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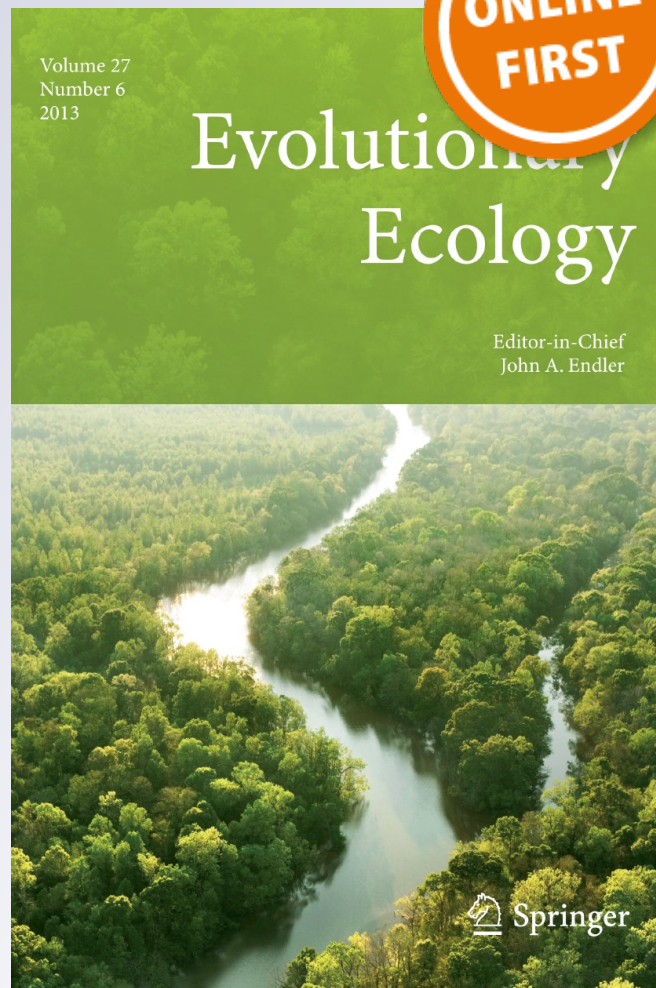
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Host plants impact courtship vibration transmission and mating success of a parasitoid wasp, *Cotesia flavipes* (Hymenoptera: Braconidae)

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Abstract Host plants provide food, shelter, and mating habitats for herbivorous and parasitoid insects. Yet each plant species is a microhabitat with distinct chemical and physical attributes that may drive selection and diversification of insects. This study examines differences in courtship vibration signal transmission through leaves of three host plant species that vary in physical characteristics (leaf tissue density, leaf width and percent moisture) and how signal transmission relates to mating success for a parasitoid wasp. The vibration signals transmit with a longer duration and a higher relative amplitude in the host plant leaves of the species with the lowest leaf tissue density, which was also the plant type with the highest mating frequency. Host plants may be a selective force on courtship vibration signals and may contribute to the behavioral or genetic divergence of populations on different host plant species.

Keywords Reproductive isolation · Selection · Host shift · Host associated differentiation · Sensory drive · Ecological speciation

Introduction

Host plants provide food, shelter and mating habitats for herbivorous and parasitoid insects. Yet each plant species is a microhabitat with distinct chemical and physical

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attributes that may drive selection and diversification of insects. Colonization of new host plants can result in divergent selection of insect populations, resulting in reproductive isolation and ecological speciation (Via 1999; Schluter 2001; Abrahamson et al. 2003). Many factors can contribute to insect population divergence on different host plant species, or host associated differentiation, including life history parameters such as parthenogenesis, limited dispersal ability, and univoltinism (Craig et al. 1993; Via 1999; Drès and Mallet 2002; Vialatte et al. 2005; Medina 2012). Host plant associated insect populations often exhibit oviposition preference for their natal host plants and assortative mating (Diehl and Bush 1984, Craig et al. 1993; Funk 1998; Wood et al. 1999), behaviors which reinforce population divergence and adaptation. Few studies have investigated the behavioral mechanisms (olfactory, acoustic, visual, etc.) that could lead to population divergence on different host plants (Craig et al. 1993; Via 1999; Stireman et al. 2005; Dorchin et al. 2009; Forbes et al. 2009; Coccoft et al. 2010; Sim et al. 2012).

The behavioral mechanisms involved in maintaining divergent host plant associated populations have been investigated in several systems. For example, the gall forming fly *Eurosta solidaginis* (Tephritidae) has an oviposition preference for, and assortatively mates with, insects from its natal host plant (Craig et al. 2001; Abrahamson et al. 2003), as does *Dasineura folliculi* (Diptera: Cecidomyiidae) which induces galls on *Solidago rugosa* and *S. gigantea* (Dorchin et al. 2009). For *E. solidaginis*, there is evidence for a male pheromone (Craig et al. 1993) which contributes to assortative mating of individuals from the two closely related host plants. Populations of the parasitoid *Diachasma alloeum* (Braconidae), which host shifted from *Ragoletis mendax* on blueberry to *R. pomonella* on apple, prefer the odor of their natal host plant (Forbes et al. 2009). Plant chemistry has been shown to influence the composition of insect pheromones (Landolt and Phillips 1997). Similarly, physical and structural characteristics of host plants such as leaf thickness, surface compounds and sap constituents can select for insect behaviors suitable for herbivores and their predators and parasitoids to survive and reproduce on different plant species. Trichome density, leaf waxes, and plant architecture influence predator and parasitoid host searching behaviors (Bottrell et al. 1998; Casas and Djemi 2002; LeGrand and Barbosa 2003; Olson and Andow 2006). In addition, insects may exhibit phenotypic changes in response to foraging on novel host plants (Carroll and Boyd 1992). Host plant physical characteristics could exert selective pressure on courtship behaviors such as vibrational signals which are tied to mating and reproductive success (McNett and Coccoft 2008).

Many insects and arthropods use substrate vibration signals which transmit through host plants as courtship communication signals (Greenfield 2002; Čokl and Virant-Doberlet 2003; Coccoft and Rodríguez 2005; Joyce et al. 2008). The structure of host plants affects the transmission of vibratory signals (Michelsen et al. 1982; Magal et al. 2000; Čokl et al. 2005), and variation in the plant or mating substrate can impact reproductive success (Elias et al. 2004; Joyce et al. 2008). Courtship vibration signals are often species specific but can vary among geographically isolated or host plant associated populations (Claridge et al. 1988; Ryan et al. 1996; Joyce et al. 2010a, b). Both vibrational signals as well as airborne courtship acoustic signals are heritable (Hoy 1974; Claridge et al. 1988; Virant-Doberlet et al. 2000). Differential mating success on host plant species which vary in their vibrational signal transmission properties could lead to behavioral divergence among insect populations (McNett and Coccoft 2008). Although a number of studies have demonstrated differences in courtship vibration signal transmission through host plants, few have related these differences to how they impact mating success.

Parasitoid wasps use both chemical and vibrational courtship signals (Field and Keller 1993; Ayasse et al. 2001). Male parasitoid wasps in the family Braconidae (Hymenoptera) wing fan during courtship and produce substrate vibrations which transmit through host plant leaves (Field and Keller 1993; Joyce et al. 2008, 2010a, b). The relative amplitude and duration of male-produced courtship vibration signals impacts mating success for the parasitoid species *Cotesia marginiventris* (Joyce et al. 2008). Variation in vibrational signal durations or amplitudes on different host-plant species, along with differential mating success on host plants, could lead to behavioral or genetic divergence between parasitoid populations.

Cotesia flavipes Cameron (Hymenoptera: Braconidae) is a parasitoid wasp that develops in stem-boring larvae of moth (Lepidoptera) species in the families Noctuidae, Pyralidae and Crambidae (Polaszek and Walker 1991, Potting et al. 1997). Host plants of these moths are grass species including sugarcane (*Saccharinum* spp.), corn (*Zea mays*), sorghum (*Sorghum* spp.), and rice (*Oryza sativa*). Genetic evidence suggests the presence of cryptic species or strains in the *C. flavipes* species complex (Kimani-Njogu et al. 1998, Muirhead et al. 2006, Joyce et al. 2010b). During courtship, adult male *C. flavipes* wing fan toward females which produces substrate vibrations in the host plant leaves (Joyce et al. 2010b). The buzz duration of the courtship vibration signal varies significantly between populations of *C. sesamiae* and between species in the *C. flavipes* complex (Joyce et al. 2010b).

The objective of this study was to determine whether variation in plant physical characteristics influences the transmission of courtship vibrations on different host-plant species, and if variation in transmission of these signals is related to mating success. We addressed this question using a biomechanical and behavioral approach (Henry and Wells 2004). The courtship vibration signals produced by male *C. flavipes* wing fanning toward females were recorded on three host plants, which included sugarcane, corn and rice. In a separate experiment, the mating success of *C. flavipes* pairs was observed on leaves of the same three host plants. Denser substrates tend to dampen sounds due to acoustic absorption and frequency filtering (Rossing and Fletcher 2004). Based on these properties of vibration transmission in substrates, we expected courtship vibration signals to transmit with higher relative amplitude and longer signal durations on the plant with less dense leaves (e.g., rice plants), while vibrational signals were predicted to have lower relative amplitudes and shorter durations on thicker, denser leaves (e.g., sugarcane plants). Higher mating success was predicted on plants with higher amplitude or longer duration courtship vibration signals.

Materials and methods

Insects and plants

Colonies of the parasitoid wasp, *C. flavipes* Cameron (Hymenoptera: Braconidae), and the moth, *Diatraea saccharalis* L. (Lepidoptera: Crambidae), were obtained from the Texas A&M Agrilife Research and Extension Center in Weslaco, Texas, from laboratory colonies supplemented yearly with field specimens collected from sugarcane. The population of *C. flavipes* introduced and established in Texas originated from Pakistan (Fuchs et al. 1979). The moth *D. saccharalis* is native in much of the Western Hemisphere, but is considered an introduced pest species in the southern US and has been the target of classical biological control programs in sugarcane, corn, sorghum and rice (White et al. 2004). Both the parasitoid wasp, *C. flavipes*, and the moth, *D. saccharalis*, were reared in College Station,

Texas in laboratory colonies as described by Joyce et al. (2009). Parasitoid cocoons were isolated individually to obtain virgin male and female adults for experiments. Plants used for experiments were grown under greenhouse conditions, with natural light (14L: 10D) at $30\text{ }^{\circ}\text{C} \pm 5\text{ }^{\circ}\text{C}$ and 50–90 % rh. Sugarcane (*Saccharum* spp. var LCP 85-384, not resistant to *D. saccharalis*) plants were provided by the USDA-ARS Sugarcane Research Unit in Houma, Louisiana, and were grown from 10 cm stalks. Corn plants (*Zea mays* L.) were grown from conventional Pioneer[®] seed 34A55 (Johnston, Iowa, USA), planted in Miracle Grow[®] (Marysville, Ohio, USA) potting soil in plastic pots (13 cm diam \times 12 cm height), while rice (*Oryza sativa* var Cocodrie)(BU Seed Growers, Texas) plants were grown from seed. Plants used for experiments had at least five internodes.

Courtship vibration transmission on three host-plant species

Courtship vibration signals were recorded from pairs of courting *C. flavipes* parasitoid wasps on plant leaves that remained attached to plants. Recordings occurred in an enclosed, sound insulated room using a phonocardiograph transducer (Electro-Voice, model 5146, Burnsville, Minn) and were amplified with a Digidesign Mbox Pro 2 (Avid Technology, Inc., Tewksbury, MA) on a vibration damping table at room temperature ($25\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$ and 30–50 % rh). A new leaf (attached to a plant) and a new pair of insects were used for each courtship recording.

Prior to recording courtship behavior, the edge of a test leaf was marked in 2 cm increments with minute dots of white correction fluid (Liquid Paper[®], Newell Rubermaid, Atlanta, GA, USA). The white marks served as a point of reference to determine the distance between where the transducer contacted the leaf and the location of a courting, wing-fanning male. All males and females used for courtship recordings were virgin and standardized in age (1–2 days old). A male–female pair was placed on a host plant leaf that was adjacent to the fifth internode of the plant stem. Corn plants have one stem, but sugarcane and rice plants have multiple stems, so a leaf next to the fifth internode on one of the central stems was used for each recording (\sim 60–70 cm from the base of the plant). Courtship vibrations produced by male wing fanning were recorded for 5 min. Headphones were used to listen to courtship sounds during recordings. Each time a wing fanning sound was heard, the time on the recording and the distance between the male and the phonocardiograph were noted. In order to standardize our recordings, male wing fanning vibrations that were produced within 0–8 cm of the recording device were used for analyses. The mean distance of the courting male from the transducer was \sim 5 cm (sugarcane = 5.25 cm, corn = 4.84 cm; rice = 5.25 cm; one-way analysis of variance (ANOVA), $F_{2,52} = 0.35$, $p = 0.71$). Most wing fanning by courting males typically occurs within several cm of a female, but courtship is active and a male will pursue a female until a female remains still and allows a male to copulate (A. Joyce, personal observation).

Recordings of courtship vibrations followed a randomized block design. A block consisted of the three host plant species, and the order of recordings was randomly assigned to each of the three host plant species within the block. All recordings occurred between 8 and 11 am, and parasitoids and plants were used for only one recording. Twenty male–female pairs were recorded on each host-plant species. Each recording was digitized using a PC computer (16 bit, sampling rate 44.1 kHz) and Adobe[®] Audition[®] 2.0 software (San Jose, CA) was used for measurement of vibration parameters. The first series of buzzes produced by male wing fanning was used for measurements (Joyce et al. 2008, 2010b). The duration of the first buzz in the series (buzz 1) was measured in ms (Fig. 1). Previous studies found that the pulse duration (Fig. 1) did not vary among *C. flavipes*

populations (Joyce et al. 2010b), so they were not considered in this study. The dominant frequency (Hz) and its relative amplitude (-db) were measured 10 ms after the beginning of buzz 1. A one-way ANOVA, with Tukey's post hoc tests, was used to compare each of the three vibration parameters of the buzz 1 component among the three host plant types (SPSS 2001). Data are presented as mean \pm SE.

Determination of leaf tissue density for the three host-plant species

After each recording, the plant leaf was removed from the plant in order to determine leaf tissue density. A section of the leaf that consisted of 9 cm on each side of the recording location (total leaf length = 18 cm) was retained for measurements. Leaf width (mm) was measured at the site on the leaf where wing fanning occurred, as was leaf thickness (mm); both measurements were made using a fine scale ruler. Wet weight (g) was also obtained and used to determine leaf tissue density (g/cm^3) for each plant type. One-way ANOVA was used to determine if leaf tissue density varied among the host plants. The leaf was dried for 2 days at 35 °C to remove leaf moisture; the leaf dry weight was obtained and used to determine percent moisture (dry weight/wet weight) of each leaf type.

Comparing mating success on three host-plant species

The same three species of host plants (sugarcane, corn, rice) that were used for courtship recordings were also used for mating trials. Plants were grown in the greenhouse as described above. Mating trials of parasitoid pairs were conducted in a small enclosed room (27 °C \pm 2 °C, 30–50 % rh) on leaves that remained attached to host plants. Previous observations of *C. flavipes* found that courtship typically occurs on plant leaves. Observations of courtship and mating occurred between 9 and 2 pm. For each trial, a virgin male–female pair (1–2 days old) was placed on a leaf of the host-plant, which was surrounded by (but not touching) a transparent plastic enclosure to contain the courting male–female pair. Pairs were observed for 10 min and the mating success (copulation or no copulation) was determined. The time elapsed from the beginning of a courtship

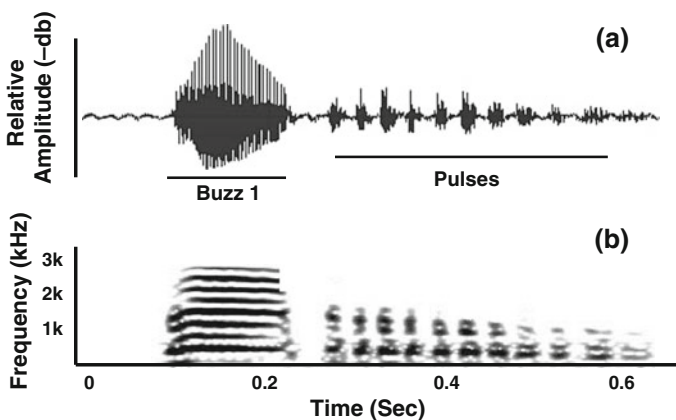


Fig. 1 The courtship vibration signal pattern produced by male wing fanning of *C. flavipes*. **a** The relative amplitude of the buzz 1 and pulses in the courtship vibration signal. **b** The frequency spectrum of the courtship vibration signal shown above in part (a)

Fig. 2 The buzz 1 duration (mean \pm SEM) produced during courtship was significantly different on the three host-plant species. Letters indicate significant differences according to a Tukey's test (One-way ANOVA, $F_{2,52} = 6.33$, $p = 0.03$)

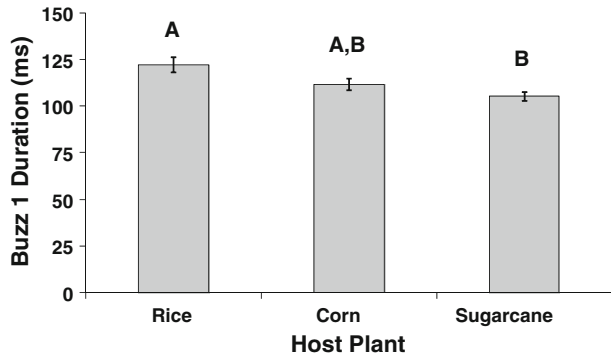
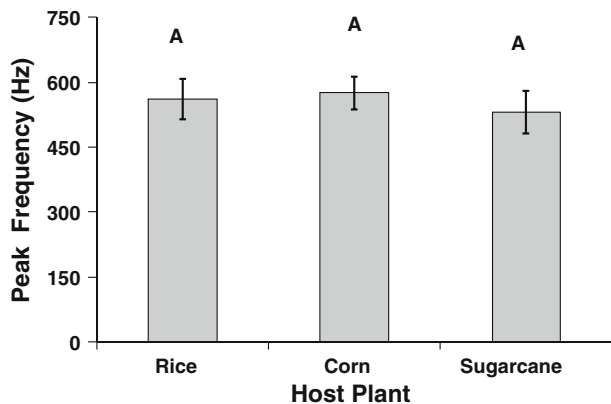


Fig. 3 There was no significant difference in the peak frequency (mean \pm SEM) of the buzz 1 component on the three host plants. Letters indicate significant differences according to a Tukey's test (One-way ANOVA, $F_{2,51} = 0.24$, $p = 0.78$)



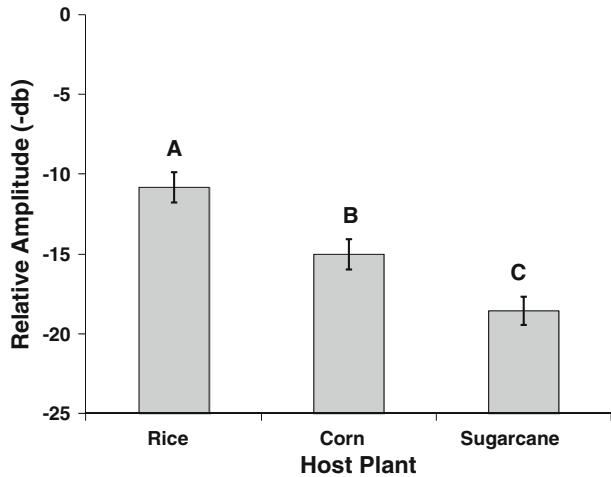
observation until mating occurred was recorded and compared among the three host plant species using a one-way ANOVA. Twenty-eight mating trials were conducted on leaves of each host plant species. All insects and leaves were used for only one trial. Mating frequency was compared among host plant species using a Chi square test with a Tukey-type pairwise comparison (Siegel and Castellan 1988).

Results

Courtship vibration transmission on three host-plant species

The buzz 1 duration varied significantly among the three host plant species ($F_{2,52} = 6.33$, $p = 0.03$) and was longest on rice, intermediate on corn, and shortest on sugarcane (rice 122.0 ± 3.97 ms; corn 111.53 ± 3.22 ms; sugarcane 105.19 ± 2.27 ms; Fig. 2). The peak frequency of buzz 1 did not differ significantly among the three host plants (rice 562.29 ± 46.83 Hz; corn 575.63 ± 36.95 Hz; sugarcane 531.47 ± 48.46 Hz; $F_{2,51} = 0.24$, $p = 0.78$; Fig. 3). However, the relative amplitude of the buzz 1 differed significantly among the three host plants ($F_{2,52} = 16.65$, $p < 0.001$), and was greatest on rice, intermediate on corn and lowest on sugarcane (Fig. 4).

Fig. 4 The relative amplitude (mean \pm SEM) of the buzz 1 component of courtship varied significantly on the three host plant species. Letters indicate significant differences according to a Tukey's test (One-way ANOVA, $F_{2,52} = 16.65$, $p < 0.001$)



Determination of leaf tissue density for the three host-plant species

Leaf tissue densities were significantly different among host plants ($F_{2,51} = 36.99$, $p < 0.001$); rice leaves were the least dense ($0.22 \pm 0.01 \text{ g/cm}^3$), corn leaves had a mean density of $0.26 \pm 0.01 \text{ g/cm}^3$, and sugarcane leaves were most dense ($0.46 \pm 0.02 \text{ g/cm}^3$) (Fig. 5). Leaf widths among host plant species were significantly different ($F_{2,52} = 148.85$, $p < 0.001$); rice leaves were most narrow, with average leaf width of $1.09 \pm 0.12 \text{ cm}$, sugarcane leaves were intermediate with a width of $3.04 \pm 0.13 \text{ cm}$, and the width of corn leaves averaged $3.93 \pm 0.12 \text{ cm}$. The moisture content of leaves varied significantly among host plants as well ($F_{2,45} = 74.65$, $p < 0.001$). Rice leaves had an average of $62 \pm 0.01 \%$ moisture, corn leaves had, on average, $80 \pm 0.01 \%$ moisture, while sugarcane leaves averaged $68 \pm 0.01 \%$ moisture.

Comparing mating success on three host-plant species

The mating frequency was significantly different on the three host plant species ($\chi^2 = 9.43$, $p = 0.01$, $N = 28$). The highest mating frequency occurred on rice (75 % mated, 21/28 pairs), followed by corn (64 % mated, 18/28 pairs), and mating success was 53 % on sugarcane (15/28 pairs) (Fig. 6). The mating frequency was significantly greater on rice than on sugarcane, while mating frequency between corn and either rice or sugarcane were not significantly different (Fig. 6). All of the males that mated exhibited wing fanning behavior. The mean time elapsed from the start of a trial until mating occurred was not significantly different among the three host plants ($F_{2,53} = 0.80$, $p = 0.45$; rice $191.05 \pm 53.29 \text{ s}$; corn $184.06 \pm 54.06 \text{ s}$; sugarcane $279.88 \pm 67.33 \text{ s}$), although there was a trend toward courting longer on sugarcane leaves before mating.

Discussion

Vibration signal transmission through host plants

Host plants affect the transmission of courtship vibrational signals (Michelsen et al. 1982; Magal et al. 2000; Casas and Djemi 2002; Cocroft and Rodríguez 2005; Čokl et al. 2005;

Fig. 5 The leaf density (mean \pm SEM) varied significantly among host plants (One-way ANOVA, $F_{2,51} = 36.99$, $p < 0.001$; mean separation by Tukey's test)

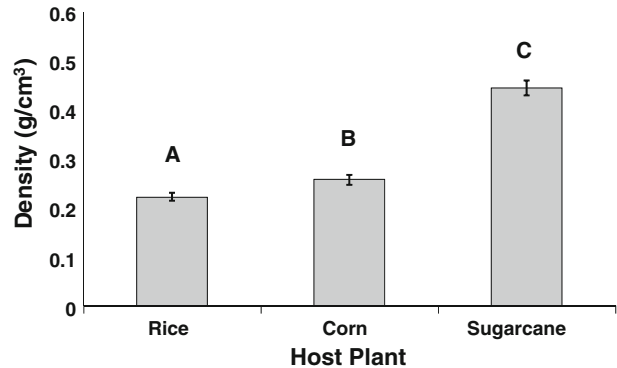
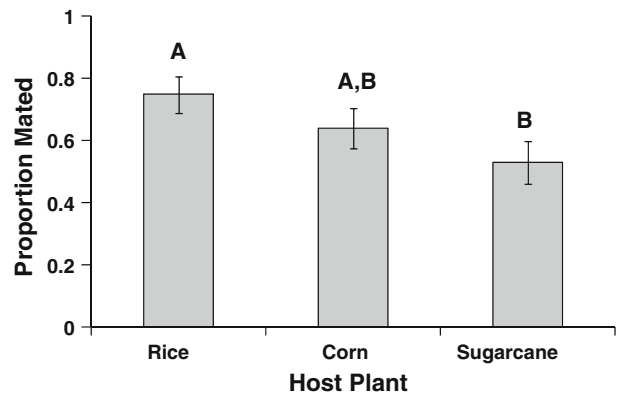


Fig. 6 The proportion (mean \pm SEM) of male *C. flavipes* mating on the three host plant species (n = 28 mating trials/per plant species ($\chi^2 = 9.43$, df = 2, $p < 0.001$, followed by Tukey's type pairwise test)



Casas et al. 2007), yet few have investigated how the vibrational signal transmission relates to mating success. We found that sugarcane, corn and rice leaves differentially impacted the courtship vibration transmission. The buzz duration of the male vibrational signal was significantly longer on rice leaves than on sugarcane leaves (~ 17 ms longer) (Fig. 2); similarly, the relative amplitude of the signal was significantly greater on rice than on sugarcane (Fig. 4). These differences related to the significantly higher mating success on rice than on sugarcane. The small differences in courtship vibration signal duration on the two host plants could lead to behavioral divergence and eventually to reproductive isolation. Differences in courtship vibration signals as small as 20 ms between divergent populations have been shown to result in reduced mating success. A previous study of the parasitoid *Cotesia sesamiae* found that courtship vibration signals of two populations varied by as little as 20 ms in the buzz duration (Joyce et al. 2010b); 30 % of pairs mated within each population, but mating frequency was reduced to 20 % between populations (Gounou et al. 2008). Another study of *Drosophila* species found that *D. persimilis* and *D. pseudoobscura* varied by 30 ms in the interpulse interval of the high rate repetition song, and mating was significantly reduced when the two species were crossed (Noor and Aquadro 1998).

Vibration transmission through leaves is subject to frequency dependent attenuation, where each frequency travels at a different speed and thus attenuates at distinct distances (Cocroft et al. 2006; Casas et al. 2007). Broadband signals are more dispersive than pure tonal signals. *C. flavipes* male wing fanning produces a broadband signal with a frequency

range up to $\sim 3,000$ Hz (Fig. 1). Little difference in vibrational signal duration was observed for courtship signals of the parasitoid *C. marginiventris* when recorded at short range (0–2 cm) on bean or corn leaves (Joyce et al. 2008). However, recordings in the present study found the buzz duration differed among host plants at up to 8 cm from the signal source. Similarly, a study of male *Nezara viridula* response to female calls found changes in signal duration at a distance of 10 cm (Mikals et al. 2001).

Host plant leaves vary in physical structures such as leaf thickness, leaf tissue density and leaf veins which can influence courtship vibration transmission (Michelsen et al. 1982; Magal et al. 2000). Denser materials such as thicker leaves absorb vibrational energy and reduce signal amplitude more than thinner leaves (Cocroft et al. 2006); they can also filter out higher frequency signal components. In our study, we found that rice leaves had a lower leaf tissue density than sugarcane leaves (0.22 vs. 0.46 g/cm³), and courtship vibration signals had a greater relative amplitude on rice as expected (Figs. 4, 5). Courtship signal durations may have been longer on rice leaves due to reduced acoustic absorption and frequency filtering compared with signal transmission through sugarcane leaves. Larger diameter leaf veins on sugarcane than on rice also absorb energy and result in signal attenuation (Magal et al. 2000). One notable difference in leaf shape was that rice leaves were narrower than sugarcane or corn leaves (1.09 cm vs. 3.04, 3.93 cm), which could contribute to reflections of vibrational signals and thus louder relative amplitude (Michelsen et al. 1982). In addition, wider leaves such as corn or sugarcane could result in a longer search time for mates than on narrower leaves such as rice (Casas and Djemi 2002). In contrast to the results of this study, Henry and Wells (2004) found no influence of host plant on the transmission of courtship vibrations for two green lacewing species that court on grasses and conifers. They suggested that for green lacewings, sexual selection may be a stronger selective force on courtship signal divergence than natural selection.

Mating success in relation to different host plant species

Courtship vibration transmission through host plants directly related to mating success in this study. *C. flavipes* mated more frequently on rice leaves, which had longer signal durations with higher amplitudes, while mating frequency was lower for *C. flavipes* on sugarcane where signals had lower relative amplitude and shorter duration. The relationship of higher reproductive success to vibrational signal amplitude and duration suggests these are critical signal characteristics involved in mate acceptance for female *C. flavipes*, as has been previously observed for the parasitoid *C. marginiventris* (Joyce et al. 2008). The variation in amplitude and duration on rice and sugarcane are not likely due to closed loop adaptation, where the parasitoid detects its self-produced vibrational signals in the leaf substrate, and subsequently fine tunes its wing fanning and energy input based on the leaf tissue density. Parasitoid wasps can detect substrate vibrations produced by potential mates and prey (Wackers et al. 1998; Meyhöfer and Casas 1999; Joyce et al. 2008). However, if *C. flavipes* males detected louder courtship vibration amplitudes on rice leaves, they did not appear to reduce their energy input into wing fanning. Courtship vibrations on rice leaves were consistently greater in amplitude than those on sugarcane, suggesting that courting males exert a relatively constant amount of energy. Variation in mating success observed for *C. flavipes* pairs on the three host plants is also not likely due to a preference for volatiles from one of the host plants. Host plant selection behavior has previously been investigated for six *C. flavipes* populations and no preference was observed for infested corn plants over sugarcane plants, regardless of the larval rearing environment (Potting et al. 1997). However, rice plants were not included in the study by

Potting et al. (1997). The *C. flavipes* used in this study was collected where sugarcane is abundant and rice is less frequently cultivated. In natural populations, greater reproductive success on a particular host plant could lead to behavioral divergence as insects adapt to physical properties of a host plant. Populations of *Enchenopa binotata* nymphs reared on novel host plants remained on the novel host plant and mated, which suggested that host shifts could eventually lead to divergent populations (Wood et al. 1999). Similarly, sensory drive suggests that communication signals will evolve for efficient transmission through the environment (Endler 1992; Boughman 2002).

Courtship vibration signal divergence might be investigated in other insect species with divergent host plant associated populations. For example, the gall fly *E. solidaginis* and apple maggot fly, *Rhagoletis pomonella*, both belong to the family Tephritidae, flies which produce wing buzzes and courtship vibration signals important to mating success (Sivinski et al. 1984). Mating of adult *Rhagoletis* flies occurs on host fruits or leaves (Prokopy et al. 1971), and courtship signals might differ in host plant associated populations. In addition, Braconid parasitoids of Tephritidae in the genus *Diachasma* are known to use courtship vibration signals (Joyce et al. 2010a), and host plant associated populations of *D. alloeum* which parasitize *R. pomonella* could have distinct vibrational signals involved in reproductive isolation.

In summary, many studies of courtship vibration signal transmission in host plants have focused on herbivores, and fewer have investigated those of plant dwelling predators and parasitoids at the third trophic level (Pfannenstiel et al. 1995; Elias et al. 2004). A parasitoid wasp such as *C. flavipes* which develops in stem-boring larvae on several host plant species could develop behaviorally divergent host plant associated populations due to differential transmission of courtship vibrational signals and mating success on structurally varied host plant leaves. Host plants are likely a selective force on courtship vibration signals, and could contribute to behavioral and genetic divergence of populations.

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