuratus latissimus*, *S. savignyi* produces a sequence of 5–6 short echemes including 3–6 syllables each (Figs 3–4). The presence of pure-tone syllables in the end of the song provides additional cue for distinguishing it from the songs of two other species. Apparently, these differences ensure reliable segregation of acoustic communication channels in these species.

Since many species of band-winged grasshoppers produce sounds during flight displays, moving distances of tens of centimeters to tens of meters while sound producing, investigation their acoustic communication in the laboratory is impossible. In addition, in Palearctic, they reach their maximum species diversity in the steppe and the desert zones, with some species inhabiting only certain landscapes (e.g., rocky deserts). For these reasons, the songs of most Palearctic species of Oedipodinae remains unstudied. It can be supposed that a study of band-winged grasshoppers in the desert zone of the Palearctic will reveal sound signals in many species for which they are presently unknown.

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