Observations of Acoustic Signaling in Three Sharpshooters: *Homalodisca vitripennis*, *Homalodisca liturata*, and *Graphocephala atropunctata* (Hemiptera: Cicadellidae)

DIANA M. PERCY,[1] ELIZABETH A. BOYD,[2,3] AND MARK S. HODDLE[2]

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ABSTRACT Observations and comparative data are presented on the acoustic signals of three sharpshooter (Hemiptera: Auchenorrhyncha: Cicadellidae: Cicadellinae) species native to North America. The acoustic signals of the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar), native to the southeastern United States, are compared with two smaller sharpshooters native to the western United States, *Homalodisca liturata* Ball and blue-green sharpshooter, *Graphocephala atropunctata* (Signoret). Each sharpshooter is a known vector of the plant pathogenic bacterium *Xylella fastidiosa* Wells et al. Male acoustic signals from all three species and female signals from *H. liturata* and *G. atropunctata* were recorded from host plant substrates. The *H. vitripennis* calls were recorded in the evening and morning, whereas *H. liturata* and *G. atropunctata* were recorded in the afternoon. Each species has a characteristic acoustic signal of which the male call structure is most complex in *H. vitripennis* and simplest in *H. liturata*. Male–female acoustic duets in *H. liturata* and *G. atropunctata* were recorded, and distinct differences were found in the reply latencies between male and female calls in these species.

KEY WORDS acoustic signal, *Homalodisca coagulata*, leafhopper, sharpshooter, substrate vibration

Sharpshooters are a group of xylophagous leafhoppers in the tribes Proconiini and Cicadellini (Hemiptera: Auchenorrhyncha: Cicadellidae: Cicadellinae). In the Americas, >1,400 species comprise these two tribes, with the greatest species diversity occurring in tropical and subtropical regions (Redak et al. 2004). Proconiine and Cicadelline leafhoppers range in size from 3.4 to >20 mm, with the largest species in the Proconiini (Redak et al. 2004). *Homalodisca vitripennis* (Germar) (=*Homalodisca coagulata* [Say] [Takiya et al. 2006]) (Cicadellidae: Proconiini), the glassy-winged sharpshooter, was accidentally introduced into California from its native range in southeastern United States in the 1990s (Sorensen and Gill 1996), and it is a serious pest due to its extensive host plant range and capacity to vector various strains of the lethal plant bacterium *Xylella fastidiosa* Wells et al. (Blua et al. 1999, Redak et al. 2004). *Homalodisca liturata* Ball (Cicadellidae: Proconiini; congener to *H. vitripennis*), and blue-green sharpshooter, *Graphocephala atropunctata* (Signoret) (Cicadellidae: Cicadellini), are both indigenous to California. These two native sharpshooter species also are efficient vectors of various strains of *X. fastidiosa* (Severin 1949b, Freitag and Frazier 1954, Hill and Purcell 1995, Krell et al. 2007), and they are considered pests of California agriculture. As a xylem feeder, *H. vitripennis* must consume large quantities of fluid to meet its nutritional requirements, and it is capable of consuming up to 100 times its body weight in a single day (Brodbeck et al. 1993), thus producing large amounts of excreta and causing physiological damage to infested flora (Andersen et al. 2003, Hix 2004). Extremely high densities of this insect in foliage result in copious amounts of excrement that can "rain" down on humans, other plants, and parked vehicles. This "honeydew" excrement dries leaving a crusty white-washed film; thus, *H. vitripennis* can be considered a substantial public nuisance in impacted areas (Grandgirard et al. 2006). *H. vitripennis* also has been unintentionally introduced into a number of South Pacific islands; and in French Polynesia (Society Islands), the extremely high densities of this insect required a classical biological control program, which was successfully implemented in 2004 by using an egg parasitoid, *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae) (Grandgirard et al. 2006).

H. vitripennis, *H. liturata*, and *G. atropunctata* differ in ecology and size, with adults of each species measuring ≈11–13 mm (Turner and Pollard 1959), 11 mm (Powers 1973), and 6–7 mm (DeLong and Severin

[1] UBC Botanical Garden and Centre for Plant Research, University of British Columbia, 6804 Southwest Marine Dr., Vancouver, BC, V6T 1Z4 Canada.

[2] Department of Entomology, University of California, 3401 Watkins Dr., Riverside, CA 92521.

[3] Current address: Division of Organisms and Environment, Department of Environmental Science, Policy, and Management, University of California, Berkeley, Kearney Agricultural Center, 9240 S. Riverbend Ave., Parlier, CA 93648 (corresponding author, e-mail: eaboyd@uckac.edu).

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1949), respectively. *H. vitripennis* can be found in both coastal and irrigated xeric habitats in California, and it is polyphagous (Redak et al. 2004). *H. liturata* occurs in both coastal and xeric habitats and also has an extensive list of host plants (Powers 1973). *G. atropunctata* is found mainly in riparian vegetation consisting of favored oviposition plants, such as wild grape, blackberry, stinging nettle, and mugwort (DeLong and Severin 1949). *H. vitripennis* and *H. liturata* are bivoltine in southern California (Blua et al. 2001) with adults living on average 2–3 mo (Turner and Pollard 1959); *G. atropunctata* is univoltine in southern California with adults living up to 10–12 mo (Boyd and Hoddle 2006). Each sharpshooter completes five instars (Severin 1949a, Turner and Pollard 1959, Powers 1973).

Cicadellids spend their entire lives on plants, and they communicate by vibrational signals transmitted via the host plant substrate (Claridge 1985, Bailey 2003, Cokl and Virant-Doberlet 2003, Percy and Day 2005). Acoustic signaling in *H. vitripennis* has been recorded, but it is not described (UCANR 2005). Acoustic signaling in *H. liturata* and *G. atropunctata* had not been examined before this study. Consequently, the objectives of this study were to record the acoustic signals of *H. liturata* and *G. atropunctata* and compare those signals to similarly recorded signals for *H. vitripennis.*

Materials and Methods

Sharpshooter colonies were housed in a temperature-controlled greenhouse at 26.7 ± 0.6°C, 24.8 ± 13.4% RH, and a photoperiod of 16:8 (L:D) h in multiple 75- by 75- by 75-cm cages at the University of California, Riverside, CA. Greenhouse populations were supplemented with field-collected insects each year. Each sharpshooter species was reared on a variety of plants, including Eureka lemon [*Citrus limon* (L.) Burm.f. 'Eureka'; Sapindales: Rutaceae], wild grape (*Vitis girdiana* Munson; Rhamnales: Vitaceae), and basil (*Ocimum basilicum* L.; Lamiales: Lamiaceae). Basil plants were selected for use in acoustic studies because all three sharpshooter species readily feed, mate, and oviposit on basil in colony cages (E.A.B., unpublished data). For all acoustic observations, fifth instars were removed from the colonies, sorted according to gender, and isolated on basil plants until the final molt to the adult stage occurred. Precise length of teneral periods for these species is not known. However, sharpshooters were observed to fly within cages ≈24 h after final molts. After ≈4 d, postteneral adults were set up on host plants for acoustic signal recordings. Thus, all colony-reared sharpshooter adults used in acoustic observations were at least 4 d postteneral.

The acoustic signals for each of the three sharpshooter species were recorded from postteneral adults that were released onto single whole basil plants (≈30 cm in height) enclosed in a transparent plastic 3-liter bottle cage (Boyd et al. 2007) to prevent sharpshooter movement off host plants. Plants used in the study had no prior insect exposure, and they were subjected to only one sharpshooter species. Acoustic signals were recorded as substrate vibrations by using optimized (Percy and Day 2005, Percy et al. 2006) substrate pickup methods developed by Claridge et al. (1985). The gramophone cartridge was positioned so the stylus made contact with the surface of the primary stem of the potted basil plants. Signals from the cartridge were amplified 10× by using an ED1241 differential amplifier (designed and constructed by C. Hardy, Department of Electronics and Electrical Engineering, University of Glasgow, United Kingdom) and recorded at a sampling rate of 44,100 samples per second (44.1 kHz) on digital audio tape (model TCD-D8, Sony DAT tape recorder).

Acoustic signaling observations were conducted in an isolated and relatively quiet room maintained at ≈25°C, with florescent lighting supplemented by ambient sunlight from nearby windows. One or more females were placed on the caged basil plant and allowed to settle. Additional females or males were then added as required. Because only one acoustic signal from a greenhouse-reared adult *H. vitripennis* was recorded after ≈4 h of monitoring (with a total of 10 males and five females), field-collected *H. vitripennis* adults from *Citrus* orchards were added to the observation arena. These newly added *H. vitripennis* adults stimulated signaling among caged *H. vitripennis* adults on basil. *H. liturata* and *G. atropunctata* did not require the addition of field-collected material because these two species began communicating relatively quickly after set up on basil. The acoustic signals were recorded during a total of 6–10 h of observations and acoustic monitoring for each of the three species. Signals from *H. liturata* were recorded in a single, continuous monitoring period of ≈6 h (8.45–14.30), whereas *H. vitripennis* and *G. atropunctata* signals were recorded in two monitoring periods on separate days: *H. vitripennis* day 1, ≈10 h (11.45–19.30) and day 2, ≈4.5 h (6.30–11.00); *G. atropunctata* day 1, 4 h (13.30–17.30) and day 2, 2 h (13.00–15.00). We used between six and 10 adults per monitoring period (two to three females and three to seven males; Table 1). General activity, feeding, and abdominal and wing movements of individuals during sound production was observed to determine whether sounds were produced by male or female sharpshooters. However, because multiple insects were used in a single cage, identification of specific individuals signaling was not always possible during multiple or overlapping acoustic signals.

The recorded sounds from all three species of sharpshooters were analyzed using Canary software, version 1.2.4 (Cornell Lab of Ornithology, Ithaca, NY). Spectrograms were computed with a filter bandwidth of 175 Hz, using a Fast-Fourier transformation (FFT), with a 2,048-point window size (frequency 21.5 Hz) and a 90–98% overlap. Dominant frequencies were measured from the amplitude spectrum computed with the same settings as for spectrograms above. The frequency response of the recording equipment is not accounted for and may affect the measures of fre-

Table 1. Descriptive characteristics of the acoustic signals produced by *H. vitripennis* (GWSS), *H. liturata* (STSS), and *Graphocephala atropunctata* (BGSS)

Species	♂ no. calls [no. ♂]	♂ mean call duration (s)	♂ mean no. pulses	♂ mean pulse rate (ms)	♂ mean dominant frequency (Hz)	♀ no. calls [no. ♀]	♀ mean call duration (s)	♀ mean dominant frequency (Hz)	Mean reply latency (s)
GWSS	8 [10]	2.75 ± 0.34	9.43 ± 2.15	94.76 ± 8.3	52 ± 4	0 [5]			
STSS	19 [5]	1.26 ± 0.09	10.26 ± 1.05	126.64 ± 9.91	95 ± 10	20 [2]	1.23 ± 0.14	95 ± 10	0.247 ± 0.096
BGSS	53 [6]	1.17 ± 0.23	6.90 ± 1.76	86.08 ± 19.95	235 ± 68	31 [6]	0.515 ± 0.13	203 ± 64	1.74 ± 0.57

The numbers of male and female calls measured are provided with the number of potentially signaling adults in brackets (see text); means reported are ±1 SD. Measurements for STSS are for typical male and female calls, whereas measurements of unusually long STSS calls are given in the text.

quency. Descriptive characteristics examined included 1) the structure of the signals (i.e., the number, placement, and type of distinct phases in a call); 2) dominant frequency; 3) duration of calls; 4) number of pulses, and 5) pulse rates (Table 1).

Results

After some initial activity upon first contact with the host plant, *H. vitripennis* and *H. liturata* settled on the primary plant stems, started to feed, and they remained mostly sedentary during observations. *G. atropunctata* is the smallest species, and it was the most active of the three sharpshooter species. *G. atropunctata* adults frequently moved around the plant, repeatedly jumped off and back onto the plant, and intermittently settled on leaf petioles and midribs to feed.

H. vitripennis and *H. liturata* shared acoustic behavior that distinguished them from *G. atropunctata.* In both *H. vitripennis* and *H. liturata,* the acoustic activity recorded was preceded and followed by long periods of acoustic inactivity. In contrast, acoustic activity in *G. atropunctata* occurred intermittently throughout the monitoring periods. In all species, feeding continued during periods of acoustic activity and inactivity.

Two monitoring periods with *H. vitripennis* were needed to capture acoustic signaling. The first monitoring period was with colony-reared adults, and the second period was with added field-captured adults from nearby cultivated *Citrus.* Acoustic signals from *H. vitripennis* were recorded in the evening between 1700 and 1900 hours and in the morning of the next day between 0830 and 1000 hours. A few single, sporadic male calls from *H. vitripennis* (eight calls in total; Table 1) were recorded, and there were no periods of multiple male calls or female responses. One monitoring period with *H. liturata* was required to record acoustic behavior. Acoustic activity was concentrated in two periods of lengthy and nearly constant signaling lasting 20–30 min between 1300 and 1400 hours, involving multiple males and females. Outside this period there were a few sporadic single calls, often of long duration (2–3.3 s) that may have been produced by either males or females (Fig. 1E). Acoustic activity of *G. atropunctata* was recorded during two afternoon monitoring periods on two separate days between 1300 and 1730 hours. In *G. atropunctata,* the individual male or female signaling was identifiable by accompanying wing vibration. Male *G. atropunctata* calls were frequent throughout the monitoring periods. Female *G. atropunctata* calls were less frequent and seemed to be in response to male calls. Upon detection of a female response, the signaling *G. atropunctata* male was usually observed to begin actively searching by moving in the direction of the female response before calling again. In contrast, no corresponding movements could be interpreted as active mate searching behavior during the concentrated periods of acoustic signaling in *H. liturata,* or during the low level of acoustic activity by *H. vitripennis.*

The concentrated periods of acoustic activity in *H. liturata* were interpreted as consisting, in large part, of male and female duetting (Fig. 1D). However, because there was little perceptible body movement during calling (other than occasional female abdominal "fluttering" and the continued production of honeydew), definitive identity of individuals emitting the calls could not be determined. The calls identified as male and female were in several call series, where calls were regularly spaced in a call-response pattern. The initiating and responding calls were clearly emitted by individuals some distance apart, and they were characteristically different in structure and frequency modulation.

H. vitripennis had the most complex structured male call of the three species, with three distinct parts (Fig. 1A). The call structure described for *H. vitripennis* is similar to the single male call published online (UCANR 2005). The *G. atropunctata* male call had two distinct parts (Fig. 1C), and the *H. liturata* had the least complex male call, which was characterized by a single train of pulses (Fig. 1B). Female calls were of simple structure in both *H. liturata* and *G. atropunctata.* In *G. atropunctata,* the female call was considerably shorter than the male call, whereas in *H. liturata,* the typical length of male and female calls was not appreciably different (Table 1). Atypically long calls in *H. liturata* also were recorded, with the lengthiest calls ranging from 3.2 to 4.7 s (Fig. 1E). Together with the structural differences described above and illustrated in Fig. 1, differences in the duration of the male call clearly distinguish the two *Homalodisca* species (*H. vitripennis* and *H. liturata*) (Fig. 2).

A reply latency between male call and female response was evident in both *G. atropunctata* and *H. liturata,* but it was much briefer in *H. liturata* (Table

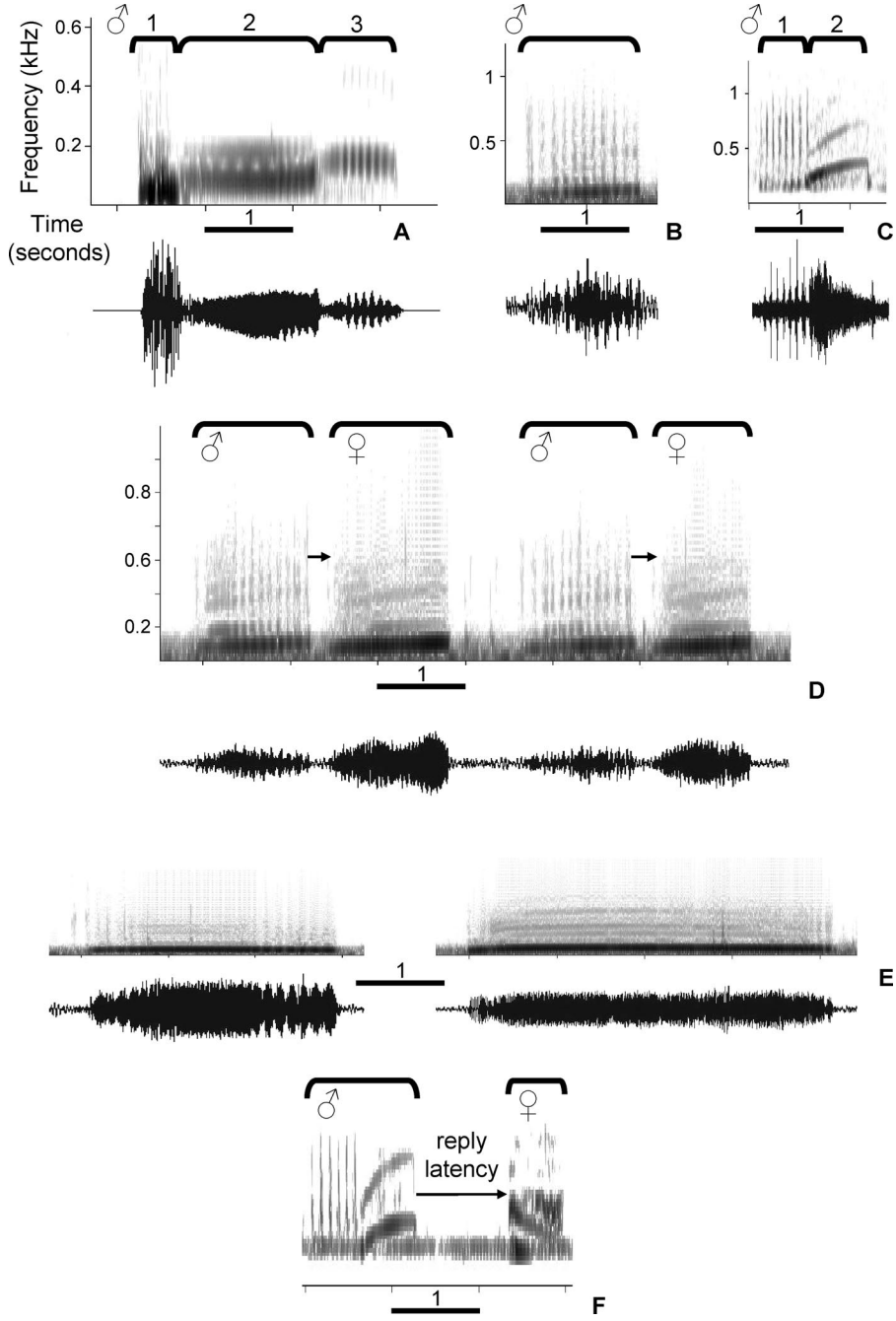

Fig. 1. Examples of *H. vitripennis*, *H. liturata*, and *G. atropunctata* male and female calls and male–female duets. (A) Male *H. vitripennis* call with three distinct parts: 1) low-frequency (mean 47 Hz), high-intensity buzz; 2) modulated and slightly higher frequency (mean 87 Hz) buzz; and 3) still higher frequency (mean 146 Hz) series of pulses. (B) Typical male *H. liturata* call consisting of a simple series of pulses. (C) male *G. atropunctata* call with two distinct parts: 1) a series of pulses and 2) a rising frequency buzz. (D) Male-female duet of *H. liturata* showing the short reply latency between male caller and female respondent (arrows). (E) Examples of atypically long calls produced by either male or female *H. liturata*, the calls were a mixture of pulses and buzz or just a sustained buzz, usually with little frequency modulation, and they may last >4 s. (F) *G. atropunctata* male and female calls from a duet, the female call was a descending frequency buzz, the relatively long reply latency was characteristic of this species and could last >3 s. In figure parts A–E spectrograms are shown above and oscillograms below; F is the spectrogram.

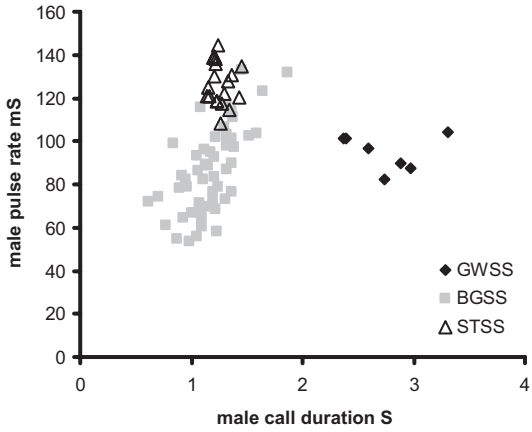

Fig. 2. Plot of two acoustic variables, male call duration and pulse rate (also see Table 1) for *H. vitripennis* (GWSS), *H. liturata* (STSS), and *G. atropunctata* (BGSS). The pulses measured were in different parts of the male call (i.e., third section of the *H. coagulata* male call, throughout the *H. liturata* male call, and in the first section of the *G. atropunctata* male call; see Fig. 1A–C). *G. atropunctata* was more variable in pulse rate, whereas the more closely related *Homalodisca* species were most clearly distinguished by call length and also call structure (see Fig. 1).

1; Fig. 1D and F). The reply latency interval between caller (male) and respondent (female) was variable, ranging from 143 to 517 ms (mean 247 ± 0.096) in *H. liturata* and from 0.9 to 3.2 s (mean 1.74 ± 0.57) in *G. atropunctata.* In both *H. liturata* and *G. atropunctata* the female calls were structured differently from the male calls. The *H. liturata* male call consisted of a train of pulses, and the female call was a buzz with a slight rise in frequency (Fig. 1D). The *G. atropunctata* male call had two parts (a train of pulses followed by a rising frequency buzz), and it was longer than the female call, ≈1.2 s for the male call versus 0.5 s for the female call. The male call was of slightly higher frequency than the female call (Table 1), which was a buzz with a slight drop in frequency (Fig. 1F). *H. liturata* male and female calls had low dominant frequencies, although not as low as the dominant frequency of male *H. vitripennis* calls (Table 1), and there was little frequency modulation throughout the calls (Fig. 1D). The dominant frequencies of *G. atropunctata* male and female calls were appreciably higher than *H. vitripennis* and *H. liturata* (Table 1). In some instances, where multiple *H. liturata* calls emitted in a series did not seem to differ appreciably from one another, there may have been multiple individuals of the same gender chorusing. However, calls in these series did not seem to be temporally organized such as those found in chorusing leafhoppers (Hunt and Morton 2001).

Other noises detected during acoustic observations were tapping and knocking noises, and a nondescript low frequency "buzz" or "rattle." The tapping was produced by males and females of *H. vitripennis* and *H. liturata*, and it might have been emitted during the location or testing of feeding sites. The low frequency buzz or rattle was recorded during *H. vitripennis* sessions, but its purpose is unknown.

It should be noted, that Table 1 indicates the number of individual calls measured and gives the potential number of signaling males and females in brackets. Because the precise number of signaling adults was not established, the results presented in Table 1 should be regarded only as preliminary observations.

Discussion

This study is the first to describe acoustic signaling in *H. vitripennis, H. liturata,* and *G. atropunctata.* Of the three sharpshooter species, *G. atropunctata* seems to have the most typical acoustic behavior, consisting of a mate search (initiating male call) and location (male movement toward female) strategy (Ossiannilsson 1949; Claridge 1985; Hunt and Nault 1991; Claridge and de Vrijer 1994; Tishechkin 2000a, 2000b; Drosopoulos and Claridge 2006). The relatively lengthy reply latency (interval between male call and female response) in *G. atropunctata* contrasts with the much shorter reply latency in *H. liturata*, even though the duration of the initiating male call in *H. liturata* is longer. This is contrary to findings that positively correlate reply latencies in some insects with male call length (Bailey and Hammond 2003). However, the length of the reply latency in sharpshooters may still be cued by specific characteristics in the preceding male call (Bailey 2003). Additionally, *G. atropunctata* had short bursts of acoustic activity throughout most of the monitoring period, whereas *H. vitripennis* was the least acoustically active, emitting only a few isolated and sporadic male calls during the monitoring period. Furthermore, the *H. vitripennis* calls were recorded in the evening and morning, whereas *H. liturata* and *G. atropunctata* were recorded in the afternoon. These behavioral characteristics indicate notable differences between the three sharpshooter species, although in some cases calling behaviors in experimental arenas may not accurately capture natural behaviors.

In *H. liturata*, acoustic activity was concentrated in 20–30-min periods of nearly continuous acoustic activity, with little or no acoustic activity in the interim periods. The call and search strategy observed in *G. atropunctata*, whereby males, after detecting a female response, move in the anticipated direction of the female before calling again was not observed in *H. liturata* or *H. vitripennis.* In fact, little or no movement was observed in the *H. liturata* or *H. vitripennis*, making it difficult to determine which individual had produced the recorded signals. The dominant frequency of all recorded sharpshooter calls was relatively low, but it seemed to be linked to body size in these three species as the mean dominant frequency in the male call of the largest species, *H. vitripennis*, was 52 Hz, whereas it was 95 Hz for the next largest species, *H. liturata*, and 235 Hz for the smallest species, *G. atropunctata* (Table 1).

The different degrees of acoustic activity observed in *H. vitripennis*, *H. liturata*, and *G. atropunctata* may

be influenced by numerous temporal factors, such as mating and egg maturation duration, or adult life span. For example, *G. atropunctata* are univoltine whereas *H. vitripennis* and *H. liturata* are bivoltine (sometimes a partial third *H. vitripennis* generation has been observed in southern California; Blua et al. 2001), and population phenology of these species may influence periodicity and duration of acoustic signaling. All sharpshooters used for the recording sessions had emerged as adults at least 4 d before the recording sessions, with the exception of the field collected *H. vitripennis* for which adult age was not determined. Hix (2001) observed that female *H. vitripennis* will not mate for up to 96 h after eclosion, and sometimes females may not mate for up to 14 d. Although adult female *H. vitripennis* were at least 4 d postteneral in our experiments, it is possible that females may not have been receptive to mating, and this may explain the lack of acoustic response to male calls. It is not known whether a premating period exists for *H. liturata* or *G. atropunctata*, but it is likely that it would be <4 d, because we were able to record male–female duets when using adults that were 4 d postteneral. Observations of the sharpshooter colonies indicate that all three species will mate within 3–5 d of adult emergence (E.A.B., unpublished data). Nevertheless, it may be that the extent of acoustic activity in the *Homalodisca* species, including receptivity of females to male calls, is dynamic due to the possibility of overlapping generations in the field.

Considerable variation in the acoustic signals of related cicadellids has been documented (Gillham 1992, Claridge et al. 1994) and the results of this study provide evidence that species in the genus *Homalodisca* also vary considerably in signal characteristics and signal complexity. *H. vitripennis* male calls have three distinct parts to the call, whereas *H. liturata* males are characterized by a monotypic one-part call. The *H. liturata* and *H. vitripennis* male frequencies were most similar of the three species recorded. The range of frequencies used by a particular species may be influenced by the relative size of the sound producing organ, the location of the calling insect on the plant, and the sound carrying capacity of the host plants (Cokl and Virant-Doberlet 2003, Cocroft and Rodríguez 2005).

Finally, research is needed to explore whether the acoustic signals of native California sharpshooters vary by geographic locality, and if the acoustic signals are systematically informative (e.g., are most similar to those of closely related species) or exhibit convergence (Henry et al. 1999, Percy et al. 2006). This information would be useful for studies investigating geographic races and speciation processes (Claridge et al. 1985, Percy et al. 2006). Furthermore, several different roles for acoustic behavior in insects have been documented, including male–male acoustic chorusing or lekking, antipredatory or defensive signals, and maternal acoustic behavior (Claridge 1985, Bailey 2003, Cokl and Virant-Doberlet 2003). The presence of long single calls in *H. liturata* outside of male–female duets could be indicative of some of these functions. There is a lower dominant call frequency in the larger, more sedentary *Homalodisca* species. It has been suggested that low frequency calls may have an antipredatory role, because lower frequencies may be less likely to be detected by predators (Bailey 2003, Cokl and Virant-Doberlet 2003). The possibility of vibrational cues aiding in parasitoid host location has been discussed previously (Meyhöfer and Casas 1999) and orientation to female stink bug sexual vibratory signals by a scelionid egg parasitoid was recently demonstrated (Laumann et al. 2007). All sharpshooters recorded in this study were readily observed mating at oviposition locations on host plants in their respective habitats (E.A.B., unpublished data), but it is not known whether the acoustic signals recorded would aid in short-range detection of oviposition locales by mymarid or trichogrammatid egg parasitoids of *H. vitripennis*, *H. liturata*, or *G. atropunctata.* Additional behavioral information on the interaction of sharpshooter acoustic signaling and parasitoids could aid in interpreting the outcomes of current classical biological control efforts against these pests. As outlined here, possible additional roles for acoustic signaling in sharpshooter species warrant future research.

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