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Sound production in *Aiolopus strepens* (Latreille, 1804) (Orthoptera, Acrididae)

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Abstract

Aiolopus strepens (Latreille, 1804) (Orthoptera, Acrididae) produces sounds in two different ways and behavioural contexts. In interaction with other individuals, whether of the same sex and species or not, it produces sounds by tapping the substrate with its hind tarsi. This sound production is sometimes also associated with aggressive movements made with the hind legs. In courtship the male stridulates by rubbing its hind femora against its tegmina. The sound produced by both methods consists of a variable number of syllables. The physical characteristics of both signals are different as a consequence of the particular type of sound production, with emission frequencies being lower in the courtship song. The mean number of syllables can be as high as about 12 (short duration, emitted at a rate of about 60 syllables per second) in interaction sounds but is typically only 1 to 3 in courtship (long duration, ca 50 ms).

Zusammenfassung

Aiolopus strepens (Latreille, 1804) (Orthoptera, Acrididae) generiert zwei unterschiedliche Lautäußerungen in verschiedenen Verhaltenssituationen. Bei Begegnung mit anderen Individuen werden Geräusche durch Tippen der Hintertarsen auf den Untergrund erzeugt. Dabei ist es egal, ob es sich um Tiere unterschiedlichen oder gleichen Geschlechts handelt. Diese Lauterzeugung wird manchmal von ruckartigen Hinterbeinbewegungen begleitet. Beim Balzverhalten striduliert das Männchen durch Reiben der Hinterschenkel an den Flügelseiten. In der vorliegenden Arbeit werden beide Stridulationsmuster verglichen und analysiert.

Introduction

Despite the great interest paid to the acoustic behaviour of insects in Europe, researchers have neglected some groups in this geographical area. This is the case with Oedipodinae Orthoptera, the acoustic communication of which has received attention only from FABER (1953), DUMORTIER (1963), GARCÍA et al. (1997, 2001) and RAGGE & REYNOLDS (1998). This neglect may be partially due to the opinion of certain authors (e.g., RAGGE & REYNOLDS 1998) concerning the low diagnostic value of the sounds they produce. However, the complexity and diversity of sound production mechanisms among Oedipodinae may also be considered as a handicap to their study, although, as regards North American Oedipodinae, OTTE (1984) maintains that the differences in the communicative aspect of different species can be used to solve taxonomical problems between very simi-

lar species. It is along these lines that we are completing a study on the Oedipodinae of the Iberian Peninsula, during which we are gathering acoustic displays of their species. In so far as the sound production mechanisms are concerned, OTTE (1984) recognized both visual (mute) and acoustic signals made with the hind legs. Among the acoustic signals, OTTE (1970) distinguished stridulation, produced by rubbing the hind leg (femur or tibia) against the tegmen, from other kinds of signal such as drumming, crepitation and mandibular sounds. In the case of *Aiolopus strepens* (Latreille, 1804), there is only one previous reference to sound production (FABER 1953) and it involves abdomen percussion against the substratum. The present paper documents all the sounds produced by this species, along with accompanying behaviour.

Table 1: Summary of information on origin of *Aiolopus strepens* specimens, date and locality of recording, number of registered recording and type of song of recordings studied (all recordings made in the laboratory)

Specimen	**Locality of capture**	**Date of capture**	**Date of recording**	**Recording number**	**Type of sound**
Male 1	Laguna de Lor, Ablitas (Navarra)	16/July/ 2001	3/September/2 001	Cinta 10/2001 ID0	Interaction
Male 2	Punta Entinas (Almería)	30/August/ 2001	3/September/2 001	9/2001 ID0 9/2001 ID1	Courtship
Male 3	Pedro Muñoz, Laguna de Navalafuente (Ciudad Real)	25/Septemb er/2001	30/September/ 2001	11/2001 ID5 11/2001 ID6 11/2001 ID7 11/2001 ID8 12/2001 ID5	Interaction
				12/2001 ID0 12/2001 ID1	Interaction/ Courtship
Male 4	Monterrubio de la Serena (Badajoz)	27/Septem-ber/2001	30/September/ 2001	11/2001 ID6 11/2001 ID8	Courtship
Female 1	Laguna de Sariñena (Huesca)	15/July/ 2001	-	-	-
Female 2	Punta Entinas (Almería)	30/August/2 001	-	-	-
Females 3, 4, 5	Pedro Muñoz, Laguna de Navalafuente (Ciudad Real)	25/Septem-ber/2001	-	-	-

Materials and Methods

The signalling behaviour of the specimens summarised in Table 1 was studied. After collection with an entomological net, the specimens were transported in plastic cages with natural vegetation to the laboratory, where they were kept in other cages separated by sex, and watered daily. They were mainly fed lettuce and bread. The wooden cages had a glass front and a metallic mesh top. They measured 40 x 30 x 40 cm, and were lit 12 hours per day by a 25 W bulb.

Observations and sound records were carried out in a soundproof room, in the Faculty of Biology of the University of Murcia. For this purpose, the specimens were placed in a wooden cage of similar design to the holding cages but measuring 32 x 42 x 32 cm. Two adjustable table lamps were used, one beside the cage and the other over it, in order to provide both light and heat to the specimens. Ambient temperature inside the cages varied between 30 and 36 °C.

Observations and sound recordings were made from 17 August 2001 to 16 October 2001. Several observation and recording sessions were carried out, grouping 4 males, or 2 males and 2 females, or 1 male and 1 female, in the recording cage, since no sound production was observed when individuals were isolated. The specimens, marked with a dab of nail polish or marking pen to distinguish them, were not disturbed during the observation and recording process, which lasted a minimum of an hour to ensure that the specimens were adapted both to the cage and to silence. Sound was recorded using an AVL 600 condenser electret omni directional microphone, placed on the cage floor, into a Tascam DA-P1 digital audio tape recorder. The frequency response of this recording system was 20 Hz – 20 kHz ± 0.5 dB. During the sound recordings, a video camera (JVC GR-ax70 or JVC GR-DVX8) was used to register the accompanying behavior. In addition, a human observer followed the specimen activity visually, describing, in detail, the movements of the insects. The videotapes were studied later with a JVC HR-S7851EU video attached to a color monitor (Sony Kx-14CP1).

To study the sound, the analog signal was digitized using a Sound Blaster® 16 with Advanced Processor Upgrade (Creative Technology Ltd.); at 48 kHz sampling rate and then analysed using Avisoft® SAS Lab Pro 4.15 (Avisoft Bioacoustics) and the Syntana analytical package (AUBIN 1994). Terminology used to describe the acoustic signals is that of RAGGE & REYNOLDS (1998):

- Song: Acoustic output of a particular species or individual.
- Courtship song: special song produced by a male when close to a female.
- Syllable: sound produced during a complete cycle of movement of the stridulatory apparatus or the sound producing apparatus, such as the whole up and down movement of the hind femur against the tegmen or one tapping movement of the hind tarsi.
- Syllable interval: considered between two consecutive points of maximum intensity when the syllable length is so short that its measure becomes impossible.

- Echeme: a train of syllables.

In addition the following term is used:

- Interaction song (GARCÍA et al. 2001): sound produced when specimens seem to be disturbed by the nearby movements of other individuals, males or females, conspecifics or not.

In relation to the spectral analysis of the sound, the following term should be defined:

- Quartile: Each one of the three frequencies dividing the spectrum of a signal into four parts. The quartiles allow us to characterize the distribution of energy across the spectrum. The distance between the lower (25%) and upper (75%) is a measure of the central tendency or pureness of the sound.
- Amplitude spectrum (linear), using a Hamming window type at FFT length of 512 points and a Frame size of 100%.

Ninety-six interaction and 12 courtship songs, produced by three males, were studied. Sound recordings used for this study are identified with the numbers: Cinta (Tape) 10/2001 ID0; 9/2001 ID01, Cinta (Tape) 11/2001 ID5, ID6, ID7, ID8; 12 ID0, ID1, Cinta (Tape) 11/2001 ID6, ID8. (Table 1).

The sound and video recordings are kept in the Fonoteca of the Área de Zoología of the Universidad de Murcia. The specimens form part of the collection at the same institution. Sample songs are available at OSF (http://osf2.orthoptera.org) (EADES 2001).

Data analysis

For every considered song parameter the minimum and maximum values and the median value were calculated for every song of each singing male. Afterwards, the mean value of the medians was calculated for each male.

The mean of the median values of all three males is used to describe the parameters, as well as the minimum and maximum values of the whole data.

The statistical analysis was made using the SPSS 11.0 program.

Results

Interaction song

An individual, male or female, produces sound, when disturbed by other specimens, by tapping the substratum with its hind tarsi. This sound is produced when another individual, male or female, is close by, or in contact with it. It is also produced by a male when another male tries to mount it. Sound duration depends on the interaction length. Aggressive movements, such as raising the hind femora or kicking with the tibiae may accompany this song. This signal can be described as the result of percussion or tapping insert.

We consider as one syllable the sound produced by a blow of the tarsus against the substratum (sound produced by a complete movement of the sound producing mechanism), while an echeme is composed of all the knocks produced from the beginning until there is a pause.

The sound is composed of sequences (Fig. 1) of a variable number of echemes lasting about 0.199 s (min.: 0.018 s; max.:1,260 s) (Fig. 2). Each echeme is composed of several syllables (mean: 12; min.: 2; max.: 75) (Fig. 3), emitted at a rate of about 60 syllables per second. The interval between syllables is 0.017 s (min: 0.007; max: 0.050) (Fig. 4) The number of syllables per echeme and echeme length are closely correlated (Pearson's correlation coefficient = 0.987). The frequency spectrum (Fig. 5) shows a main peak at around 6000 Hz, the bandwidth being around 4000 Hz.The minimum frequency is around 5000 Hz and the maximum around 9000 Hz. The lower quartile is around 6000 Hz, the medium quartile around 7500 Hz and the higher quartile around 11000 Hz.

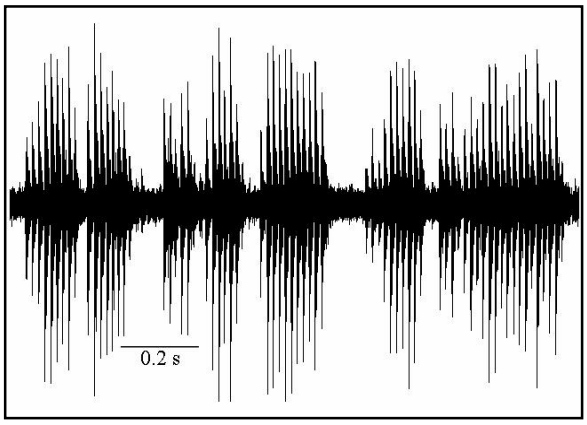

Fig. 1: Sequence of interaction song of *Aiolopus strepens*.

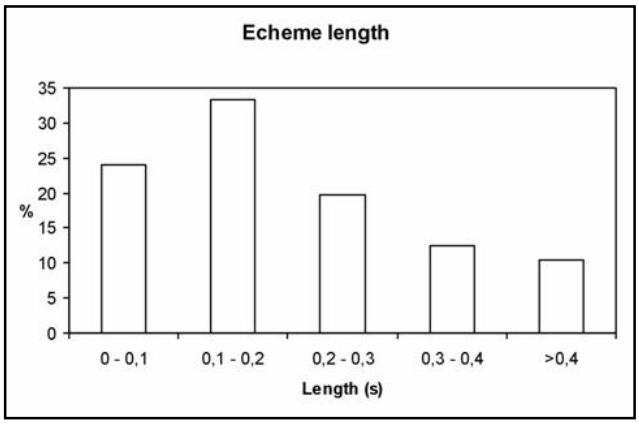

Fig. 2: Distribution of echeme length of interaction song of *Aiolopus strepens* represented as percentages of total cases.

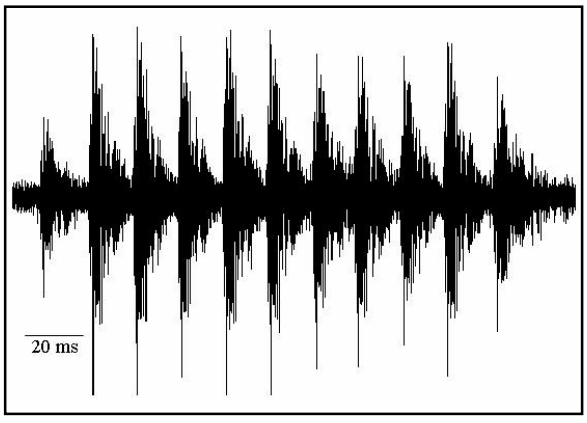

Fig. 3: A single echeme of interaction song of *Aiolopus strepens*.

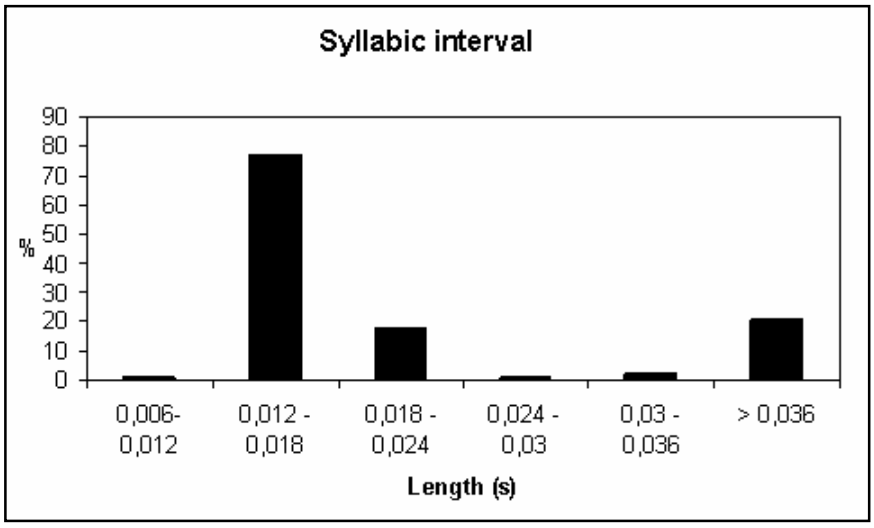

Fig. 4:

Distribution of syllabic interval in the interaction song of *Aiolopus strepens*, expressed as percentages of total cases.

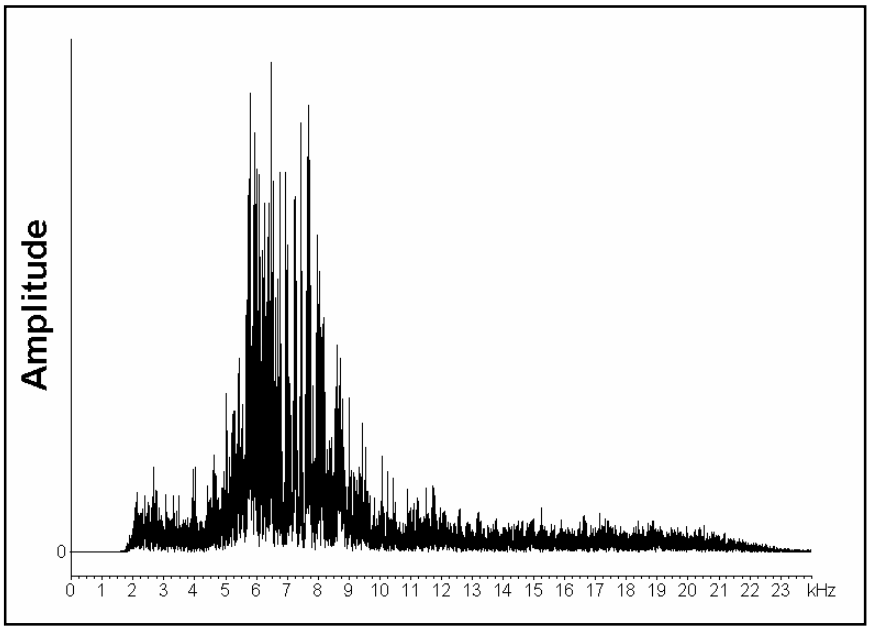

Fig. 5:

Frequency spectrum of interaction song of *Aiolopus strepens*.

Courtship song

The courtship song is produced by stridulation, that is, by rubbing the hind femora against the tegmina. A male emits this song when it is going to mount another individual, male or female, to copulate. When the song is very brief, the male sings several times before mounting the female, except if the female moves away quickly (by jumping for instance) in which case the courtship behavior ceases.

When a male tries to copulate with a female he approaches and stands at right angles to her. In this position he produces one or more courtship songs. Songs can be interspersed with movements of the hind legs, such as raising one or both femora and extending the tibiae. The last is the most frequent movement. If the tibiae extension is brusque and the tibia hits the tegmen, then a click may be produced. After singing, the male jumps on the female, except when the female declines by raising one or both hind femora or extending her hind tibiae.

When trying to copulate with another male, the starting movements and song are similar but, after the stridulation, the other male may answer with an interaction song (tarsal tapping). This provokes the first male to cease the courtship behavior and to move away.

The song consists of sequences of echemes composed of a variable number of syllables (1-3). Echemes can be monosyllabic (Fig. 6a) or composed of two or three syllables (Fig. 6b) Monosyllabic echemes last 0.049 s (= syllable duration) (min.: 0.017; max.: 0.069); longer echemes last 0.131 s (min.: 0.096; max.: 0.190), the sound length and number of syllables being related. Sounds have a frequency band of between 3000 and 8500 Hz with two peaks. The first peak occurs around 4000 Hz, and the second around 6500 Hz (Fig. 7). The lower quartile occurs around 4800 Hz, the medium quartile around 6500 and the higher quartile around 8000 Hz. The first peak was the highest in 42% of the cases and the second peak was the highest in 58%.

The courtship song is produced by asynchronically moving the hind femora up and down while hind tibiae are flexed, that is, the stridulating movements summarized in the kinetogram given in figure 8.

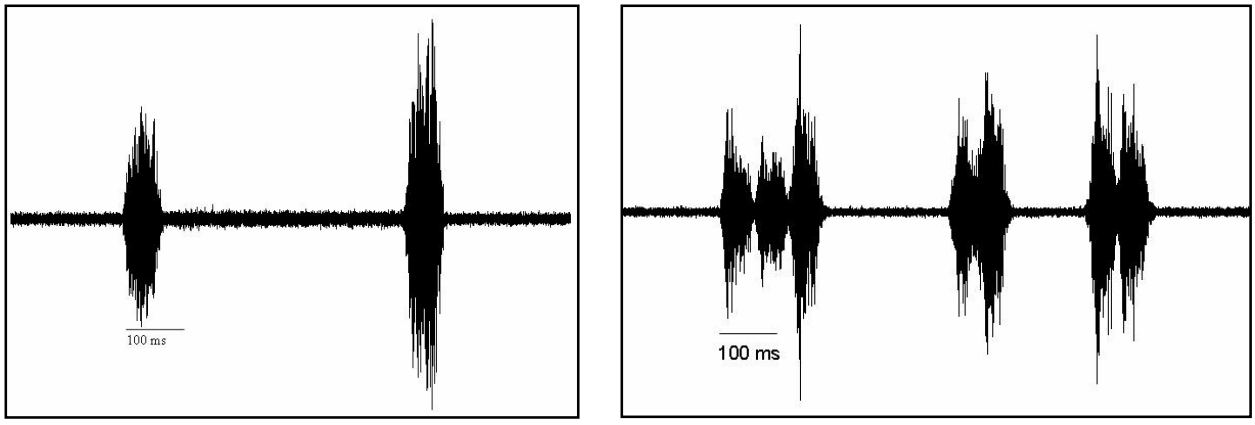

Fig. 6: Courtship song of *Aiolopus strepens.*
a: monosyllabic echemes. **b**: bi- and trisyllabic echemes.

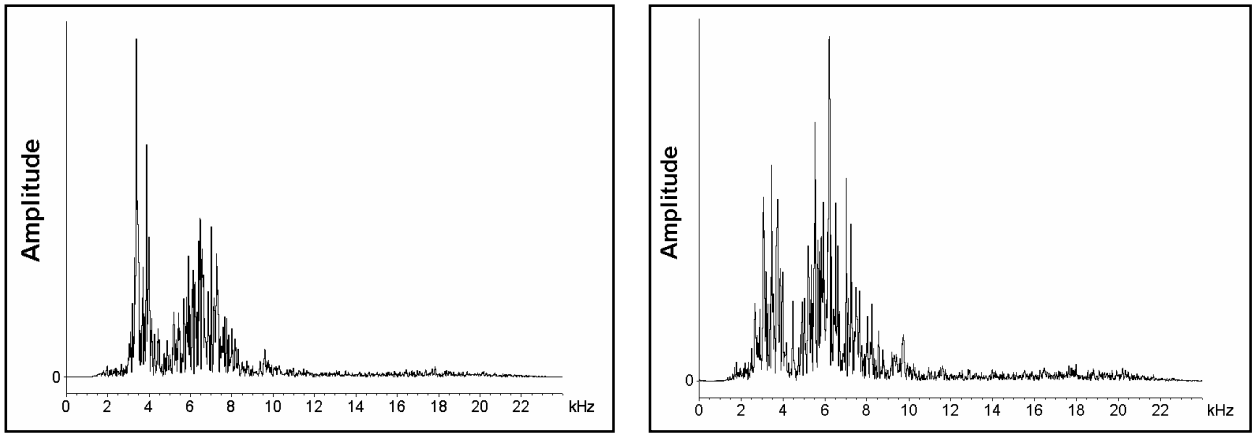

Fig. 7: Frequency spectrum of courtship song of *Aiolopus strepens*.
a: case in which the main peak is the first. **b**: case in which the main peak is the second.

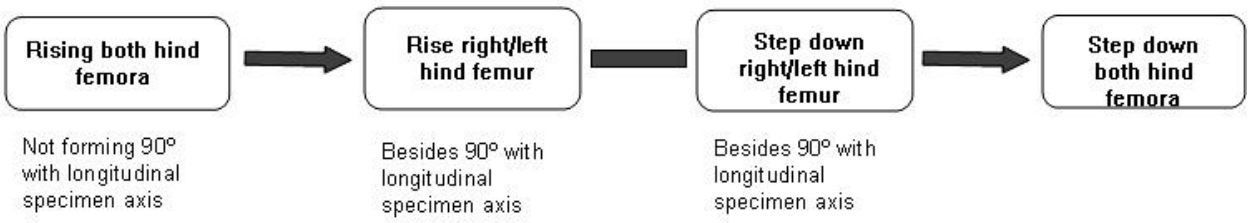

Fig. 8: Kinetogram summarizing the stridulatory movements during the courtship song of *Aiolopus strepens*.

Discussion

Aiolopus strepens emits sounds in two different behavioral situations. These sounds are different and produced in a different way. The courtship song is produced by stridulation, the courtship behavior being of the "Acrolophitus-type" (OTTE 1970), that is, male stridulate in the vicinity of the female and then attempt to mount. The courtship song can be assumed to be a recognition signal since, as OTTE (1970) pointed, courtship signals are highly species-specific. The interaction song is produced by tapping the substratum with the hind tarsi. The actual sound produced, its intensity and the quality of the air-borne sound, depends on the characteristics of the substratum (DUMORTIER 1963, RAGGE & REYNOLDS 1998), in our case the cage floor and, in the nature, grass leaves, a stem or the soil. It has been recently demonstrated the influence of the substratum in signal properties, mainly spectral characteristics (COCROFT et al. 2006). So, it can be assumed that some song characteristics, such as the frequency, may not be important in the interaction and just the sound production itself and the emission rate of the signal may be relevant.

OTTE (1970) cites the "femur-shaking" as a movement performed by both males and females of many species that causes the separation of individuals. Following him, the shaking can be silent or involving the tibiae striking the substratum or the femora striking the forewings. In our case, although the general description of the movement is similar, the sound production is different because it implies the hind tarsi. In this song case, aggressive movements, such as raising the hind femora or kicking with the tibiae may accompany the song. These movements have a probable visual intention, because they reveal the brilliant color of the tibiae, and the dark spots on the inner surface of hind femora. DUMORTIER (1963) considers that the noise produced by tapping, which evidently depends on the nature of the substratum, may act as an acoustic signal for the other specimens, but it may also be a visual signal. Nevertheless, we consider that the tapping movements are so quick and of such reduced amplitude that they hardly can be considered as a visual signal. In addition to that, the song is produced and the movement performed independent of the position of the other individual; so this can see, or not, the hind legs of the singer.

Acknowledgments

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