

STINK BUG COMMUNICATION THROUGH PLANTS DURING MATING

KOMUNIKACIJA RASTLINSKIH STENIC PREKO RASTLIN MED PARJENJEM

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ABSTRACT

Stink bug communication through plants during mating

Different aspects of substrate-borne sound communication in stink bugs are reviewed. Vibrational communication follows aggregation on the same plant, enables mate location and together with other senses promotes species recognition and copulation. Stink bug vibratory signals produced by body vibrations are transmitted with low attenuation through green host plants which resonant frequency is tuned with signal spectral characteristics. This phenomenon enables communication through the same plant at the distance of up to several meters. Species specific male and female calling and courtship songs were recorded, analyzed and described in more than 20 species of the subfamily Pentatominae. Male-male vibratory interaction occurs during rivalry. All recorded vibratory emissions have similar frequency characteristics with the fundamental and dominant frequency around 100 Hz and harmonic peaks generally not exceeding 500 Hz. Species and sex specificity of signals is preserved in their amplitude modulation and time pattern. The subgenual organ, leg joint chordotonal organs and campaniform sensilla together with antennal mechanoreceptors constitute the receptor system which sensitivity exceeds the intensity of emitted signals for about 60 dB. Male vibrational directionality is enabled by resolution of the difference in the time of stimulation of leg receptors of different sites by female calling song signals.

Key words: Mating behaviour, vibrational communication, insects, Heteroptera, Pentatominae, insect-plant interactions.

IZVLEČEK

Komunikacija rastlinskih stenic preko rastlin med parjenjem

V članku so predstavljeni različni aspekti komunikacije rastlinskih stenic preko podlage. Vibracijska komunikacija sledi zbiranju stenic na isti rastlini in omogoča določanje položaja partnerja ter skupaj z drugimi čuti omogoča razpoznavanje vrste in kopulacijo. Vibracijski signali, ki jih rastlinske stenice proizvajajo s pomočjo nihanja telesa, se prenašajo z malo dušenja skozi zelene rastline gostiteljice, katerih resonančne značilnosti so uglasene s frekvenčnimi lastnostmi signalov. Zaradi tega lahko komunicirajo na isti rastlini na razdalji tudi nekaj metrov. Vrsto ter spolno specifične pozivne napeve in napeve dvorjenja so registrirali, analizirali in opisali pri več kot 20 vrstah poddružine Pentatominae. Do vibracijske interakcije med samci pride med rivalnim vedenjem. Vsi registrirani vibracijski signali imajo podobne spektralne lastnosti z osnovno in dominantno frekvenco okrog 100 Hz in z višjimi harmoničnimi vrhovi običajno pod 500 Hz. Vrstna in spolna specifičnost se ohranja v amplitudni modulaciji in časovnem vzorcu signalov. Subgenualni organ, kampaniformne senzile in sklepni hordotonalni organi skupaj z antenalnimi mehanoreceptorji sestavljajo senzorični sistem katerega občutljivost je približno 60 dB višja od intenzitete emitiranih signalov. Vibracijsko orientacijo samca omogoča razpoznavanje razlike v času draženja nožnih receptorjev različnih strani s signali pozivnega napeva samice.

Ključne besede: vedenje ob parjenju, vibracijska komunikacija, žuželke, Heteroptera, Pentatominae, interakcije med žuželko in rastlino.

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INTRODUCTION

Communication is a process of information exchange between sender and receiver. In the present review only »true communication« is discussed being defined as provision of information which is not accidental but benefits both the sender and receiver (BRADBURY & VEHRENCAMP 1998). Mating is a complex process running at different distances and in different media which determine whether visual, tactile, mechanic, chemical or signals of other modality will be employed. Technical problems limit investigations of many sensory modalities involved in communication. Nevertheless the study of insect communication is important because it plays the central role in animal societies, it can elucidate general evolutionary principles like signal optimization as the sign of the intensity and process of natural selection, together with morphological traits it can be used for taxonomic classification and finally it can be recruited as a solution to various practical issues.

The use of some type of mechanical disturbance propagating through medium like airborne near- or far field sound, substrate vibration, watersurface vibration or underwater sound is a most common form of communication between insects (GREENFIELD 2002). Among them the exchange of vibrational (substrate-borne sound, seismic) signals prevails whether counted by species, family or phylogenetic distribution (COCROFT & RODRIGUEZ 2005). 80% of families in which some or all species use one of the mentioned mechanical channels communicate also with vibratory signals transmitted through substrate and 74% of them use vibratory signals alone. It is estimated that 92% of such species (more than 195,000 taxa) use vibratory communication alone or together with other forms of mechanical signalling; again about 71% (150,000 species) communicate exclusively through substrate. These estimations (GREENFIELD 2002) are low because investigations of diversity of insect vibrational communication has been intensified only in the last decades with development of more precise and sensitive methods to record and analyse weak signals transmitted through tiny structures.

Phylogenetic distribution (phylogenetic tree from GULLAN & CRANSTON 2000) of mechanical signal modalities among insect orders demonstrates that Hemiptera represent the only group in which species communicate through air in the near- and far field, over surface or through water and through substrate (GREENFIELD 2002). First known descriptions of sound emission and sound producing mechanisms are known from the 18th century (RAY 1710, PODA 1761). The land-dwelling bugs Heteroptera (Geocorisae) represent the group of Hemiptera with most investigated vibrational communication (ČOKL & VIRANT-DOBERLET 2003, GOGALA 2006). The aim of the review is to describe different aspects of stink bug communication through green plants which represent their usual substrate on which they feed and mate.

The family Pentatomidae (stink bugs) is one of the largest families within

Heteroptera, occurs worldwide and includes a large group of phytophagous and predaceous species. It is estimated that among 36,096 described Heteroptera species 4,123 of them belong to Pentatomidae. Their general biology, distribution, taxonomy and economic importance are described in detail by MCPHERSON & MCPHERSON (2000) and PANIZZI et al. (2000). The family Pentatomidae together with several other families like Cydnidae, Thaumastellidae, Parastrachiidae, Tessarotomidae, Scutelleridae, Plataspidae, Acanthosomatidae, Piesmatidae, Lygaeidae *sensu lato* and Colobathristidae belongs to the superfamily Pentatomoidea (infraordo Pentatomorpha) (FREEMAN 1940, SCHAEFFER 2003). In all of them the presence of vibrational communication has been identified and described at different levels.

Pentatomidae include eight subfamilies: Asopinae, Cyrtocorinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae and Serbaninae (SCHUH & SLATER 1995). Members of the largest subfamily Pentatominae are entirely plant feeders and many of them are economically important pests feeding on different crops.

The southern green stink bug (*Nezara viridula*) represents a model species among Pentatominae with intensively investigated substrate-borne communication at different levels (ČOKL & VIRANT-DOBERLET 2003, VIRANT-DOBERLET & ČOKL 2004). The species originates from eastern Africa (HOKKANEN 1986, JONES 1988, KAVAR et al. 2006) and occurs now throughout the tropical and subtropical regions of all the continents (TODD 1989). The species is highly polyphagous attacking mono- and dycotyledonous plants. By inserted stylet into the food source they suck up nutrients and cause injury to plant tissues resulting in plant wilt and, in many cases abortion of fruits and seeds. More than 145 species of 32 plant families have been identified as species hosts (KIRITANI et al. 1965, TODD 1989, PANIZZI 1997); however a preference for leguminous plants has been reported (PANIZZI 1997). During the year the southern green stink bug can be found on different plants and none of them was identified so far as specific for mating. In the United States the species feeds and mates in clover, small grains, early spring vegetables, corn, tobacco and weed hosts where they complete the first generation. The second generation is completed on leguminous weeds, vegetable and row crops, cruciferous plants, and okra as typical mid-summer hosts. The third generation migrates into soybean where the fourth and the fifth generations are completed (TODD 1989). Similar migrations have been described in Parana State (Brazil) (PANIZZI 1997). 57 parasitoid species have been recorded for *N. viridula* (JONES 1988), various arthropod predators feed on it (TODD 1989) and substantial kill of *N. viridula* by birds in Argentina has been described (BELTZER et al. 1988).

BEHAVIOUR AND COMMUNICATION DURING MATING

Mating behaviour was first described in two pentatomine species *Cosmopepla bimaculata* (Thomas) and *Chlorochroa ligata* (SAY) (FISH & ALCOCK 1973) and the same pattern was later confirmed for *N. viridula* by several authors (HARRIS et al. 1980, BORGES et al. 1987, KON et al. 1988, OTA & ČOKL 1991, ČOKL et al. 2000). Chemical and vibratory signals play the key role during calling and courting. Male emitted pheromone was

described in genera *Nezara* (ALDRICH et al. 1989, ALDRICH 1995, MCBRIEN & MILLAR 1999), *Eushistus* (ALDRICH et al. 1991), *Acrosternum* (MCBRIEN et al. 2001), *Thyanta* (MCBRIEN et al. 2002), *Chlorochroa* (HO & MILLAR 2001a, 2001b), *Biprorulus* (JAMES et al. 1994), *Plautia* (SUGIE et al. 1996) and *Piezodorus* (LEAL et al. 1998). Vibratory signals were described in more than 20 species. Although pheromones and vibratory signals are species specific they do not isolate species completely. High interindividual variation in pheromone composition has been reported for *N. viridula* (RYAN et al. 1995) and in some southwestern regions in Japan interspecific copulation occurs between *N. viridula* and the oriental green stink bug (*Nezara antennata* SCOTT) (KIRITANI et al. 1963, KON et al. 1993).

Male *N. viridula* sex pheromone attracts females (PAVIS & MALOSSE 1986, ALDRICH et al. 1987, BORGES et al. 1987, BREZOT et al. 1994). Pheromone specificity is achieved by the ratio of trans- to cis-(Z)- α -bisabolene epoxide which is different among geographically isolated populations (ALDRICH et al. 1989, 1993). *Acrosternum hilare* (SAY) males emit the same compounds as *Nezara*, but with the reversed relative abundances of the epoxide isomers (ALDRICH et al. 1989). Furthermore the blend of male volatiles of *A. pennsylvanicum* is almost the same as that of Japanese *N. viridula*.

The male pheromone is produced and released continuously starting 8-10 days after the final moult in *N. viridula*. Mating decreases pheromone emission (BREZOT 1994) and stimulation with the conspecific female calling song increases both the percentage of males releasing pheromone and its amount (MIKLAS et al. 2003a). The latter reaction is song specific: stimulation with the male rival song has no effect and the amount of released pheromone decreases by stimulation with 100 Hz pure tone. By modulation of pheromone release males reduce metabolic costs, attract less their parasitoids and they offer a better synchronization of sexual activity.

Chemical signals are effective as sex attractants on a long range scale but wind and local air turbulences prevent precise mate location on a plant. Substrate transmitted signals offer a better choice. They have been described in *Acrosternum hilare* (SAY) (ČOKL et al. 2001), *Acrosternum impicticorne* (STAHL) (BLASSIOLI-MORAES et al. 2005), *Eushistus heros* (FABRICIUS) (BLASSIOLI-MORAES et al. 2005), *Eushistus conspersus* UHLER (MCBRIEN & MILLAR 2003), *Holcostethus strictus* (FABRICIUS) (PAVLOVČIČ & ČOKL 2001), *Murgantia histrionica* (HAHN) (ČOKL et al. 2004), *Nezara antennata* SCOTT - (KON et al. 1988), *Nezara viridula* (LINNAEUS) (ČOKL et al. 2000), *Palomena prasina* (LINNAEUS) (ČOKL et al. 1978), *Palomena virridissima* (PODA) (ČOKL et al. 1978), *Piezodorus guildinii* (WESTWOOD) (BLASSIOLI-MORAES et al. 2005), *Piezodorus lituratus* (FABRICIUS) (GOGALA & RAZPOTNIK 1974), *Thyanta custator accerra* MCATEE (MCBRIEN et al. 2002), *Thyanta pallidovirens* STAHL (MCBRIEN et al. 2002) and *Thyanta perditor* (FABRICIUS) (BLASSIOLI-MORAES et al. 2005). Unpublished data also exist for *Eysarcoris aeneus* (SCOPOLI), *Graphosoma lineatum italicum* (LINNAEUS), *Aelia acuminata* (LINNAEUS), *Raphigaster nebulosa* (PODA), *Sciocoris cursitans* (FABRICIUS) and *Eurydema oleraceum* (LINNAEUS) (GOGALA 2006).

The calling phase of mating behaviour runs at distances at which other senses are not employed. In most (but not all) cases a female starts vibrational communication and there are no experimental data to show which signals trigger them to sing in natural conditions.

During calling a female *N. viridula* remains at the same place on a plant. The male *N. viridula* emits on the other hand its calling song during movement. The female calling song is emitted continuously also in the absence of a male and the stable time and frequency structure of the song is preserved during the whole singing period (ČOKL & BOGATAJ 1982). A typical male response to female calling is directional movement to her (ČOKL & OTA 1991, ČOKL et al. 1999, VIRANT-DOBERLET et al. 2006), increasing of pheromone release and emission of the calling or courtship song. No direct female response to male calling song has been observed so far.

Female calling song signals mediated male vibrational directionality, as described in *N. viridula* (OTA & ČOKL 1991, ČOKL et al. 1999, VIRANT-DOBERLET et al. 2006), is lacking in small pentatomine bugs like *Holcostethus strictus* (FABRICIUS) (PAVLOVČIČ & ČOKL 1991) and *Murgantia histrionica* (HAHN) (ČOKL et al. 2004). The role of female singing is minimized in both species and the calling phase of mating behaviour is significantly shorter.

Male songs have been described in most investigated stink bug species but its role in a duet with a female needs to be experimentally confirmed. It appears also as a transitional form from courtship to rival singing. The latter male-male vibratory interaction is present when more males are calling or courting one female.

Although communication in the courtship phase of behaviour runs at distances where different senses are potentially involved experimental data about the role of vision, touch, near field sound or chemical signals are lacking. In two congeneric species *N. antennata* and *N. viridula* mates first approach by waving antennae up and down and when close they antennate each other (KON et al. 1988). In both species females usually first antennate males indicating that male emitted chemical signals are also involved. When a male antennates a female first he can enter the next phase of the behavioural sequence without her response. After antennation a male moves to the rear of the female and puts his head under her abdomen butting its venter. When a female accepts a male for copulation she rises the abdomen and the male turns facing away from her. The male rises the abdomen with extended aedeagus and by sweeping the aedeagus in a zigzag pattern against the venter of the abdomen he attempts to copulate. When genital linkage is achieved both lower their abdomen. Shaking of the body from side to side was described frequently in response to female antennation in male *N. antennata* (KON et al. 1988) and was observed also in *N. viridula* (ČOKL, unpublished data). Antennation and shaking of the body elicit tactile signals as well as air particle movement in the near field. Trichobotria are sensitive enough to detect the latter signals (BARTH 2002). The female thus accepts or rejects a male by synthesis of multimodal information including visual and chemical signals. The lack of experimental data on multimodal communication in close range is caused mainly by technical problems connected with recording, analyzing and reproducing such signals in the relevant behavioural context.

Male and female courtship songs of most investigated pentatomine species are more species specific than their calling songs. Specificity was determined on statistically verified differences between signal time and frequency parameters but the impact of the substrate on these characteristics was in most cases ignored. Investigations of signal recognition conducted on *N. viridula* in artificial surroundings (ČOKL et al. 1978) need critical

revision in the view of new data on plant-insect interaction during substrate-borne sound communication.

EMISSION OF VIBRATORY SONGS

Stink bugs produce vibratory signals by body vibration; no other sound producing mechanisms have been described so far. The fundamental frequency of their songs ranges between 70 and 180 Hz and as a rule, harmonic peaks do not exceed 500 Hz. Similar fundamental and dominant frequency values were measured for signals recorded from the body of a singing bug by a laser vibrometer (ČOKL et al. 2005) or piezo-crystal (AMON 1990), from surface of a non-resonant loudspeaker membrane (ČOKL & VIRANT-DOBERLET 2003) or from resonating plant surface (ČOKL et al. 2004, 2005) or from signals recorded as airborne sound (ČOKL et al. 1972, 1978, KON et al. 1988).

The intensity of vibratory signals was measured by laser vibrometer from abdomen, wings and prothorax of a singing bug as well as from the plant surface immediately below (ČOKL 1988, OBLAK 2002). Velocity values measured on abdomen varied individually between 9 and 31 mm/s, on prothorax between 4 and 16 mm/s and on wings between 7 and 25. Intensity values recorded from the plant surface below the singing bug (distance less than 0.5 cm) varied individually between 3 and 18 mm/s on bean leaf, between 2 and 10 mm/s on bean stem, and between 1 and 14 mm/s on cyperus stem. In 15 of 20 tested bugs signals were attenuated by transmission from the body to the substrate and in the rest 5 they were amplified. Comparison of fundamental and dominant frequencies did not show significant differences between signals recorded from different parts of the body and between body and plant recorded signals. The body thus vibrates as a unit and in phase with the substrate without any filtering in the fundamental and dominant frequency domain.

The low frequency vibratory signals are produced by vibration of abdomen versus thorax as consequence of contraction of muscles connecting the abdominal tergal plate with thorax at one and with the rest of abdomen at the other side (KUŠTOR 1989, GOGALA 2006). Similar sound producing mechanism was described in *Riptortus clavatus* (Alydidae) (NUMATA et al. 1989). The anatomy of the green stink bug skeletal motor mechanism with vibration producing muscles was described by MALOUF (1932) and KUŠTOR (1989). The last part of the first tergum and second abdominal tergum are fused into a plate previously called tymbal (GOGALA 1984). The tergal plate is connected by a thin chitinous membrane anteriorly to thorax and posteriorly to the third abdominal tergum. The medial part of the plate is narrow and thin compared with broader lateral parts. A pair of strong tergal longitudinal muscles (TLI) connects the metaphragma of thorax with the median part of the plate antecostal ridge and their contraction moves the plate anteriorly. The plate is moved posteriorly by contraction of another set of tergal longitudinal muscles (TLII) fixed on the plate ridge anteriorly and posteriorly on the anterior edge of the third abdominal tergum. Two pairs of lateral compressor muscles (LCrI and LCrII) and one pair of the depressor tymbali muscle (DrTy) are laterally fixed on the tergal plate.

The activity of muscles during singing was recorded by copper wire electrodes implanted into TLI, TLII and LCrI muscles (KUŠTOR 1989, AMON 1990); LcrII muscles did not contract during singing and due to delicate position of the DrTy muscles their electromiograms could not be recorded in freely moving bugs. The muscles contract synchronously and in phase. The one-to-one relation was recorded also between muscle potentials and vibration cycles of body or substrate recorded signals. Muscle potentials were recorded extracellularly and the amplitude of summed potentials can be correlated with the corresponding cycle amplitude. The repetition rate of muscle potentials determines the repetition rate of evoked cycles of the vibratory emission so that any frequency modulation is based on the modulated repetition rate of action potentials controlling contractions of corresponding muscles.

TIME AND FREQUENCY CHARACTERISTICS OF STINK BUG SONGS

According to behavioural contexts songs are usually determined as calling, courtship and rival songs. In the last years these names are frequently replaced by abbreviations of the succession number of song appearance in communication like MS1 (male song appearing first), MS2 (male song emitted after MS1) etc. To avoid differences which may occur as potential feed-back caused by substrate resonance we compare only frequency and time characteristics of signals recorded from bugs singing on a non-resonant substrate (loudspeaker membrane).

Frequency characteristics

Frequency characteristics of all until now recorded stink bug vibratory signals reveal similar position of the fundamental (and usually dominant) frequency and a different number of higher harmonics with variously expressed frequency modulation. The dominant frequency lies generally in the frequency range between 70 and 180 Hz and the main emitted energy with distinct harmonic spectral peaks lies with few exceptions below 500 Hz.

The position of the fundamental and dominant frequency varies individually, between populations of the same species and between different congeneric species (ČOKL et al. 2000, MIKLAS et al. 2003, BLASSIOLI-MORAES et al. 2005). The dominant frequency of the female calling song of *N. viridula* lies around 94 Hz for the Slovene population, around 123 Hz for the Florida population, around 133 Hz for the Guadalupe and around 108 Hz for the French population. Different parts of a complex songs can have different dominant frequencies like in the first female song of *A. impicticorne* in which the fundamental and dominant frequency of the long pulse lies around 125 Hz and around 100 Hz for the short pulse. The same male *A. impicticorne* emits different songs with different dominant frequencies (rival song has the dominant frequency of around 107 Hz and the second song around 130 Hz) and changes it from around 130 Hz when singing alone to 92 Hz when singing in a duet. Despite of intra-species differences some species can be differentiated from others by the dominant frequency range of their songs. Mean values range between 136 and 173 Hz in *E. heros* and between 79 and 122 Hz in *T. perditor*. The range of do-

minant frequencies between 102 and 136 Hz is the same for the consperse bug *E. conspersus* (MCBRIEN & MILLAR 2003) and for different songs of *T. pallidovirens* and *T. custator accerra* (MCBRIEN et al. 2002). There are no experimental data supporting correlation of the dominant frequency with the body size.

Harmonic, not dominant peaks (amplitudes less than 60 dB below the dominant frequency value) of vibratory signals recorded on non-resonating loudspeaker membrane are generally restricted to the frequency range below 500 Hz. One of very few exceptions are for example pulses of the *N. viridula* broad-band male calling song or the female repellent song (ČOKL et al. 2000).

Within the limited frequency range spectra of narrow band low frequency signals can be expanded either by a combination of spectrally different units within the same signal or by frequency modulation. The female calling song pulse train of the southern green stink bug is for example composed of one or more frequency modulated prepulses of broad band and higher frequency characteristics, followed by a narrow band longer pulse (ČOKL et al. 2000). The first female song pulse train of *A. impicticorne* is composed of short and long pulses which dominant frequencies differ significantly (BLASSIOLI-MORAES et al. 2005). Extensive frequency modulation has been recorded in several pentatomine species like *P. lituratus* (GOGALA & RAZPOTNIK 1974, BRVAR 1987, GOGALA 2006) or *Thyanta* spp. (MCBRIEN et al. 2002).

The role of frequency characteristics for signal recognition has been studied in *N. viridula* (ČOKL et al. 1978) and in *P. lituratus* (BRVAR 1987). Male *N. viridula* responds to synthesized female calling song of frequencies between 50 and 200 Hz with optimal alternation between 100 and 150 Hz. Males respond with the rival song to the opponent rival in natural (GOGALA & RAZPOTNIK 1974) and in an artificial situation (BRVAR 1987, GOGALA 2006). Male rival song with frequency modulation reversed according to the natural signal did not evoke the rival but another male song. Increasing or decreasing the dominant frequency significantly depressed male responding. Increasing the number of higher harmonics in stimulatory rival song evoked mainly the rival and in less cases other male songs. Different types of male songs were evoked also by stimulation with signals of lower or higher dominant frequency accompanied by several higher harmonics. On the other hand stimuli with damped dominant frequency and several higher harmonics did not evoke responding in stimulated males.

Time characteristics

Female calling songs

The female calling song described in *A. hilare*, *A. impicticorne*, *E. conspersus*, *E. heros*, *M. histrionica*, *N. antennata*, *N. viridula*, *P. prasina*, *P. viridissima*, *T. custator accerra*, *T. pallidovirens* and *T. perditor* are characterized by long sequences of readily repeated pulses (or pulse trains) of stable duration. In *N. viridula* pulse trains composed of different number of pulses can be exchanged in the same sequence (ČOKL et al. 2000). Pulse train duration of female songs of the above mentioned species ranges between 0.2

and 1.6 s and repetition time (the time between onsets of two consecutive signals) between 0.4 and 2.0 s. In species with smaller body size like *H. strictus* and *P. guildinii* the female calling differs significantly. Several seconds long first female song pulses are irregularly repeated in *P. guildinii* and about 50 ms long pulses repeated every 0.3 s evoked by male singing constitute the *H. strictus* female calling song pulse train.

Regular stereotypic male responses to the female calling song inspired several investigations on the informational value of different song parameters. Responding to artificial stimuli with duration and repetition rate outside the conspecific female calling song characteristics explain male *N. viridula* responding also to stimulation with the natural female calling song of *Palomena prasina*, and mutual responding of males of both *Palomena* species to the female calling song of the sympatric species (ČOKL et al. 1978). *Nezara viridula* males responded stereotypically (directional movement and emission of the courtship song) also to *Thyanta* spp. songs which resembled time characteristics of the conspecific female calling song (HRABAR et al. 2004). Signal duration differences occurring during transmission through a plant (MICHELSEN et al. 1982) have to be respected in investigations of the informational value of signals transmitted on longer distances. MIKLAS with co-workers (2001) demonstrated that male *N. viridula* differentiated conspecific female calling song pulse trains of two types on a non-resonating loudspeaker membrane but not on a plant.

Male calling songs

Stink bug male first emitted songs are less fixed to the calling phase of mating behaviour. The song appears less frequently as first in several species like *N. viridula* but regularly in *H. strictus* (PAVLOVČIČ & ČOKL 2001) and *M. histrionica* (ČOKL et al. 2004). The male first song of *P. guildinii* (BLASSIOLI-MORAES et al. 2005) is emitted as the first in a couple after antennation by a female. In *P. lituratus* no female but eight different male songs were described (GOGALA & RAZPOTNIK 1974, BRVAR 1987). The species song repertoire needs reinvestigation in natural conditions to confirm the absence of female signalling and to determine the behavioural context of such a diversity of male songs. Male consperse bugs *E. consperus* started to sing first in a couple in 46% either with the MS-3 or MS-1 song (MCBRIEN & MILLAR 2003). The first male song is composed of around 0.5 s long pulses repeated every 0.7 s when emitted without female responding and of around 0.3 s duration when singing in a duet with a female. The first male song of the Neotropic relative *E. heros* is emitted always as response to the calling female and single pulses are the transitional form to fully developed MS-1 pulse trains of various duration and repetition time.

The male calling song of *N. viridula* is characterized by a sequence in which narrow band 0.08 to 0.26 s long pulses are exchanged with 0.07 to 0.15 s long broad-band (and frequency modulated) pulses grouped into pulse trains (ČOKL et al. 2000). The repetition time varies between different populations between 0.15 and 0.45 s for the broad-band and between 0.43 and 1.2 s for the narrow-band pulses. The song rarely appeared as first on a loudspeaker membrane on which males usually immediately respond with the courtship song to the calling female probably as consequence of limited space where signals of other

modalities are immediately available. On a plant the male calling song is emitted during walking and there are no data about any direct female response to it. Furthermore, the song appears as transitional form to the male courtship song or from the courtship to the rival song. Similar temporal pattern of the male calling song was recorded and described for both *Palomena* species (ČOKL et al. 1978) as well as for the sympatric *N. antennata* (KON et al. 1988) with the main difference in the lower pulse repetition rate.

The second male song of *A. hilare* has temporal characteristics similar *N. viridula* but is emitted during courtship (ČOKL et al. 2001). The complex pulse train of *A. hilare* first male song lasts about two seconds with the repetition rate determined by female calls. Male calling song pulses of both *Thyanta* species last between 0.3 and 0.5 s and are repeated every 0.7 or 1.1 s in *T. pallidovirens* and *T. custator accerra* respectively. The first male song of the Neotropical species *T. perditor* is triggered by female calling but is emitted also if the female was removed (BLASSIOLI-MORAES 2005). Contrary to most stink bug species the song with several seconds long and irregularly repeated pulse trains does not carry calling song characteristics.

Female courtship songs

The several seconds long pulses of the second female song of *N. viridula* are emitted during courtship and carry many characteristics of the male courtship song (ČOKL et al. 2000). The song does not appear as regularly as in males and in many cases a female copulates without its emission. A comparable song but with different time characteristics has been described in *N. antennata* (KON et al. 1988).

Female courtship songs were described also in *T. pallidovirens* and *T. custator accerra* (MCBRIEN et al. 2002). Three to four seconds long pulse trains are in both species repeated irregularly and mainly in duets with courting males. Less clear is the role of the second female song of the Neotropical relative species *T. perditor* (BLASSIOLI-MORAES et al. 2005). Longer pulse trains are emitted in the absence than in the presence of a male. The second female song of another Neotropical species *E. heros* is composed of irregularly repeated and several seconds long pulse trains of extensive amplitude modulation (BLASSIOLI-MORAES et al. 2005).

The time pattern of the female courtship song of *H. strictus* differs from the above mentioned examples (PAVLOVČIČ & ČOKL 2001). Pulse trains are emitted together with male courtship song signals and partly overlap each other. Duration of the pulse train varies extensively between 2 to 85 s according to different number of about 0.2 s long pulses repeated approximately twice per second.

No female courtship songs have been recorded in *P. prasina* and *P. viridissima*. In *A. hilare* females emit only the calling song (ČOKL et al. 2001) and in the Neotropical species *A. impicticorne* the second female song appears also in the absence of a male indicating that this song is either another form of the calling song or has a role not directly connected with courtship (BLASSIOLI-MORAES et al. 2005). Clearly separated 1-2 s long pulse trains are composed of pulses which are repeated regularly approximately every 3 s when singing alone or every 5 s when singing in a duet. Such a time pattern is characteristic for the second (pulsed) type of the female calling song pulse trains in *N. viridula* (ČOKL et al.

2000). Females of the consperse bug *E. conspersus* emit the second song type spontaneously in contrast with other stink bug species (MCBRIEN & MILLAR 2003). In genus *Piezodorus* the second female song was recorded in the Neotropic species *P. guildinii* in the male absence (BLASSIOLI-MORAES et al. 2005).

Male courtship songs

High species specificity of male courtship songs is expressed in the time pattern and amplitude modulation of pulses constituting complex and several seconds long pulse trains which repetition rate is determined by the singing female.

The male courtship song of *N. viridula* has its origin in the calling song pulses which repetition rate increases to fuse in the most part of the signal (ČOKL et al. 2000). Single pulses at the onset of the pulse train disappear in fully developed alternations with the female. The pulse train lasts about 3 s and is usually followed by a 0.1 s long frequency modulated post-pulse. In the sympatric *N. antennata* species from Japan (KON et al. 1988) the AM-2 song of different characteristics is emitted during female approach, antennation and butting.

The southern green stink bug (*N. viridula*) lives together with different pentatomine species. Similarity in the time pattern of the male courtship song is obvious by comparison with *E. heros* and *T. perditor*. In both, single pulses are fused into a several seconds long pulse train with constant amplitude (BLASSIOLI-MORAES et al. 2005) throughout most of the signal in the former and with increasing amplitude of fused pulses in the latter species. Male songs of other two *Thyanta* species emitted during courtship differ: in *T. pallidovirens* pulses within a pulse train are not completely fused and their amplitude decreases throughout the signal while in *T. custator accerra* the origin from single pulses can not be observed in extensively amplitude modulated and several seconds long MS-2 signals (MCBRIEN et al. 2002). The courtship song (MS-2) of *E. conspersus* represents an exception among all until now investigated stink bugs songs being characterized by short about 0.5 s long pulses of repetition rate about 0.7 s (MCBRIEN & MILLAR 2003).

The first male song (MS-1) of *A. hilare* is the usual response to female calling and shows similar basic pattern as the male courtship song of *N. viridula*. The amplitude of pulses increases and remains at the same level through the signal in *N. viridula* while in *A. hilare* the amplitude of single pulses at the onset of the pulse train remains constant but the amplitude of the fused part decreases (ČOKL et al. 2001). The *A. hilare* second male song (MS-2) emitted prior to copulation silences the female. Its time characteristics are similar to those of the male calling song of *N. viridula* but the behavioural context of the song is completely different. Pulse trains of the of *Nezara* Neotropic sympatric relative *A. impicticorne* have similar duration but pulses are not completely fused (BLASSIOLI-MORAES et al. 2005).

Palomena prasina and *P. viridissima* are sympatric with *N. viridula* and their song repertoire differs mainly at the level of male courtship songs (ČOKL et al. 1978). In *P. prasina* pulses of the MS-2 pulse train are completely separated and in *P. viridissima* the pulse train is composed characteristically of four pulses separated from each other with pause decreasing from the first to the last one. Contrary to many male songs described in

P. lituratus (GOGALA & RAZPOTNIK 1974, BRVAR 1987) no male song was recorded in connection with courtship behaviour in *P. guildinii* (BLASSIOLI-MORAES et al. 2005).

A different pattern of male songs was described for the harlequine bug *M. histrionica* (ČOKL et al. 2004). The first male song is composed of about 10 s long pulse trains repeated with a low rate when a male is far from a female. When coming closer males emit the second song of a very complex pulse train structure. The pulse trains of the male courtship song of *H. strictus* are repeated irregularly and are composed of three different types of pulses of which the first and the second one last around 0.05 s and the third one around 0.4 s (PAVLOVČIČ & ČOKL 2001).

In *M. histrionica* two more male songs were described during courtship as MS-3 and MS-4 (ČOKL et al. 2004). Their behavioural context is not clear. More male songs emitted during courtship and prior to copulation have been described also in *N. antennata* (KON et al. 1988), *N. viridula* (ČOKL et al. 1972), *E. conspersus* (MCBRIEN & MILLAR 2003) and *T. custator accerra* (MCBRIEN et al. 2002). Their temporal pattern is rather uniform characterized by irregular sequences of less than 0.5 s long pulses repeated several times per second with a highly variable repetition rate. During emission of these songs a female usually stops singing and accepts or rejects a courting male.

Male rival songs

Rival songs were recorded only in males when more of them were courting one female. They were described in *A. impicticorne*, *E. heros*, *P. guildinii*, *T. perditor* (BLASSIOLI-MORAES et al. 2005), *N. viridula* (ČOKL et al. 2000), *P. lituratus* (GOGALA & RAZPOTNIK 1974, BRVAR 1987), *M. histrionica* (ČOKL et al. 2004) and in *Raphigaster nebulosa* (unpublished data). In fully established rivalry, pulses are exchanged in a true a-b-a-b-a... fashion until the winning male silences the other(s). During rivalry the female usually stops singing. Contrary to high diversity of the first (calling) male song the time parameters of the rival song show higher uniformity and low species specificity. Rival song consists of single pulses which duration varies between 0.2 (*N. viridula*) and 1.3 s (*A. impicticorne*) with repetition time between 0.7 (*N. viridula*) and 1.6 s (*P. guildinii*). Extensive male-male interactions of *P. lituratus* need reinvestigation.

Other songs

The female repelling signal of *N. viridula* was recorded as a broad-band and several seconds long vibration without any characteristic time pattern (ČOKL et al. 2000). Although the main emitted energy lies below 100 Hz a secondary (harmonic?) peak between 600 and 700 Hz was recorded as well. Signal producing mechanism is not clear because it was frequently recorded simultaneously in the same sequence with signals produced by body vibration. The song silenced courting males immediately and was emitted when females refused male attempts for copulation.

In *A. hilare* a copulatory song was recorded several minutes after copula was established (ČOKL et al. 2001). It is not clear whether signals were emitted by a male or a female. The song is composed of low frequency (dominant frequency between 92 and 129 Hz) about 0.04 s long pulses repeated approximately every 0.2 s. The male copulatory

song was described also in *H. strictus* (PAVLOVČIČ & ČOKL 2001) as a sequence of vibrations of very irregular temporal structure.

Eushistus heros males emit a different song during head butting or following an unreceptive female (BORGES et al. 1987, BLASSIOLI-MORAES et al. 2005). The song is composed of irregularly repeated pulse trains consisting of a different number of about 0.05 s long pulses repeated every 0.2 s. The song determined as MS-3 was accompanied by female first emitted song. A similar song was (MS-3) recorded before copulation in *T. perditor* silences the female (BLASSIOLI-MORAES et al. 2005).

We can expect in the future new data on informational value of vibrations emitted during activity other than singing. Among first deserve attention the low frequency tremulatory signals and almost pure tone signals produced by trembling of wings.

VIBRATIONAL RECEPTORS

Because of stink bug small size has the airborne component of body produced vibrations low intensity in the relevant frequency range. To radiate efficiently airborne sound the diameter of the vibrating body has to be at least one third of the wavelength of the emitted sound (MARKL 1983); in practice it means that stink bugs of the size usually below 1 cm can not produce efficiently sounds of frequencies below 10 kHz. Like many other insects (GOGALA et al. 1974, MICHELSEN et al. 1982) stink bugs use the substrate-borne component for communication. Although the most sensitive receptors are situated in and on the legs we can not exclude that other mechanoreceptors are involved as well.

DEBASIEUX (1938) described leg vibrational receptors in *Pyrrhocoris apterus* and DEVETAK et al. (1978) in *Sehirus* species. Anatomy (MICHEL et al. 1983) and function (ČOKL 1983) of the leg vibrational receptors with a few identified higher order neurons (ČOKL & AMON 1980) has been investigated only in *N. viridula*. Data on vibrational receptors in Heteroptera were recently reviewed by ČOKL and co-workers (2006).

All the six legs of the southern green stink bug are equipped with a lower number of non-grouped campaniform sensilla at the surface, with the subgenual organ inside the haemolymph channel and with joint chordotonal organs. The subgenual organ, situated in the haemolymph channel in the subgenual (proximal) part of tibia (MICHEL et al. 1983) is composed of two scolopidia, each of them with one sensory cell. The body of the organ is proximally fixed to the epithelium of the haemolymph channel wall whereas the scolopals with cilia and ligament are stretched out in haemolymph. The sensory nerve with axons of both sensory cells joins the nerve innervating the femoral chordotonal organ. Distally, the ligament formed by two cap cells flattens into a thin flag-like structure which is only loosely fixed at the epidermis of the blood channel wall and at both main tibial nerves.

Chordotonal organs controlling the position of the joint and detecting the angular velocity during joint movement were described in *N. viridula* in femur (the femoral chordotonal organ), tibia (the tibial distal chordotonal organ) and in the last tarsal joint (the tarso-pretarsal chordotonal organ) (MICHEL et al. 1983). They are sensitive to low fre-

quency vibration of the leg and as such contribute in sensing of low frequency components of stink bug vibratory signals (ČOKL 1983). The femoral chordotonal organ is situated in the lateral distal third of femur at its anterior ridge and controls the joint between femur and tibia. The organ is divided into the anatomically distinct condensed and dispersed scoloparium. Each of the twelve scolopidia of the organ contains two sensory cells. Their axons form the sensory nerve branch which joins the subgenual organ sensory nerve and reaches the main leg nerve in the posterior part of femur close to the femur-trochanter joint. The proximal condensed scoloparium contains eight scolopidia and the distal dispersed scoloparium four. The body of the condensed scoloparium is fixed to the wall. Cap cells of the proximal three scolopidia form a ligament which is attached to the *musculus levator tibiae*. The other five scolopidia of the condensed scoloparium form a separate ligament which is distally fixed directly to the apodeme. Four scolopidia of the dispersed scoloparium were identified and described within this ligament.

The other joint chordotonal organs are composed of a lower number of scolopidia with less complex anatomy. The tibial distal chordotonal organ controls the joint between tibia and tharsus and lies in the blood channel about 400 μm proximally to the joint. The ligament formed by cap cells of both scolopidia (one with one and the other with two sensory cells) is attached to the joint membrane between tibia and the first tarsal joint. Sensory cells are fixed to the dorsal side of *nervus tibialis anterior*, their dendrites separate from the nerve and scolopals are freely stretched in the blood channel. Axons of sensory cells join other nerve fibers of the *nervus tibialis anterior*. The tarso-pretarsal chordotonal organ controls the position of the claws. The proximal scoloparium contains two scolopidia one with one and the other with two sensory cells distally fixed by a ligament at the tendon of the unguitactor moving the pretarsus. The distal scoloparium is composed of three scolopidia which are arranged into two separate parts. The cap cell of the one-celled scolopidium is distally attached with a separate ligament to the inner wall of the posterior claw. The cap cells of the second part of the distal scoloparium with two scolopidia (one with two and the other with one sensory cells) are attached to the inner wall of the anterior claw. Axons of sensory cells run to the ventral cord within the *nervus tibialis anterior*.

Responses of receptor cells to vibratory stimulation of the legs were recorded from single neurons at the entrance of a leg nerve in the appropriate part of the ventral nerve cord in *N. viridula* (ČOKL 1983). Backfilling of the leg nerve neurons revealed that all sensory fibers finally terminate at the ipsilateral side of the prothoracic ganglion for the first and at the meso- or metathoracic part of the central ganglion for the second or third leg pair respectively (ČOKL & AMON 1980, ČOKL 1983). For any stimulated leg were identified and described the group of low frequency receptor neurons responding optimally below 100 Hz, a middle frequency receptor neuron tuned to frequencies around 200 Hz and the high frequency receptor neuron tuned to frequencies between 0.7 and 1 kHz. According to the response pattern, tuning and comparative data on burrower bugs (DEVETAK et al. 1978), bushcrickets and locusts (KÜHNE 1982) we can conclude that responses to low frequency tuned neurons have their origin in stimulation of campaniform sensillas and/or joint chordotonal organs, and that both receptor neurons tuned to higher frequencies originate in

both sensory cells of the subgenual organ.

Phase-locked response pattern below 120 Hz and threshold velocity sensitivity between 3 and 6×10^{-5} m/s between 50 and 70 Hz are characteristic for the low frequency vibratory receptor neurons. Threshold curves run parallelly with the line of equal displacement value around 10^{-7} m (ČOKL 1983). Three subgroups of low frequency receptor neurons were identified within the group: neurons responding to the rising or falling phase of a cycle and neurons responding to its peak amplitude. Simultaneous intracellular recording and staining of two low frequency receptor neurons with Lucifer Yellow showed that fibers enter the central ganglion in the posterior third of the leg nerve and finally terminate at the ipsilateral side of the pro-, meso- or metatoracic part of the ventral cord (ZOROVIĆ et al. 2003, 2004). The main branch projects anteriorly to the ganglion midline and side branches diverge mostly anteriorly and decrease in size towards the midline; the branching pattern is generally similar to the described one in locusts (BURROWS 1996).

V-shaped threshold curves of the subgenual organ receptor neurons have approximately 10^{-5} m/s peak velocity threshold (around 200 Hz) for the middle frequency (MFR) and between 1 and 2×10^{-6} m/s (between 0.7 and 1 kHz) for the higher frequency receptor neuron type (HFR) (ČOKL 1983). Their threshold curves run parallelly with the line of equal acceleration value (around 10^{-2} m/s²) up to the frequency of highest velocity sensitivity where they turn and follow the line of equal displacement values (between 10^{-7} and 10^{-8} for MFR and between 10^{-9} and 10^{-10} m for HFR). The middle frequency receptor neuron responds optimally in the frequency range between 0.05 and 1 kHz. The response range of the high frequency receptor neuron extends up to 5 kHz with displacement threshold between 10^{-10} and 10^{-9} m) and at frequencies below 0.2 kHz their sensitivity sharply decreases. With increasing stimulus frequency the spike repetition rate increases in the frequency range above 200 Hz up to 300 spikes/s in the phasic part and 200 spikes/s in the tonic part of the response in which every second cycle is followed by a spike up to 500 Hz.

Central projections of *N. viridula* subgenual receptor cells were described only for the middle frequency receptor cell of the mid- and hind legs in the central ganglion of *N. viridula* (ZOROVIĆ et al. 2004). Mid- and hindleg receptor cells enter the central ganglion in the posterior third of the leg nerve and finally terminate at the ipsilateral side of the meso- or metatoracic part of the ventral cord with dense terminal arborizations. Their similar branching patterns suggests that they both originate in the same receptor organ and confirms the hypothesis that sensory structures repeated in successive segments have similar ganglionic organisation (EIBL & HUBER 1979). Similar arborisations were described in bushcrickets (KALMRING et al. 1996) and crickets (EIBL & HUBER 1979) for the T5 auditory receptor neuron but not for those originating most probably in the subgenual organ (EIBL & HUBER 1979, ESCH et al. 1980). Recently ZOROVIĆ et al. (2004) demonstrated presynaptic inhibition of the middle frequency vibratory receptor cells as described for crickets (POULET & HEDWIG 2003), locusts (BURROWS 1996) and stick insects (STEIN & SAUBER 1999). Presynaptic inhibition may be caused by inhibitory central neurons connecting the proprioceptor sensory system (WOLF & BURROWS 1995).

Antennation of the plant (OTA & ČOKL 1991) and of the mate (KON et al. 1988) sug-

gest that antennal mechanoreceptors can be involved as additional sensory input for vibratory signals. On antennae of *N. viridula* were described twelve campaniform sensillas with six of them grouped on the basis of their first antennal segment and inside the Johnston's organ with the centrally positioned central chordotonal organ was described (JERAM & PABST 1996, JERAM & ČOKL 1996). The Johnston's organ is located in nymphs in the distal part of pedicel and in adults in the distal part of the second pedicellite. 45 amphinematic scolopidia distributed around the periphery of the distal part of the third antennal segment (distal pedicellite) constitute the Johnston's organ. Axons of 17 scolopidia run to the brain within the first antennal nerve and 28 scolopidia of the opposite side in the second. The central organ located in the pedicel is composed of seven mononematic scolopidia positioned proximally and centrally from the amphinematic scolopidia. Four scolopidia form two scoloparia each with two scolopidia. Together with three separate scolopidia they attach to the same place as amphinematic scolopidia of the Johnston's organ.

The axons of four scolopidia run to the brain within the first antennal nerve and the other three within the second. Back-fill staining of *N. viridula* antennal nerve (JERAM 1996) showed that mechanosensory receptor neuron axons pass the antennal lobus and finally terminate in the suboesophageal or prothoracic ganglion at the ipsilateral side. Some axons project into the central ganglion and finally terminate in its abdominal region. These fibers show many characteristics of *Drosophila* long axons originating in campaniform sensilla of the pedicel (STRAUSFELD & BACON 1983). Vibration of the antennal proximal flagellar segment elicited responses of mechanosensory system in antennae. Single cell recording from the antennal nerve show best responsiveness below 100 Hz with highest velocity sensitivity of 2×10^{-3} m/s around 50 Hz (JERAM & ČOKL 1996, JERAM 1993, 1996). Receptor neurons respond in a phase-locked manner. The origin of single cell responses and their coupling to higher order neurons is not known. Nevertheless the antennal mechanosensory system is sensitive enough to detect low frequency parts of stink bug vibratory signals transmitted through plants.

Central processing of the vibratory information received by leg vibratory receptors has been first investigated by ČOKL & AMON (1980). Functional properties of four different higher order vibratory interneurons were described. ZOROVIC (2005) recently described morphology and function of more than 15 different types of vibratory higher order neurons in the meso- and metathoracic part of the central ganglion (article in preparation).

PLANTS AS THE MEDIUM FOR TRANSMISSION OF STINK BUG SONGS

Bugs of the subfamily Pentatominae entirely feed on plants (PANIZZI et al. 2000) and their role as transmission medium for vibratory signals has been directly demonstrated in *N. viridula* (MIKLAS et al. 2001). Many stink bug host plants are light and loading with accelerometers or any other mechanical contact devices to pick-up vibrations change significantly substrate's mechanical properties. Development of laser technology enabled relevant investigations of biophysical background of transmission of naturally emitted vibra-

tions through biological materials like plants. In the pioneering work in the field MICHELSEN with co-workers (1982) demonstrated that bending waves excited by singing insects are used for communication. In broad bean *Vicia faba* 200 Hz pure tone signals propagate with measured propagation speed of 39 m/s and at 2000 Hz with 120 m/s (MICHELSEN et al. 1982). Through a banana plant (leaves and the pseudostem) 100 and 500 Hz pure tone vibrations are transmitted with propagation velocity of less than 50 m/s (BARTH 1985, 1998) and for *N. viridula* we can expect values below 40 m/s according to their dominant frequency around 100 Hz.

Bending waves are reflected with little loss of energy at the border between different media (plant-air) at the top and at roots of the plant so that vibratory signals travel several times up and down the plant before decaying (MICHELSEN et al. 1982). The attenuation values of pure tone vibratory signals transmitted through different monocotyledonous plants is below 0.5 dB/cm (BARTH 1985). The amplitude of vibration does not decrease monotonically with the distance from the source (MICHELSEN et al. 1982, BARTH 1998) and the occurrence of echoes and low damping of vibratory signals indicates that we can expect standing wave conditions at least in plant rod-like structures like stems and stalks (MICHELSEN et al. 1982). The same authors conclude that filtering brings about complicated pattern of frequency dependent standing waves which is of similar nature in plants with different mechanical properties. Branched dicotyledonous plants are more mechanically heterogenous than monocotyledonous ones so that reflections, frequency-dependent standing-wave patterns, and changes in mechanical impedance complicate the vibration pattern (BARTH 1998). Distortion of signal pattern has to be expected due to mechanical heterogeneity and to interference and superposition caused by reflections from plant's ends.

MICHELSEN with co-workers (1982) suggested that the use of broad-band signals is a better strategy for communication through plants because at any place on a plant some of the frequency band is likely to get through to the listening animals. Until now this hypothesis has not been experimentally confirmed. On the contrary, communication with hypothetically less convenient low frequency narrow-band vibratory emissions shows many advantages.

The interaction of plants and insects during substrate-borne communication was recently investigated on a model of *N. viridula* and species host plants (ČOKL et al. 2005). It has been demonstrated that spectra of naturally emitted signals recorded on the body of singing bugs contain peaks which can not be attributed to vibration of the body but to induced vibration of the plant. Spectra of body recorded signals differ when bugs are singing on a non-resonant (loudspeaker membrane) or resonant (plant) substrate. The dominant resonant frequency of sound-induced vibrations in stink bug different host plants lies in the frequency range between 160 and 215 Hz; the harmonic resonant peaks do not exceed 600 Hz. The plant resonates as whole because no difference could be found in spectra of signals recorded at its different parts. The position of the dominant resonant peak corresponds to best frequency sensitivity of the subgenual middle frequency receptor cell (ČOKL 1983). Harmonic resonant peak around 100 Hz optimizes transmission of about 100 Hz dominant frequency signals emitted by *N. viridula* and other stink bugs

investigated until now. These results agree with frequency filtering and attenuation of a sinusoidal vibration on *Thesium bavarum* (MICHELSEN et al. 1982). It has been shown that with increasing distance from the source 100 Hz signals are also amplified and not only attenuated. The use of narrow band signals of frequencies around 100 Hz is thus an advantage according to broad-band signals.

Spectral characteristics of *M. histrionica* vibratory signals are characterized by several harmonic frequencies above 80 to 100 Hz dominant frequency (ČOKL et al. 2004). The species was found to mate also on big cabbage leaves which are structurally different as the usual green plants. MAGAL et al. (2000) investigated transmission of vibratory signals through apple leaves and demonstrated that the loss of signal energy for the midvein decreases between 80% at the base and 40% at the leaf apex. The loss by transmission through lamina was about 40%. Investigations on cabbage leaves showed that transmission is more efficient through veins than through lamina; attenuation rate for transmission through veins is comparable with the one measured in plant stalks and stems. Observations of harlequin bugs mating on cabbage leaves confirmed preferred routes for communication: bugs were singing and moving preferentially on veins. The relative amplitude of frequency peak varies with distance from the source so that spectral peak amplitude minima and maxima lie at different distances. Consequently at any distance from the source a different relationship between spectral peak amplitudes could be recorded. Attenuation of the dominant frequency peak amplitude did not decrease more than 5 dB at the distance of 7 cm. On the other hand 5 cm from the source the amplitude of the first harmonic spectral peak decreased for 15 and 20 dB for the male and female song respectively.

Topics concerning insect-plant interactions during substrate-borne communication deserve further attention. Low frequency narrow band signals are widely used not only in stink bugs but also in other arthropods (BARTH 2002). Even in »small cicadas« and burrower bugs which signals are broad-band with low and high frequency components, the low frequency one dominates in substrate-transmitted signals (MICHELSEN et al. 1982). Simultaneously recorded airborne and substrate-borne signals of a planthopper *Euides speciosa* BOH. (TRAUE 1978) have different spectral properties: the airborne sounds are at maximum around 550 Hz and vibrational signals between 150 and 250 Hz. Spectra of stridulatory signals emitted by some cydnide bugs (GOGALA et al. 1974) extent up to 12 kHz with the main energy between 3 and 4 kHz when recorded as airborne sound. Spectra of simultaneously recorded signals from plants extend below 2-3 kHz with the main energy mostly below 0.5 kHz.

Recently was demonstrated that spectral properties of burrower bugs *Scaptocoris castanea* and *Sc. carvalhoi* stridulatory signals are significantly changed during transmission through a green plant: the broad peak around 500 Hz as recorded close to the singing bug disappears and is replaced by narrow peaks around 100 and 200 Hz with a strong low frequency (<50 Hz) component as characteristic for narrow-band low frequency signals emitted by stink bugs (ČOKL et al. 2006).

Mechanical properties of plants determine communication range and enable distance discrimination and mate location. The communication range of stink bugs signalling through plants is determined by the intensity of emitted signals (ca. 10 to 40 mm/s) (ČOKL

1988), sensitivity of relevant receptors (ca. 0.01 mm/s) (ČOKL 1983) and attenuation rate during transmission through a plant (below 0.5 dB/cm). Theoretically the communication range could reach 1 to 1.5 m on the same plant but behavioural experiments on *Cyperus alternifolius* LINNAEUS (Umbrella Flat Sedge) showed that it extends to longer distances. We can explain this by lower damping of frequency components around 100 Hz, standing wave conditions and tuning of plant resonance spectra with frequency characteristics of stink bug vibratory signals. Distance discrimination has not been explained yet and the role of signal components of frequencies below 50 Hz has to be investigated in this context (VIRANT-DOBERLET et al. 2006).

Vibrational directionality has been first described among stink bugs in the southern green stink bug (*N. viridula*) by OTA & ČOKL (1991) on ivy. A male walking to the female responds to her calls with the emission of the calling and courtship song, and when he reaches a crossing of the stem with stalks or side branches he stops and straddles his legs across the fork waiting there for female calls which enable him to orient to the female. Such a behavioural pattern was recorded at distances which did not allow orientation by other mechanical, optical or chemical cues. The role of female calling song signals in male vibrational directionality was confirmed by artificial vibration of a plant (ČOKL et al. 1999). Directionality is sex specific, females do not react to vibration with the conspecific female calling song. In non-stimulus (control) conditions none of 28 males sang, 20 remained at their place and 8 walked to the other branch. During stimulation with the female calling song all 28 males responded with the courtship song, 22 males moved and 21 of them located the vibration source; only 6 males remained at their place. Most generally a male can bring a decision about direction on a crossing when two demands are fulfilled: different signals have to arrive on the left and right (or front and back) side of the relevant receptor system and these differences have to be recognized in the central nervous system as the information about direction. Suprathreshold time of arrival or amplitude differences can be achieved by a critical distance between legs, by low propagation velocity and high damping of transmitted signals. *Nezara viridula* legs are spread on the crossing of bean stalks and the stem with maximal distances of 2 cm. The intensity difference between two sites does not seem to enable vibrational directionality: with the expected attenuation rate of 0.4 dB per cm the amplitude difference would reach 0.8 dB which is below discrimination threshold of the species vibratory receptor system (ČOKL 1983). Furthermore, intensity variation with distance is not linear and at some distances 100 Hz signals have higher amplitude than at the source. Simultaneous recording of naturally emitted signals on a bean crossing of stalks with the stem at the distance of 2 cm between the left and the right stalk showed that in one third of examples the intensity at the opposite (contralateral) side was higher than on the side leading to the calling female (ZOROVIĆ 2005). On the other hand calculated time delays at the distance of 2 cm and 40 m/s propagation velocity would be 0.5 ms. Such a delay is above 0.2 ms behaviourally determined threshold triggering vibrational directionality in scorpions (BROWNELL & FARLEY 1970). Nevertheless shorter distances between the legs were observed in males which correctly turned to the side leading to calling female indicating that either propagation velocity is lower or some other effect underlies male decision. The last hypothesis is

confirmed by simultaneous recoding of *N. viridula* naturally emitted signals on a crossing on bean with two identical laser vibrometers (ZOROVIĆ 2005); at the distance of 2 cm several ms long delays could be measured. The reason for such a delay at the short distance on bean crossing is not known yet but gives a reasonable explanation about mechanisms underlying vibrational directionality in small plant-dwelling insects.

SUMMARY

Principles of stink bug communication through plants are reviewed. All until now investigated species of the subfamily Pentatominae are entirely plant feeders. Male emitted pheromone plays an important role in the field attracting mates to the same plant. When on it, females and males start calling each other. Usually a female starts vibrational communication by emitting the calling song continuously from one place even without male responding. It is not clear what triggers her to start singing. A male responds to a calling female with emission of the calling song and approaches her with well expressed searching behaviour and vibrational directionality on plant's crossings. The courtship phase of behaviour runs at short distances by multimodal information exchange including visual, tactile, air particle movement in the acoustic near-field, olfactory and vibratory signals. At the basis of the analysis of the received complex information a female decides to accept or reject the courting male. Rival song is emitted in male-male interaction when more males are courting the same female. Species and sex specific calling and courtship songs were recorded, analyzed and described in more than 20 stink bug species. Songs are produced by vertical vibration of the abdomen as consequence of synchronous contraction of muscles connecting the abdominal tergal plate with the rest of abdomen and thorax. All until now recorded vibrational signals emitted by stink bugs have uniform frequency characteristics with signal species and sex specificity expressed in their time and amplitude pattern. The dominant frequency of low frequency and narrow band signals lies around 100 Hz and most of the emitted energy is restricted to the frequency range below 500 Hz. Most sensitive vibrational receptors are located in and on the legs: campaniform sensilla and joint chordotonal organs are low frequency receptors and both sensory cells of the subgenual organ are highly sensitive in the frequency range around 200 and between 700 and 1000 Hz. Spectral properties of signals are tuned with resonant characteristics of green plants. Low attenuation rate during transmission, standing wave conditions and frequency tuning between songs and plants together with high sensitivity of relevant receptors enable long distance communication of stink bugs through the same plant.

POVZETEK

V preglednem članku je opisana vibracijska komunikacija rastlinskih stenic. Vse do sedaj opisane vrste stenic poddružine Pentatominae so rastlinojede. Samčev feromon igra pomembno vlogo pri privabljanju partnerjev na isto rastlino. Na njej začno samci in sami-

ce klicati drug drugega. Običajno začne vibracijsko komunikacijo samica tako, da z enega mesta kontinuirano oddaja pozivni napev tudi v primeru, ko ji samec ne odgovarja. Do danes še ni znano kaj sproži samičino petje. Samec odgovori samici z oddajanjem svojega pozivnega napeva in jo prične iskati z dobro izraženo orientacijo na križiščih rastline s pomočjo samičinih vibracijskih signalov. V fazi dvorjenja na krajših razdaljah komunicirata s signali različnih modalitet kot so vid, tip, gibanje zračnih delcev v bližnjem polju, vonj in vibracije. Na osnovi analize kompleksne informacije samica odloči ali bo prišlo do kopulacije ali ne. Rivalni napev je interakcija med samcema, v primeru ko več samcev dvori isti samici. Spolno in vrstno specifične napeve so registrirali pri več kot dvajsetih vrstah skupine. Vibracijske napeve proizvajajo rastlinske stenice z vertikalnim nihanjem zadka kot posledica istočasne kontrakcije mišic, ki so pripete na abdominalno tergalno ploščo na eni strani in na oprsje oz. preostali del zadka na drugi strani. Vsi do sedaj registrirani vibracijski signali rastlinskih stenic podružine Pentatominae imajo podobne frekvenčne karakteristike, njih spolna in vrstna specifičnost pa je izražena v amplitudnem in časovnem vzorcu signala. Osnovna in hkrati dominantna frekvenca nizkofrekvenčnih in ozkopasovnih signalov leži okrog 100 Hz, večina oddane energije pa se nahaja v frekvenčnem pasu pod 500 Hz. Najobčutljivejši vibracijski receptorji leže na površini in v notranjosti nog: kampaniformne senzile in sklepni hordotonalni organi so občutljivi na signale nizkih frekvenc, obe senzorični celici subgenualnega organa pa sta najbolj občutljivi v frekvenčnem pasu okrog 200 Hz in med 700 in 1000 Hz. Spektralne lastnosti vibracijskih signalov so uglasene z resonančnimi spektralnimi značilnostmi zelenih rastlin. Slabo dušenje med prenosom po rastlini, stoječe valovanje in frekvenčna uglasenost napevov med rastlino in stenico skupaj z visoko občutljivostjo receptorjev omogočajo komunikacijo tudi na večje razdalje po isti rastlini.

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