Journal of Natural History

Stridulation in <emph type="2">Aphodius</emph> dung beetles: Songs and morphology of stridulatory organs in North American <emph type="2">Aphodius</emph> species (Scarabaeidae)

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Published online: 06 Dec 2010.

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Stridulation in *Aphodius* dung beetles: Songs and morphology of stridulatory organs in North American *Aphodius* species (Scarabaeidae)

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Abstract

The acoustic behaviour of four *Aphodius* dung beetle species from the Pacific Northwest of the USA was investigated. Male *Aphodius* produce substrate vibrations when they meet a conspecific female in a dung pat. The temporal structure of the substrate vibrations and the stridulatory organs are described. The vibrations are species-specific songs that are emitted during courtship. The stridulatory organ is of the abdomino-alary type in the investigated species. Morphological differences with regard to the detailed structure are present.

Keywords: Aphodius*, Scarabaeidae, stridulation, dung beetles*

Introduction

Among many insects, sounds are known to have an important function in the species communication system (Alexander 1967; Bailey 1991). They are widely used as species-specific recognition signals between opposite sexes to attract mates at long distance or in difficult habitat. Such calling behaviour is especially conspicuous in groups that produce loud airborne sounds with frequencies audible to the human ear as known from cicadas and Orthoptera (Pierce 1948). Substrate borne vibrations, however, are also used as an intra-specific signalling mode in some primitive cicadas (Claridge et al. 1999) and Orthoptera (Field and Bailey 1997). In planthoppers and leafhoppers faint substrate vibrations, transmitted via the host plant, are used in the same context (Claridge 1985a, 1985b). Airborne sounds and substrate vibrations both serve as specific mate recognition signals (SMRS) (*sensu* Paterson 1985). Insects also produce sounds at close range or direct bodily contact that have a function within the species courtship or mating behaviour (Ewing 1984). Although not necessarily used in species recognition, the sounds are usually species-specific (Barr 1969; Neems et al. 1997). They are sexual signals that are strongly influenced by competition for mates, leading to rapid divergent evolution of the signals compared to other, more 'conservative' characters (West-Eberhard 1984).

Sound production is widespread and common in many beetles (Gahan 1900; Dudich 1921a, 1921b, 1922). Sound-producing organs and stridulatory behaviour have been

described in detail in a number of different groups, particularly Scarabaeidae (Arrow 1904), Silphidae (Bredohl 1984), Curculionidae (Lyal and King 1996), Scolytidae (Barr 1969) and several aquatic taxa (Aiken 1985). Especially in scarabs the ability to produce sounds by means of a stridulatory organ is frequently observed. Dudich (1922) mentioned 124 genera in which stridulation was found, and Arrow (1904) seemed deeply impressed by their ability to produce sounds, stating that 'The special importance of stridulation in the Lamellicorns is probably in part due to a mental development higher than that of most other beetles'. Among *Aphodius* Illiger dung beetles, a large genus within the Scarabaeidae, sound production and the morphology of the abdomino-alary stridulatory organ has only recently been described in detail in the European *Aphodius ater* DeGeer (Hirschberger and Rohrseitz 1995) (Figure 1).

The beetles produce sounds when they are disturbed (for a description of disturbance sounds see Masters 1979, 1980) but their acoustic activity is more conspicuous during courtship and mating. Male beetles produce a complex song that is comprised of different temporal patterns when they meet a female and mate (Hirschberger 2001).

Presently, there are more than 1200 *Aphodius* species described worldwide. Many *Aphodius* have an abdomino-alary stridulatory organ (unpublished data). Thus, sound production within this genus seems to be widespread, and perhaps is a characteristic feature of their reproductive behaviour. It has been shown that the two sibling species, *A. ater* and *A. convexus* Erichson, produce sounds during courtship that are very similar but still more distinct than morphological features and, thus, allow a better discrimination between the two species (Hirschberger, unpublished data). Similarity in songs may reflect relatedness and could be a useful character in phylogenetic research. At present, however, it is necessary to take a first step and survey the presence and structure of stridulatory organs in further *Aphodius* species and investigate the sound production in stridulating species. As a first attempt we have recorded four *Aphodius* species in North America, of which three are nearctic, and one is palaearctic but introduced to North America (Hatch 1971). We describe the general structure of the stridulatory pattern, the behavioural context of the species' songs and the morphology of the stridulatory organs.
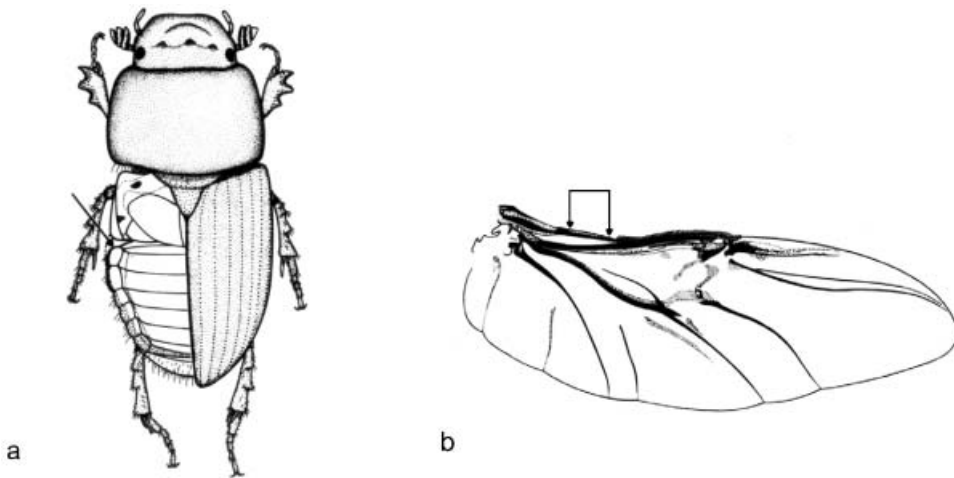

Figure 1. The abdomino-alary stridulatory organ of *Aphodius* sp. The plectrum is on the first abdominal segment (a) and the file is on the underside of the hindwing (b).

Materials and methods

Animals

Aphodius pectoralis. LeConte, a nearctic species, was collected on 21 May 1999 from horse dung west of Seattle, WA on Kitsap Peninsular at an elevation of *ca* 100 m. *A. granarius* Linné has originally a palaearctic distribution but the species has become cosmopolitan, probably through human influence. Specimens of *A. granarius* were collected on 9–10 July from horse dung south-west of Wenatchee, WA at an elevation of *ca* 300 m. *A. rainieri* Hatch and *A. sigmoideus* Van Dyke, both nearctic, were collected on 29 August from sheep, deer and horse dung north of Mt Rainier, WA at Corral Pass at an elevation of *ca* 1700 m. The sheep dung was previously frozen and exposed 1 day before collecting.

In *A. pectoralis*, *A. rainieri* and *A. sigmoideus*, living male and female beetles can be distinguished by three little protuberances on the head that are larger in males than in females in *A. pectoralis*, and are present only in males in *A. rainieri* and *A. sigmoideus*. Sex differentiation in *A. granarius* is possible by the tubercles on the head (usually present in males but may be missing), beetle size (males are slightly larger) and shape of the pronotum, which is more prominent in males. The characters in *A. granarius* are, however, not very reliable.

Recordings

The beetles were kept individually on moist tissue without any dung for 1 or 2 days prior to the recordings. The experiments were carried out using a small portion of defrosted sheep dung. Two beetles were released to the dung, which they quickly entered. In *A. pectoralis*, *A. rainieri* and *A. sigmoideus* the male was always released prior to the female. In *A. granarius* two individuals were chosen randomly. The first beetle was given a few minutes to settle in the dung before the second individual was released in all experiments. Sounds of the beetles were recorded on the surface of the dung using an electro-dynamic system after Strübing and Rollenhagen (1988). The detailed experimental design is given in Hirschberger (2001). The beetles' acoustic behaviour was observed for a minimum of 30 min. In case they started to produce sounds, the acoustic emissions were recorded on a portable Sony DAT-Recorder TCD-D8 until the beetles were silent again for at least 10 min.

Analysis of sounds

Song sequences of 30 s were analysed for every pair using Avisoft-SAS Lab Pro. The sequences were sampled with 16,000 Hz and a high pass filter of 200 Hz was applied to the data if necessary. The repetition rate of syllables (Figure 2) was measured in *A. pectoralis*, *A. granarius* and *A. rainieri*. The song of *A. sigmoideus* is very irregular so that syllable repetition rate was not measured. In all species the lengths of the syllables were measured and the number of pulses per syllable counted.

Sonograms of characteristic parts of the songs were obtained for each species. Since the frequency distribution of the sounds depends on the condition of dung and the position of the beetle within the dung, the sonograms were only used to describe major differences between species. A detailed analysis of the frequencies was not carried out.
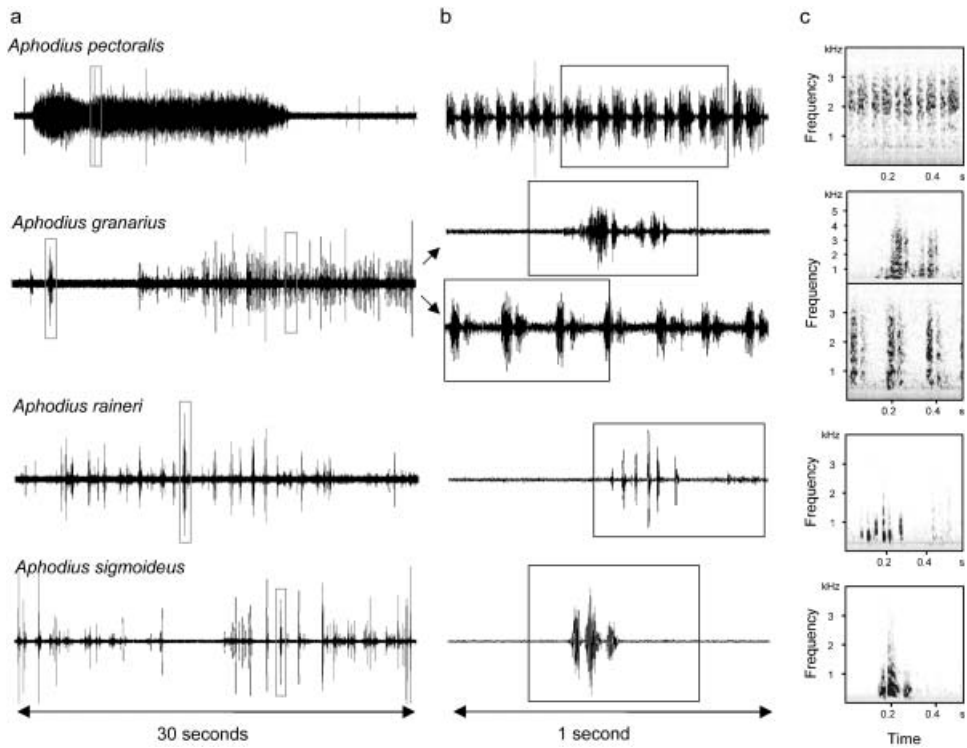
Figure 2. Sonagrams with duration of 30 s (a) and 1 s (b) of *A. pectoralis*, *A. granarius*, *A. rainieri* and *A. sigmoideus*. Spectrograms show the frequency during 0.5 s (c).

Morphology of stridulatory organs

The morphology of the stridulatory organs was investigated using scanning electron microscopy. Prior to SEM males and females were determined by dissecting the genital organs. The hindwings and the abdomen were dissected and dehydrated by passing through a series of ethanol (70%, 85%, 96% and 100%), 1 day in each. The beetles were dried in a critical point dryer (CPD 030, Baltec), coated with gold–palladium (90:10) in a sputter SCD 050 (Balzers) and scanned in an SEM JSM 6300 (Jeol). One male and two females of *A. rainieri*, four males of *A. pectoralis*, two males and three females of *A. granarius* and one male and female of *A. sigmoideus* were investigated.

Results

The investigated species produce songs under two circumstances. Firstly, when the beetles are still disturbed by handling, immediately after being released to the dung. Such disturbance sounds always consist of regularly emitted syllables with high repetition rate. They are produced by males as well as females and are relatively similar in the investigated species. Secondly, songs are produced when male and female meet in an undisturbed situation in the dung. Within this behavioural context the sounds are exclusively produced by the male beetles. They sing for a period of 10–20 min. Females do not answer and no duetting was observed. The male songs are species-specific (Figure 2). *A. pectoralis* emits a

Table I.   Characteristics of the stridulatory patterns of four species of *Aphodius* dung beetle.

Species	Size (mm)	No. of investigated individuals	No. of measured syllables	Mean duration between syllables $\pm$ SD (mm)	Mean length of syllables $\pm$ SD (mm)	No. of pulses per syllable
A. pectoralis	4.1–5.2	4	80	0.097 ± 0.0083	0.083 ± 0.0098	2
A. granarius	3.6–5.8	12	240	0.156 ± 0.0438	0.095 ± 0.0247	2
A. rainieri	5.7–6.8	4	82	0.99 ± 0.491	0.19 ± 0.312	2–7
A. sigmoideus	6.1–10.0	3	36	Irregular	0.13 ± 0.029	2–3

continuous buzzing sound that is comprised of a series of syllables in rapid succession. The duration of the buzz varies between 5 and 30 s. Its frequency distribution is between 2 and 3 kHz. The song of *A. granarius* consists of two different patterns: irregular chirps with variable length and a series of regularly emitted syllables. The frequency distribution of both chirps and syllables lies between 0.4 and 3–4 kHz. In *A. pectoralis* and *A. granarius* the syllables consist of two parts that are separated by a small pause. Both parts have the same intensity in *A. pectoralis* while in *A. granarius* the second part is of lower intensity than the first one.

The repetition rate is much higher in *A. pectoralis* with about 10 syllables per second compared to six syllables per second in *A. granarius* (Table I). Males of *A. rainieri* produce syllables that consist of a variable number of pulses. The number is not individually characteristic but varies within an individual's song. The syllables have a frequency distribution of 0.4–1.5 kHz and are emitted with a relatively low repetition rate of 1 per second. In *A. sigmoideus* the number of pulses within a syllable is lower, the syllables are irregularly produced and have a frequency of 0.2–2 kHz.

Morphology of the stridulatory organs

As described in *A. ater* (Hirschberger and Rohrseitz 1995), the stridulatory organ of the four investigated species is an abdomino-alary apparatus. The plectrum on the first abdominal segment consists of a small number of parallel sclerotic lamellae (Figure 3a). When the abdomen stretches and contracts the plectrum is moved across a file on the underside of the hindwing. The file is a specialized area of a wing-vein with a large number
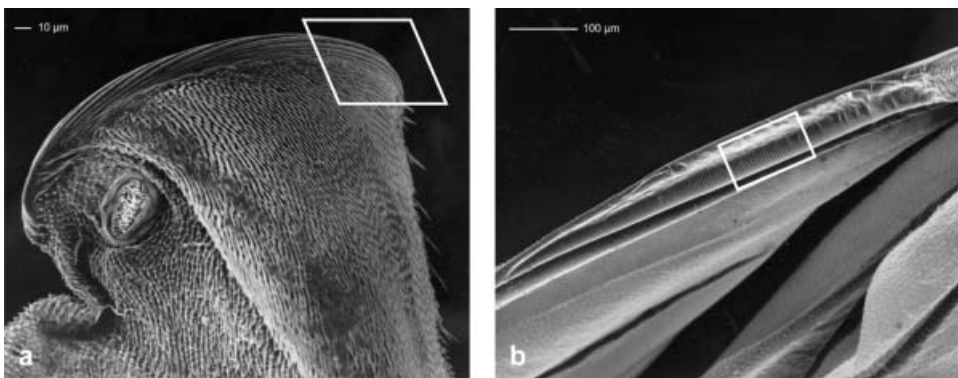
Figure 3. SEM of the plectrum (a) and the file (b) of *Aphodius rainieri*.

of parallel ridges (Figure 3b). None of the investigations revealed any differences between males and females with regard to the morphology of the stridulatory organ. Thus, only one sex is shown for each species in Figure 4.

The lamellae and ridges of both parts of the stridulatory organ are very thin and close together in *A. pectoralis* (Figure 4a, b). The lamellae of the plectrum are flat and twisted in *A. granarius*. At the upper end they become thin and diffuse (Figure 4c). The ridges of the file are thicker than in *A. pectoralis* but also relatively close together (Figure 4d). The lamellae of the plectrum are also twisted but round in *A. rainieri* and *A. sigmoideus* (Figure 4e, g). The intervals between the lamellae of the plectrum are deeper in *A. rainieri* (Figure 4e), and the intervals between the ridges of the file are very wide (Figure 4f). The ridges of the file are still further apart and very thick in *A. sigmoideus*. They are more erect and bifurcate on both ends (Figure 4h).

Discussion

The four *Aphodius* species produce specific songs when male and female are in an undisturbed situation in the dung. The same behavioural context of sound production has been observed in *Aphodius ater* and is described in detail by Hirschberger (2001). The few cases in which the beetles could be observed while stridulating (*A. granarius*, *A. sigmoideus*) showed that, as in *A. ater*, only males sing during the male–female interactions, and that copulation takes place during singing pauses. It seems conceivable that the male singing behaviour plays an important role during courtship in *Aphodius* dung beetles. Singing is time- and energy-consuming and thus, the sounds may serve as an honest signal (Zahavi 1975) of the males. Choosiness in female dung beetles seems likely since they have considerable investment in their offspring. Eggs are large, and suitable places for egg-laying have to be found: different parts of dung pats are preferred in different species (Holter 1982; Gittings and Giller 1997), and competitive interactions may force the female to engage in an extensive search for competitor-free space (Hirschberger and Degro 1996; Hirschberger 1998, 1999).

In *A. ater* (Hirschberger and Rohrseitz 1995) it was shown that stretching and contracting the abdomen produces syllables that are comprised of two parts with a small pause in between. This mode of sound production seems to be equivalent in *A. pectoralis* and *A. granarius*. The syllables of their song show the same structure. In *A. rainieri* and *A. sigmoideus* the mode of sound production must be slightly different when syllables with a number of small pulses are produced (Figure 2). The plectrum may only be in contact with the file during part of the movement along the wing, resulting in the patterned syllables.

The frequency of the sounds lies between 0.4 and 4 kHz with *A. pectoralis* singing with the highest frequency and having the ridges of the file packed tightest of the four species. Song frequency may be correlated to the density of the ridges but further investigation is needed to prove this hypothesis. The repetition rate (number of syllables per unit of time) is highest in *A. pectoralis* and lowest in *A. sigmoideus*. It seems conceivable that smaller species generally sing at a higher speed because the abdomen can be moved faster. Still, more species have to be investigated to prove this assumption.

The morphology of the stridulatory organs is species-specific and does not differ between males and females. At present it is, however, not possible to indicate its value for phylogenetic research. *A. raineri* and *A. sigmoideus*, the species that are assigned to one subgenus (Hatch 1971; Dellacasa 1988) show considerable difference with regard to the morphology of the file. They show, however, the highest similarity with regard to their
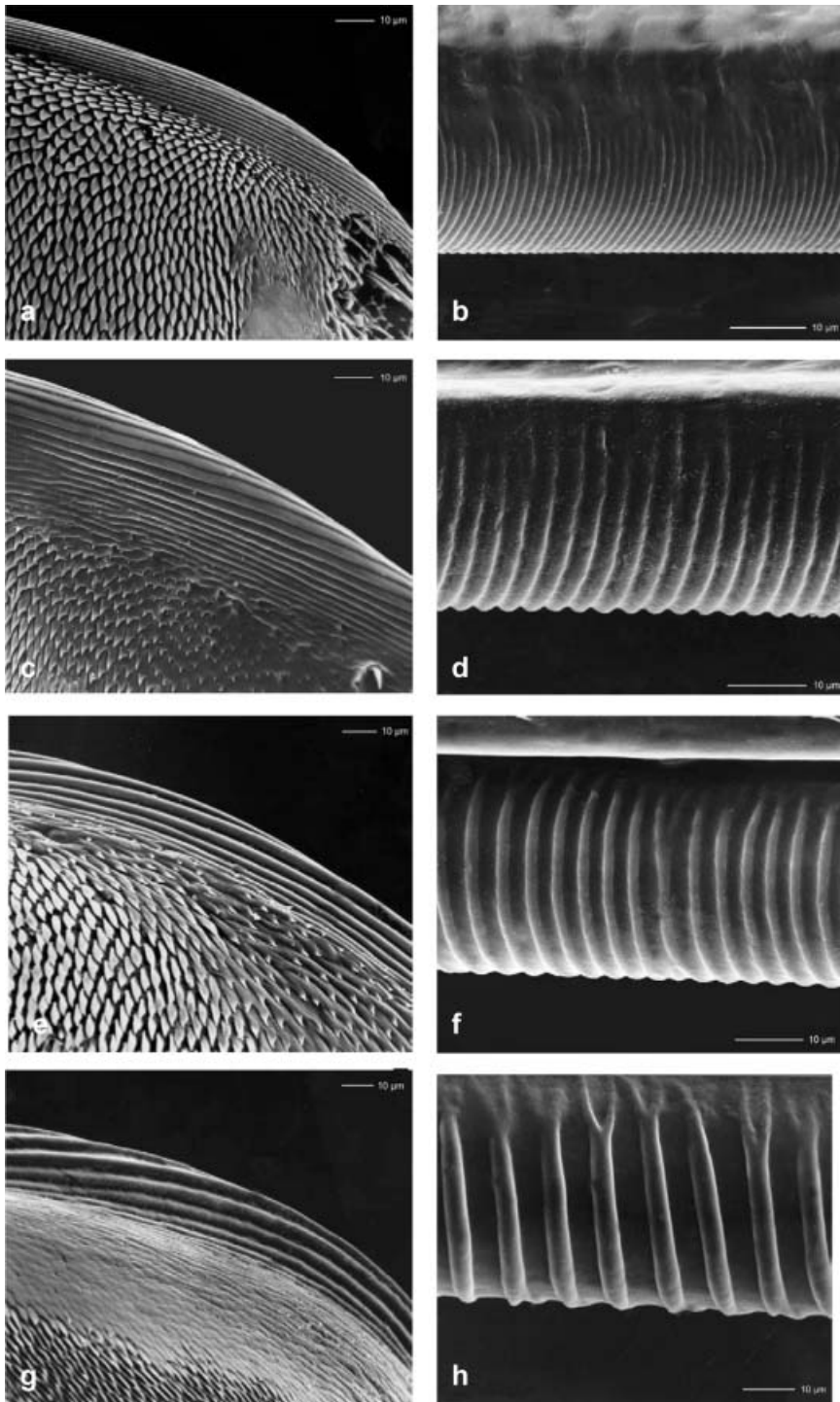
Figure 4. SEMs of the stridulatory organ. (a) Plectrum of *A. pectoralis*; (b) file of *A. pectoralis*; (c) plectrum of *A. granarius*; (d) file of *A. granarius*; (e) plectrum of *A. rainieri*; (f) file of *A. rainieri*; (g) plectrum of *A. sigmoideus*; (h) file of *A. sigmoideus*.

song. Considering that the species were found in the same dung pats at the same time at high densities, thus co-occurring spatially and temporally, it could be assumed that it would be most effective if their courtship songs were distinct. This is not the case, their songs are instead very similar but most distinct from all other species investigated so far. This unexpected result suggests the presence of unknown elements of the SMRS (Paterson 1985) in these two species.

Acknowledgement

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