Courtship Behavior of the Corn Leafhopper Dalbulus maidis (DeLong & Wolcott) (Hemiptera: Cicadellidae)

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Abstract *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera: Cicadellidae) is one of the most important pathogen vectors on maize, but its courtship behavior has never been documented. In the present study, we recorded length of courtship and mating periods and behavioral transitions for *D. maidis*. According to these observations, we built ethograms for both sexes to create a comprehensive description of their courtship behavior. The mean courtship duration was 110.04 (±66.84) min and the mean mating period was 51.61 (±19.75) min. Both sexes showed similar, stereotyped behavioral transitions. However, females exhibited a lower frequency of several behavioral transitions and behaviors compared with males. Before mating, females were more frequently *resting* or performing an *abdomen movement*. Less frequently, they were *walking* or flapping the wings (*wing fanning*). Meanwhile, males exhibited three main behaviors before mating; the most frequent was *wing fanning*, followed by *walking* and *approaching*. However, during courtship, rapprochement between individuals of both sexes was not common so it is deduced that physical contact is not essential. In this regard, we discuss possible acoustic and chemical communication during the courtship process of *D. maidis*.

Introduction

Maize (*Zea mays mays* L.) is one of the most important crops worldwide (Tsai 2008). During cultivation, maize can be damaged by several insect pests, including the corn leafhopper, *Dalbulus maidis* (DeLong & Wolcott) (Hemiptera: Cicadellidae) (Chiang 1978; Nault 1990). This leafhopper has rarely been reported as a pest producing direct damage on maize, caused by feeding and removal of plant sap (e.g. Bushing and

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Burton 1974; Waquil 1997). However, *D. maidis* is a significant pest due to its role as a vector of three major phytopathogens, corn stunt spiroplasma (*Spiroplasma kunkelii*), maize bushy stunt phytoplasma (16SrI-B (rp-L)), and maize rayado fino virus (*Marafivirus*) (Nault 1980; Gámez 1969). At least one of these three pathogens has been reported wherever *D. maidis* is found (Nault 1998). The geographic distribution of *D. maidis* ranges from the Southern United States to Argentina (Triplehorn and Nault 1985). Eggs of *D. maidis* hatch about 6 days after oviposition and the nymphal stage lasts about 18 days at 21 °C (Davis 1966). Adult longevity is about 51 days under optimal conditions at 21 °C and 60 % RH (Davis 1966). Adult females can mate within 1 or 2 days after emergence and lay 400–500 eggs over their lifetime, which lasts about 7–8 weeks (Nault 1998).

Despite the economic importance of *D. maidis*, relatively few behavioral studies have been performed for this species. Previous work on the feeding behavior of *D. maidis* reported that this species differs from other Deltocephalinae in probing and feeding behavior (Wayadande and Nault 1996). Todd et al. (1990a) studied the response of *D. maidis* to different color stimuli and found that this species exhibited a strong orientation to yellow. In another study, it was reported that *D. maidis* populations from Brazil and Mexico move faster than those from Peru, Costa Rica and Colombia in response to plant shaking. In the same study it was found that male leafhoppers move faster than female conspecifics (Heady and Nault 1985).

Sexual behavior is a prerequisite for reproductive success, and to some extent is related to a species' population dynamics and prevalence (Cordero 1999; Futuyma 2004). As part of sexual behavior, courtship is a communication process by which insects can ensure successful conspecific mating as well as phenotype selection among sexual partners before copulation (e.g., Yang and Wang 2004). More specifically, courtship can be defined as the close-range, intersexual behavior that induces sexual receptivity prior to mating (Gullan and Cranston 2005). In this way, knowledge of courtship behavior can be helpful in gaining a better understanding of more complex processes such as sexual selection or mate choice (Matthews and Matthews 2010). Additionally, knowledge of courtship behavior of insect pests can be helpful in improving control of their reproduction and developing behavior-based pest control strategies, e.g., use of synthetic sex pheromones for mating disruption or trap-and-kill programs (Lingren et al. 1982; Charmillot et al. 2000; Matthews and Matthews 2010).

Some descriptions of courtship and mating behavior have been performed in other Cicadellidae. Downham et al. (1997) studied the mating behavior of *Cicadulina storeyi* China and *C. mbila* Naudé. Hix (2001) reported courtship and mating durations and mating and oviposition behavior for *Homalodisca coagulata* (Say). Duan and Messing (2000) examined the mating process and oviposition behavior of the two-spotted leafhopper *Sophonia rufofascia* (Kuoh & Kuoh). For the genus *Dalbulus*, Heady et al. (1986) provided a basic pattern of courtship behavior, although these authors stated that some variations exist among species. Later, Heady et al. (1989) described the courtship behavior for three *Dalbulus* species, *D. chapensis* Triplehorn & Nault, *D. quinquenotatus* DeLong & Nault and a hybrid between *D. quinquenotatus* (male)×*D. chapensis* (female). The authors focused mainly on the male, reporting its behavioral transitions and characteristic

behaviors: *stationary* (staying motionless), *walk to the female, walking but not to the female, contact with the female*, and *attempt to join the genitalia*. However the courtship behavior for the leafhopper *D. maidis* was not reported. Aiming to provide fundamental information on this species, the objective of the present study was to describe the courtship behavior of *D. maidis* by constructing ethograms for both sexes and reporting the pre-mating and mating duration.

Materials and Methods

Plants

Zea mays (var. Tuxpeño) seeds were supplied by the International Maize and Wheat Improvement Center (CIMMYT, Mexico) and by Dr. Moisés Morales Rivera (University of Guadalajara, Mexico). Seeds were grown in plastic pots (14 cm height×18 cm diameter) containing commercial soil (Nutrigarden ®) in a greenhouse. Plants were watered three times a week and used for colony rearing and experiments when they reached the four- to six-leaf stage.

Dalbulus maidis

A colony of the leafhopper *D. maidis* was established from individuals collected in El Grullo, Jalisco, Mexico (19°50′ N latitude, 104°16′ E longitude), in January 2008. Subsequently, leafhoppers from the same location have been added once a year to this colony to maintain culture vigor. This general colony was maintained in mesh wooden cages (Fig. 1a) containing four maize plants for feeding and reproduction under greenhouse conditions. These plants were frequently examined and replaced when necessary.

Dalbulus maidis (Virgin Leafhoppers)

In order to obtain known-age virgin leafhoppers, 200 adults from the general colony were confined into a mesh wooden cage (Fig. 1a) for 72 h to allow oviposition. Oviposition cages were placed in a room with the following environmental conditions: 25±5 °C; 60 % ±30 % RH, and an L12:D12 photoperiod. After the oviposition period, the leafhopper adults were removed and cages were observed daily until the appearance of second or third instar nymphs. Second or third instar nymphs were individually isolated in cylindrical clip-cages (Fig. 1b), which were clipped to a maize leaf to provide food. Each clip-cage was checked daily until adult leafhopper emergence. One day after emergence, leafhopper adults were identified to gender and individuals of each sex were separately placed in rectangular plastic cages (Fig. 1c) attached to a maize leaf to provide food. Leafhopper adults were used in the experiment when they were 7 to 14 days old. Virgin females were used in all bioassays because they can mate only once in their life (Heady et al. 1986). Occasionally (following the procedure described by Heady et al. 1989), when virgin females were ready for use but not enough virgin males were available, males from the colony were used after being isolated for 24–48 h, as males can mate several times.

a)

47.3 cm

29.7 cm

29.7 cm

b)

Clip cage
1.5 cm diameter
1.8 cm height

Hair clip

Corn leaf

Piece of sponge

c)

Rectangular plastic
cage:
5 cm height
4 cm length
2 cm width

Corn leaf

Rubber band

Entry hole

Piece of sponge

Wood support

d)

6.0 cm

9.0 cm

Corn leaf
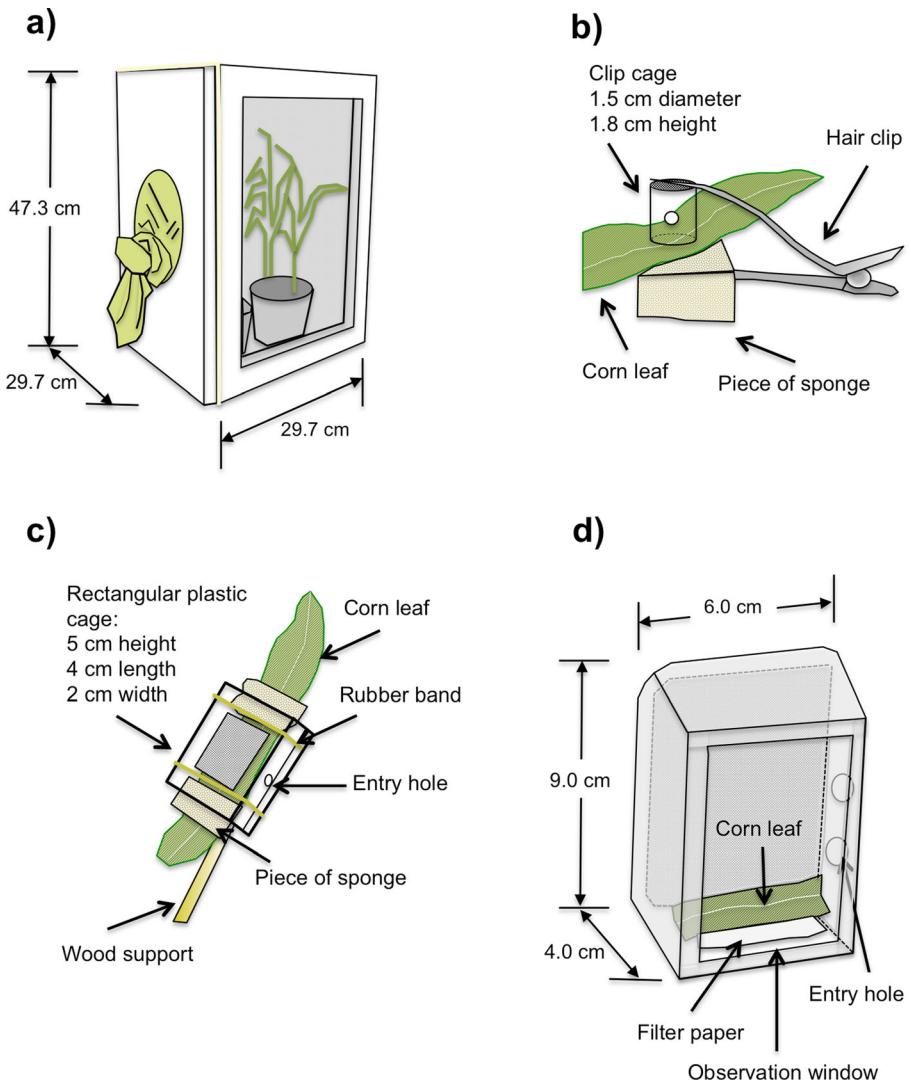
4.0 cm

Entry hole

Filter paper

Observation window

Fig. 1 Experimental cages for courtship observation and rearing of *D. maidis* to obtain virgin adults: **a)** rearing cages, **b)** clip cages (to keep virgin individuals), **c)** rectangular plastic cages (to keep individuals grouped by sex) and, **d)** arena to observe courtship

Courtship Behavior

Behavioral observations were conducted in a room with environmentally controlled conditions (25±2 °C, 60±10 % RH and 150 lux). For the observations, individuals were placed inside a plastic box (hereafter, 'arena') (Fig. 1d) with its lid replaced by transparent cling film to enable observations. The opposite side to the lid was replaced with insect-proof mesh to enable air circulation inside the arena. Before observations began, a piece of maize leaf (3 cm long) was placed inside the arena over a piece of wet filter paper (3 cm length×2 cm width) to provide food and humidity to leafhoppers during observations.

Based on preliminary observations, a catalogue of eleven distinctive behaviors was built for *Dalbulus maidis* (Table 1). This catalogue was used for all observed groups because leafhoppers displayed similar behaviors in the bioassays performed in the current study.

Behavioral observations started between 09:00 and 10:00 am and continued until mating occurred or for 5 h if mating did not occur. When mating did not take place, the observation was called invalid and a new pair of leafhoppers was observed. Behavior was only recorded for one member of each pair. The individual whose behavior would not be recorded was introduced first into the arena. Subsequently, we introduced the individual whose behavior would be recorded (hereafter referred to as 'observed individual'). Behavioral observations started when the observed individual was introduced into the arena. All behaviors displayed by the observed individual (see below) were recorded. In addition, courtship duration (i.e., time elapsed between the introduction of the observed individual and the beginning of mating) and mating duration (i.e., time elapsed between the beginning of mating and separation of the couple) were also recorded. As a result, courtship was described separately for two groups: i) females that did mate (hereafter referred to as 'mated females') and ii) males that did mate (hereafter referred to as 'mated males'). Each observed group was replicated 13 times (for a total of ~130 h of observation), as this has been the observation time for similar behavioral studies (e.g. Todd et al. 1990b; Heady et al. 1989). For each replicate, a new pair of

Table 1 Catalogue of behaviors displayed during *D. maidis* courtship. The relative frequency of each behavior performed by 52 individuals is indicated (13 replicates per group; total of ~230 h of observation)

Behavior *	Description of the behavior	Mated Females	Unmated Females	Mated Males	Unmated Males
Walking	Walking anywhere inside the arena	0.24 a A	0.27 a	0.31 a B	0.25 b
Cleaning	Rubbing the legs together, against the head, wings or the side of the body	0.21 a A	0.14 b	0.07 a B	0.07 a
Jumping	Displacement by means of jumping or flying (not possible to determine if the wings were opened)	0.04 a A	0.11 b	0.13 a B	0.22 b
Resting	Standing still	0.46 a A	0.44 a	0.38 a B	0.43 b
Approaching	Target individual gets closer to the other individual (to within 1.0–1.5 cm)	0.003 a A	0.02 b	0.01 a B	0.02 a
Abdomen movement	Movement of the abdomen (up and down)	0.01 a A	0.01 a	0.00 a B	0.0006 a
Wing fanning	Flapping the wings	0.008 a A	0.004 a	0.09 a B	0.01 b
Mating	Evident joining of genitalia	0.007 a A	0.00 b	0.005 a A	0.00 b
Separation	Separation of the genitalia	0.007 a A	0.00 b	0.005 a A	0.00 b
	Total Frequency	1,704	2,124	2,482	2,870

* Significant differences between mated and unmated females and mated and unmated males are indicated with different lowercase letters (chi-square tests with Bonferroni correction). Significant differences between mated females and mated males are indicated with different capital letters (chi-square tests with Bonferroni correction)

leafhoppers, a new piece of maize leaf, and a new piece of humidified paper were used. After each observation, the arenas were washed, rinsed, and cleaned with 70 % ethanol.

Behavior of Couples that did not Mate

To clearly differentiate courtship behavior (i.e., the close-range, intersexual behavior that induces sexual receptivity prior to mating) from other behaviors, we also described the behaviors and behavioral transitions of couples that were placed together but did not mate. For this, we first followed the same procedure to obtain virgin individuals as described previously. Then, we performed observations using the same procedure and environmental conditions as for the courtship bioassay. From these observations, behavior was described separately for two groups: i) females that did not mate (hereafter referred to as 'unmated females') and, ii) males that did not mate (hereafter referred to as 'unmated males'). Each observed group was replicated 13 times and each replicate consisted of 4 h of observation (The results of the courtship bioassay indicated that 4 h was enough time for a mating to take place). Therefore, a total of ~104 h of observation were performed for this bioassay. If individuals mated within the 4 h, the observation was called invalid for this analysis and a new couple was observed. For each replicate, a new pair of leafhoppers, a new piece of maize leaf, and a new piece of moist paper were used. After each observation, the arenas were washed, rinsed, and cleaned with 70 % ethanol.

Data Analysis

For each observed group, the frequencies of transitions from one behavior to another were first tabulated and then consolidated into a transition probability matrix using only first-order, preceding-following behavioral transitions (Lehner 1996). Self-transitions (i.e., repetitions of the same behavior) were not included in these matrices. A transition matrix was created for each group (13 individuals per group). Furthermore, for each group, another global transition matrix was created by pooling values from all 13 individuals. The principal diagonal elements of these matrices were logical zeros since behaviors could not follow themselves in our records. Expected transition frequencies were calculated as follows: Expected=(row sum×column sum) / (grand sum) (Lehner 1996). The statistical significance of the overall table was evaluated using a log-likelihood ratio (G) test. Yates correction for continuity was applied throughout. When deviations in the overall table were found to be statistically significant, the significant transitions were found by collapsing the tables into 2×2 matrices around each transition and performing separate G tests. The significance of these individual tests was adjusted to a table-wide alpha level of 5 % using the sequential Bonferroni method (Rice 1989). The results of the analyses of behavioral transition matrices are presented graphically in flow diagrams (Joyce et al. 1999; Ramirez-Romero et al. 2012). Finally, to analyze differences between mated and unmated leafhoppers, the relative frequency of each behavior was compared between mated and unmated individuals (within each sex) using chi-square tests with Bonferroni correction for multiple comparisons (Rice 1989). Chi-square tests and the Bonferroni correction were also employed to compare the relative frequency of each behavior between mated females and mated males (to analyze differences between sexes).

Results

Courtship Behavior

As stated previously, only couples where mating had place were taken into account for analysis of courtship.

Females

The most frequent behaviors (relative frequency) displayed by *D. maidis* females during courtship were *resting*, followed by *walking*, *cleaning*, and *jumping*, which together represented more than 95 % of the behaviors seen during courtship (Table 1). During courtship, females usually *walked* into the arena and then they frequently *rested* (Fig. 2a). After *resting*, females performed one of the following behaviors (in decreasing order of frequency): *walk*, *clean* themselves, *jump*, or engage in *mating* (Fig. 2a). After *cleaning* themselves or *jumping*, females mainly returned to *rest* (Fig. 2a). Before *mating*, females more frequently performed *resting* or *abdomen movement* and, less frequently, *walking* or *wing fanning* (Fig. 2a).

Males

The most frequent behaviors (relative frequency) displayed by *D. maidis* males during courtship were *resting*, followed by *walking*, *jumping*, *wing-fanning* and *cleaning* which together represented more than 95 % of the behaviors seen during courtship (Table 1). Comparing the relative frequency of these behaviors between mated females and mated males, we found that males exhibited a higher relative frequency than females of *walking* ($X^2 = 22.808$; 1df; $P < 0.0001$), *jumping* ($X^2 = 95.245$; 1df; $P < 0.0001$), and *wing fanning* ($X^2 = 121.55$; 1df; $P < 0.0001$). Meanwhile, females exhibited a higher relative frequency of *resting* ($X^2 = 28.866$; 1df; $P < 0.0001$) and *cleaning* ($X^2 = 198.13$; 1df; $P < 0.0001$) (Table 1). During courtship, males frequently *walked* into the arena and then performed any of the following behaviors (in decreasing order of frequency): *rest*, *jump*, *wing fanning*, or engage in *mating* (Fig. 2b). After *resting*, males performed one of the following behaviors (in decreasing order of frequency): *walk*, *jump*, *cleaning* themselves or *wing fanning*. After *wing fanning*, males either *walked* or *rested*. After *jumping*, males frequently *rested* or *walked*. Before *mating*, males most frequently flapped their wings (*wing fanning*) and less frequently *walked* or *approached* the female (Fig. 2b). Overall, during courtship males displayed displacement behaviors (e.g. *walking*, *jumping*, and *approaching*) more frequently than females; males also exhibited more behavioral transitions (greater than 2 % relative frequency) than females. Meanwhile, females more frequently exhibited behaviors without displacement (e.g. *resting*, *cleaning*, and *abdomen movement*). Before mating (although at different frequencies), both sexes *walked*, *rested* or flapped their wings (*wing fanning)*. Also, prior to mating, males *approached* the females and females performed *abdomen movement* (Fig. 2a and b).
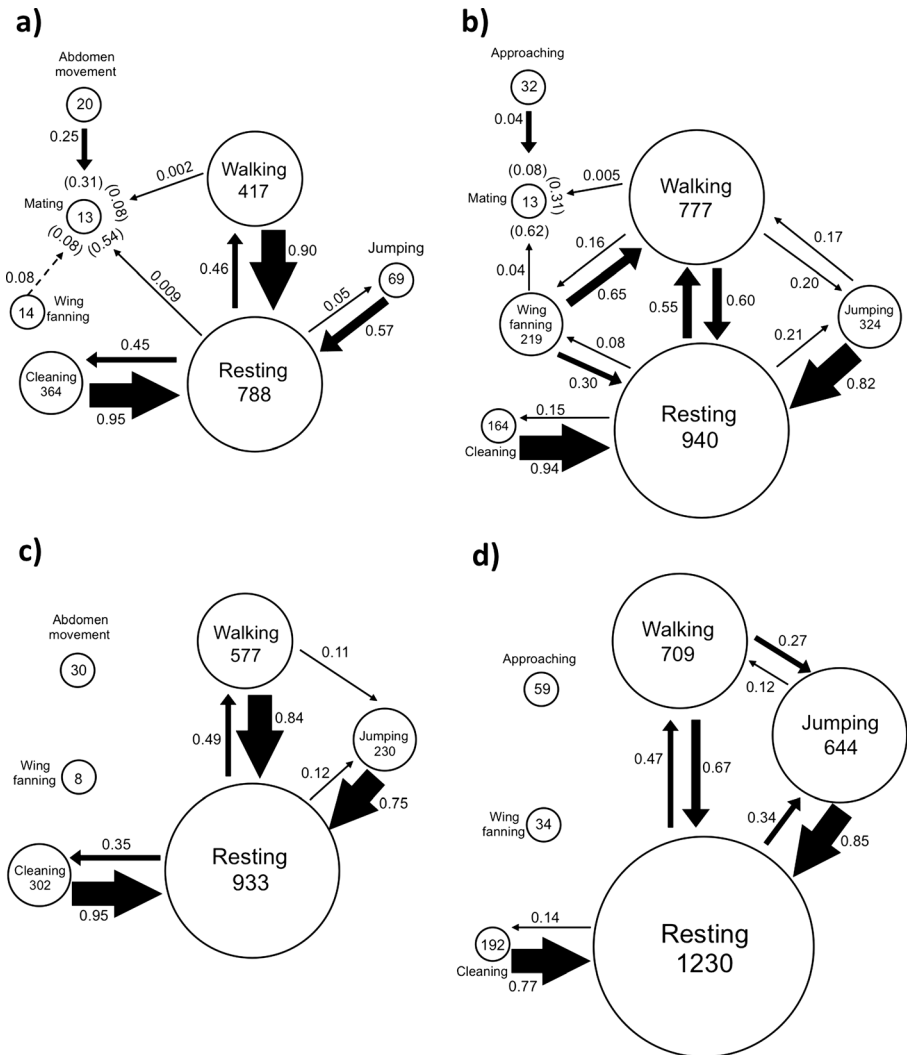
Fig. 2 Flow diagram showing the behavioral transitions for: **a)** mated *D. maidis* females, **b)** mated *D. maidis* males, **c)** unmated *D. maidis* females, and **d)** unmated *D. maidis* males. Boxes represent behaviors (Table 1); numbers inside the boxes are behavioral repetitions. Solid arrows represent transitions significantly different from expected (non-random), and dashed arrows represent transitions not significantly different from expected (random). The numbers next to the arrows indicate the proportion of transitions. The numbers in parentheses refer to the relative frequency of the behavior that precedes mating. Only transitions with a relative frequency higher than 2 % or transitions found to be related to mating are shown

Courtship and Mating Times for *Dalbulus maidis*

After pooling data from observation of 26 individuals, we found a mean courtship duration (±SD) for *D. maidis* of 110.04 (±66.84) min. The mean mating time was 51.61 (±19.75) min.

Behavior of Couples that did not Mate

As stated previously, this bioassay considered only couples for which mating did not occur.

Unmated Females

The most frequent behaviors (relative frequency) of *D. maidis* unmated females, together representing more than 95 % of the behaviors seen were the same as those exhibited by mated females (Table 1). However, unmated females exhibited a significantly higher relative frequency of *jumping* (X^2=59.407; 1df; P<0.0001) and a lower relative frequency of *cleaning* (X^2=33.070; 1df; P<0.0001) compared with mated females (Table 1). When unmated females were introduced into the arena, they exhibited similar behavioral transitions to those performed by mated females, except for the absence of those transitions related to *mating* and the transition *walking-jumping* (greater than 2 % relative frequency) (Fig. 2c).

Unmated Males

The most frequent behaviors (relative frequency) for unmated *D. maidis* males were *resting*, *walking*, *jumping* and *cleaning*, which together represent more than 95 % of the behaviors seen (Table 1). When the relative frequency of these behaviors was compared with that for mated males, significant differences were found. Unmated males exhibited a higher relative frequency of *jumping* (X^2=78.495; 1df; P<0.0001) and *resting* (X^2= 13.511; 1df; P=0.0002) behaviors, and a lower relative frequency of *walking* (X^2= 28.592; 1df; P<0.0001) and *wing fanning* (X^2=170.75; 1df; P<0.0001) behaviors (Table 1). When unmated males were introduced into the arena, they displayed similar behavioral transitions to mated males, although mated males exhibited additional transitions (or greater than 2 % relative frequency) related to *mating* and *wing fanning*, compared to unmated males (Fig. 2d).

Discussion

According to our observations, *D. maidis* individuals displayed stereotyped courtship behavior (Fig. 2a and 2b). During courtship, males exhibited a higher relative frequency of displacement behaviors (e.g. *walking*, *jumping*, and *approaching*) and more behavioral transitions (greater than 2 % relative frequency, such as those related to *wing fanning* and *jumping*) than females (Fig. 2a and 2b). Females, on the other hand, exhibited a higher relative frequency of behaviors without displacement (e.g. *cleaning*, *resting*, and *abdomen movement*) relative to males (Table 1). This indicates a more active role during courtship for *D. maidis* males compared with females. This is consistent with observations from previous studies that *Dalbulus* spp. males *fly* or *walk* around the female, actively courting, while females are less active (Heady et al. 1986). This pattern has also been reported for other leafhopper species such as *C. mbila* and *C. ehavi*. The virgin males of these species approach females by means of rapid

walking accompanied by wing-flicking movements, while virgin females remain stationary most of the time and do not approach males (Downham et al. 1997).

Previous studies reporting a general courtship pattern for *Dalbulus* (Heady et al. 1986) and describing the courtship behavior of other *Dalbulus* species (Heady et al. 1989) have mainly focused on male behavior. Our results showed that *D. maidis* females also exhibit a clearly stereotyped behavioral sequence during courtship. In this sequence, females are more frequently *resting* and less frequently *walking*, *cleaning*, or *jumping*. Before *mating* takes place, females are more frequently *resting* and less frequently *moving their abdomen*, *walking*, or *wing fanning* (Fig. 1a). This indicates that, prior to *mating*, females are mainly waiting (*resting*) and perhaps emitting some signals through the *wing fanning* behavior and the *movement of the abdomen*. Indeed, it has been reported that wing fanning is related to acoustic signals emitted by insects (Joyce et al. 2010) and could be related to previous courtship calls reported for *Dalbulus* females (Heady et al. 1986). Abdomen movement could also be related to acoustic or chemical signals. Indeed, in other insects such as cockroaches, during courtship, some species move down the abdomen and, genital membranes are expanded and relaxed (Schal and Bell 1985). The production of sex attractants by cockroach females has been related to these postures (Gemeno et al. 2003). *Dalbulus maidis* courtship, then, might include the release of a sex attractant. This last possibility could warrant further study, since acoustic communication in some Cicadellidae species has been extensively studied (e.g. Saxena and Kumar 1984; Heady et al. 1986; Mazzoni et al. 2009), while chemical communication in this family has not received much attention. This contrasts with pheromonal communication research on other families within the order Hemiptera (reviews by Dawson et al. 1990; Moraes et al. 2008).

Our observations of male *D. maidis* courtship behavior partially agree with a previous analysis of other *Dalbulus* species (Heady et al. 1989). This previous study reported the following characteristic behaviors: *walk to the female, walking not to the female, contact with the female*, and *attempt to join the genitalia*. In our study of *D. maidis*, behaviors such as *resting*, *walking*, *jumping*, and *wing fanning* were displayed with a higher relative frequency than *approaching* (males approaching the females). This may indicate that *D. maidis* male courtship is rather a medium-distance behavior, including acoustic communication (Heady et al. 1986) or chemical signals. Moreover, prior to engaging in mating itself, *D. maidis* males mainly performed the *wing fanning* behavior (Fig. 1b), which suggests that for this species, signals emitted by *wing fanning* are important components of courtship. These signals emitted by the *wing fanning* behavior are likely the courtship calls previously reported for *Dalbulus* males (Heady et al. 1986). However, additional observations are needed to verify that *wing fanning* is producing such calls.

Behaviors of mated males differed significantly from those of unmated males. For example, males performing courtship more frequently exhibited behaviors such as *walking* and *wing fanning*. In contrast, behaviors such as *jumping* and *resting* were exhibited more frequently by unmated males. This confirms that during male courtship, *wing fanning* and *walking* are important behaviors, whereas in other situations, males are mainly *resting* and *jumping*. In addition, it was observed that during courtship, males who mated exhibited more transition behaviors (greater than 2 % relative frequency) than unmated males. Overall, this indicates that although the same behaviors can be displayed under different conditions, their frequency and sequence may be

different. This is consistent with previous observations that the same behaviors may be performed but with different frequency, depending upon the conditions (e.g. Field and Keller 1993). It is also consistent with other studies reporting that different species can exhibit similar behaviors but at different frequencies or in different sequences (e.g. Phelan and Baker 1990; Curkovic et al. 2006).

The times spent during the courtship and mating phases for *D. maidis* were 110.04 (±66.84) and 51.61 (±19.75) minutes, respectively. This contrasts with previous reports for other *Dalbulus* species which reported courtship and mating periods lasting from 8 to 16 min and 1 to 4 min, respectively (Heady et al. 1989). Previous studies with other Cicadellidae such as *Sophonia rufofascia* (Kuoh and Kuoh) show that this leafhopper spent 64.7 (±1.20) min in a back-to-back copulation (Duan and Messing 2000). In contrast, *C. mbila* and *C. ehavi* spent less time in the mating phase, 22.2 (±4.8) and 5.50 (±2.0) minutes, respectively (Downham et al. 1997). Various factors may have selected for differences in the duration of courtship and mating periods of different species, such as predation risk and competition (Maier et al. 2000; Candolin 1997). Competition between males may decrease courtship activity and reduce total time spent on courtship (Candolin 1997), while the possibility of increased predation risk while the couple remains in back-to-back copulation might result in strong predation pressure selecting for shorter mating periods.

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