Analysis of the Stridulation in Solifuges (Arachnida: Solifugae)

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Analysis of the Stridulation in Solifuges (Arachnida: Solifugae)

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Abstract Stridulation in solifuges has not been investigated yet. We performed a comparative analysis of the stridulatory organs and sounds produced by juveniles of various developmental stages and adults (both sexes) of *Galeodes caspius subfuscus* Birula. The stridulatory organ is of similar morphology in all developmental stages. The sound that they produced was a broad frequency hissing, composed of one or two chirps with maximum at 2.4 kHz. The intensity of the sound was found to increase with body size. Otherwise, no differences were observed between stridulation in juvenile, male and female individuals. Therefore, we suggest that the stridulation in solifuges has primarily a defensive role. As solifuges are neither venomous nor unpalatable, they might imitate an accoustically aposematic organism that shares the same habitat and has similar circadian activity, e.g. vipers. It may also have an intraspecific function in reduction of cannibalistic tendencies.

Keywords Camel-spiders · defensive behaviour · sound production · stridulatory organ · warning sound

Introduction

Communication in animals is based on several different stimuli, namely visual, chemical, tactile, vibratory or acoustic. Although the latter is quite widespread in arthropods, only five of 11 arachnid orders (Amblypygi, Araneae, Opiliones,

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Scorpiones and Solifugae), are known to use it (Dumortier 1963a). Within these orders, only few species have been observed to produce sounds. The function of acoustic communication thus remains to be unravelled in most arachnids. In scorpions, the sound appears to deter potential predators (Alexander 1958, 1960, Acosta and Maury 1990). In spiders the role of sound is important in few ways: in some species it is used to threaten enemies or conspecifics (Uetz and Stratton 1982; Marshall et al. 1995; Vol 2002), while in others it is used for communication between opposite sex during courtship (Gwinger-Hanke 1970; Edwards 1981; Gwynne and Dadour 1985; Maddison and Stratton 1988; Uhl and Schmitt 1996). The role of sound production in solifuges has not been investigated yet and thus is unclear.

In arachnids, the stridulatory organs are situated in various body parts, mainly on the chelicerae, legs and/or on the pedipalps. Thus, many types of stridulatory mechanism have been described in this group. In harvestmen and in scorpions there are at least four types of stridulatory mechanisms (Šilhavý 1978; McCormick and Polis 1990) and in spiders there are even eight different types (Uetz and Stratton 1982). In solifuges, however, only one type has been observed so far, in which the sound is produced by chelicerae rubbing against one another (Cloudsley-Thompson and Constantinou 1984). This type of stridulation has not been found in other arachnids with the exception of theraphosid spiders (Legendre 1963). Stridulatory organ in solifuges was observed for the first time more than a hundred years ago (Dufour 1862) and since then it was described only in few genera (Hansen 1893; Cloudsley-Thompson and Constantinou 1984).

In many solifuge species, particularly in the small ones, the stridulation is inaudible to human ear (Punzo 1998; Pekár and Hrušková, unpubl.). So far, it has been noticed mainly in large species, such as those of the genus *Ammotrechella, Rhagodessa* or *Galeodes* (Roewer 1934, Cloudsley-Thompson and Constantinou 1984). Solifuges had been observed to produce sound as a response to a disturbance (Pocock 1898; Warburton 1909). Cloudsley-Thompson (1961) has described stridulation as a part of a high intensity threat display. At low intensity threat the solifuge raises pedipalps and sways forward and backward with chelicerae moving soundlessly, if the disturbance continues, the movements of the chelicerae become more tight and more intensive therethrough the threatening behaviour is accompanied by stridulation.

Although this observation suggests an interspecific (defensive) role of the stridulation in solifuges, the sound can be used in intraspecific (intersexual) communication as well. Defensive and intersexual sounds differ in their characteristics. Defensive sounds are most frequently broad frequency signals with an increased number of pulses *per* a chirp. This physical characteristic assures that the sound is intensive and perceived by a wide array of enemies. Intersexual signals are, in turn, narrow-frequency signals with a perfectly defined pattern and frequency gaps in order to be specific (Dumortier 1963b).

Our aim was to find out the role of the sound produced by a solifuge *Galeodes caspius subfuscus* Birula, 1937. For this purpose the sound should be recorded, analysed and then its role investigated in a manipulative experiment. We succeed to record and analyse the sound in a semifield conditions but failed to demonstrate its role in a controlled experiment as solifuges ceased to stridulate in few hours when brought to the laboratory. Thus we performed a comparative analysis of the stridulatory organ and of the sounds produced by different developmental stages of this species. We hypothesised that if the sound is produced by only adult specimens then the role of the stridulation would be primarily intersexual. In such case we expected male and female producing different sounds due to possible differences in their stridulatory organs. If the sound is produced by all developmental stages then the role would be primarily defensive. In which case the sound characteristics would be similar, for all stages and both sexes. The morphology of stridulatory organs would be similar as well.

Material and Methods

The solifuges were collected in June 2005 in Kapshagay valley, a semi-desert area on the border with Taukum desert in south-east Kazakhstan. In that locality a single solifuge species occurs. *G. caspius subfuscus* is nocturnal, thus all individuals of different developmental stages were collected during nights. As no classification for developmental stages of this species exists and we did not find any feature usable for the classification, we were not able to distinguish particular juvenile instars. Thus we classified juvenile individuals according to the width of their propeltidium to six classes (rounding to the nearest millimetre): class 1 ($n = 2$) 2.5–3.5 mm; class 2 ($n = 4$) 3.6–4.5 mm; class 3 ($n = 3$) 4.6–5.5 mm; class 4 ($n = 9$) 5.6–6.5 mm; class 5 ($n = 9$) 6.6–7.5 mm; and class 6 ($n = 2$) 8.6–9.5 mm represented by subadult females. The adults were determined by the presence of developed copulatory organs (females) or the presence of flagellum on chelicera (males). The width of propeltidium in males was on average 8 mm ($n = 5$) and in females it was on average 10 mm ($n = 6$).

We noticed the circumstances under which solifuges produced sounds both in the field and in semifield (shelter) conditions. In a shelter, solifuges were introduced singly ($n = 40$) or in pairs (male and female, $n = 5$) in a plastic box (25 × 12 × 8 cm) and the sound that they produced was recorded. Single solifuges were disturbed by approaching the head of the microphone.

All sound recordings were performed in a shelter a few hours after collection of solifuges. The sounds were recorded using portable devices. A highly directional condenser microphone (Sennheiser ME 67 with K-6) was used to eliminate background sounds. The recording device was a minidisc recorder (Sony MZ-NHF800) using linear PCM with the sampling frequency of 44.1 kHz. An individual solifuge was disturbed by the microphone head approached at a distance of 3–5 cm. When paired, the sound was recorded close to one of the individuals. Altogether 40 individuals were used. Stridulation in tiny specimens was inaudible, thus we used specimens with at least 4 mm width of propeltidium.

For each individual two tracks of approximately 1min duration were recorded. The sound files were then analysed with Adobe Audition 1.5 and Sigview 1.9. In the analysis we used a single chirp of each track with the lowest background noise. The power spectrum of each chirp was determined from a 10ms long (central) signal using Fourier transform technique (with 1,024 bites).

The morphology of the stridulatory organ that is situated on chelicerae was studied under stereomicroscope. We recorded number of stridulatory ridges and the number of the stridulatory bristles in two individuals of each class. Then one left chelicera of each class was placed on a stub, coated with gold and studied under scanning electron microscope Joel JSM-6380LV. By means of the image analysis software (UTHSCSA ImageTool v. 3.0) we measured size of stridulatory ridges, as well as the length and basal thickness of the stridulatory bristles from SEM pictures.

Statistical analyses were performed within R (R Development Core Team 2004). As the data came from normal distribution, analysis of variance (ANOVA) or linear regression (LM) was used (Crawley 2002). ANOVA was performed in order to find differences between developmental stages (coded by categories). If ANOVA was significant LM with the size as a continuous explanatory variable was used to find whether the difference could be explained with the size of solifuges. To test for isometric increase generalised linear models (GLM) with offset were used. As the intensity of recorded sounds differed between instars, comparative analysis was based on residuals. These were obtained by subtracting actual intensities from an average intensity computed from the interval of 1–20 kHz.

Results

Stridulatory Organ

Stridulatory organ was found in all developmental stages including the first free instar. The organ consists of two identical files each situated opposite to each other on the inner face of the chelicera. Each file consists of two components, smooth area corrugated with prominent horizontal ridges and anteriorly oriented bristles, readily distinguishable by their noticeable thickness. The size of files increased linearly but allometrically with the solifuge size [GLM, offset, $n = 8$, p value = 0.0026, $\ln(y) = 12.06 + 1.74*\ln(x)$]. The stridulatory ridges were short and were situated only on the upper half of the proximal margin of the smooth area (Fig. 1). The number of ridges was similar for all stages being 15 on average ($n = 16$). Similarly, the number of stridulatory bristles did not differ between stages, being 35 on average ($n = 16$). The length of the bristles increased isometrically (GLM, offset, $n = 8$, p value = 0.25) with the solifuge size [LM, $n = 8$, p value = 0.003, $\ln(y) = 3.4 + 1.26*\ln(x)$]. Similarly the thickness of the bristles increased isometrically (GLM, offset, $n = 8$, p value = 0.57) with the body size [LM, $n = 8$, p value = 0.0009, $\ln(y) = 1.54 + 1.07*\ln(x)$].

Sound Analysis

All study solifuges stridulated when they were disturbed, handled or when they encountered a conspecific including that of an opposite sex. Some females allowed male to mate her without producing a sound. The sound produced by juvenile and adults solifuges was similar, no differences were found between stridulation in males and females as well. Each sound was composed of one to two chirps. The duration of a chirp was on average 0.53 s (SE = 0.02) with no difference between developmental stages (ANOVA, $n = 40$, p value = 0.27).

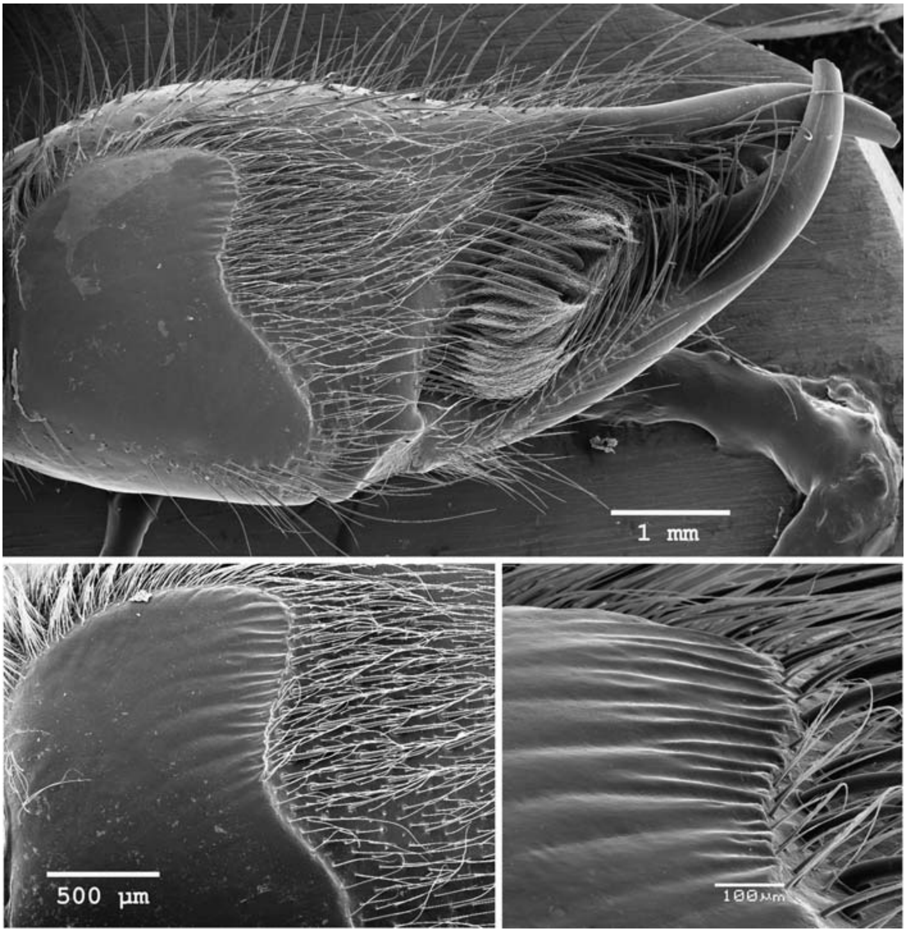


Fig. 1 Stridulatory organ of juvenile *G. caspius* with 6mm large propeltidium. **a** Overview of the organ on the inner face of chelicera. **b** Detail of the stridulatory organ, showing the ridges and bristles. **c** Detail of the ridges. All SEM pictures.

The peak frequency of the produced sound was similar for all stages (ANOVA, $n = 40$, p value = 0.1). It was 2.4 kHz on average (SE = 87). The band maximum lied between 1.5 and 4.5 kHz (Fig. 2). No consistent frequency gaps were found in the chirp of any stage. Visual analysis of the sonogram (Fig. 3) and oscillogram (Fig. 4) showed that there was no modulation of the intensity within a chirp in any stage.

The average intensity of a chirp (computed from the range of 1–20 kHz) increased significantly with the size of solifuges (LM, $n = 40$, p value < 0.0001, Fig. 5). The sum of intensities was markedly higher for the range of 1–11.9 kHz than for the range of 12–20 kHz for all stages. The sum of (standardised) intensities over particular ranges was found to be similar for all stages in the range of 1–2.9 kHz (ANOVA, $n = 40$, p value = 0.8), 3–5.9 kHz (ANOVA, $n = 40$, p value = 0.58) and 12–20 kHz (ANOVA, $n = 40$, p value = 0.77). But in the range of 6–11.9 kHz the sum of intensities declined significantly with the size of solifuges (LM, $n = 40$, p value = 0.03, Fig. 6). The difference was particularly in the range of 8–11 kHz.

Fig. 2 The power spectrum of the sound produced by *G. caspius* (pooled for males, females and juveniles).

Discussion

The morphology of the stridulatory organ in *G. caspius subfuscus* was very similar in all developmental stages and in both sexes. There were no significant differences in the main characteristics, such as the number of stridulatory ridges and specialized stridulatory bristles. If any differences were observed, these were accounted to the increase of body size due to ontogenetic development.

In contrast to uniformity on intraspecific level, the stridulatory organ in various solifuges species varies in shape and structure. In some species, the organ is extensive and well developed, in others it is less conspicuous (Cloudsley-Thompson and Constantinou 1984). Particularly nocturnal solifuges have well developed

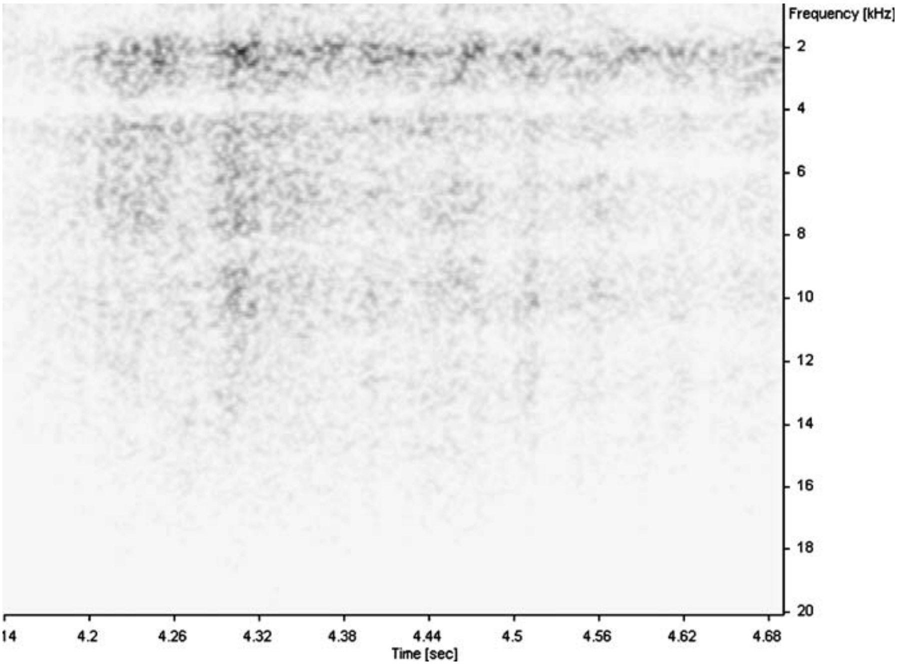


Fig. 3 A sample sonogram of a single chirp of a juvenile solifuge with 7mm large propeltidium.

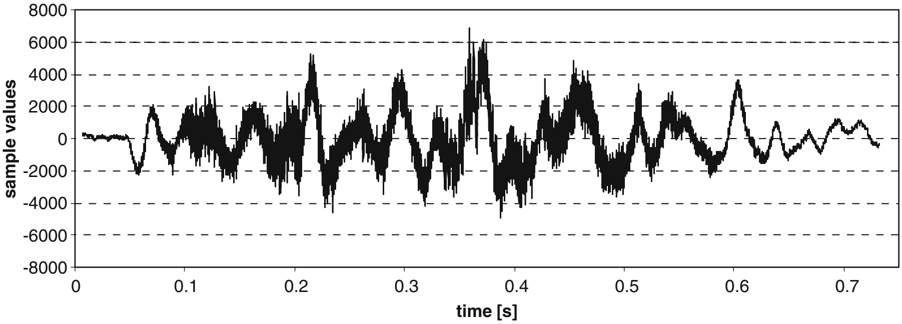


Fig. 4 A sample oscillogram of a single chirp of a juvenile solifuge with 7mm large propeltidium.

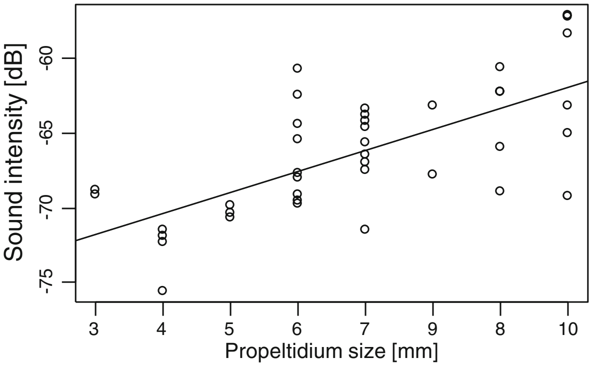
stridulatory organ, while in diurnal it is reduced or absent (Hewitt 1919). The stridulatory organ of *G. caspius subfuscus* is very similar to that of other species of the same genus (cf. Cloudsley-Thompson and Constantinou 1984). Therefore, the sound produced might not be species but genus specific.

It is not clear which morphological structures, ridges, hairs or both, are involved in the stridulation. Cloudsley-Thompson and Constantinou (1984) suggested that the sound is produced by rubbing the bristles against each other only. However, it rather seems that the sound is either produced by rubbing ridges only or bristles against ridges as the chelicera move tightly. Ablation experiments could provide a clear answer.

Alike the morphology, a sound produced by individuals of *G. caspius subfuscus* was similar in the main characteristics for all juvenile stages and adults. Only one characteristic, i.e. overall intensity of produced sound and the intensity of higher frequencies, changed with the ontogenetic development. This characteristic is a function of body size as has been shown previously for other sound-producing organisms (Bennet-Clark 1971). For example, smaller rattle snake individuals tended to have higher frequency of the rattle sound than larger individuals (Young and Brown 1993; Kinney et al. 1998).

What is the function of the stridulation in solifuges? Since we failed to obtain direct evidence we can only hypothesise about it. As the stridulation is produced by all developmental stages and both sexes a role in sexual behaviour is excluded. The

Fig. 5 Relationship between the sound intensity and size of solifuges. The linear model is $y = -75.98 + 1.41x$, $R^2 = 0.44$.



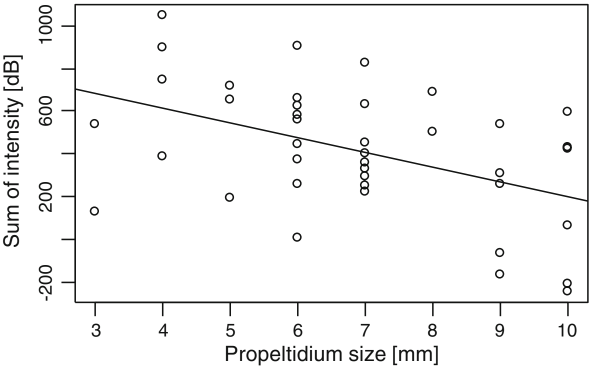


Fig. 6 Relationship between the amount of energy produced in the range of 6–11.9kHz and the size of solifuges. The linear model is $y = 886.6 - 68.4x$, $R^2 = 0.19$.

fact that it is elicited by a disturbance strongly indicate that the primary role is defensive—to repel the intruder. This is further supported by comparison of observed sound characteristics with defensive sounds produced by other animals. Masters (1980) analysed defensive sounds in dozens of insects and found that the sounds are (1) intermittent noisy squeaks of a broad frequency bandwidth, (2) peaking at 2.6kHz, (3) without harmonic components, (4) without temporal structure, (5) lasting on average for 80ms. The recorded sounds of *G. caspius subfuscus* agree well with all these characteristics.

The defensive sounds should have an aposematic function—to signal to a potential predator that the organism is venomous or unpalatable. The evidence is, however, scarce, indirect or controversial. Kirchner and Röschard (1999) showed that bumblebees chased away mice from their nests using hissing that should resemble snake hissing. West (1993) assumed that the stridulation of theraphosid spider is to warn coati from eating it due to release of urticating setae that can cause an extreme irritation. Alexander (1958) observed in a controlled experiment that hedgehogs refused to consume stridulating scorpions but the rat and mongoose ate it without hesitation.

Solifuges are not known to be unpalatable nor venomous. Therefore, they might imitate accoustically aposematic organism that shares the same habitat and has similar circadian activity. These are with two venomous viper species, *Macrovipera lebetina* (L.) and *Agkistrodon halys* Pallas, and few scorpions, such as *Mesobuthus eupeus* (C.L. Koch) and *M. caucasicus* (Nordmann). The vipers produce a strong hissing sound (Gans and Maderson 1973) but *Mesobuthus* scorpions have not been observed to produce defensive sound yet (McCormick and Polis 1990). Thus it appears that *G. caspius* solifuges imitate the sound of the vipers.

Who might be the receiver of the defensive stridulation in *G. caspius*? Solifuges have several different enemies, such as spiders (Gromov, unpublished), the great bustards (Zhatkonabayev, personal communication) and eagle owls (Birula 1938). However, as the defensive sounds are working at short distance only, it might be ineffective to birds. It is rather directed to epigeic predators, such as hedgehogs, reptiles and scorpions, which are all very common in the Kapshagay valley.

Stridulation in solifuges may have an intraspecific function as well. Many solifuge species exhibited frequently cannibalism in captivity (Cloudsley-Thompson 1977; Muma 1967; Hrušková-Martišová et al. 2007). The extent to which cannibalism occurs under natural conditions is not known (Punzo 1998), but it appears to be rare (Muma 1967). This suggests that the stridulation may reduce cannibalistic tendencies of solifuges in the nature. Since they are nocturnal, visual signals would be ineffective for mutual recognition, thus selection might have favoured the use of defensive acoustical signals for the intraspecific communication. The cannibalism observed frequently in captivity could be caused by the fact that the solifuges ceased to stridulate when brought to the laboratory.

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