

# 3 Mating Behavior of the Asian Citrus Psyllid

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Many aspects of the mating behavior of *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), the Asian citrus psyllid (ACP) are shared by other members of the Psylloidea. Adults are reproductively mature within about 2 days post-eclosion, and both sexes mate multiple times during their lifetime. Typically, courtship is mediated by short-range, substrate-borne vibrational communication and semiochemicals. In citrus orchards, *D. citri* courtship is facilitated by host-seeking and foraging behavior, as both sexes are attracted to green and yellow colors, as well as to volatiles of young flush shoots on the host tree, and short-range communication is sufficient for finding mates in aggregations that develop soon after the flush opens. Courtship behavior includes a series of duets, in which a searching male produces vibrational calls that elicit rapid replies from receptive females, enabling him to focus on willing partners. Both sexes produce vibrational communication signals by extending and fanning their wings while their legs hold on to the plant. The signal is transmitted to the host plant structures and then detected by vibration-sensitive, chordotonal organs in the legs of the receiving conspecific. During the duetting bouts, male *D. citri* call intermittently, with an interval of  $9 \pm 1.4$  s (mean  $\pm$  standard error) between calls, and females reply within  $0.95 \pm 0.09$  s. Males

produce signals ranging approximately 150–500 ms in duration, and females 331–680 ms. The spectra of communication signals produced by *D. citri* have prominent frequencies that are multiples (harmonics) of the 170–250 Hz wing-beat frequency, and both sexes respond behaviorally to synthetic signals containing three or more wingbeat harmonics. When the male finds the female, he moves alongside with their heads pointing in the same direction and grasps her with his adjacent legs, bringing his abdomen from underneath to meet the opening of her genital segment. They remain in copulation for about 48 min. Dispersal and mating behavior of *D. citri* is influenced by abiotic factors including light, temperature, storms and barometric pressure, and by biotic factors including host plant flush, host plant structure, aggregation behaviors and learning behaviors. Opportunities exist to co-opt *D. citri* mating behavior for purposes of detecting and managing populations, enabling reductions in the incidence and spread of the bacteria causing huanglongbing, a devastating disease of citrus. This chapter describes details of what is currently known about *D. citri* mating behavior and how such knowledge has been applied in development of methods that apply vibrational communication to disrupt mating or trap males.

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### 3.1 Introduction

*Diaphorina citri* Kuwayama (Hemiptera: Liviidae) native to India (Hollis, 1987), initially was reported as a significant psyllid pest of *Citrus* spp. in China, Taiwan, Japan and the Philippines in the early 20th century (Crawford, 1912); however, little was reported about its ecology, life cycle and mating behavior (Husain and Nath, 1927; Catling, 1970; Pande, 1971) until it became important as a worldwide vector of huanglongbing (HLB), a devastating bacterial disease in citrus orchards (Halbert and Manjunath, 2004; Gottwald *et al.*, 2007). The bacterium *Candidatus Liberibacter* spp. (Alphaproteobacteria) resides in symbiotic bacteriomes within the *D. citri* hemocoel that also contain nutritional and defensive symbionts in mutually indispensable associations, all of which are transmitted transovarially (Dan *et al.*, 2017). Economic damage caused by HLB has stimulated interest in development of knowledge about *D. citri* biology and mating behavior that could be used for an integrated, multidisciplinary approach to management of *D. citri* and thereby HLB (Aubert, 1990; Grafton-Cardwell *et al.*, 2013; Hall *et al.*, 2013), as has occurred also with other economically important insect pests (Mankin, 2012; Benelli *et al.*, 2014; Takanashi *et al.*, 2019). In this chapter, we focus on aspects of mating behavior that can be co-opted to reduce *D. citri* populations in citrus and other hosts in the Aurantioideae subfamily of Rutaceae (Halbert and Manjunath, 2004; Hall *et al.*, 2017). The life stages of *D. citri* on rough lemon *Citrus jambhiri* Lush, sour orange *C. aurantium* L., grapefruit *C. paradisi* Macfadyen, and orange jessamine *Murraya paniculata* (L.) Jack were described by Tsai and Liu (2000). These and other host species have a range of different physical and structural characteristics that, as discussed further below, strongly affect vibrational signal amplitudes and the efficacy of mate-seeking behaviors (Cocroft *et al.*, 2006; Mankin *et al.*, 2018).

### 3.2 General Aspects of Mating Behavior in *Diaphorina citri* and Other Psylloids

Members of the Psylloidea, a group of about 3850 phloem-feeding Sternorrhynchan species

(Burckhardt and Ouvrard, 2012; Martoni *et al.*, 2017), share numerous aspects of reproductive biology and mating behavior (Lubanga *et al.*, 2014, 2016a). Psylloids reproduce only sexually, unlike some hemipterans (Kennedy and Stroyan, 1959). Many male psylloids reach reproductive maturity within about 2 days post-eclosion, and both sexes mate several times (Burts and Fischer, 1967; Van den Berg *et al.*, 1991; Wenninger and Hall, 2007; Guédot *et al.*, 2012; Lubanga *et al.*, 2018) during a typical lifetime of 49 days or longer (Wenninger and Hall, 2008). Refractory periods have been reported for females of some psyllid species (Lubanga *et al.*, 2016a) but have not been reported in *D. citri*. Newly emerged *D. citri* females have immature ovaries that remain without mature eggs until mating occurs (Dossi and Cònsoli, 2010). Mating stimulates vitellogenesis and rapid development of oocytes, and females often begin laying eggs on the day of mating (Wenninger and Hall, 2007). Because oocyte maturation is metachronous, with only one oocyte developing per oogenic cycle, the stimulatory effects of mating (Dossi and Cònsoli, 2010) may contribute to the polyandry (Wenninger and Hall, 2008) observed in this species. General aspects of several different male reproductive systems in the Psylloidea are described in Schlee (1969), Macharashvili and Kuznetsova (1997) and Kuznetsova *et al.* (1997); and the male *D. citri* genitalia and reproductive system were described in Stockton *et al.* (2017b) and Alba-Alejandre *et al.* (2018). Dossi and Cònsoli (2014) and Stockton *et al.* (2017b) described the *D. citri* female reproductive organs.

Short-range semiochemicals have been demonstrated to play a role in mate-finding of several (Wenninger *et al.*, 2008; Brown *et al.*, 2009; Guédot *et al.*, 2009, 2010; Mann *et al.*, 2013) but not all psylloids (Lubanga *et al.*, 2016b). Wu *et al.* (2016) investigated the antennal and abdominal transcriptomes of male and female *D. citri* to consider whether chemosensory proteins could be identified for development of attractants or repellents. It was found that a large proportion of chemosensory genes were similar in male and female antennae and terminal abdominal tissues, but two were expressed at higher levels in male than female antennae (Wu *et al.*, 2016), which is consistent with a potential role of antennal chemosensilla in *D. citri*

mate-finding or species identification (Onagbola *et al.*, 2008).

In addition, substrate-borne vibrational communication is an important mechanism for mate location in many psylloids (Ossiannilsson, 1950; Virant-Doberlet and Čokl, 2004; Tishechkin, 2005; Percy *et al.*, 2006; Lubanga *et al.*, 2014, 2016b; Eben *et al.*, 2015; Liao and Yang, 2015, 2017; Liao *et al.*, 2016), as well as other Hemiptera (Cocroft and Rodríguez, 2005) including the Auchenorrhyncha (Percy and Day, 2005) and the Cicadellidae (Gordon *et al.*, 2017). The capability to detect and produce vibrations is essentially ubiquitous in terrestrial invertebrates, which attests to the importance of vibrational cues for reproduction and predator avoidance (Cocroft and Rodríguez, 2005; Pollack, 2017; Takanashi *et al.*, 2019). In many Hemiptera, sexual communication involves a duet, in which a searching male will call and a sedentary female will reply, which facilitates searching behavior as well as mate recognition (Bailey 2003; Derlink *et al.*, 2014).

Unlike in air, a relatively uniform substrate, the physically non-uniform characteristics of the interiors and interfaces within plant structures strongly affect propagation of vibrations from their sources to the sensing insect (Michelsen *et al.*, 1982). Reflections from surface edges, frequency-dependent attenuation and background noise make it difficult to locate or estimate the distance to a vibration source precisely (Michelson *et al.*, 1982; Mankin *et al.*, 2011, 2018; Dent, 2017; Gordon *et al.*, 2019). In addition, the small size of *D. citri* (and many other psylloids) as well as frequency-dependent attenuation observed in plant structures essentially reduces the 'active space', i.e. the maximum communication distance, of vibrational communication signals to 1–2 m (Ichikawa 1979; Michelsen *et al.*, 1982; Mazzoni *et al.*, 2014). Consequently, the information that vibrational communication provides is typically transmitted over only a short range.

Males of *Nezara viridula* (L.) and other large hemipteran species have been reported to use the time delay between vibrational signals that reach two different legs as a directional cue for locating the female (Čokl *et al.*, 1999). The distances between the legs of psylloids, however, may be too small to use this delay effectively in search behavior (Tishechkin, 2007). Virant-Doberlet and Čokl (2004) suggested that even

small insects can stretch their legs between branches at bifurcations, thereby increasing the time delay, which could provide directional cues at bifurcation points. Nevertheless, background noise from wind or other loud sound or vibration sources masks the weak signals produced by small insects and interferes with precise identification of the direction of a replying female psyllid (Tishechkin, 2013). To accommodate directional uncertainties and signal masking, many hemipterans augment their searching behavior with a 'call-fly' strategy under which a searching male produces substrate-borne vibrational calls spontaneously when it first lands on a host plant and then moves upward and/or towards a receptive female who has produced a duetting reply in response to his call (Hunt and Nault, 1991). Such a strategy is beneficial when the females aggregate towards the upper perimeter of the plant, as is discussed in Section 3.4 below.

### 3.3 Substrate-borne Communication in *Diaphorina citri*

Substrate-borne communications associated with mating behavior of virgin male and female ACP, 5–7 days post-eclosion, were characterized by Wenninger *et al.* (2009a). Males and females both produce low-amplitude vibrational signals, 140–700 ms in duration, by extending and flapping their wings rapidly while holding on to the substrate with their legs, as in many other psylloids (Tishechkin, 1989, 2005). The signal then is transmitted through the legs to the substrate and connected structures. The communication signal spectral frequencies are harmonics of the 170–250 Hz wingbeat frequency (i.e. the fundamental frequency) (Mankin *et al.*, 2016), which is negatively correlated with body mass (Wenninger *et al.*, 2009a). ACP production of sounds consisting of wingbeat fundamental and harmonic frequencies is similar to that observed in many flying insects such as mosquitoes and bumblebees, the aerodynamics of which are described in Bae and Moon (2008). Due to its small size, ACP produces only faint sounds and the signal is carried primarily through vibrations transmitted through the leaf or twig surfaces (Michelsen *et al.*, 1982), which have signal attenuation and other structural characteristics

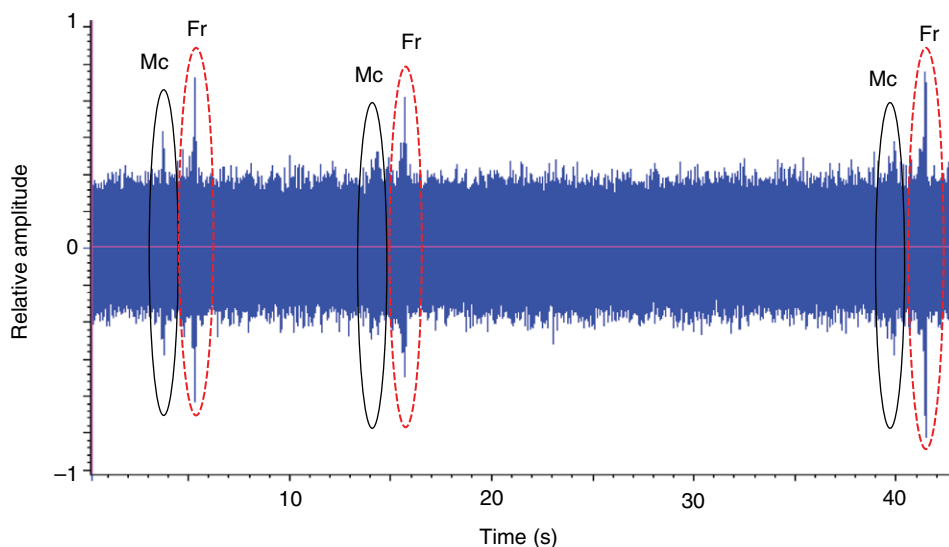
that vary considerably among the different plants that are ACP hosts (Mazzoni *et al.*, 2014; Ebert *et al.*, 2018). Several other psyllids have rows of teeth on the axillary cords of the wing mesoscutellum and metascutellum which can serve as a stridulatory organ for sound production (Heslop-Harrison, 1960; Taylor, 1985a; Liao *et al.*, 2019). However, stridulatory organs usually produce chirps with high-amplitude fundamental frequencies and weak harmonics (e.g. Mankin *et al.*, 2009; Grant *et al.*, 2014) caused by the friction of the pars stridens scraping over the plectrum. Because such spectral patterns are not observed in its signals (Mankin *et al.*, 2016), ACP possibly uses only wing-flapping and not stridulation as a sound-production mechanism.

ACP searching and mating activity on citrus occurs primarily on new leaf flush between 10:00 am and 3:00 pm (Wenninger and Hall, 2007). As with *Cacopsylla pyri* (L.) (Eben *et al.*, 2015), male *D. citri* usually produce calls spontaneously within about 15 min after landing on a host plant, except during extreme changes in weather or barometric pressure (Zagvazdina *et al.*, 2015). Receptive females produce a duetting reply within  $0.95 \pm 0.09$  s (mean  $\pm$  standard error) after the male call (Wenninger *et al.*, 2009a). The female remains sedentary while the male moves intermittently towards the female. Durations of male

calls range from approximately 148 to 544 ms, and female replies from 331 to 680 ms (Wenninger *et al.*, 2009a). After detecting a female reply, a male that has begun searching on a leaf or branch of a citrus tree typically moves in the direction of the reply for a few seconds until it reaches a bifurcation or other visually identifiable transition point. There it pauses, calls again, and then continues or returns back along the original path. Males call intermittently during the duetting bouts, with an interval of  $9 \pm 1.4$  s between calls (Lujo *et al.*, 2016).

Typical movement speeds of males involved in searching behavior are  $> 9$  mm/min (Zagvazdina *et al.*, 2015). Several instances of reciprocating behavior may occur before the male finds the female or ceases searching. Lujo *et al.* (2016) reported that, in 17 mating tests on small citrus trees, a male placed on a separate branch from a female searched for  $15.9 \pm 2.4$  min before finding the female. An example of a 45 s section of a duetting bout recorded from a small tree in an anechoic chamber is shown in Fig. 3.1.

It should be noted that only virgin *D. citri* males and females were tested in the Mankin *et al.* (2013), Rohde *et al.* (2013), Lujo *et al.* (2016), and Hartman *et al.* (2017) studies, and there is evidence that males learn female-produced olfactory cues and associated environmental odors



**Fig. 3.1.** A 45 s period of a *D. citri* duetting bout recorded on a small tree in an anechoic chamber. Solid oval (Mc) designates male call; dashed oval (Fr) designates female reply.

during their first mating encounter and subsequently are attracted to such odors (Stockton *et al.*, 2017a). Similar learning responses have been observed in mice (Remedios *et al.*, 2017). Previously mated *D. citri* males may be more responsive than virgins to female odor and associated environmental odor cues, as well as to vibrational reply cues when searching for females. In addition, there is evidence that females can learn cues associating male color with subsequent reproductive success and thereby increase fecundity (Stockton *et al.*, 2017b). Learning may be particularly beneficial (Dukas *et al.*, 2006) when multiple movement biases or other factors result in aggregations with high encounter rates between males and females, the topic of the next section. There is evidence that male cuticular hydrocarbons, including dodecanoic acid (Mann *et al.*, 2013), degradation products of citrus volatiles (George *et al.*, 2016; Lapointe *et al.*, 2016; Zanardi *et al.*, 2018), and combinations of yellow, green and ultraviolet light (Paris *et al.*, 2017a, b) may serve as significant cues in male searches for mates and host plants, as well as in female searches for host plants.

Once the male finds the female, he moves to her side with their heads pointing in the same direction, similarly as in *Trioza erythrae* (Del Guercio) (Van Den Berg *et al.*, 1991). If she is receptive, he holds on to her abdomen with his nearest legs, bending his upward-pointing genital segment down to meet the opening of the female segment, while supporting himself on the substrate with his remaining legs, and begins copulation (Husain and Nath, 1927). They copulate while the male holds the female with legs on one side of his body and supports himself on the plant with his remaining legs (Husain and Nath, 1927). The mean duration in copula has been measured as  $48.3 \pm 8.4$  min, ranging from 15.2 min to 98 min (Wenninger and Hall, 2007). The female usually begins ovipositing on the day of mating (Wenninger and Hall, 2007) and may lay up to 800 eggs over a lifetime of 2 months (Husain and Nath, 1927).

It has not been established whether differences among the temporal or spectral components of female replies affect ACP male mating preference although preference has been observed in fulgorid males (Mazzoni *et al.*, 2015). It may be relevant, however, that ACP females infected with the CLas pathogen are more fecund

and therefore have greater reproductive fitness than uninfected females, which may facilitate the spread of HLB (Pelz-Stelinski and Killiny, 2016). It is not known whether mating behavior itself is affected by CLas infection but increased fecundity could result from multiple matings with high-fertility partners, from changes in hormonal regulation of immune function and metabolic allocation (Harshman and Zera, 2007) or from increased movement leading the female to healthier flush (Martini *et al.*, 2015).

In addition, there are numerous abiotic factors that could interfere with different aspects of communication, physical activity or physiological processes associated with mating behavior. These include weather extremes and barometric pressure extremes (Zagvazdina *et al.*, 2015; Martini and Stelinski, 2017; Udell *et al.*, 2017; Martini *et al.*, 2018), high altitude (Jenkins *et al.*, 2015) and high levels of wind and other interfering vibrational background noise (Tishechkin, 2013).

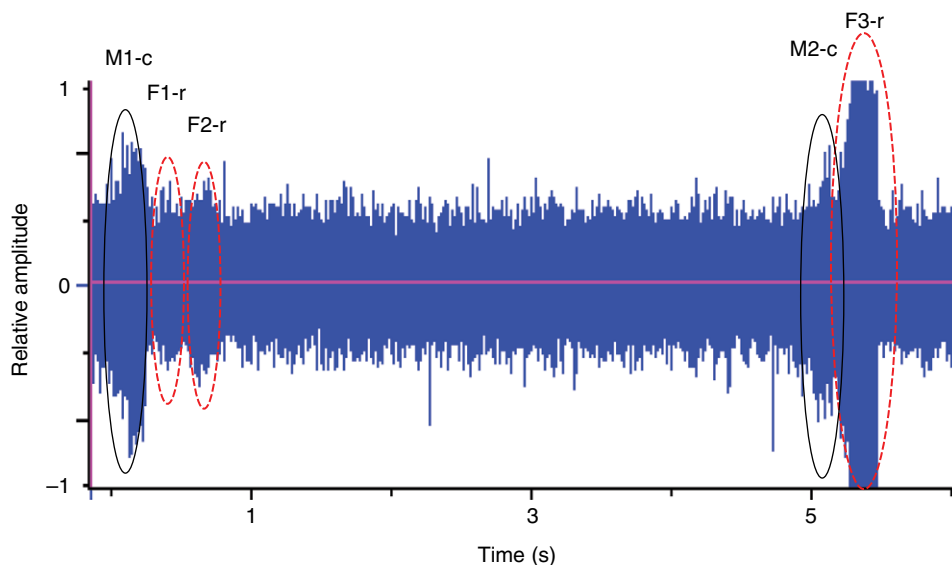
### 3.4 Movement Bias towards Light and Flush: Impacts on Mating Behavior

As with many psylloids, *D. citri* females and males exhibit phototaxis, both when flying (Sétamou *et al.*, 2011; Anco and Gottwald, 2015; Paris *et al.*, 2015) and walking (Pregmon *et al.*, 2016; Paris *et al.*, 2017a). They are attracted to green and yellow colors (Paris *et al.*, 2015); yellow colors are known to induce settling of many hemipteran herbivores on host plants (Döring, 2014). There is evidence that citrus tree volatiles play a role in attraction to the host (Wenninger *et al.*, 2009b). In addition, *D. citri* are attracted to new leaf flush (Catling, 1970; Hall and Albrigo, 2007; Patt and Sétamou, 2010; Sule *et al.*, 2012; Sétamou *et al.*, 2016; Hall and Hentz, 2016; Stelinski, 2019) on which eggs are laid and nymphs develop. Nutrient availability (Steinbauer, 2013), ability to easily probe the thinner structure of citrus leaf veins in young flush (Ammar *et al.*, 2013) and phagostimulants (George *et al.*, 2016; Lapointe *et al.* 2016) may play a role in such attraction. Oviposition cues detected by sensilla on the legs and female ovipositor also may play a role in

flush attraction (Zhang *et al.*, 2019). Such movement biases can result in both-sex aggregations on upper canopies (Soemargono *et al.*, 2008), border trees (Sétamou and Bartels, 2015) and flush (Tsai *et al.*, 2000; Sétamou *et al.*, 2008; Hall *et al.*, 2015). Aggregation and social behaviors also have been documented in numerous other hemipterans (e.g. Kennedy *et al.*, 1967; Way and Cammell, 1970; Lin, 2006). The occurrence of aggregations may reduce predation, partly by increased tending by ants (e.g. Navarrete *et al.*, 2013) which would lead to more rapid increases of *D. citri* populations.

Given that the volume of upper-canopy flush is generally only a fraction of the volume of the complete canopy, mate-seeking males that move towards light and flush will, on average, have less distance to cover in searching for a female than males that search at random. Consequently, such biases are reproductively advantageous. Likewise, when the density of nymphs and adults increases to levels that reduce flush healthiness, it is reproductively advantageous to migrate to areas with lower ACP populations (Martini *et al.*, 2015; Martini and Stelinski, 2017), as has been observed frequently in auchenorrhynchans (Taylor, 1985b).

A relatively unstudied impact of ACP aggregations is whether the presence of nearby conspecifics of both sexes may affect mating behavior. Until now, social interactions involving vibroacoustic communication have been studied primarily in social insects (Hunt and Richard, 2013) but interactions also have been documented in Delphacidae (Ott, 1994) and Cicadellidae (Hunt and Morton, 2001), and acoustic interactions are well documented in mating swarms of mosquitoes and midges (Mankin, 2012; Simões *et al.*, 2016; Jakhete *et al.*, 2017). Recordings from *D. citri* in infested orchard trees (Mankin *et al.*, 2016) as well as in greenhouse trees with *D. citri* maintained for behavioral bioassays (Paris *et al.*, 2013, and unpublished), suggest that social interactions in which multiple males and females take part in duets occur frequently in aggregations during the time of day when mating typically occurs, an example of which is shown in Fig. 3.2. The notable differences in the amplitudes and fundamental frequencies of the signals in Fig. 3.2 suggest that two different males and three different females had participated in the duets. Unpublished studies suggest that the duetting frequency per number of aggregated individuals decreases relative to the



**Fig. 3.2.** A 6 s period of duetting recorded from a tree in a *D. citri* colony reared for behavioral bioassays: solid ovals, M1-c and M2-c, indicate male calls; dashed ovals, F1-r, F2-r, and F3-r, indicate female replies. Differences in the amplitudes and fundamental frequencies of the signals suggest that two male calls and three female replies were produced by different individuals.

duetting frequency of isolated pairs, possibly because males can locate females in the aggregation readily by random movement without calling. Also, it has been observed that previously mated ACP males are less likely than virgin males to begin calling spontaneously (Wenninger *et al.*, 2009a), which may reduce the rate of calling in aggregations.

### 3.5 Potential for Mimicking or Interfering with Vibrational Communication Signals to Trap Males or Disrupt Mating

Soon after *D. citri* vibrational signals were first characterized in 2009, interest developed in the possibility of devices that mimicked the female reply signal to attract and capture males or disrupt mating. An understanding of *D. citri* population densities and spatial distributions in citrus groves is important for development and timing of management decisions (Sétamou *et al.*, 2008), but commonly used stem-tap and sweep-net sampling methods (Hall *et al.*, 2013; Monzo *et al.*, 2015) have limited efficiency at low population densities, and sampling with yellow sticky traps is costly and requires a relatively large time commitment (Hall and Hentz, 2010; Hall *et al.*, 2010; Monzo *et al.*, 2015). Mating disruption seemed feasible, having been demonstrated previously by Saxena and Kumar (1980) on cotton leafhopper *Amrasca devastans* Dist. and rice brown planthopper *Nilaparvata lugens* Stål. Disruption of substrate-based communication is a natural competitive practice in the leafhopper *Scaphoideus titanus* Ball (Mazzoni *et al.*, 2009). Therefore, a series of investigations was conducted to develop methods to trap and/or disrupt *D. citri* mating behavior.

Initially, recordings of duets (Rohde *et al.*, 2013) as well as synthetic mimics (Mankin *et al.*, 2013) were bioassayed for their potential to elicit female replies and male searching behavior in citrus trees. The bioassays demonstrated that males were attracted to the recorded replies as well as to synthetic mimics in which three or more harmonics of the fundamental frequency were present (Mankin *et al.*, 2016). Such knowledge of the spectral and temporal patterns needed for *D. citri* species recognition and male attraction thereafter led to development of

prototype signal-mimicking devices that disrupted mating (Lujo *et al.*, 2016) and attracted male *D. citri* to traps (Mankin *et al.*, 2016; Hartman *et al.*, 2017).

A potentially useful result of the male *D. citri* trapping study (Hartman *et al.*, 2017) was that males were found to be variably responsive to searching cues. Also, Zagvazdina *et al.* (2015) had previously reported variability in male searching behavior, demonstrating that changes in barometric pressure affected the proportions of males who moved either  $> 9$  mm/min or  $< 9$  mm/min towards the synthetic female reply from the prototype device. Similarly, variability in courtship behaviors of male *D. citri* was observed by Stockton *et al.* (2017b). A better understanding of such variability can help guide additional efforts to co-opt mating behavior for integrated pest management applications.

Mating disruption has been demonstrated in several different hemipterans since the initiation of studies with *D. citri*. Mating disruption of *S. titanus* (Eriksson *et al.*, 2012) and *Homalodisca vitripennis* (Germar) has been accomplished in vineyards (Gordon *et al.*, 2017; Krugner and Gordon, 2018). There is potential to disrupt mating in *Halyomorpha halys* (Stål), given that males have been attracted to synthetically produced signals (Mazzoni *et al.*, 2017). Field testing and device improvements coupled with experimentation to identify the best locations from which to deploy such devices ultimately may result in *D. citri* being one of the first insects for which the co-opting of vibrational communication becomes an important component of an integrated pest management program. Knowledge of *D. citri* movement biases enables pest managers to increase the efficiency of vibrational traps and mating disruption devices by operating them near potential sites of aggregation.

It should be noted also that a potent modulator of transient receptor potential channels in insect chordotonal organs has been developed recently (Kandasamy *et al.*, 2017) to which *D. citri* has been demonstrated to be susceptible (Chen *et al.*, 2018). Given the importance of vibration sensing in *D. citri* courtship, insecticides that target chordotonal organ function, reducing the perception of vibrational signals, are likely to have strong negative impacts on *D. citri* mating behavior at sublethal dosages.

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