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Sound production and chorusing behaviour in larvae of *Icosium tomentosum*

Communication

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Abstract: Substrate-borne vibrations produced by the larvae of non-lamiinae longicorn *Icosium tomentosum* Lucas, 1854 (Cerambycidae: Cerambycinae) are also emitted as loud sounds audible to humans. The vibrations consists of a long sequence of regularly repeated pulses at a rate of 8 pulses per second. The duration of the pulses are 0.061±0.009 s and the interpulse intervals are 0.065±0.015 s. The mechanism of vibration generation is the scraping by strongly sclerotised mandibles against the bark. Chorusing behaviour previously unknown in Cerambycidae larvae have been observed when the larvae feeding in the same or nearby branches starting to produce the audible vibrations in reaction to the vibrations of another larva.

Keywords: *Acoustics • Vibration • Chorusing • Behaviour • Defense • Larvae • Icosium • Cerambycidae • Coleoptera*

1. Introduction

Many beetles are able to generate diverse sounds by a few well-known mechanisms, such as stridulation, percussion or click mechanisms [1,2]. The reason for the sound or vibration emission in adult beetles is usually to attract and recognize one's own sexual partner, to demarcate and guard territory, or in defense against predators [3-5]. Less frequently, beetles use the sound as a component of social or subsocial behaviour or as an acoustic mimicry [1,6]. In contrast, the sound or substrate-born vibration production in beetle larvae, excluding that produced by feeding, is rare and has been documented in representatives of only few families [1,7]. The reason for beetle larvae song production, while not well understood, is generally associated with territorial behaviour [e.g. 1,8].

Sound production in larvae of Cerambycidae was observed and described by Leiler [9] in two species of lamiine longicorns (Cerambycidae: Lamiinae) – *Niphona pecticornis* Mulsant, 1839 and *Ceroplesis aestuans* (Olivier, 1795). The author assumed that the larvae emit the songs by knocking their heads with heavily sclerotised mandibles against the wall of the empty larval burrow. The substrate-borne vibrations produced by both species are emitted as sounds readily audible to humans from the distance of a few meters. Sound production has also been observed in two other species of the same subfamily - *Monochamus alternatus* Hope, 1842 [10] and *M. sutor* L., 1758 [8]. Both the authors established that the sound was produced by the scratching of mandibles against the beetle gallery walls. These authors discussed the significance of the larval sound production and suggested that it helps the larva secure resources by keeping away other potentially competitive larvae. Victorsson & Wikars [11] also observed cannibalistic behaviour among larvae of *M. sutor* when placed in close contact, which confirmed their assumption.

Sound production in the larvae of non-lamiinae longicorn is described for the first time in this contribution for the species *Icosium tomentosum* (Cerambycidae: Cerambycinae). The songs and the mechanism of their

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production are described and the possible significance is discussed.

2. Experimental Procedures

The larvae of *Icosium tomentosum* were collected by V. Kabourek (Zlín, Czech Republic) in Greece, Crete Island: Chania, Vrisses env., GPS N35°23'41'', E024°10'14 on 25th May 2007. The habitat is comprised of open woodlands dominated by *Cupressus* sp. trees of varying ages. The branches invaded by *I. tomentosum* were cut from a dry *Cupressus* tree with a trunk diameter of about 15-20 cm. The branches (diameter 4-8 cm, length to 50 cm) were placed in a well-ventilated insectarium where the larvae maintained until they hatched. All the larvae were in the last instar stages during the recordings and experiments.

The songs were recorded and analyzed as air-born vibrations (sounds) with a mini-disc recorder (SONY MZ-RH1) with condenser microphone (type MCE-2500). The response of the recording apparatus falls off between 40 Hz and 20 kHz. The sound had been recorded in wav format and processed on a PC using BatSound software ver. 3.31 (BatSound, Pettersson Electronics, Uppsala, Sweden). The temporal characteristics of the song were determined from the long-term laboratory recordings at a temperature of 24°C. The songs of larvae were recorded from the distance of 1-2 cm above the bark where the larva in the gallery had been located previously. The sound files of five different larvae were used for analysis. Sound characteristics were calculated from 100 individual songs, and the results of measurements are presented as the mean ± SD. Statistical analysis was performed using the software Microsoft Excel 2002 (Microsoft, Seattle, WA).

Two highly infected branches were used for detailed observations. The bark was removed from approximately one-half of each branch and was replaced by a transparent covering which permitted detailed visual observation of the larvae behaviour in the galleries. The interactions between larvae released into the same tunnel were easily observed in branches modified in this way.

3. Results

3.1 Sound structure and the mechanism of sound production

The sound produced by *I. tomentosum* larvae consists of a long sequence of repeated pulses in rate 8 pulses per sec, lasting as long as 3 min. The duration of the pulses were 0.061±0.009 s and the time between individual pulses (interpulse interval) was 0.065±0.015 s. The pulses have irregular structure with short gaps of different duration (Figure 1). The amplitudes of pulses within the songs also varied and the songs were composed of distinctive pairs of pulses with each even pulse being different from uneven. The results of the t-test show that there are significant differences in the maximum intensity of the even and uneven pulses (two-tailed paired t-test; $P<0.001$; $t=-11.301$; $df=49$), when the duration of the pulses are rather similar (two-tailed paired t-test; $P=0.42$; $t=-0.205$; $df=49$). The presence of differences in each pair of pulses reflects the mechanism of their production, namely, by scraping of mandibles in right and left directions (see section 3.2). The frequency of the song shows a band between 1-18 kHz with the main frequency between 3-5 KHz.

3.2 Induction of sound production and chorusing behaviour

Larvae produce the sounds within the air-filled space (tunnels) between the wood and bark. The mechanism of sound generation is the scraping by strongly sclerotised mandibles against the bark, when the larva moves with the first third of body in horizontal direction at an angle of 30°. The mandibles are outspread during the scraping. No special morphological adaptations associated with the the scraping were observed on the larvae mandibles. Pulses generated by scraping of mandibles in one direction show some distinct patterns by comparison with those generated in the opposite direction, so each even pulse is slightly different than the others (see Figure 1 and Discussion).

The larvae produced songs spontaneously, and independently ofthe time of day (studied only in laboratory conditions) and also as a direct response to some external stimuli. The stimulus could be knocking or scraping on the surface of the bark or wood, or some non-specific louder sounds, e.g. human voice. When the first larva starts to produce the sound, it is joined by other larvae; the simultaneous sound production by these animals is known as chorusing. Chorusing larvae usually occupy the same branch or other branches in close proximity up to 0.5 m (data not shown). The sounds of individual larvae are not synchronized during the chorusing.

3.3 Interactions between larvae

When a larva had been experimentally released into the tunnel occupied by another one, the domestic larva tries to push away the invader and attacks with open

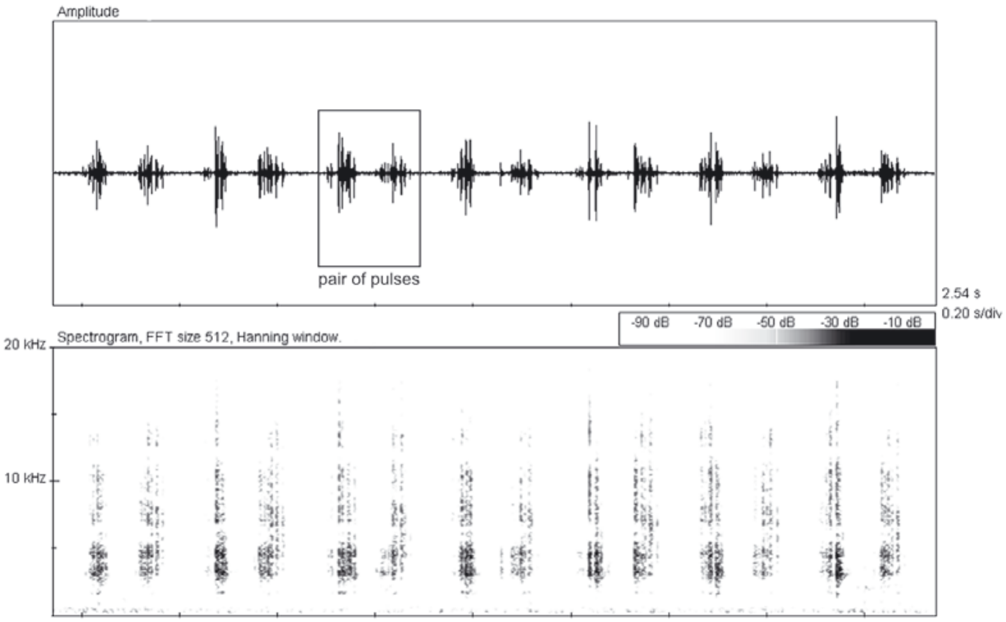

Figure 1. Oscillogram (relative amplitude *vs.* time in seconds) and spectrogram (frequency in kHz *vs.* time in seconds) of the song produced by larva of *Icosium tomentosum*; above - oscillogram, below – spectrogram. One pair of even and uneven pulse is indicated by the box. Recorded on 6 June 2008 at an air temperature of 24ºC.

mandibles, but not through the production of vibration signals. The invader larva usually tries to leave the tunnel (7 cases out of 10) and the domestic one follows the invader and bites it. In three cases, each of the larvae tried to bit its rival. When the invader larva could not exit the tunnel, the domestic one haunted the invader during each contact and finally killed it. The killed larvae were retained in the tunnel for one day, though cannibalism was not observed in any case. One observed interaction ended with death of both fighting larvae within 2 h.

4. Discussion

Sound production in larvae of Cerambycidae is a rare phenomenon described in only few species of lamiine longicorns (Cerambycidae: Lamiinae) [8-10]. Larvae probably emit the sounds by the scratching of mandibles (or other specialized sclerotized structures [12,13]) against the beetle gallery walls, although Leiler [9] assumed sound production occurred by knocking of the head against the wall of larval burrow. The song is propagated as substrate-born vibrations and simultaneously as air-borne sounds. The sounds are relatively loud and readily audible to humans from the distance of a few meters. The acoustics are favourable because of the thin bark remaining above the gallery which functions as a "drumhead" and the presence of resonant airspace within the larval galleries.

The songs have irregular structure with short gaps of different duration between individual pulses, which correspond to the mechanism of sound production (described above). The character of the sound and the individual pulses are influenced by the structure of the irregular inner bark surface, which is a consequence of the preceding larvae feeding. For that reason, high variability of individual pulses can be observed (see Figure 1). Pulses generated by scraping of mandibles in one direction shown some distinctive patterns compared to pulses generated in the opposite direction, so each even pulse is slightly different than uneven in relation to the character of the bark surface.

Victorsson and Wikars [8] suggested that *Monochamus sutor* larvae used sound production in territorial defense, signalling their presence to other larvae to avoid competition and cannibalism under the bark, when the food source (wood mass within the branch and especially the underbark) is limited and it can support only a limited number of beetle larvae. Saliba [14] showed that *Cerambyx dux* (Faldermann, 1837) larvae were able to move sharply in feeding galleries to avoid other larvae in close proximity and speculated that the more winding galleries in densely colonized regions (as compared with more straight ones where the larva worked alone) are a result of the larvae avoiding contact with each other by excavating their galleries in a direction from which no vibrations are registered. Larval cannibalism documented in some studies on cerambycid larvae [8,11,15,16, *etc.*] may have been a factor in reduced survival of larvae. Rose [15] reported that when *M. scutellatus* larvae density was high, particularly in earlier instar stages, cannibalism was the cause of considerably elevated mortality. The mortality caused by nonspecific bites was observed also in *M. alternatus* [11]. During the manipulative experiments with the larvae of *I. tomentosum* used in this study, cannibalism was not observed. However, if two larvae meet each other in a tunnel, the observed aggressive interaction usually ended with death of one or both fighting larvae. Larvae of many xylophagous Cerambycidae probably register the vibrations generated during the feeding of another larva, as well as deliberate vibration production, and avoid contact within their feeding galleries [8]. This territorial behaviour leads to the more equal distribution of larvae within the branch and prevents close encounters. How, then, does one explain the production of loud sounds and, especially, the chorusing? The loudness of the sound evidently does not decrease larval contacts, because it is not effective to warn potential competitors over long distances. The purpose of the sound production is probably not primarily the territorial behaviour. Simultaneous sound production can also aggravate the localization of the position of another larva.

A general disadvantage of acoustic communication is the fact that the signals are heard not only by nonspecific recipients but also by other species for those the signals were not primarily intended, namely, predators and parasites. Larvae of all long-horn beetles produce vibrations and sounds while moving inside the branches or eating the wood and predators and parasites can determine their location according to these vibrations [17]. Thus, for a beetle larva living under bark, it is hazardous to emit any loud sound.

Studies conducted in Australia [18] reported that two species of parasititoid wasps, *Syngaster lepidus* Brullé, 1846 and *Callibracon limbatus* (Brullé, 1846) (Hymenoptera: Braconidae), actively search the bark surface of eucalyptus logs and apparently located their wood-boring hosts by substrate vibrations associated with feeding. Some species of predatory or parasitoid wasps that search for concealed prey, including bark beetles and leafminers, have evolved specialized traits, such as modified antennae to tap on substrates to detect prey position through vibrational sounding [17,19-23, and others]. Likewise, their prey have evolved a sensory apparatus to detect the presence of their potential attackers and respond with defensive or evasive behaviours [24-26, and others]. The importance of sound or vibration in prey localization of hosts was illustrated by the brief period that wasps search for hosts in a log that contained no larvae [18]. Other important group of longicorn larvae predators that use the sounds for prey location are woodpeckers [8].

A very interesting phenomenon is the chorusing behaviour observed in *I. tomentosum* when the sound produced by one larva causes sound production of other larvae in the same and surrounding branches. One of the most plausible explanations could be an adaptation which reduces the rate of larvae localization by parasitoids and predators. Because parasitoids use vibrations to search for hosts [27,28], generating vibrations (substrate-borne as well as air-born) can be an effective tactic for disrupting or increasing the costs of the search process of parasitoids. The relatively loud sound extends across the dry branch to all directions, thereby obscures the exact location of the source of the sound for parasitoids and predators, especially when larvae produce the sounds at the same time from different positions within the branch. The startle effect of the loud scraping sound of many larvae on some predatory birds, especially woodpeckers, is speculative and may also be contradictory in that such birds might learn to utilize it to locate a highly infested tree from a long distance away.

More studies are clearly needed to fully understand the context and function of vibration-generating behaviour of *I. tomentosum*. In particular, experiments with real parasitoids and predators are required to confirm the possible functionality and the adaptive value of the transmitting vibrations.

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