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Observations of unusual acoustic behaviour in two Australian leafhoppers (Hemiptera; Cicadellidae)

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Abstract
Acoustic substrate-borne communication between hoppers has been well studied with certain patterns of acoustic behaviour considered typical. We report observations of acoustic behaviour in two Australian leafhoppers, *Stenocotis depressa* (Walker) and *Austrolopa brunensis* Evans, that are markedly atypical. Two types of unusual acoustic behaviour were observed: female–female interactions, and the transmission of an elaborate male call through direct physical contact with the female. We discuss the evolution of these acoustic displays based on our observations of these hoppers and their environments, including the potential roles of intra-sexual competition and the carrying capacity of the plant substrate. The discovery of these unusual behaviour patterns emphasizes the need for broader surveys of the diversity of acoustic behaviour in the Hemiptera.

Keywords: *Acoustic communication, female interaction, leafhopper, substrate transmission*

Introduction

Acoustic behaviour in many insects is an integral part of courtship and mating, as well as interactions with competitors and predators (Bailey 1991; Cocroft and Rodríguez 2005). In the leafhoppers and planthoppers (Auchenorrhyncha), a diversity of acoustic behaviour and signals have been recorded and documented (Ossiannilsson 1949; Moore 1961; Ichikawa 1976; Claridge 1985; Claridge and de Vrijer 1994; Tishechkin 2000a, 2000b). Ossiannilsson (1949) undertook the first survey of the acoustic signals of hoppers in which he examined the morphology of presumed mechanisms, observed acoustic behaviour, and analysed the acoustic signals of more than 80 species. From these studies certain patterns of acoustic behaviour came to be considered typical for the majority of hoppers. For instance, the acoustic signals were in most cases thought to involve vibrations transmitted via a substrate. We now recognize certain patterns of hopper acoustic behaviour as typical, including (1) substrate-borne vibrational communication as a mechanism for mate location, during which males and females come together by the recognition of species-specific signals; (2) some body movement in conjunction with acoustic signals, but not involving prolonged physical contact; (3) female signals that are less complex than male signals and are issued in response to male calls.

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In this study, we report two unusual examples of acoustic behaviour in the Australian leafhoppers *Stenocotis depressa* (Ledrinae; Stenocotini) and *Austrolopa brunensis* (Ulopinae; Ulopini). The presence of receptive adults and the propensity to produce signals is likely to be seasonal and is difficult to control for the purposes of experimental design. We therefore report these findings as preliminary observations that are of interest because such behaviour has rarely been observed. Both these leafhoppers were believed to retain a number of plesiomorphic features within the Cicadellidae (Evans 1966). However, when members of the Ulopinae and Ledrinae were included in a recent analysis of relationships in the major lineages of Membracoidea using molecular data (based on the nuclear ribosomal 28S DNA gene; Dietrich et al. 2001), the derived placement of both groups in the phylogeny does not support the interpretation of these taxa as ancestral.

Classification

The subfamily Ledrinae is distributed worldwide, with some 70 genera and 450 described species. Evans (1966) suggested that this group represented an ancient lineage of Mesozoic origin, based on morphological characters such as forewings often having numerous supernumerary veins. Other characteristics of the subfamily include hind femora with three short stout macrosetae, and males with ligulate genital plates. The molecular data of Dietrich et al. (2001), in addition to supporting a relatively derived position within the Cicadellidae, shows the Ledrinae to be polyphyletic, with the Australian ledrine tribes (Stenocotini and Thymbrini) more closely related to the Australian subfamily Tartessinae than to the New World ledrine tribes (Xerophloeini and Petalocephalini). The Stenocotini is an endemic Australian tribe, and includes six genera (Day and Fletcher 1994). Four of these genera are monotypic, including *Stenocotis*.

The subfamily Ulopinae has a worldwide distribution and includes around 33 genera and 180 species. Ulopines have also been described as ''relict forms'' of Mesozoic origin (Evans 1966). This view is based on several morphological characters, including the retention of a maxillary suture, ocelli on the crown, greatly reduced chaetotaxy, and alary dimorphism. The tribe Ulopini is recorded from Europe, Asia, Africa, Madagascar, New Zealand, and Australia. Four of the five Australian genera are monotypic, and the fifth, *Austrolopa*, contains two described species (*A. brunensis* Evans and *A. victoriensis* Evans).

Biology of *Stenocotis depressa*

Little is known about the life cycle of species in five of the six genera of Stenocotini, except that they are all believed to feed on the stems and trunks of smooth-barked *Eucalyptus* species. The sixth genus is *Stenocotis*, represented in eastern Australia by a single, large, conspicuous and markedly dimorphic species (*S. depressa*, males 10–15 mm, females 21–24 mm). This species has been frequently collected and is often highly variable in colour, with the result that it has been described under several names by different authors. It is now generally accepted that these are all synonyms of *Stenocotis depressa* (Walker) (Day and Fletcher 1994). This leafhopper has markedly flattened nymphs and the adults are illustrated in *Insects of Australia* (Fletcher et al. 1991, Figures 30, 32C). Nymphs and adults are mottled cream and brown, providing excellent camouflage on eucalypt trunks. In the populations studied, males are considerably darker than females or nymphs. When

disturbed, males tend to move away rapidly, while females and nymphs tend to remain stationary.

In the Australian Capital Territory (ACT) *S. depressa* overwinters as an egg. Nymphs appear in early spring (October) with adults approximately 5 months later in summer (December) through to winter (May). The species has been found on several *Eucalyptus* species (*E. camaldulensis*, *E. obliqua*, *E. delagetensis*, *E. ovata*, as well as others), but in ACT most often on *E. mannifera*. Nymphs and adults may remain stationary for days. Individuals sometimes produce droplets of excreta every few minutes but have not been seen attended by ants, despite the abundant presence of several ant species on the same trunk. At times both nymphs and especially adults are mobile, moving surprisingly fast around a tree trunk; adults also fly but are rarely seen to do so. Males appear to locate females by random search movements around the tree trunk, and occasionally more than one male may attend a single female. Neither adults nor nymphs are able to adhere to the waxy surface of the leaves of the *Eucalyptus* hosts.

Biology of *Austrolopa brunensis*

Austrolopa brunensis is a widespread ulopine species found in all states in eastern Australia. Little is known about the biology of the group. These insects are inconspicuous and brown coloured, of small size (male length ca 4 mm, females ca 4.5 mm) and generally believed to inhabit "concealed" (epigeal) habitats, as ground feeders (Evans 1966). However, *A. brunensis* has been captured on a number of plants from several plant families (*Podocarpus*, Podocarpaceae; *Bossiaea*, *Pultenaea*, Fabaceae; *Richea*, Epacridaceae) (Evans 1966), though it is uncertain whether these records signify food plants or incidental capture during random collecting. Recently, we have collected *A. brunensis* on numerous occasions from the shrub *Cassinia* (Asteraceae) in New South Wales and ACT, and have been able to maintain nymphs and adults on this host for several weeks in the laboratory.

Details of the life cycle are unknown, but although the shrub *Cassinia* is locally abundant, the insect is sparsely distributed with individuals on widely separated plants, and often with only one individual to a plant. Of the three local *Cassinia* species, *A. brunensis* appears to show a preference for *C. quinquefaria* and *C. aculeata*, and is not found on *C. longifolia* in the same localities. Males are found less often than females but both sexes occupy the same habitat. Another unusual biological feature is that adults have been collected in all months of the year, even in mid-winter when few other insects are to be found.

Materials and methods

Acoustic signals were recorded using substrate pickup methods developed by Claridge et al. (1985) and optimized by D. Percy as described below. Recordings were made inside a transparent acrylic tube (15 cm × 4 cm diameter). Cork plugs were used to seal both ends. A crystal gramophone cartridge was attached firmly to a cork at one end with adhesive putty and positioned where the stylus made contact with the surface of the host plant stem. The plant stem was trimmed (ca 10–13 cm in length) and placed inside the tube with the base inserted in the adhesive putty. Signals from the cartridge were amplified × 10 using an ED1241 Differential Amplifier (designed and constructed by C. Hardy, Department of Electronics and Electrical Engineering, University of Glasgow, UK) and recorded at a

sampling rate of 44.1 kHz on digital audio tape (Sony DAT tape recorder, model TCD-D8).

Adults collected in the field, and adults reared from nymphs on their host plants, were used to obtain recordings. Acoustic signals and behaviour were recorded and observed in *A. brunensis* using a total of 13 females and two males in three separate sessions: one with two females, one with four females, and one with seven females and two males. For *S. depressa* we used five females and three males in two separate sessions: one with two females and one male, and a second with three females and two males. To record the acoustic signals, a female was released into the tube and allowed to settle on the plant stem, and then additional females or males were released into the tube. The male signal of *S. depressa* was transmitted through the female and picked up from the plant stem that was in contact with the abdomen of the female (she was not sitting on the stem). Room temperature was unregulated, but was approximately 18°C. The recorded sound was analysed using Canary software (version 1.2.4). Oscillograms and sonograms were prepared for illustrations using Canary and PaintshopPro. We examined the structure of the signals, frequency, duration of calls, and pulse rates. Measurements are given in seconds and milliseconds with standard deviations. Frequencies are given in kilohertz and relative intensity in decibels.

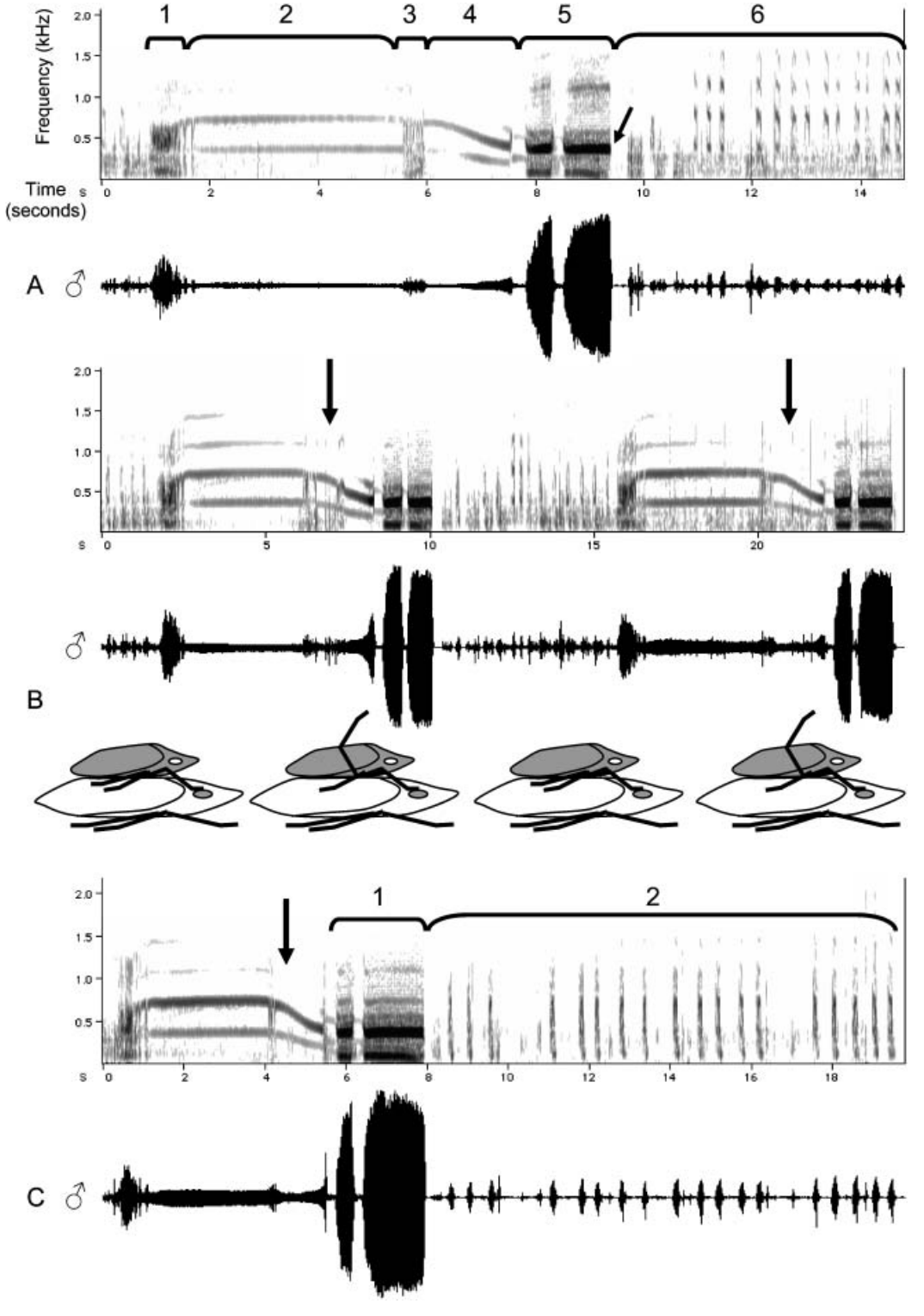
Results

Stenocotis depressa

In the first of the two sessions with this species, the male was observed producing the complex acoustic signal, together with the accompanying movements illustrated in Figure 1. Shortly after being released into the tube the male made contact with and climbed on top of one of the females, facing in the same direction with his foreleg tarsi positioned just behind the female's eyes. He then immediately commenced producing a continuous series of 17 highly structured calls, each lasting about 14 s (mean 13.94 ± 1.23 s). Each call consists of a high diversity of frequencies and amplitudes, and can be divided into six stages (Figure 1A). Although there is no obvious break between calls, there does appear to be a "rest period" of short pulses at the end of each call, which lasts to the beginning to the next call (stage 6). No part of this signal is produced by the female based on the continuity of frequency and periodicity in each call.

The first stage of the call is a sharp ascent in frequency (stage 1), followed by an extended frequency plateau of 3.74 ± 0.17 s (stage 2), before a sharp descent in frequency (stage 4). During the descent in frequency, we observed that both hind legs are rotated up above the male's head where they remain motionless (for ca 1 s) until the end of the descent when they are brought down rapidly, signifying the start of two forceful, high-intensity pulses (stage 5). Throughout stages 1–5 of the call, the greatest relative intensity is concentrated in

Figure 1. *Stenocotis depressa*. (A) A single male call which lasts ca 14 s can be divided into six stages, stage 1 is a rapid frequency ascent accompanied by a "trill"; stage 2 is a prolonged frequency plateau; stage 3 is a "trill" preceding the frequency descent that is stage 4; stage 5 is two high-intensity pulses (the diagonal arrow indicates the band of highest relative insensity: −35 dB between 0.3 and 0.4 kHz), and stage 6 is a series of short pulses, which appears to be a "rest period". (B) The male calls are produced in a continuous series with the sychronized rotation of the hind leg upwards (indicated by the vertical arrows and cartoon) and then downwards at the same point in each call. (C) The "finale call" was the last of the series of 17 calls and differed in the length of the high-intensity pulses (1), and the rate and duration of the series of short pulses at the end (2). In each figure part, spectrograms are shown above and oscillograms below.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two frequency bands. During the plateau (stage 2) the lower of these bands has a peak relative intensity of -65.3 ± 4.8 dB at 0.35–0.37 kHz, and the upper band has a peak relative intensity of -62.2 ± 5.6 dB at 0.72–0.74 kHz. During the two pulses (stage 5) the intensity of these two bands is greatly increased (lower band: -48.9 ± 2.6 dB at 0.08–0.09 kHz; upper band: -35 ± 2 dB at 0.36–0.37 kHz). The call then ends with a series of short pulses (6–17, mean pulse rate 0.38 ± 0.17 s, stage 6) before the next call starts.

The last call of the series differed from the preceding calls in the length of the two pulses (stage 5) and therefore appeared to be a ''finale call''. The first of the high-intensity pulses in the ''finale call'' is shorter (0.45 s) than the preceding calls (0.51–0.63 s), and the second pulse is considerably longer (1.55 s) than in the preceding calls (0.76–1.08 s). The relative intensity of the signal in the two pulses is also marginally greater in the ''finale call'' (lower band: -43.9 ± 1.6 dB; upper band: -33.4 ± 2.4 dB). The series of 17 calls lasted a total of 4 min followed by a further 57 s of short pulses ($n=59$) similar to the ''resting'' pulses at the end of each preceding call, but produced less frequently (mean pulse rate 0.89 ± 0.78 s; Figure 1C (2)). Apart from the rotation of the hind legs in the male, no body movement could be detected in the male or female during the series of calls, and no acoustic signal was produced by the female.

Mating was not observed directly after this acoustic behaviour, but several hours later the male was observed mating with one of the two females. During copulation male and female were positioned back to back facing in opposite directions, which differs from the positions during the acoustic display and is the typical copulatory position in many Hemiptera. In the second session, using different males and females, no acoustic behaviour was observed.

Austrolopa brunensis

Acoustic exchanges between females took place in all three sessions when multiple females were present on the plant stem. These sounds were produced when females were stationary, except on one occasion when a moving female produced brief intermittent signals. This aids in distinguishing which individuals are emitting signals, as the signal is interrupted when that individual moves. In sessions one and two (using field-collected adults) a single female was released into the tube and allowed to settle on the plant stem; isolated females did not produce signals during up to 15 min of initial observations. However, in each case the arrival of an additional female (multiple females are released into the tube over several minutes) on the plant illicited an almost immediate series of acoustic exchanges. During these exchanges females typically move close together, positioned either facing each other (a few millimetres apart) or on opposing sides of the stem (illustrated in Figure 2A). The acoustic exchanges between females occurred within the first 30 min of each session (session one lasted 45 min, and sessions two and three lasted 1 h). After the first 30 min females remained silent, either moving away or moving off the plant altogether. Exchanges between females lasted from 17 s to over 5 min. Eight exchanges lasting from 17 to 81 s (mean 43.8 ± 26.1) were recorded in session one, and 11 exchanges lasting from 23 to 313 s (mean 94.4 ± 81.2) were recorded in session two.

In a third session, using adults raised from nymphs, a female was allowed to settle on the plant, a male was then released into the tube. On making contact with the plant stem the male produced a single call, but there was no response from the female. Additional females and males were then released into the tube. When the second male made contact with the plant stem, a single call was produced, but again there was no female response. Two further calls were produced by the second male but these were partially masked by a continuing

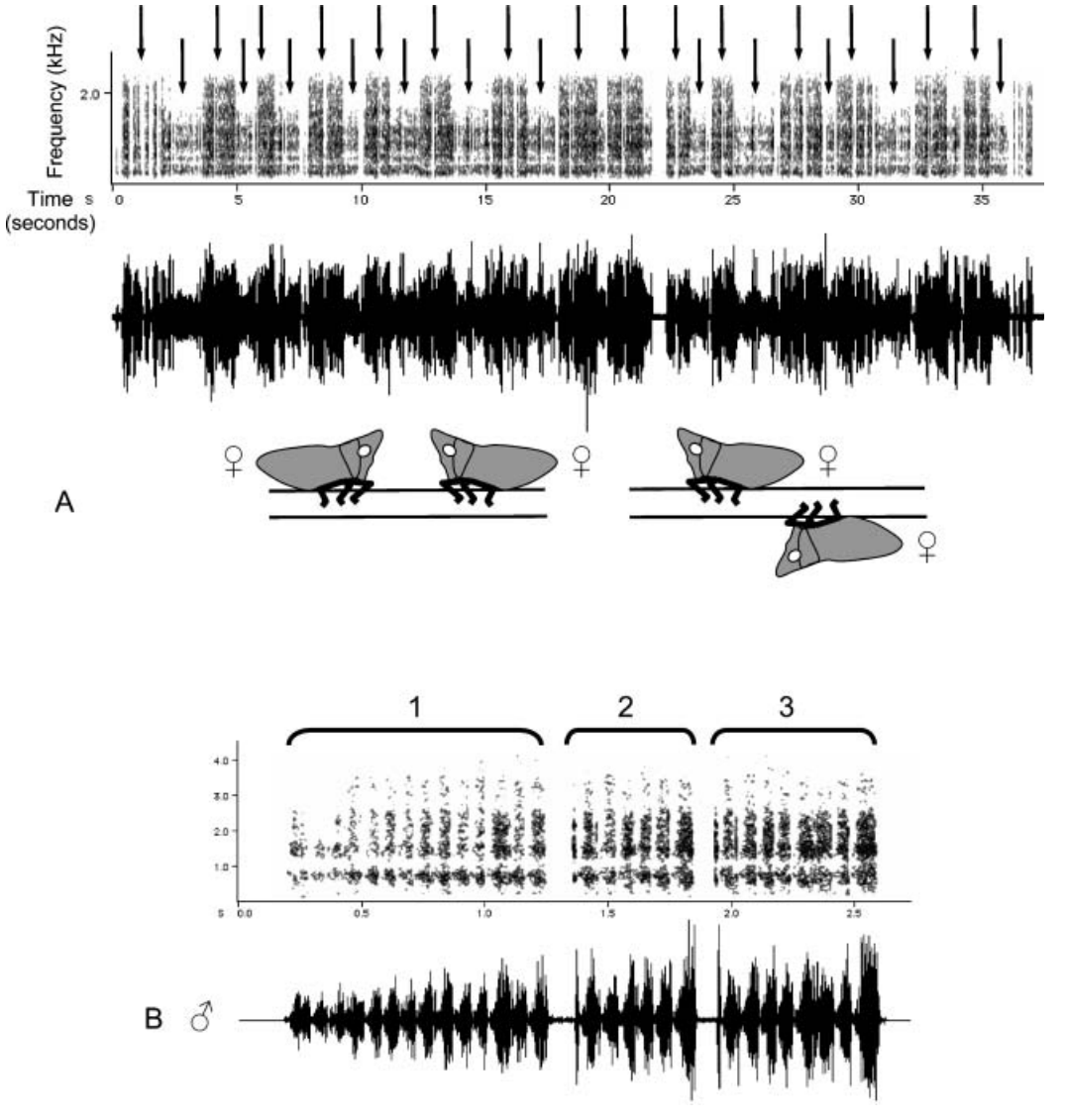

Figure 2. *Austrolopa brunensis.* (A) An acoustic exchange between two females. The two individuals can be distinguished by different frequencies of the signal (the lower and higher frequency signals are indicated by the arrows). Individual calls also overlap in part. The cartoon illustrates the typically close proximity of the females during these exchanges. (B) The male call which is usually divided into three distinct phrases of regular pulses. In each figure part, spectrograms are shown above and oscillograms below.

female–female exchange, and there was no obvious female response to these male calls. There were several exchanges between females as for sessions one and two. Two female–female exchanges were recorded lasting 55 and 135 s. As the males called more readily on initial contact with the host, removing the males from the plant with a small paint brush and allowing them to climb back on to the plant stem elicited additional calls. In this way, we captured on tape five complete and two partial male calls. None of the seven females

used in this session responded to the male signals. It is not clear what accounted for the lack of female response, but it is possible that females were unresponsive due to seasonal influences (this session was conducted in September, which is early spring) or were not yet sexually mature (laboratory-raised adults were 2–7 days old). Both females and males were raised from nymphs for this session and then isolated, but it is possible mating took place prior to isolation.

Our observations indicate that female–female exchanges take place both with and without the presence of males. The female signal is unstructured and consists of a continuous or intermittent low-frequency ''crackling'' and ''buzzing''. When multiple females are engaged in acoustic exchanges, individual females can often be identified by the different frequencies of their signals (Figure 2A). In contrast to the female signal, the male has a structured call consisting of three phrases of repeated pulses, with a gradual escalation in amplitude from start to finish of the call (Figure 2B). Each phrase of the male call is usually distinct with a break between phrases (Figure 2B). However, in one male call, phrase one and two were run together without any apparent break. The first phrase of the call is usually longer (mean length 1.14 ± 0.46 s; mean number of pulses 13.8 ± 4.8) than phrase two or three (mean lengths 0.77 ± 0.28 s and 0.64 ± 0.09 s; mean number of pulses 9.3 ± 2.6 and 8 ± 0.9). The pulse rate in all three phrases is similar (phrase 1: 83.2 ± 14.7 ms; phrase 2: 88.2 ± 11.4 ms; phrase 3: 86.7 ± 12.6 ms). No body movement could be detected during sound production in either females or males.

Discussion

In both *Stenocotis* and *Austrolopa* we have found evidence of atypical acoustic behaviour. Based on our observations of *Stenocotis*, both in recording sessions and in the native environment on *Eucalyptus* trunks, the male appears to locate the female prior to any acoustic mating or courtship display. The male acoustic signal we recorded was transmitted during direct physical contact with the female. This behaviour contrasts with typical male hopper signalling, which is usually initiated and carried over some distance, and is therefore an important part of mate location on the host plant. If acoustic signalling in *Stenocotis* is only used in direct physical contact, then there may be other types of signal that are more critical for initially locating females (e.g. chemosensory, or mechanical searching behaviour). The unusual behaviour we found in *Austrolopa* consists of lengthy acoustic exchanges between females. Acoustic signalling between female hoppers has been documented only rarely, and there are no reported experiments that have assigned a specific function to such signals. In both cases the acoustic behaviour we report is uncommon in hoppers, with few records of analogous behaviour in other species.

The acoustic behaviour we observed in *Stenocotis depressa* constitutes a remarkable performance. The use of direct physical contact in the transmission of the signal, together with the synchronized leg movement, suggests an important tactile component in the communication. The male appears to be ''drumming'' the sound into the female. The repeated and simultaneous raising of the hind legs at the same point in each call, combined with the rapid descent of the hind legs at the start of the two high amplitude pulses, emphasizes the use of sound and movement together as the strategy of the signalling male. The leg movement may be either reinforcing the acoustic effect, or acting as a separate physical stimulant. Selection for this direct physical contact during signal production may have arisen as a result of the poor transmission qualities of the habitat (i.e. tree trunks rather than more easily vibrated stems or leaves). The direct physical transmission may also

have allowed the development of the particularly long and complicated call structure, which is unusual for substrate signals (Bailey 1991), although relatively complex signals are know for some hoppers (de Vrijer 1984, 1986). The long duration of each individual call (ca 14 s), together with an apparent ''finale call'' at the end of the uninterrupted series of calls, is also notable.

We are unable to confirm whether *S. depressa* relies solely on tactile rather than acoustic information to locate females. Our observations of these insects on eucalypt trunks does suggest that random search movements are employed, but further studies are required to establish if acoustic signals are emitted during this search behaviour. Comparative studies of the habitats and reproductive biology of other hoppers that exhibit similar acoustic behaviour may shed light on the evolution and selection for direct contact acoustic transmission (e.g. Cocroft 2003; Tishechkin 2003). The few descriptions of similar acoustic behaviour in other male hoppers include frenetic male activity whereby the male either runs up and down on top of the female or issues abrupt body jerks (Ossiannilsson 1949; Tishechkin 2003). In contrast, apart from the synchronized rotation of the hind legs, the male *S. depressa* does not move. Thus, the male ''dancing'' on top of the female, described in *Megophthalmus scanicus* (Megophthalminae), *Utecha trivia* (Ulopinae), and two species of the Membracidae (*Centrotus cornutus* and *Gargara genistae*) differs from the acoustic behaviour of *S. depressa*. In a study of the treehopper *Vanduzea arquata*, Cocroft (2003) showed that a variation of the male's long-distance signalling behaviour was produced when the male climbed on top of the female, and this appears to be a closer equivalent to our observations of *S. depressa*.

The only previous reports of acoustic signals in the Ulopinae are by Ossiannilsson (1949) of *Ulopa reticulata*, and more recently, work by Tishechkin (2003) on *Utecha trivia*. Ossiannilsson (1949) reported that both sexes of *Ulopa reticulata* produced ''weak, unrhythmical clacking'', and noted that each of these ''clackings'' corresponded to a rapid movement in the lateral part of the first abdominal tergum. In addition, he reported a second call of short ''rolls'' lasting 2–3 s, which is apparently produced by the male. These acoustic descriptions suggest similarities to the signals we recorded from *Austrolopa brunensis*.

The distribution of *A. brunensis* is sporadic in the field, and this species does not typically form aggregates on the host plant. In addition, our observation that females are more frequently encountered on the host plant (*Cassinia* spp.) suggests that females may be more sedentary than males. If this is the case, the acoustic interaction between females that we observed may be territorial and aggressive due to competition between females for resources and/or mates. Our behavioural observations support this interpretation because after acoustic exchanges females move away from each other and sometimes leave the plant altogether. In contrast to females, males were surprisingly reticent to produce sound. Males elicited a single call on first settling on the host plant but infrequently thereafter. In contrast, females readily initiated and sustained virtually unbroken periods of acoustic signalling in the presence of another female, lasting from a few seconds to several minutes.

Acoustic interactions between female hoppers were not observed in studies by Ossiannilsson (1949). However, aggressive acoustic behaviour by females towards males was observed by Tishechkin (2000). Ossiannilsson (1949) referred to a type of female signal produced in the absence of a male as a ''distress'' signal, and a spontaneous female call (not induced by a male call) was referred to as a female ''invitation'' call serving to lead the male to the female; and Cocroft (1996, 1999) has documented maternal behavioural and acoustic responses to nymphal alarm signals in social treehoppers. Yet, although no

female calls initiated by the presence of another female were recorded in these studies, both M. Claridge (personal communication) and D. Tishechkin (personal communication) have observed some form of female–female interaction. In addition, Moore (1961) recorded acoustic signals from spittlebug (Cercopidea) females that were isolated or grouped with other females. Further studies are needed to determine how common acoustic exchanges between females are, and what their function may be. These examples of unusual acoustic behaviour in two Australian leafhoppers emphasize the extensive diversity of acoustic interactions, as well as questions concerning function and selection of signal types, that require further investigation.

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References

Bailey WJ. 1991. Acoustic behaviour of insects: an evolutionary perspective. London: Chapman & Hall. 225 p.

Claridge MF. 1985. Acoustic signals in the Homoptera: behaviour, taxonomy, and evolution. Annual Review of Entomology 30:297–317.

Claridge MF, de Vrijer PWF. 1994. Reproductive behaviour: the role of acoustic signals in species recognition and speciation. In: Denno RF, Perfect TJ, editors. Planthoppers: their ecology and management. London: Chapman & Hall. p 216–233.

Claridge MF, den Hollander J, Morgan JC. 1985. Variation in courtship signals and hybridization between geographically definable populations of the rice brown planthopper, *Nilaparvata lugens* (Stål). Biological Journal of the Linnean Society 24:35–49.

Cocroft RB. 1996. Insect vibrational defence signals. Nature 382:679–680.

Cocroft RB. 1999. Parent–offspring communication in response to predators in a subsocial treehopper (Hemiptera: Membracidae: *Umbonia crassicornis*). Ethology 105:553–568.

Cocroft RB. 2003. The social environment of an aggregating, ant-attended treehopper (Hemiptera: Membracidae: *Vanduzea arquata*). Journal of Insect Behavior 16:79–95.

Cocroft RB, Rodríguez RL. 2005. The behavioral ecology of insect vibrational communication. Bioscience 55:323–334.

Day MF, Fletcher MJ. 1994. An annotated catalogue of the Australian Cicadelloidea (Hemiptera: Auchenorrhyncha). Invertebrate Taxononomy 8:1117–1288.

de Vrijer PWF. 1984. Variability in calling signals of the planthopper *Javesella-Pellucida* (F) (Homoptera, Delphacidae) in relation to temperature, and consequences for species recognition during distant communication. Netherlands Journal of Zoology 34:388–406.

de Vrijer PWF. 1986. Species distinctiveness and variability of acoustic calling signals in the planthopper genus *Javesella* (Homoptera, Delphacidae). Netherlands Journal of Zoology 36:162–175.

Dietrich CH, Rakitov RA, Holmes JL, Black WC. 2001. Phylogeny of the major lineages of Membracoidea (Insecta: Hemiptera: Cicadomorpha) based on 28S rDNA sequences. Molecular Phylogenetics and Evolution 18:293–305.

Evans JW. 1966. The leafhoppers and the froghoppers of Australia and New Zealand (Homoptera: Cicadelloidea and Cercopidea). Australian Museum Memoirs 12:1–347.

Fletcher MJ, Evans JW, Carver M. 1991. Superfamily Cicadellidae. In: CSIRO, editor. Insects of Australia. Volume 1. Melbourne: Melbourne University Press. p 468–473.

Ichikawa T. 1976. Mutual communication by substrate vibration in the mating behaviour of planthoppers (Homoptera: Delphacidae). Applied Entomology and Zoology 11:8–23.

Moore TE. 1961. Audiospectrographic analysis of sounds of Hemiptera and Homoptera. Annals of the Entomological Society of America 54:273–291.

Ossiannilsson F. 1949. Insect drummers. Opuscula Entomologica, Supplement 10:1–145.

Tishechkin DYu. 2000a. Vibrational communication in Aphrodinae leafhoppers (Deltocephalinae auct., Homoptera: Cicadellidae) and related groups with notes on classification of higher taxa. Russian Entomological Journal 9:1–66.

Tishechkin DYu. 2000b. Vibrational communication in Cicadellinae sensu lato and Typhlocybinae leafhoppers (Homoptera: Cicadellidae) with notes on classification of higher taxa. Russian Entomological Journal 9:283–314.

Tishechkin DYu. 2003. Vibrational communication in leafhoppers from Ulopides subfamilies group (Homoptera: Cicadellidae) and Membracidae with notes on classification of higher taxa. Russian Entomological Journal 12:11–58.