Chapter 22
Vibrational Communication in Psyllids

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Abstract Psyllids are small insects that can vector causal agents of serious plant diseases, such as greening in citrus and zebra chip disease in potatoes. Several invasive psyllid species are expanding their geographic range, but there are few pest management tactics available at present. Vibrational communication is a primary intra-specific communication channel within Psylloidea, being widespread among almost all the families. In psyllids, vibrational signals are used for mate location and mate choice by means of a male–female duet. Depending on the species, the first call can be emitted either by the male or the female and if a potential mate replies, the duet is eventually established. Some psyllid males produce a specific response signal when a female replies to their call, while in most other species the male uses a unique type of vibrational signal throughout the mating

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process. Most psyllids likely emit vibrations by means of stridulation, in which signals can be produced when the sclerotised areas of the anal vein of the wings rub against the scutellum, which bears scale-like denticles. Recent evidence suggests that novel methods of trapping or mating disruption using vibrational communication could provide solutions for monitoring and control psyllid pests. For instance, the vibrational signals of the Asian citrus psyllid, *Diaphorina citri*, and the North American tomato potato psyllid, *Bactericera cockerelli*, have been tested as monitoring and trapping tools, and similar studies have been initiated on other species.

22.1   Introduction

Psyllids are small sap-feeding insects belonging to the superfamily Psylloidea, which consists of eight hemipteran families (Aphalaridae, Calophyidae, Carsidaridae, Homotomidae, Liviidae, Phacopteronidae, Psyllidae, and Triozidae) and comprises more than 3500 species (Ouvrard 2016). They are distributed in almost all the world's climatic regions (Hodkinson 2009) and some are agricultural pests that can cause damage to the host plant, either by feeding or by transmitting pathogens including bacteria, phytoplasmas, and viruses (Munyaneza 2010; Burckhardt et al. 2014). Vector species have received great attention from researchers and pest managers because of the economic importance of the diseases that they transmit to plants (Hodkinson 1974; Munyaneza et al. 2007; Munyaneza 2010; Hall et al. 2013; Coutinho-Abreu et al. 2014). For example, the bacterium *Candidatus* Liberibacter, which is transmitted by four known psyllid species, causes important diseases in citrus and several solanaceous crops (Haapalainen 2014). A psyllid-transmitted disease known as Huanglongbing or "citrus greening disease" is associated with three species of *Ca.* Liberibacter and is considered a global threat to citrus cultivations (Gottwald et al. 2007). Another economically important disease is apple proliferation, transmitted by two *Cacopsylla* species that are controlled by insecticide treatments in Europe (Tedeschi et al. 2012).

Studies on the biology, physiology, ecology, and behaviour of these insects could provide useful information to support the development of effective control strategies. A review examined the biotic and abiotic factors affecting the life cycle in psyllids, and temperature and humidity in ecological context seemed to play major roles in psyllid evolution (Hodkinson 2009). A simple temperature-driven phenological model, based on psyllid biology and on the host plant development across a wide geographical range, demonstrates how both northern and southern limits of latitude and climate affect the insects' life cycle (MacLean 1983). The geographical range also determines whether a psyllid species can exploit different hosts or plant tissues. For instance, in the northern regions of Greenland, the willow psyllid *Cacopsylla groenlandica* (Psyllidae) develops solely on the catkins of *Salix glauca*, even in the presence of other willow species, while in southern regions the insect can complete the cycle on different plant tissues of four *Salix* species (Hodkinson 1997). In the case of psyllid vectors, similar information could be used to develop risk maps

on the epidemiology and the potential outbreaks of the plant disease transmitted by the insect. Climate change should to be taken into account when modelling risk maps as well, since global warming could influence the developmental range of both pest species and pathogenic microorganisms in several ways (Ladányi and Horváth 2010). Psyllids have adapted to a range of host plants (Hodkinson 1974, 1986; Van Klinken 2000), in that most species are strictly monophagous or oligophagous and feed especially within Solanaceae, Umbelliferae, and Cruciferae (Hodkinson 2009). Host alternation during the year is common in psyllids, and adults can migrate from overwintering plants to colonise host and shelter plants (Burckhardt et al. 2014). Long-range dispersal can be a challenge for such small insects, but some migrations cover remarkable distances, as in the Asian citrus psyllid *Diaphorina citri* (Liviidae), which can move to different citrus groves even in the presence of geographical barriers such as fields and roads (Lewis-Rosenblum et al. 2015). The colonisation of a new area can lead to a shift in host range, as reported for the tomato potato psyllid *Bactericera cockerelli* (Triozidae), a major pest of potato (Knowlton and Thomas 1934). Host shifting is considered to be one of the most important drivers of speciation in psyllids (Percy et al. 2004) and depends in the first instance on the initial attractiveness of a novel host (Lapis and Borden 1993; Tsai and Liu 2000), and secondly on the ability to exploit it as a food source (Hodkinson 2009). Some psyllids accordingly inject salivary secretions to influence the physiology of the plants to enhance availability of nutrients and assist nymphal growth (Laurema 1989). Such secretions can be phytotoxic, causing necroses, galling, and malformations in the host plants (Markkula and Laurema 1971; Burckhardt et al. 2014).

Most psyllids live in dense, mixed-sex colonies (Hodkinson 2009), and research has therefore investigated the mechanisms that underlie aggregation, host location and selection. In general, psyllids reproduce sexually, but parthenogenesis has been reported in some species (Nokkala et al. 2008). Notwithstanding the available literature on the psyllid biology and ethology, there is still need for more information regarding the sexual behaviour, and particularly the sensory modalities used by these insects for mate location and selection. In fact, knowledge about the signals emitted during pair formation is an important prerequisite in order to develop successful integrated pest management strategies (Polajnar et al. 2015; Pertot et al. 2016; Takanashi et al. 2019). For this reason, besides studies on the communication of some species from Australia, e.g., Triozidae (Taylor 1985; Percy et al. 2006) and Russia, e.g., Psyllidae, Triozidae, and Aphalaridae (Tishechkin 1989, 2005, 2006, 2007), the most detailed description of psyllids' vibrational signals associated with mating has involved pest species, i.e. *Cacopsylla pyri, Cacospylla picta, D. citri,* and *B. cockerelli* (Wenninger et al. 2009; Eben et al. 2015; Oppedisano et al. 2020; Avosani et al. 2020). In this regard, since current control practices (i.e., insecticide treatments) against *B. cockerelli* did not eliminate zebra chip disease in New Zealand (Vereijssen 2020); alternative methods of control such as mating disruption and behavioural manipulation remain under investigation within this country.

22.2 Mating Communication and Pair Formation in Psyllids

Mating communication allows transfer of relevant information about the species and physiological status of the sender to the receiver (West-Eberhard 1984; Candolin 2003; Cocroft and Rodríguez 2005). Most psyllids reach sexual maturity within 24–48 h after adult eclosion and females of some species mate several times during their lifespan to continuously produce fertile eggs (Burts and Fischer 1967; Van den Berg et al. 1991). After mating, males usually search for other potential partners, while females require a longer refractory period before resuming sexual receptivity (Percy et al. 2006; Tishechkin 2007; Lubanga et al. 2014). In general, signalling systems differ between species and usually involve interactions among multiple modalities. Similarly, both vibrational and chemical communication promotes pair formation within Psylloidea, although the relative weight of the cues involved in mate finding and selection depends on the species (Wenninger et al. 2008, 2009; Lubanga et al. 2014).

22.2.1 Vibrational Communication: Mechanisms and Behaviours

Vibrational communication is considered to be the main intra-specific communication channel, being widespread among the majority of Psylloidea; it has been reported in Liviidae (Yang et al. 1986; Wenninger et al. 2009), Triozidae (Percy et al. 2006; Tishechkin 2007; Liao et al. 2016: Avosani et al. 2020), Homotomidae (Liao and Yang 2017; Liao et al. 2019), Carsidaridae (Liao et al. 2019), Aphalaridae (Tishechkin 2007; Wood et al. 2016), and Psyllidae (Eben et al. 2015; Liao and Yang 2015). Acoustic signalling in psyllids was first described by Ossiannilsson (1950) while vibrations were recorded and described in the sixties (Heslop-Harrison 1960; Campbell 1964). Much later, several studies demonstrated that vibrational signals carried along the plant surface play a key role in the mating behaviour of many species and likely constitute the primary sensory modality used to identify and locate a suitable mate in many species (i.e., Yang et al. 1986; Tishechkin 1989, 2005; Percy et al. 2006).

A proposed mechanism for signal production in psyllids is stridulation, which involves the movement of the wings in a vertical plane, along the body of the insect (Heslop-Harrison 1960; Taylor 1985; Tishechkin 2006, 2007; Eben et al. 2015; Wood et al. 2016; Oppedisano et al. 2020). In this way, vibrational signals can be produced when the sclerotised areas of the anal vein of the wings rub against the scutellum, specifically against the meso- and metathorax axillary cords, which bear scale-like denticles. The anal vein acts as a "plectrum" scraping against the surface of the axillary cord, which represents the *pars stridens* (Taylor 1985; Tishechkin 2006), as shown in Fig. 22.1. In five species of psyllids (*Macrohomotoma gladiata*
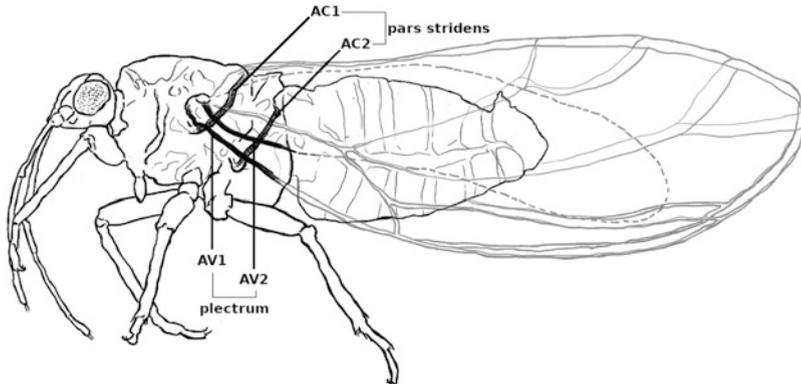
Fig. 22.1 Drawing of a male of *Cacopsylla spp*. The stridulatory organs that could be involved in the production of vibrations, as suggested by Eben et al. (2015), are coloured in black. The movement of the wings in the vertical plane enables the anal veins to act as a plectrum when they scrape against the *pars stridens,* which consists of the axillary cords. AC1: axillary cord of the mesoscutellum; AC2: axillary cord of the metascutellum; AV1: forewing anal vein; AV2: hindwing anal vein. Dashed line: hind wing (drawing courtesy of S. Avosani)

(Homotomidae), *Trioza sozanica* (Triozidae), *Mesohomotoma camphorae* (Carsidaridae), *Cacopsylla oluanpiensis* and *Cacopsylla tobirae* (Psyllidae)) vibrations are produced by means of two stridulatory mechanisms, which work together. In particular, one component involves friction between the anal area of forewings and the axillary cords on mesothorax, while the other consists in stridulation between the axillary sclerites of the forewings and the thorax (Liao et al. 2019). With this study, Liao and colleagues (2019) confirmed the crucial role of the forewings and showed for the first time that the axillary sclerites are also involved in signal production within Psylloidea. However, in the case of the five species under analysis, the hindwings are not used to emit vibrations (Liao et al. 2019), as previously hypothesised by Taylor (1985) and Tishechkin (2006). Moreover, Liao et al. (2019) demonstrated that frictional mechanisms such as the rubbing between wing–wing, leg–abdomen, or leg–wing do not play a role in signalling. Interestingly, the rapid wing vibration is hypothesised to be the source of the faint sound that was first noted in Psylloidea (Heslop-Harrison 1960). *Diaphorina citri* males and females, by contrast, use wingbeat signals for vibrational communication and have not been reported to stridulate (Wenninger et al. 2009). Indeed, signal production cannot be achieved solely via wingbeat in other psyllid species, where the stridulatory organs are found in the forewings and the thorax. As a fact, wing beat cannot be the source of substrate-borne signals when the wing beating frequency does not correspond with either the dominant or fundamental frequency of the emitted vibrational signals (Liao et al. 2019). Tishechkin (2006) described stridulatory organs in species that did not emit vibrations, while these structures were not found in some Australian species that possibly do not communicate by means of vibrations or use an alternative stridulatory organ (Percy et al. 2006).

Although stridulation appears to be a simple frictional mechanism, the resulting signals are diverse among species in terms of amplitude and temporal pattern; therefore, comparative analyses of the temporal and spectral properties of the signals could enable discrimination among different species (Tishechkin 2005; Liao and Yang 2015). In fact, the denticulate surface of the axillary cords slightly differs between psyllid families and even between morphologically identical/similar species, and these differences influence the characteristics of stridulatory signals, therefore supporting species discrimination and determining taxonomic positions (Tishechkin 2006; Liao et al. 2019). A similar relatedness between the morphology of stridulatory organs, vibrations/sound characteristics, and taxonomic relationships has been proposed and discussed for other insect species. In the genus *Typhlocharis* (Coleoptera: Carabidae), for instance, the presence of the *pars stridens* is potentially a useful character that can elucidate the taxonomic relationship between species (Zaballos and Perez-Gonzalez 2011). In velvet ants, on the contrary, the link between the structure of stridulatory organs and call patterns seems to be weak, even when characteristics of stridulatory organs are species-specific (Polidori et al. 2013). Signals generally differ substantially between sympatric species to avoid potential interference during intra-specific communication, as a form of precopulatory reproductive barrier (Claridge 1985, 1990; Coyne 2007; Tishechkin 2008). Sympatric psyllids could nonetheless produce vibrations with similar spectral and temporal patterns, if they complete their life cycle on different host plants (Tishechkin 2005, 2007; Percy et al. 2006). Signal characteristics are indeed a reliable tool that can support morphological analyses for taxonomy (Claridge 1985, 1990; Tishechkin 2014) as vibrational characters can reveal phylogenetic relationships between psyllids species, explaining if two or more species have either recently diverged or are allopatric (Percy et al. 2006). The use of vibrational features as phylogenetic characters is still under debate (Percy et al. 2006), and before using vibrational data in phylogenetic studies, it is necessary to take into account the types of selection (i.e. environmental, sexual, etc.) that operated during the process of speciation (Claridge 1990; Percy et al. 2006). At any rate, while the mere organisation and shape of sound/vibration organs cannot resolve phylogenetic problems, a multidisciplinary approach that integrates molecular data with both morphological and developmental studies could be a more effective strategy (Jost and Shaw 2006).

Psyllid signals mostly consist of short pulses, which can be arranged in longer songs (Tishechkin 2007; Eben et al. 2015). These pulses can have different spectral characteristics and be grouped in pulse trains or syllables, which in turn can be arranged to produce more complex signals used to achieve mating (Tishechkin 2005, 2007; Percy et al. 2006). As an example, a detail of the male calling signal of *B. cockerelli*, which consists of a series of pulse trains, is provided in Fig. 22.2 (Avosani et al. 2020).

As in other hemipteran insects (Virant-Doberlet and Čokl 2004), vibrational signals are species- and gender-specific and play a crucial role during pair formation within Psylloidea (Percy et al. 2006; Tishechkin 2006). In this regard, male and female tightly synchronise their signals to identify and finally locate the most suitable mate (Tishechkin 2005, 2006, 2007; Liao and Yang 2015). In most species,
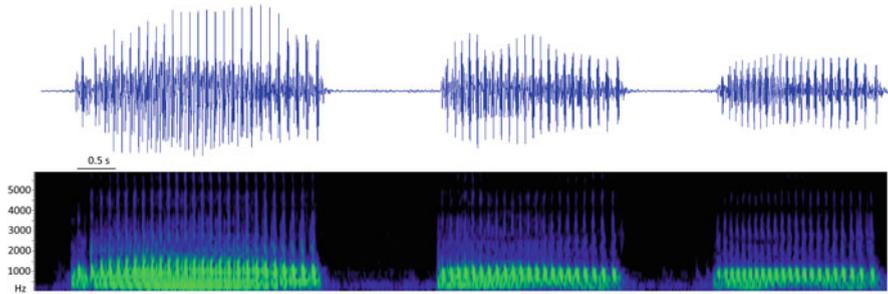
Fig. 22.2 Oscillogram and spectrogram of a section of the first part of a calling signal emitted by a *Bactericera cockerelli* male (FFT size = 256, overlap = 75%). Similarly to other psyllid species such as *Cacopsylla pyri* (Eben et al. 2015), the male call is composed of pulses arranged in pulse trains (Avosani et al. 2020). The figure shows three successive pulse trains (courtesy of S. Avosani)

the male produces the first call, to which a sexually-mature female may reply, and if so, a duet is established (Percy et al. 2006; Tishechkin 2007). In some cases, females spontaneously produce vibrational signals before or in absence of the male, as in *D. citri* and *C. pyri* (Wenninger et al. 2009; Eben et al. 2015; Mankin et al. 2020). Contrary to other psyllid species, pair formation in *C. picta* mainly started with the emission of a female calling signal, which was followed by the male signal and, potentially, the duet. Even so, the female calling activity could have been a consequence of an increased sexual motivation since the females were tested near the end of their reproductive period, as stated by the authors of the study (Oppedisano et al. 2020). In general, when the duet is established, the male starts to search for the female, who remains stationary on the plant (Percy et al. 2006; Tishechkin 2007; Liao et al. 2016; Lujo et al. 2016; Liao and Yang 2017; Oppedisano et al. 2020). Mating is eventually achieved when the male reaches the replying partner on the plant (Wenninger et al. 2009; Liao et al. 2016; Liao and Yang 2017; Oppedisano et al. 2020).

Depending on the species, the male and female signals can differ greatly in their structure, with male signals being generally longer and more complex than those of females (Percy et al. 2006; Lubanga et al. 2016; Oppedisano et al. 2020). In three *Cacopsylla* species, by contrast, the female reply has a longer duration compared to the male call, probably to provide more directional information to the searching mate (Liao and Yang 2015). In a very recent review, Liao and colleagues analysed and classified the vibrational communication of 107 species within 47 genera, providing evidence that, notwithstanding many similarities, the psyllid repertoire of vibrational signals and mating strategies are rather variegated (Liao et al. 2022). Males of *Macrohomotoma gladiata* and *Macrohomotoma robusta* (Homotomidae), for example, produce a specific response signal whenever a female replies to their call, while in other species the male uses a unique type of vibrational signal to both call and duet with the potential mate (Liao and Yang 2017). In both *Macrohomotoma* species, the male response signals resemble the female reply in
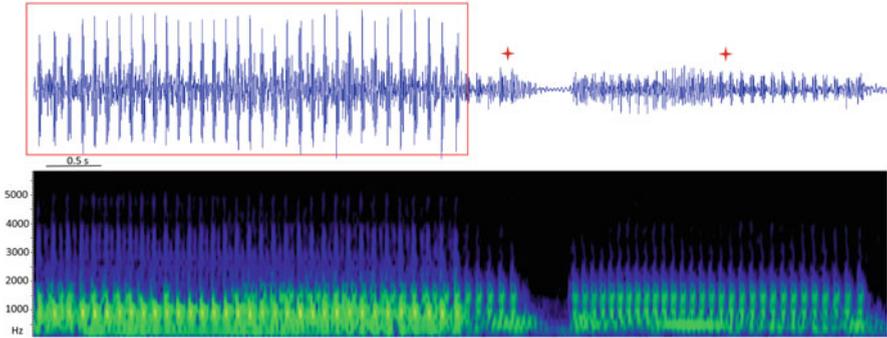
Fig. 22.3 Oscillogram and spectrogram of a section of a male–female duet in *Bactericera cockerelli* (FFT size = 256, overlap = 75%). Similarly to other psyllid species (Percy et al. 2006), the female response partially overlaps the last section of the male signal (red rectangle) and then continues after the male ceases to call (red diamonds) (Avosani et al. 2020)

the temporal structure, probably as a strategy to deceive rival males while duetting (Liao and Yang 2017). In this way, an eavesdropping male could potentially not be able to discriminate between the male and the female and consequently not reach the duetting female before the signalling male (Liao and Yang 2017). In some stonefly species, similarly to the two *Macrohomotoma* psyllids, the male signal mimics the female response during the duet (Boumans and Johnsen 2015). At any rate, the exchange of signals within the duet can be more or less synchronised in psyllids, and the reply of the female can either partially overlap or follow the male call (Eben et al. 2015; Liao and Yang 2015; Liao et al. 2019; Mankin et al. 2020; Avosani et al. 2020; Liao et al. 2022). An example of partial overlap between the male and female signal is shown in Fig. 22.3. Since the female remains stationary throughout the duet, the overlap of the male and female signals could possibly decrease the risk of eavesdropping by predators, such that "one signal" is perceived as coming from two different positions (De Groot et al. 2012). As in many other hemipterans, the male searching behaviour is characterised by the alternation of walking and calling (Polajnar et al. 2014). Male calls elicit female replies, which likely give directional information on the female's location to the male and, in this way, mediate the directional choices of the male (Percy et al. 2006; Wenninger et al. 2009). The process of pair formation in insects as small as psyllids can be very complicated in that the distance between legs is likely too short to perceive and correctly process directional information (Virant-Doberlet and Čokl 2004), but it has been demonstrated that even small insects can acquire directional information using vibrational signals (Mazzoni et al. 2014). For instance, in *Aacanthocnema dobsoni* (Triozidae), searching efficiency was experimentally confirmed on one-dimensional surfaces (i.e. plant branchlets), where males located the replying females within 30 s of duetting (Lubanga et al. 2016). Besides evaluating the calls to assess the quality of the male, psyllid females probably use other cues and accordingly choose to stop signalling before being located (Liao and Yang 2015, 2017). As an example, the

responsiveness of females of *Anoeconeossa bundoorensis* (Aphalaridae) was not influenced by the parameters of male calls, which varied significantly between individuals. Since the differences in the male calls were associated with the size and the age of the insects, it is possible that females evaluated other male features to assess the quality of the potential partner (Lubanga et al. 2016). In this regard, when the male reaches the female, signal modalities other than vibrations, such as odours, could be involved and be decisive in mate preference (Wenninger et al. 2009), provided that the use of multiple cues in mate choice is common within insects (Candolin 2003).

Psyllids usually form dense populations, and this situation could be advantageous for males, which could intercept and copulate with a female without the support of vibrational signals (Tishechkin 2007). Besides occasionally achieving mating without signalling (Avosani et al. 2020), *B.cockerelli* males also try to mount other males (Avosani and Sullivan, personal observations). Similar same-sexual behaviours occur in at least 110 species among insects and arachnids and may be a result of high sexual responsiveness (Scharf and Martin 2013). Although fascinating, alternative reasons that proposed an adaptive significance for male–male interactions have been mainly rejected (Scharf and Martin 2013). Probably, a copulation attempt towards a rival does not provide any direct advantage to the mounting male, while the cost of losing the opportunity of mating with a nearby female is greater than the cost of approaching a male (Scharf and Martin 2013).

Male competitive behaviours have been described in many insect species such as delphacid planthoppers (Ichikawa 1982), leafhoppers (Mazzoni et al. 2009), and sharpshooters (Nieri et al. 2017), and may involve the production of vibrational signals aimed at decreasing the mating success of a rival male. For instance, in the leafhopper *Scaphoideus titanus,* a specific male rivalry signal is used to disrupt an ongoing duet (Mazzoni et al. 2009). Although rivalry signals have not yet been reported in psyllids, there is evidence that males interact by exchanging signals and future studies on potential rival interactions are worth being conducted (Tishechkin 2007). Male choruses have been accordingly described for some species belonging to the family Triozidae, in which chorusing may be either a cooperative strategy to increase the active space of the male calls or simply a random sum of vibrational signals emitted in unison (Tishechkin 2007; Greenfield 2015). Males of the Australian psyllid *Anoeconeossa unicornuta* (Aphalaridae) also perform choruses, regardless of the presence of a female on the plant. In particular, the male call may trigger the emission of signals from surrounding males, creating a prolonged and continuous chorus, whose role is still unknown (Liao et al. 2022).

Specific courtship vibrations are common among hemipterans such as leafhoppers (Mazzoni et al. 2009) and stinkbugs (Virant-Doberlet and Čokl 2004) to elicit the acceptance of a partner (usually the female) at short-range and differ from the signals used in the first phases of the pair formation process. In *S. titanus*, for example, pair formation is a dynamic process, whose stages are associated with different male signals, while the repertoire of the female is limited to a response signal. In this way, signals are optimised for reliability in the first stages of the

mating process (identification and localisation), while the more energy-demanding signals aimed at evoking the acceptance of the female are used in proximity of the latter (Mazzoni et al. 2009). Comparable short-range courtship signals have not been reported within Psylloidea, since the male usually uses the same vibrational signal throughout the pair formation process (Tishechkin 2007). Although the repertoire of vibrational signals within Psylloidea is commonly limited to the male call and the female response, in some species signals are produced also during copulation (Tishechkin 2007). In *Colposcenia aliena* (Aphalaridae), the male produces vibratory signals, which consist of a sequence of pulses, each composed of shorter high-amplitude and longer low-amplitude fragments (Tishechkin 2007). Similarly, long signals with a varying structure are produced by the male of *Calliardia anabasidis* (Aphalaridae) once his genitalia are in contact with the female (Tishechkin 2007). Similar "copulatory" signals seem rather common among the Aphalaridae family, considering that also the male of *A. unicornuta* emits a long buzzing signal while copulating (Liao et al. 2022).

Indeed, many questions remain on the role of vibrational communication in the sexual behaviour within Psylloidea. Indeed, it seems to be important but not always necessary, since mating could occur in the absence of vibratory signals, especially in situations of high population densities (Tishechkin 2006, 2007; Liao and Yang 2017).

22.2.2 Chemical and Other Communication Modalities

Chemical cues are used by many phytophagous insects to find suitable hosts for reproduction, especially in specialist species where a correct decision during host selection is crucial for survival (Dicke 2000). Odors leading the insect to the host can derive from the plant or from conspecifics (Dicke 2000), and some psyllid species accordingly use olfaction for host finding (Moran and Brown 1973; Lapis and Borden 1993). In *D. citri*, plant volatiles play a crucial role in host selection (Patt et al. 2011; Patt and Setamou 2010; Robbins et al. 2012). Citrus trees infected by the bacterium *Candidatus* Liberibacter asiaticus released more methyl-salicylate than uninfected plants and, for this reason, were more attractive to *D. citri* (Mann et al. 2012; Martini et al. 2014). Similarly, the bacterium *Ca.* Liberibacter solanacearum, which is transmitted by *B. cockerelli*, caused an upregulation of volatiles in capsicum plants (Mas et al. 2014). The bacterium also altered the hemolymph pH and oxygen tension in the insect's body (Molki et al. 2019), but the effects on other aspects of the physiology and behaviour are not known. It would be interesting to assess whether the infection could change the attractiveness of *B. cockerelli* females and males to each others. At any rate, attractant compounds emitted by psyllids have been reported previously in the species *Cacopsylla chinensis* (Psyllidae) (Wan et al. 2013), *Cacopsylla bidens* (Psyllidae) (Soroker et al. 2004), *Cacopsylla pyricola* (Psyllidae) (Guédot et al. 2009a,b), *B. cockerelli* (Triozidae) (Guédot et al. 2010), and *D. citri* (Liviidae) (Wenninger et al. 2008).

While semiochemicals used for long-range communication have not been yet described (Lubanga et al. 2014), odors are important at short distances, considering that female-specific cuticular hydrocarbons may attract nearby males and probably enhance the efficacy of vibrational communication (Guédot et al. 2009b; Mann et al. 2013). Indeed, the role of odours depends on the species, considering that *D. citri* males increase their calling rate in absence of female odorants (Wenninger et al. 2009). Psyllid mating behaviour also relies on visual cues, as in the case of *D. citri*, where mated females can use visual cues such as male colour to assess the quality of the potential partner (Stockton et al. 2017). Besides mate choice, vision seem to be important in orientation during mate searching, as the presence of light is an important factor affecting the mating frequency of species such as *C. pyricola* and *D. citri* (Krysan 1990; Wenninger and Hall 2007). Furthermore, geotaxis and phototaxis support the male during mate finding (Yasuda et al. 2005; Wenninger et al. 2009).

22.3 Vibrational Control of Psyllid Pests

Acoustic devices can detect insect presence or absence in the field and therefore monitor the activity of potential pest populations (Mankin et al. 2011). Moreover, several studies have shown that vibrational signals can be used to manipulate the behaviour of hemipteran pests (Polajnar et al. 2015; Takanashi et al. 2019). Species-specific vibrations can accordingly attract an insect target into traps (Hartman et al. 2017; Mazzoni et al. 2017) or interfere with the communication of mating pairs (Polajnar and Čokl 2008; Čokl and Millar 2009; Eriksson et al. 2012, Lujo et al. 2016; Gordon et al. 2017; Laumann et al. 2018; Nieri and Mazzoni 2019). Many factors such as the behaviour and the size of the insect affect the efficiency of these methods, provided that broadband signals emitted by large insects can be easily discriminated from low-frequency background noise, while smaller insects can be detected when very close to the sensor or when they reach high densities and their signal active space is consequently enlarged (Mankin et al. 2011). Giving that psyllids live in dense colonies and can damage economically important crops (Munyaneza 2010), there is an increasing interest in characterising their vibrational communication and developing monitoring and behavioural manipulation control strategies by means of mechanical stimuli.

The first encouraging attempts on Psylloidea involve *D. citri*, which, as mentioned above, transmits a devastating disease to citrus trees (Bové 2006). The vibrational signals of *D. citri* were used to create a monitoring and trapping device, which is currently under implementation (Mankin et al. 2013). In particular, the female reply was transmitted to citrus plants to direct males towards the signal source, exploiting the psyllid mating duet (see Sect. 22.2.1) (Wenninger et al. 2009). Therefore, the researchers developed a device consisting of a micro-controller platform operating a piezoelectric buzzer, which mimicked the female by simulating her response after the detection of a male call on the plant (Mankin et al. 2013, 2015;

Hartman et al. 2017). The buzzer elicited behavioural responses in both males and females (Mankin et al. 2013) and successfully led males towards the signal source, reducing their mating success (Hartman et al. 2017). In fact, tested males moved preferentially towards the device than towards females and the number of matings was significantly lower in the stimulated group than in the control (Lujo et al. 2016). The signals produced by the buzzer were longer and louder than those of the female psyllids, suggesting that higher amplitude signals were more effective at disrupting mating (Polajnar et al. 2015). Even if the device competed with the females, it rarely masked their signals; thus, the authors hypothetised that a continuous application of the playback could result in a more effective disruption of mating by covering the female replies. On the other hand, since the mating duet is properly mimicked when the playback is triggered after the male call, the authors also pointed out that the continuous transmission could be disadvantageous in terms of mating disruption (Lujo et al. 2016). Besides determining what signal features and timing could underlie the most effective control strategy, an economic and convenient application method must be developed before the vibrational device could integrate the farmers' toolbox. In the case of *D. citri*, since the device needs to be applied to multiple trees in large citrus groves, studies are ongoing in order to provide a future efficient field method.

In this regard, the technology to detect and transmit insect signals is rapidly improving, enabling acoustic and vibrational stimuli to become reliable tools for pest monitoring and control (Mankin et al. 2011). Small shakers are currently applied (at 50 m intervals) to the wires that support grapevines in vineyards and used to successfully disrupt mating in the leafhopper *S. titanus* by means of species-specific interference signals (Polajnar et al. 2015; Mazzoni et al. 2019). Cosidering that a similar approach is less feasible for the control of *D. citri* on citrus groves; other strategies have been proposed and should be tested in the future (Lujo et al. 2016). The vibrations could be, for instance, induced in the host plant by means of sounds transmitted aerially by audio-speakers, as it has been tested for the control of the hemipteran pest *Amrasca devastans* and *Nilaparvata lugens* (Saxena and Kumar 1980). Sound sweeps of 90 dB have been similarly tested on *D. citri,* and provided that the preliminary results are encouraging (Lujo et al. 2016), a reliable device may be available for farmers in the near future. Nonetheless, the use of sounds in field conditions has several disadvantages, such as costs due to broadcasting over large areas, which are relatively higher than those of pesticides (Mankin and Hagstrum 2012). Moreover, the effective range of airborne signals could be reduced by frequency-dependent attenuation over distance, which is often difficult to predict in natural habitats (Nelson 2003).

Mass trapping could support both monitoring and pest control, especially if employed before the psyllid populations reach high densities within the crop, but, again, there is need of implementation of the devices to ensure economic viability and efficiency. In addition, given that *D. citri*, *B. cockerelli,* and other species also use semiochemicals for mate finding (Wenninger et al. 2008, Guédot et al. 2010, 2013), plant volatiles and/or conspecific odours could increase the attractiveness of

the transmitted vibrational signals and support the development of traps, as demonstrated in the case of a stinkbug pest (Polajnar et al. 2019).

To conclude, vibrational communication plays a crucial role in the biology and ethology of psyllids, whose signal repertoire may be more or less complex, depending on the species. For these reasons, the signals emitted by these small insects may be used by researchers not only to support phylogenetic and taxonomic studies, but also to develop sustainable strategies for the control of pest species. In this regard, we are confident when affirming that mechanical stimuli are reliable tools that will integrate other pest management strategies to control and monitor psyllid populations in the field.

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