



Characterizing Substrate-Borne Vibrational Mating Signals Produced by Pear Psylla, *Cacopsylla pyricola* (Hemiptera: Psyllidae)

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Abstract Tactics that manipulate insect behavior are a component of many pest management strategies. Pheromone-based mating disruption is one such tactic widely used in agricultural systems, but few studies have assessed disrupting other mate communication mechanisms, such as acoustic signals. The most destructive pear pest in the Pacific Northwest USA, pear psylla (*Cacopsylla pyricola*) is believed to use acoustic signals to find mates, making it a candidate for this type of disruption. This species has two adult morphs, overwintering adults (winterforms)

that emerge in the spring and subsequent generations (summerforms). Our study characterized the mating signals for both sexes and morphs of pear psylla, and assessed whether temperature and previous exposure to adult conspecifics altered signals and likelihood of signaling. While there are descriptions for acoustic signals of other psyllid species, this study provides the first evidence that *C. pyricola* communicates acoustically. The two sexes communicate via duetting; males signal to attract a female and the female signals back if she is receptive for mating. We showed that both morphotypes' male signals contain a group of chirps followed by a trill, while females respond with chirps. Male signal trills differed significantly in frequency (Hz) between winterform and summerform psylla. The signal frequency among morphs also had a positive linear relationship with temperature, suggesting that dissimilarity in signals among morphs had some relationship to temperature. Males were more likely to signal when they had previous exposure to females compared to males without exposure to females. Our results provide new information on how pear psylla communicate acoustically for mating, advancing the potential to develop mating disruption strategies for integrated pest management (IPM).

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Introduction

Sustainable pest management in agricultural systems relies on strategies that reduce overall insecticide use and exploit species-specific behaviors or life history traits (Weddle et al. 2009). Mating disruption, for example, is used to exploit a pests' mating behavior in ways that reduce mating opportunities (Cardé and Minks 1995). Many insects communicate with mates using species-specific pheromones that can be synthesized and used to interfere with mate-location and, consequently, female-production of fertile eggs (Cardé and Minks 1995). Pheromone-based mating disruption has in turn been used to control species such as domestic silk moth, oriental fruit moth, and codling moth (Butenandt 1959; Wright 1964; Ridgway et al. 1990; Cardé and Minks 1995; Brunner et al. 2002; Howse et al. 2013). While insects also communicate with potential mates through non-chemical means, such as acoustic signals, there are few examples of mating disruption tactics that disrupt signals other than pheromones (Miller and Gut 2015).

Many insects use vibrational signals for communication (sometimes referred to as songs) and the study of substrate-borne vibration has a long history; this form of communication is common in many Hemipteran, Coleopteran, and Hymenopteran insect families, including pest groups (Cocroft and Rodríguez 2005). Studies show that sap-feeding pests such as *Homalodisca vitripennis* (Nieri et al. 2017), *Diaphorina citri* (Mankin et al. 2015), *Halyomorpha halys* (Polajnar et al. 2016), and *Cacopsylla pyri* (Eben et al. 2015) all use substrate-borne vibrational signals that might be targeted to reduce mating success. Although recent advances in vibration sensing and recording technologies offer an opportunity to disrupt this form of communication, there are few examples of such behavioral manipulation within integrated pest management (IPM) programs outside of brown marmorated stink bugs (Mazzoni et al. 2017b) and in two leafhopper pests in grapes (Mazzoni et al. 2009, 2017a; Nieri et al. 2017).

One potential barrier to using vibrational signals for pest management is that insect signals are rarely static, with signal characteristics affected by variation in abiotic or biotic conditions (McNett et al. 2010; Virant-Doberlet et al. 2014; Oberst et al. 2019). In the *Enchenopa binotata* species complex of treehoppers, for example, temperature fluctuations affect

characteristics of male mating signals as well as responses by females (Jocson et al. 2019). This suggests that changes in temperature can induce physiological changes that allow males to produce vibrations at varying frequencies. This suggests disruptive signals might need to be modulated to match species-specific patterns under various temperature ranges, or based on other abiotic factors. Biotic factors, such as the presence of conspecifics or natural enemies, or the number of mating attempts, may also affect mating behavior (Fowler-Finn and Rodríguez 2012).

The goal of this study was to characterize vibrational communication signals of pear psylla, *C. pyricola*, as a step toward testing an acoustic mating disruption approach. Pear psylla is the most economically damaging pest of pears in Washington, Oregon, and California (Follett et al. 1985; DuPont et al. 2021; Murray et al. 2021). Pear psylla has two morphs: the winterform and the summerform (Oldfield 1970), and we characterized vibrational signals of male and female psylla of both morphs. After signals were characterized, we assessed how temperature variation and previous exposure to adult conspecifics affected signal characteristics. We predicted that psylla would produce higher frequencies (Hz) in their signals at warmer temperatures (Jocson et al. 2019), and that males would be more likely to produce mating signals if they had previously encountered females compared to naïve males. Our experiments characterizing pear psylla mating signals across a range of realistic abiotic and biotic conditions are a first step towards potentially incorporating acoustic mating disruption as a tactic for control of pear psylla.

Methods and Materials

Study System

Pear psylla is the most damaging pest of pears in the Pacific Northwest USA (Oregon and Washington), a region that produces nearly 80% of pears in the USA (NASS U 2022; NHC 2022). Current strategies to manage pear psylla in the Pacific Northwest USA rely on pesticides, and growers have been estimated to spend nearly \$3,700 per hectare per year on average for chemical control, with 10 to 14 pesticide applications used between February and October (DuPont et al. 2021; Murray et al. 2021). However, due to its phenology, multiple overlapping generations, and

overuse of broadly toxic chemicals, pear psylla has a history of developing pesticide resistance (Harries and Burts 1965; Follett et al. 1985; Whalon et al. 2008). In turn, there is an urgent need to develop more integrated tactics that conserve natural enemies or manipulate psylla behavior (Dupont et al. 2021; Murray et al. 2021). For example, behavioral manipulation using kaolin clay and reflective mulches can disrupt flight behavior of winterform pear psylla and subsequent injury to pear trees (Nottingham and Beers 2020; Nottingham et al. 2022).

Pear psylla uses a multi-modal communication system for attracting and finding mates that include pheromones (Guédot et al. 2009) and, as shown in this study, substrate-borne vibrations. It is thought that vibrational communication and pheromones with low volatility act in concert to bring the sexes together for mating (Lubanga et al. 2014), with the vibrational signals bringing the sexes into near proximity of one another through “duetting” and the pheromone acting as a contact recognition signal. Duetting is the back and forth signaling behavior of psyllids that males use as a location beacon to find stationary females (Percy et al. 2006; Liao et al. 2022). Vibrational communication, like duetting, between the males and females is thus expected to be essential in mate-searching and may be an important target for disruption.

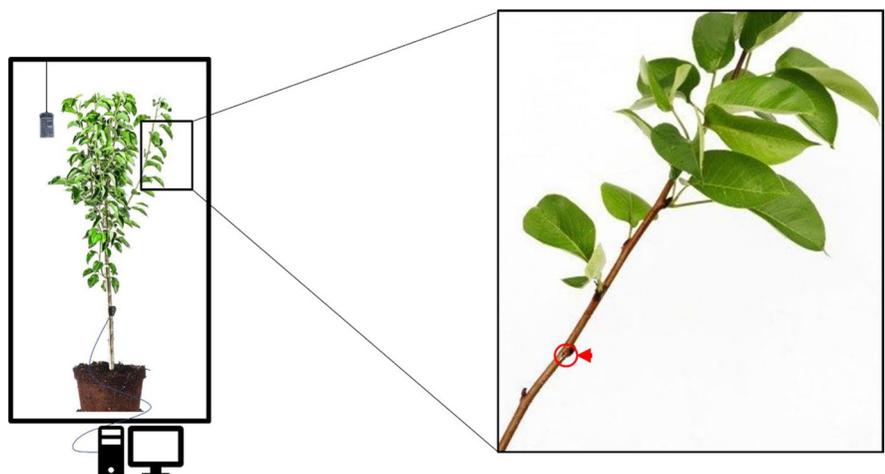
Our study attempted to assess signals of both male and female pear psylla of both morphs. The large, dark winterform adults develop in autumn in response to shortening day lengths, then overwinter,

and re-emerge in the spring to mate. The smaller and light-colored summerform psylla emerge during the long-day conditions of the growing season. Winterform females may be a particularly good target for mating disruption because they overwinter in an unmated condition (Krysan and Higbee 1990). Courtship and mating begin in late winter, meaning that acoustic signaling by winterforms begins while temperatures are relatively low. These conditions stand in contrast to the much warmer ambient temperatures experienced by courting summerforms.

Recording set-up

Inside a soundproofed room at Washington State University, assays were conducted by placing a potted pear plant inside a clean rectangular meshed cage (BugDorm-44590F Insect Cages, MegaView Science Co., Ltd., Taiwan) with a temperature sensor (HOBO Onset, Bourne, MA) hanging from the top (Fig. 1). An accelerometer (PCB Piezotronics, Depew, NY) was attached to the pear stem using beeswax to monitor vibrations produced on the stem. The accelerometer was connected to an audio interface (Tascam 4×4, Los Angeles, CA). Vibrations were recorded on a computer using the Audacity program (Version 2.3.0, Muse Group, San Francisco, CA). Potted plant size, placement of accelerometer head, placement of psylla, and input volume were kept similar or consistent across assays.

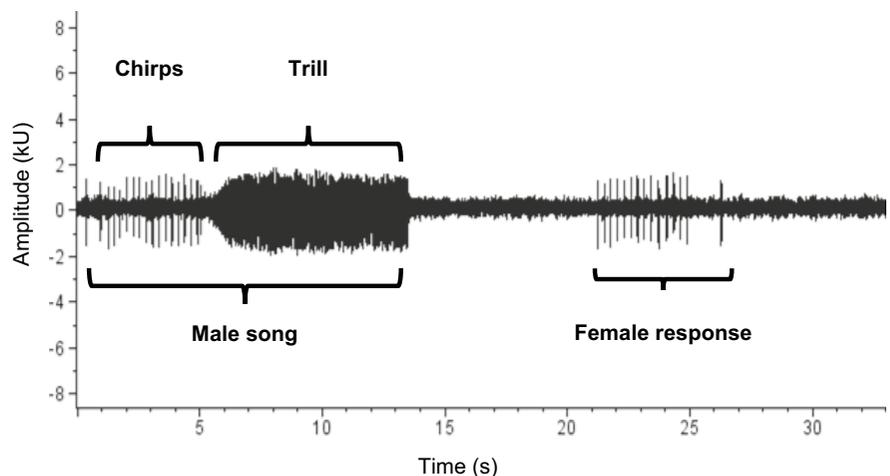
Fig. 1 Set-up of observation assays to record and listen to pear psylla. The potted pear plant is placed inside a mesh cage (black rectangle) and the head of the accelerometer placed on the stem of the pear plant. Zoomed in rectangle shows a part of the pear plant where the pear psylla (red circle with an arrow pointing to it) may be on



Measuring Acoustic Signals

Assays with field-collected (winterform) and greenhouse-reared (summerform) pear psylla were conducted on potted pear trees (cv. ‘Bartlett’) provided by the Central Washington Nursery (Quincy, WA, USA) in 14 L pots with potting soil (Sunshine® LC1, Sun Gro® Horticulture, Agawam, MA, USA). Plants were kept in greenhouses (16:8 h light:dark, 21–24°C:16–18°C) at Washington State University, Pullman, WA, USA. Winterform pear psylla were collected from pear trees in experimental pear orchards using beat trays and aspirators. In 2019, psylla were collected from orchards in Yakima, WA, USA; in 2020 and 2021, psylla were collected from the Washington Tree Fruit Research and Extension orchard in Wenatchee, WA, USA. After collection, winterforms were kept in the greenhouse in long-day conditions to break reproductive diapause and were tested three days after placement in the greenhouse. Summerforms were produced by rearing insects in long-day conditions (16:8 h light:dark, 21–24°C:16–18°C). As new summerform adults emerged they were separated by sex onto 12 pear plants (six with males and six with females). We used mesh cages (30×30×100 cm) with one plant and 30 to 50 adults. Males and females were also placed in six mixed-sex mesh cages to give both males and females pre-assay contact with the opposite sex. Psylla were assayed seven to ten days after having been placed in their respective cages. Psylla were randomly chosen from the mesh cages to assay.

Fig. 2 Oscillogram from Audacity showing a summerform male signal and a summerform female response. Male signals comprise of multiple chirps in the beginning followed by a trill. Females respond using chirps only



Male song assay

Males were collected from rearing cages (randomly chosen from cages with female exposure and without) by aspirating individuals into vials and brought into the recording lab. For one replicate, a single male was placed on a single pear plant inside the observation arena. Recording began immediately. Each male was allowed 30 min to produce a courtship signal. Temperature could not be controlled in the soundproof room, so was monitored to assess the effects of this variable on song traits. At the end of each 30 min assay, temperature at the stem surface was recorded with an infrared surface-temperature gun (Etekcity, Lasergrip 800) pointed at the stem adjacent to the assayed psylla. Ambient temperature over the duration of each assay was also recorded, using a HOBO temperature sensor (HOBO UA-001-64 Pendant Temperature 64 K Data Logger). Surface temperature and ambient temperature were strongly correlated (Pearson correlation test, $r=0.81$, $t_{222}=20.8$, $P<0.0001$); surface temperature data were used in the analyses. Winterforms and summerforms were recorded at different times of the year corresponding with their natural phenology in the orchards.

If males produced courtship signals, the recordings were saved (at 44100 Hz sample rate) and analyzed for multiple signal traits (Fig. 2): number of chirps, trill length, number of complete signals (a set of chirps and a trill), number of bouts (groupings of signals that are less than 5 s apart), trill peak frequency (Hz), inter-chirp interval, and inter-signal intervals. Trill peak frequency (Hz) and trill length were

measured using the Raven Program (Raven Pro 1.5, Cornell Lab of Ornithology), while inter-chirp interval, inter-signal intervals, number of chirps, number of signals, and number of bouts were quantified with the Audacity program.

Recording pear psylla duet and female response

We placed two male and two female summerform pear psylla, randomly chosen from those with and without previous exposure to conspecifics of the opposite sex, on a pear plant inside a 30 × 30 × 100 cm mesh cage. Recording set-up was the same as above. We recorded for 24 h to allow individuals time to perform and produce mating signals and responses. Recordings were analyzed to describe male–female communication signals. Visual observations could not be recorded. Frequencies (Hz) from our recordings were compared to noted frequencies (Hz) in existing literature of closely related species (Eben et al. 2015; Liao et al. 2022).

Statistical analyses

Statistical analyses were conducted in *R* (V4.3.1; R Core Team 2022). We first used Pearson's correlation coefficients to assess linear relationships between different song traits. Next, we conducted linear regression models to assess whether trill peak frequency (Hz), number of chirps, trill length, and interchirp interval were affected by surface temperature, morphotype, and their interaction; morphotype was a categorical variable in these analyses. Logistic regression was used to examine whether likelihood (odds ratio) of a male signaling (a binary yes/no variable) depended upon temperature and experience (i.e., previous exposure to females).

Results

Signal Characteristics

Male signals (of both morphs) had between 8 to 20 chirps (mean = 15.8) followed by a trill that lasted between 3 and 41 s (Fig. 2). Summerform psylla signal had a mean frequency (Hz) of 1180 (SE = 92.8) while winterforms had a mean frequency (Hz) of 639 (SE = 90.6). Inter-chirp intervals ranged from 122 to

443 ms (mean = 275.5). Psylla produced one to three complete signals on average and one to two bouts of these signals within the 30-min lab assay. Signal frequency and trill length were significantly negatively correlated ($r = -0.41$, Fig. 3), but other signal characteristics were not significantly correlated (Fig. 3). These results reflect pooled data from males with and without previous exposure to conspecifics of the opposite sex.

Effects of Temperature and Morphotype on Signals

Signal frequency was significantly positively correlated with temperature (Pearson's correlation, $r = 0.27$, $P = 0.047$, Fig. 3), while trill length was negatively correlated with temperature (Pearson's correlation, $r = -0.22$, $P = 0.002$, Fig. 3). Winterform signal frequency was significantly lower than that for summerforms (linear model, $t_{93} = -6.60$, $P < 0.0001$, Fig. 4), but there was no interaction between temperature and morphotype (linear model, $t_{92} = -0.57$, $P = 0.57$, Fig. 4). Other signal characteristics, like inter-chirp interval, trill length and number of chirps, were not significantly affected by temperature, morphotype, or interaction between these two variables (Table 1).

Effects of Experience on Signals

Males were 1.79 more times likely to signal if previously housed on plants in the presence of females (mixed) compared to males that had been isolated from females (binomial glm, Mean = 1.79, SE = 0.48, $Z = 3.72$, $P = 0.0002$, Fig. 5). There was no effect of temperature on the likelihood of males signaling (binomial glm, Mean = -0.19, SE = 0.15, $Z = -1.25$, $P = 0.21$).

Discussion

Mating signals are species-specific, and insects must detect them in varying environmental contexts. For example, the acoustic signal of male *C. pyricola* is similar to that of male *C. pyri*. Peak signal frequency for male *C. pyri* is 1,600 Hz (Eben et al. 2015) while that for *C. pyricola* was 1,200 Hz at a similar temperature. Yet, the peak frequency of *C. pyricola* males ranged from 180 to nearly 1,900 Hz across

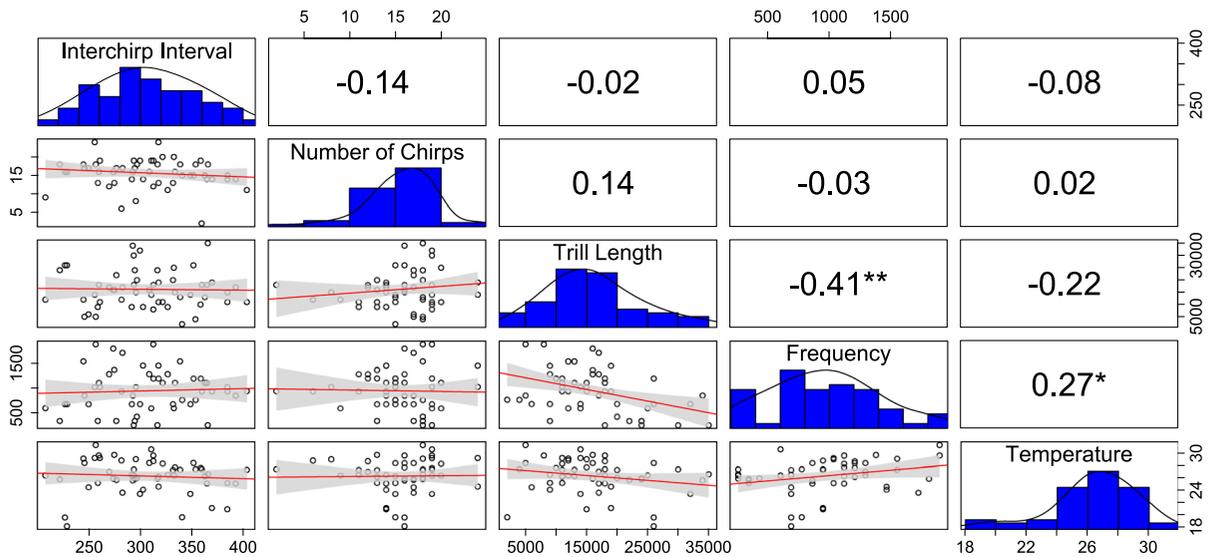


Fig. 3 A correlation plot of male signal characteristics and temperature. Units of measurements are as follows: Interchirp-interval = milliseconds (ms), Temperature = Celsius (C), Number of chirps = counts, Trill length = milliseconds (ms), Frequency = Hertz (Hz). The lower panel shows a scatterplot

of the data with a linear regression fitted line with 95% confidence interval ribbon. The diagonal shows a histogram of how the data are distributed with a fitted curve. The upper panel shows correlation values with significant correlations shown with asterisks

different temperatures, showing trill peak frequency can overlap across species. Moreover, trill frequency was negatively correlated with trill length, possibly because the energy required to produce a high frequency trill reduced the length of the trill. This suggests entire signals may be perceived to discern mates, and individuals within species must discern how variable features of signals may be influenced by environmental factors to enable mate discrimination (Gerhardt 1978; Jocson et al. 2019). Vibrational signals, as an example, are susceptible to frequency changes as insects cannot regulate temperature independent of the environment. As temperatures increase, insect activity rates increase, which translates to higher frequency vibrational signals. Other species, such as the vibration-producing insect *Enchenopa binotata*, have been seen to exhibit temperature coupling (Jocson et al. 2019), where males produce higher frequency signals at higher temperatures that the females recognize and prefer. Our study similarly shows a broad range in the values for signal traits, such as frequency and trill length, suggesting pear psylla may be able to discern variable signals as abiotic conditions shift.

As with treehoppers (Jocson et al. 2019), the signals of male pear psylla varied based on temperature and were more complex than the female signal. This dimorphism can be seen in many animals, such as peacock males having ornamental feathers to attract choosy peahens. The reverse has been seen in glow worms, where females that produced brighter glows were more successful at attracting males (Hopkins et al. 2015). More complex signals in males have been linked to both polygyny and female choice, where males mate with multiple females and are thus less discerning than females that mate a single time (Fitzpatrick and Servedio 2018). In species with polygyny, such as pear psylla, more complex signals have been suggested to communicate higher fitness because of increased energy put into signaling (Andersson 1994). The dimorphism observed in pear psylla may thus be related to the need for females that mate singularly to be fairly choosy, while mobile males use signals to locate females but perhaps do not use them to discern which females have greatest fitness.

Our results suggest that some winter and summerforms signal traits most likely differ because

Fig. 4 **A** With increasing temperature both winterforms and summerforms had decreasing inter-chirp intervals. **B** Trill length shown in milliseconds (ms) is not affected by temperature in either form. **C** The number of chirps was not affected by temperature in either form. **D** The dominant frequency measured in Hertz (Hz) show an increasing trend as temperature increases. This is shown in both winter and summerform. Summerforms are more likely to signal at warmer temperatures while winterforms are more likely to signal at cooler temperatures

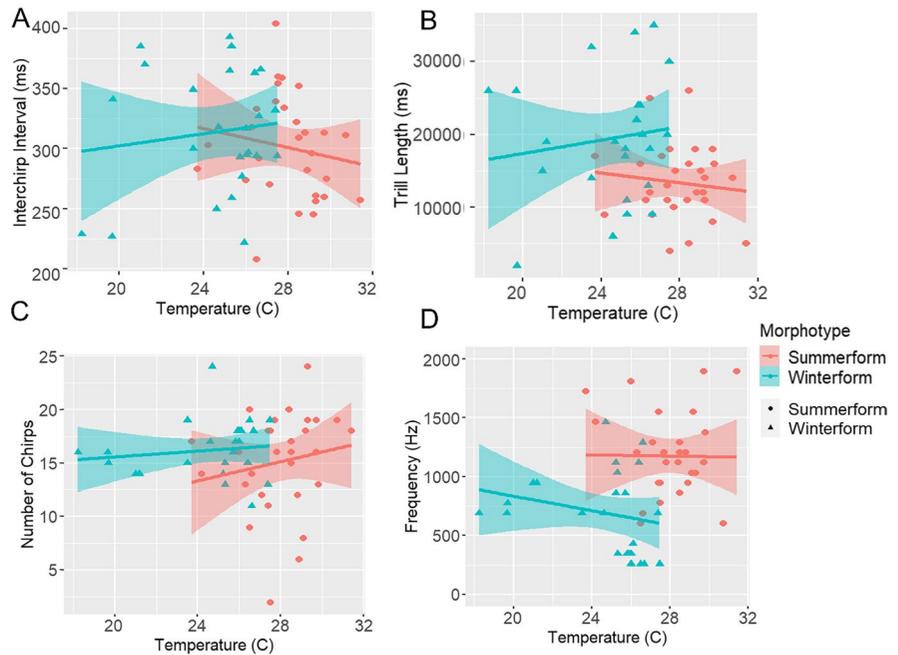


Table 1 Statistics for the four signal characteristics measured as response variable with temperature, morphotype, and the interaction between temperature and morphotype as the explanatory variables

Response Variable	Explanatory Variable					
	Temperature		Morphotype		Temperature x Morphotype	
	t	P	t	P	t	P
Interchirp interval	-0.766	0.447	-0.928	0.358	1.013	0.316
Trill length	-0.442	0.661	-0.574	0.569	0.843	0.403
Number of chirps	1.053	0.298	0.723	0.473	-0.592	0.556
Frequency	-0.901	0.372	-6.597	<0.001*	-0.573	0.569

*Significant effect of morphotype to signal frequency

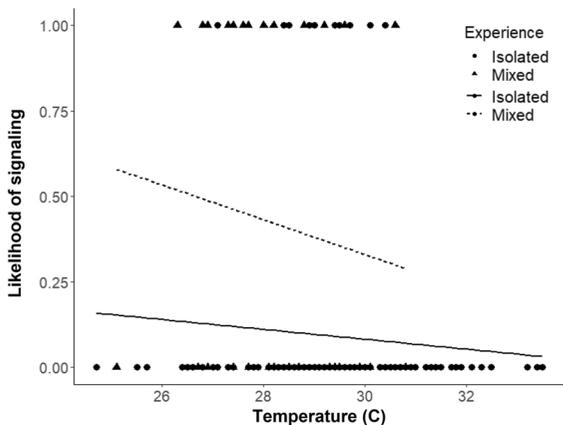


Fig. 5 Likelihood of males from mixed (triangle points and dotted line) and isolated (circle points and solid line) environments to signal across temperature

winterform and summerform psylla call at unique temperature ranges (Fig. 4). For example, our study shows that winterforms and summerforms produced vibrational signals at different frequency ranges, even while the patterns of the signals were broadly similar across the two forms (Fig. 4). However, signal traits were more similar for the temperature range where both morphs signaled (24 to 28°C) (Fig. 4). As winterform pear psylla have a single reproductive generation, during late winter and early spring when temperatures are cool, they should produce signal traits under low temperatures. In contrast, summerforms have up to three generations in the field and experience a broader range of abiotic conditions, suggesting summerforms may need to discern signals that are highly variable or not be as choosy when it comes to signal frequency

(Hz). In addition, acoustic signaling might be variable even over the course of a single day. For example, in Pacific Northwest USA, temperature extremes in a single 24-h period may vary between the mid-30 s (C) and the mid-teens. It may be that signaling occurs optimally during certain times of the day and temperatures. Targeting disruption during those optimal times of activity, and knowing characteristics of different signal traits at these times, will provide a baseline for disrupting mating in ectothermic animals that are unable to regulate internal temperature (Kingsolver 2009). Differences in song traits may reflect signaling at different temperatures, but this could also be a product of evolution between the morphs to discern intramorph signals versus intermorph signals when both morphs are present in early spring.

Additionally, variation among insects in signal traits may also have been driven by innate differences between morphotypes. Winterforms are larger than summerforms, and size alone could possibly have contributed to variation among insects in certain signal traits (Bennet-Clark 1998). Results that show significant correlation between temperature and frequency are dictated by the morphotypes singing at different temperatures with slight overlap between 24 and 28C. But as the data shows, summerforms and winterforms are noticeably signaling at different frequency within this overlapping range. This can also be the case for the negative correlation between trill length and temperature. As winterform and summerform adults do overlap in the field for a period of four to six weeks during the late spring/early summer, we hypothesize that differences in signal traits such as trill link may be adaptive and allow the unique forms to discern mates of the same morphotype.

Our assays also showed that the likelihood of signaling was affected by whether males had previously encountered females, but not based on other traits. Males that had been kept in culture with females were more likely to signal than males that had been in contact only with other males. This suggests males may avoid energetic costs of producing signals if they do not discern females nearby. Although we did not assess how density of pear psylla affects possible signals, the density of males and females in our mating arenas suggest that males were more likely to signal to attract females especially in a mixed-sex context. It is possible that if pear psylla density increased considerably, such that males are encountering receptive females frequently, they might also be less likely to signal

because they do not need to attract females with vibrational signals. We provide further evidence of experience-mediated behavior influencing mating behaviors, similar to previous studies on treehoppers and crickets (Rebar et al. 2011; Fowler-Finn and Rodríguez 2012; Rebar and Rodríguez 2016).

Our study provides the first evidence that *C. pyricola*, like other psyllids, engages in an acoustic duet. We describe that duet, and show how biotic (morphotype, previous contact with females) and abiotic (temperature) factors affect the male signal. While we still need to better understand potential interactions between pear psylla density, the probability of signaling, and signal traits, this study provides a fundamental step in understanding pear psylla behavior and biology. Now that traits of this species have been identified and synthesized, we can expand our work and assess how signal playbacks may affect pear psylla mating behavior in the field. We observed evidence regarding the complex mating strategies used by insects, and show that studies capturing species biology, life history, and environment can be used to develop mate disruption strategies that are species-specific and environmentally friendly.

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Author contributions Downen Mae I. Jocson wrote the main manuscript text, designed the experiments, collected data, analyzed data, and prepared figures. Mark Chester T. Gonzales helped design the experiments and collected and analyzed data. David R. Horton, Elizabeth Beers, and David W. Crowder conceived the project. Louis Nottingham and Liesl C. Oeller made major contributions to revisions and edits. All authors reviewed the manuscript.

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Data Availability The data for this paper is available in a project withing the Open Science Framework: https://osf.io/5hb8v/?view_only=fe8fe6e68d5e4cdd881451030c5f2a26

Declarations

Competing interests The authors declare no competing interests.

Conflicts of interest All authors declare there are no conflicts of interest.

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