Context-Dependent Mating Success in *Murgantia histrionica* (Hemiptera: Pentatomidae)

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ABSTRACT   Animals must find and select mates in environments that naturally vary in both space and time. Of particular importance for many species are the availability and phenology of host plants for feeding and oviposition sites. Here, we used *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae), a herbivorous insect, to determine mating preferences and success using mating assays and preferences based on odor cues. We manipulated the natal and encounter contexts using two different host plants, mustard and broccoli. We found that both the natal host plant and the host plant where insects encountered potential mates significantly affected mating success in this insect. Broccoli-reared individuals were more likely to mate in general; however, all individuals were more likely to mate when placed in an encounter context of mustard. Using a separate assay, we also found that the natal host plant affected female preference based on odor cues; females preferred the odors of males from the same natal environment that the females experienced as nymphs. In addition, we examined color and body size for host plant effects as both size and color are important factors for many species during mate choice. We found that individuals reared on mustard were larger than those reared on broccoli. However, the proportion of orange color on the dorsum of insects was not significantly affected by the natal host plant. In summary, these results suggest that changes in host plants, as commonly occurs seasonally, may have implications for sexual selection via mate choice.

KEY WORDS   sexual selection, mate preference, host plant effect, *Murgantia histrionica*, harlequin bug

Variation in natural environments is ubiquitous. This variation can take many forms, can be studied at different spatial and temporal scales, and can affect animal behavior. Relatively few studies have examined the effects of one common source of environmental variation, host plant availability, on sexual selection. Changes in host plant availability can affect the phenotypic expression of a variety of traits, including mating behaviors and fecundity (Landolt and Phillips 1997, Awmack and Leather 2002), which are components of fitness.

Female mate choice, an important agent of sexual selection, may be affected by resource variation. For example, female preferences and choosiness can change according to the physical condition of potential mates (Cotton et al. 2006, Hebets et al. 2008). Male condition is often highly sensitive to food quality (Uetz et al. 2002; Cotton et al. 2004a,b; Hebets et al. 2008) and likely affects multiple components of male courtship signals (Candolin 2003, Hebets et al. 2008). In addition, accumulating research suggests that females may alter their mating decisions based on their own condition and their resource context (Cotton et al. 2006, Hebets et al. 2008). Here, we manipulate host plant availability to determine the effects on traits potentially related to female preferences in one species of herbivorous insect, the harlequin bug, *Murgantia histrionica* (Hahn) (Hemiptera: Pentatomidae).

M. histrionica naturally feeds and oviposits on a variety of cruciferous plants (Family, Brassicaceae; Sullivan and Brett 1974, Ludwig and Kok 2001). The plants from the family Brassicaceae differ in characteristics such as physical structure and secondary compounds (Lin and Harnly 2010); thus, the environment that offspring experience during rearing can be strikingly different depending upon host plant availability. In particular, many of the cultivated species in the Brassicaceae produce a wide variety of glucosinolates (Aliabadi et al. 2002); the glucosinolate profiles of these cruciferous plants are dependent upon both the species and the environmental conditions present (Halkier and Gershenzon 2006).

In many insects, chemical cues are important at both long- and short-ranges for location of conspecifics and courtship behavior. Chemical cues are common among stink bugs (Family, Pentatomidae) that typically release odoriferous compounds from their thoracic glands as adults and from abdominal glands as nymphs (Aldrich 1988b). Some of the compounds present in the chemical cues of *M. histrionica* have been identified (Aldrich et al. 1996). For example, adult males produce an aggregation pheromone, mur-

gantiol, which attracts both sexes (Zahn et al. 2008b). Males can also produce a male-specific pheromone during the late morning (Zahn et al. 2008b). These chemical cues likely function in a natural environment to aggregate males and females on the same plants (Zahn et al. 2008b), facilitating the location of potential mates.

During the year, individuals must locate conspecifics within a heterogeneous environmental landscape. Broccoli (*Brassica oleracea* L. variety *italica* Plenck), cabbage (*Brassica oleracea* L. variety *capitata* L.), cauliflower (*Brassica oleracea* L. variety *botrytis* L.), mustard (*Brassica juncea* (L.) Czern.), and other cruciferous crops are commonly found within home gardens as well as in larger-scale agriculture. However, although these crops can grow through much of the year in northern Florida, the availabilities of these crops differ throughout the year on individual farms. As host plant availability and suitability change spatially and temporally, *M. histrionica*, like other stink bugs, moves among wild host plants and cultivated agricultural crops to feed (McPherson and McPherson 2000). Therefore, one pervasive form of environmental variation experienced by this species is host plant availability.

In Florida, *M. histrionica* can be active year-round; therefore, eggs are laid on different host plants during the year and result in nymphs being provided with food sources of differing type and quality. The developmental host plant environment is known to influence the preoviposition period (Ludwig and Kok 2001). Effects on adult size, if present, may impact reproductive success because female size in insects is often correlated with fecundity. Different qualities of diet may also affect coloration (Taylor et al. 2011), a potentially important factor in mate choice.

Here, we use a series of experimental manipulations to investigate whether environmental variation in host plant availability is likely to influence sexual selection for *M. histrionica.* To do so, we conducted two kinds of behavioral assays, one involving physical contact and the other where female preferences were measured based solely on odor cues. We also measured color and size, two variables important for sexual selection in many species. *M. histrionica* is excellent for this research because this species naturally feeds on a wide variety of host plants from the family Brassicaceae during the year and uses different modalities of cues to find and select mates. Based on preliminary observations that demonstrated female preferences as the likely dominant factor in mating success, we focused our attention on female choice as an agent of sexual selection likely to be important for this species. To generate ecologically relevant environmental variation, we reared individuals on and then introduced them to potential mates on mustard or broccoli, common host plant species.

Materials and Methods

Insects. Adults of *M. histrionica* were field-collected from a variety of host plants in the University of Florida Organic Gardens in Gainesville, FL, during October and November 2010, and brought to the lab for breeding. We provided this parental generation with a variety of cruciferous plants in their rearing containers.

The offspring of the parental generation were split into groups of even-sex ratios with 2–6 adults per container, after Streams and Pimentel (1963b). For this experiment, all individuals were housed in clear plastic deli containers (11 by 15 cm) under controlled environmental conditions (mean temperature = 24.9°C; relative humidity [RH] 49%; and a photoperiod of 16:8 [L:D] h). The offspring of the first generation adults were maintained throughout development on one of two different randomly assigned mustard (*Brassica juncea* (L.) Czern.) or broccoli (*Brassica oleracea* L. variety *italica* Plenck) plant species; these second-generation individuals comprised the experimental population used in this study.

Plant varieties used for insect rearing and trials were obtained from local farms. Thus, the plants used for the experiments reflected those actually available to the focal species during this time frame. All plants used in this study were grown without pesticides. Each rearing container was supplied with a fresh segment of plant every 2–3 d. All the lab-reared *M. histrionica* were maintained on their assigned plant type provided ad libitum throughout their life cycle. During both maintenance and behavioral trials of these bugs, the mustard consisted of the vegetative portions of the plant (i.e., leaves and stems) while the broccoli consisted of the leaves, stem, and florets of the plant. The plant structures used reflected those commonly available in the field to *M. histrionica* during the same time period and therefore were biologically relevant.

The insects were reared with one clutch per container and maintained in these groups until they eclosed to adults; clutches of this species typically consist of 12 eggs laid in two rows (Streams and Pimentel 1963a). In the field, nymphs from a single clutch will typically be found on the same plant variety because of their inability to fly until adulthood and their tendency to aggregate, primarily during the first instar (Canerday 1965). Because sexual maturation occurs ≈7 d after eclosion to adulthood (Canerday 1965, Zahn et al. 2008a), we isolated second-generation insects in individual containers within 48 h of adult eclosion to ensure they remained unmated before behavioral trials.

Contact Trials for Mating Success. Once individuals have come into contact with one another, males often begin courting females. The courtship behavior of this species is well defined and readily observable; courtship typically begins with the antennation of the female by the male and then proceeds with extension of the pygophore by the male and rotation of the male to a 180-degree position in relation to the female (Lanigan and Barrows 1977, Zahn et al. 2008a). These behaviors were observed consistently during the current study and were typical of this population from north–central Florida.

To assess the effects of host plant variation on mate choice, we conducted behavioral trials between virgin males and females that were reared on one of two host plant species. Individual adult males and females were paired for behavioral trials no earlier than 12 d after eclosion to ensure sexual maturity; the adults used for these trials ranged in age from 12 to 59 d (mean age = 34 d) after eclosion to the adult stage. Each adult pair included individuals that were similar in age (mean age difference = 0.597 d) but from different clutches. Individuals used during the trials in late April and early May were typically older than those used both before and after this period. For the behavioral trials, one female and one male were removed from their rearing environments and paired in a new environment (i.e., 11 by 15 cm clear plastic deli container) with an encounter treatment of either mustard or broccoli. This design was suitable for this experiment because this species likely makes sequential mating decisions when one female encounters one male.

Behavioral trials were performed between 1000 and 1600 hours. This time period encompasses most reproductive activity in this species; most courtship behavior is confined to the photophase from 1000 to 1400 hours (Zahn et al. 2008a). In total, 119 behavior trials were performed including all possible combinations of natal environment (i.e., the plant used in the rearing containers) and encounter environment (i.e., the plant in the containers used for the behavioral trials). For all treatment combinations including a broccoli-reared male, 18 behavioral trials were performed; for all treatment combinations (except one combination) including a mustard-reared male, 12 trials were performed (Supp. Table 1 [online only]). During the behavioral trials, eight pairs were observed concurrently in separate clear deli containers for 1 h. This time period was sufficient for observations; latency to mate with individual pairings of males and females is usually less than 1 h (Lanigan and Burrows 1977). To ensure that 1 h was sufficient for behavioral observations, the initial 32 trials for this study were performed for 4 h each; these trials resulted in 20 matings, all of which occurred during the first hour of observation. As a result, all data analyses were performed with a 1-h observation period (i.e., the additional 3 h of observation were discarded before statistical analysis for the initial 32 trials).

Presence or absence of copulation was recorded for each trial; copulation was defined as successful coupling of the genitalia with the anterior portions of the male and female positioned 180 degrees from each other. We used copulation as a proxy for mating success in this study. Attempted copulations were also recorded. All males attempted to mate during the behavioral trials; therefore, mating success was under female control during these trials.

Assays for Female Preference Based on Odor Cues. Sixty trials were performed using a Y-tube olfactometer (common arm 15 cm in length; choice arms 12 cm in length each and placed at a 90-degree angle from one another with a 135-degree angle between each choice arm and the common arm; tube diameter was

≈3 cm). In 47 trials, the focal female fed on broccoli as a host plant; in the remainder of the trials, the focal female fed on mustard. During this portion of the study, fewer mustard-reared females were available for trials because of a lack of sufficient mustard available for colony maintenance. For these trials, one male from each natal environment was placed at the ends of the Y-tube olfactometer. A female was then placed into the base of the olfactometer and allowed 20 min to choose one male. A female was considered to have made a choice when entering and remaining completely within the end section of the arms of the Y for at least 15 s continuously. Preliminary trials demonstrated that the presence of a female for 15 continuous seconds in one arm of the olfactometer was sufficient to record a choice being made.

Color and Size. We photographed a subset of the lab-reared colony and measured the photographed insects using ImageJ (Rasband 2012) image processing software available from the National Institutes of Health and available in the public domain. The measurement tools of ImageJ were used to outline the dorsal area and orange portions of the photographed insects. Dorsal area and relative proportion of orange on the dorsum were calculated from the photographs for each individual with an included scale to calibrate the measurements. For the statistical analyses, size was measured as total dorsal area (excluding head). Differences were also noted in the intensity or hue of orange as variation in color was observed in these bugs. As a result, a color standard was included in the photos to facilitate use of intensity or hue in analyses. However, the bugs also differed in proportion of orange. Proportion of orange was selected as a more objective measurement because of the observation that the photos varied in the intensity of lighting.

Statistical Analysis. The generalized linear model (GLM) with the binomial distribution and logit link function was used with the Wald χ^2 test to analyze the likelihood of mating. Factors included in the final model were male natal plant, female natal plant, encounter plant, date of behavioral trial, and the interaction of date and male natal plant. Because of the wide range of ages used in the mating trials, age was also included as a main effect in initial analyses; however, age was not a statistically significant factor and was removed from the final model. Size data were available for a subset ($n = 77$) of the behavioral trials; therefore, an additional GLM was constructed on these data to evaluate the significance of size as a predictor of mating success. However, size was not significant in any of the models with this subset of data; therefore, this factor was removed and the entire data set ($n = 119$) used for the final explanatory model (Table 1). Initial descriptive statistics revealed a time-dependent shift in the likelihood of mating by males reared on the different natal plants. As a result, the date and the interaction of date and male natal plant were added to the GLM as significant factors (Table 1).

In addition, we used logistic regression to determine whether female natal treatment had a significant effect on their choice of males based on chemical cues in an olfactometer. The GLM was used with the Wald

Table 1.   Factors in the final generalized linear model affecting likelihood of mating during behavioral trials ($n = 119$)

Treatment	df	χ^2	P value
Male natal host plant	1	5.212	$P = 0.0224$
Female natal host plant	1	7.888	$P = 0.0050$
Encounter host plant	1	6.197	$P = 0.0128$
Date of behavioral trial	1	8.434	$P = 0.0037$
Date * male natal plant	1	12.233	$P = 0.0005$

All factors included in the final model significantly affected the likelihood of mating.

χ^2 test to determine whether female *M. histrionica* were more attracted to the chemical cues of males reared on the same plant as they were than to males reared on a different host plant.

Statistical analyses of the proportion of orange and size were performed using a two-way analysis of variance (ANOVA). Dorsal area and pronotum width were significantly correlated ($n = 167$; $r = 0.9016$; $F = 716.771$; df $= 1,165$; $P < 0.0001$). Therefore, dorsal area was used in all analyses including size as a factor.

Results

Contact Trials for Mating Success. Both the natal and the encounter host plants significantly affected the likelihood of mating success in this species. During the behavioral trials, males reared on broccoli were more likely ($P = 0.0224$) to mate than those reared on mustard regardless of the rearing environment of the female or encounter host plant environment (Fig. 1). Females also showed this same pattern, with females reared on broccoli more likely ($P = 0.0050$) to mate regardless of the rearing environment of the male (Fig. 2). Pairs placed in a mating treatment of mustard were more likely ($P = 0.0128$) to mate than those placed with broccoli as an encounter treatment regardless of the rearing environments of the individuals (Fig. 3). Date of the behavioral trial also significantly affected ($P = 0.0037$) likelihood of mating as did the interaction of date and male natal plant ($P = 0.0005$; Fig. 4).

Assays for Female Preference Based on Odor Cues. Forty of the 60 trials with a Y-tube olfactometer resulted in the female selecting a male based on chemical cues; in 20 trials, the females did not make a choice during the allotted observation period. Overall, 31 of 47 broccoli-reared females made a choice and 9 of 13 mustard-reared females selected a male. Among the females that made a choice, female natal plant significantly affected the male chosen by chemical cues in the olfactometer ($\chi^2 = 3.8343$; df $= 1$; $P = 0.0502$), with females from both rearing environments more likely to choose a male from their common rearing environment than one from a different rearing environment (Fig. 5).

Color and Size. Females were larger ($F = 45.3663$; df $= 1,163$; $P < 0.0001$) and had proportionately more orange than males ($F = 4.8481$; df $= 1,163$; $P = 0.0291$). Males and females were both larger when reared on mustard ($F = 5.2548$; df $= 1,163$; $P = 0.0232$), but the proportion of orange color on the dorsal area was not significantly affected by the natal host plant ($F = 2.1856$; df $= 1,163$; $P = 0.1412$). Interactions of sex and the natal host plant did not significantly affect ($F = 3.9291$; df $= 1,162$; $P = 0.2801$) the proportion of orange color and were thus removed from the final model.
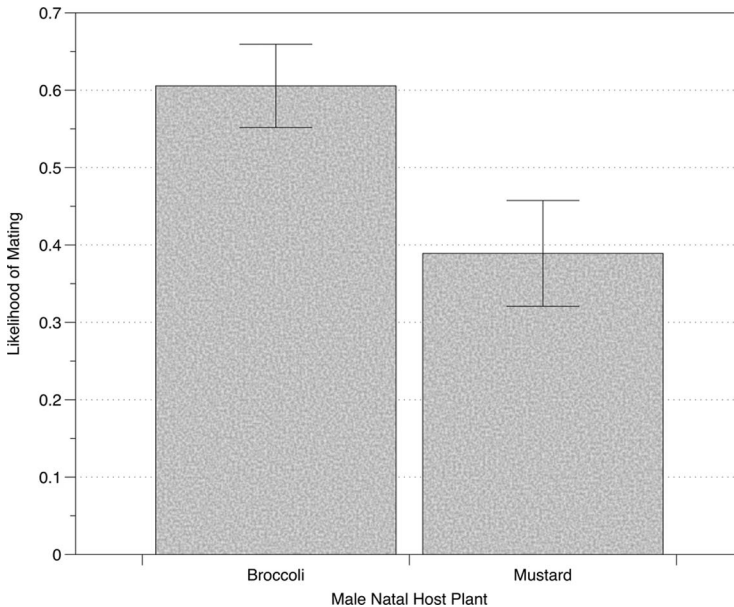
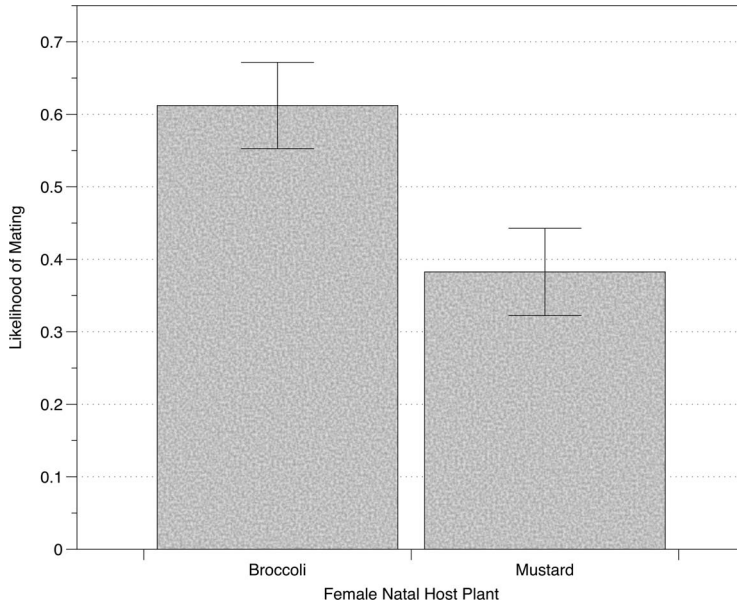**Fig. 1.**   Likelihood of mating in lab-reared *M. histrionica* based upon male natal host plant environment. Males reared on broccoli were more likely to mate during our observation period regardless of the rearing environment of the female or the encounter host plant ($n = 119$). Error bars represent ±SE.

Fig. 2. Likelihood of mating in lab-reared *M. histrionica* based upon female natal host plant environment. Females reared on broccoli were more likely to mate during our observation period regardless of the rearing environment of the male or encounter host plant (*n* = 119). Error bars represent ±SE.

Discussion

Herbivorous insects naturally experience environmental variation in the form of host plant availability and phenology. This environmental variation can affect reproductive success and fitness in general (Awmack and Leather 2002, Hebets et al. 2008). Many species of stink bugs (Family Pentatomidae) have a wide range of host plants on which they can feed and reproduce (Jones and Sullivan 1982, McPherson and McPherson 2000), however, current environmental factors can affect the host plants used at a particular time (Reeves et al. 2010).

Both the natal and encounter host plants affected mating preferences and success in the current study
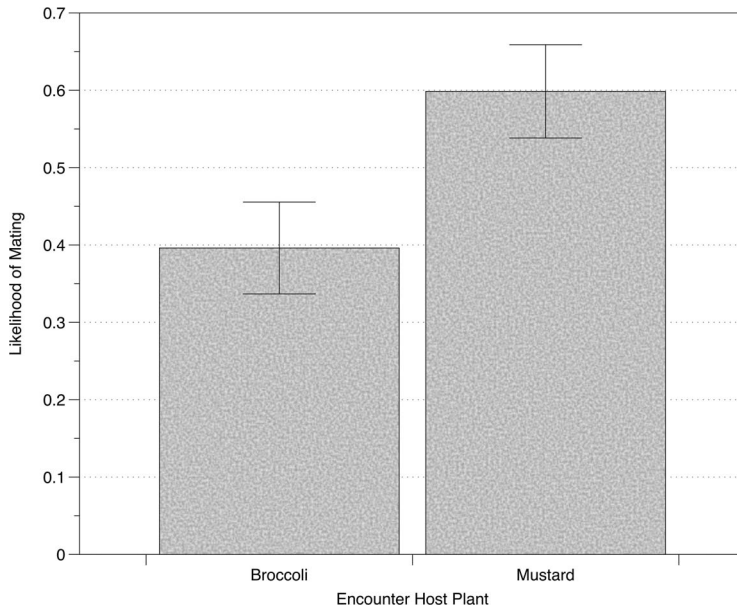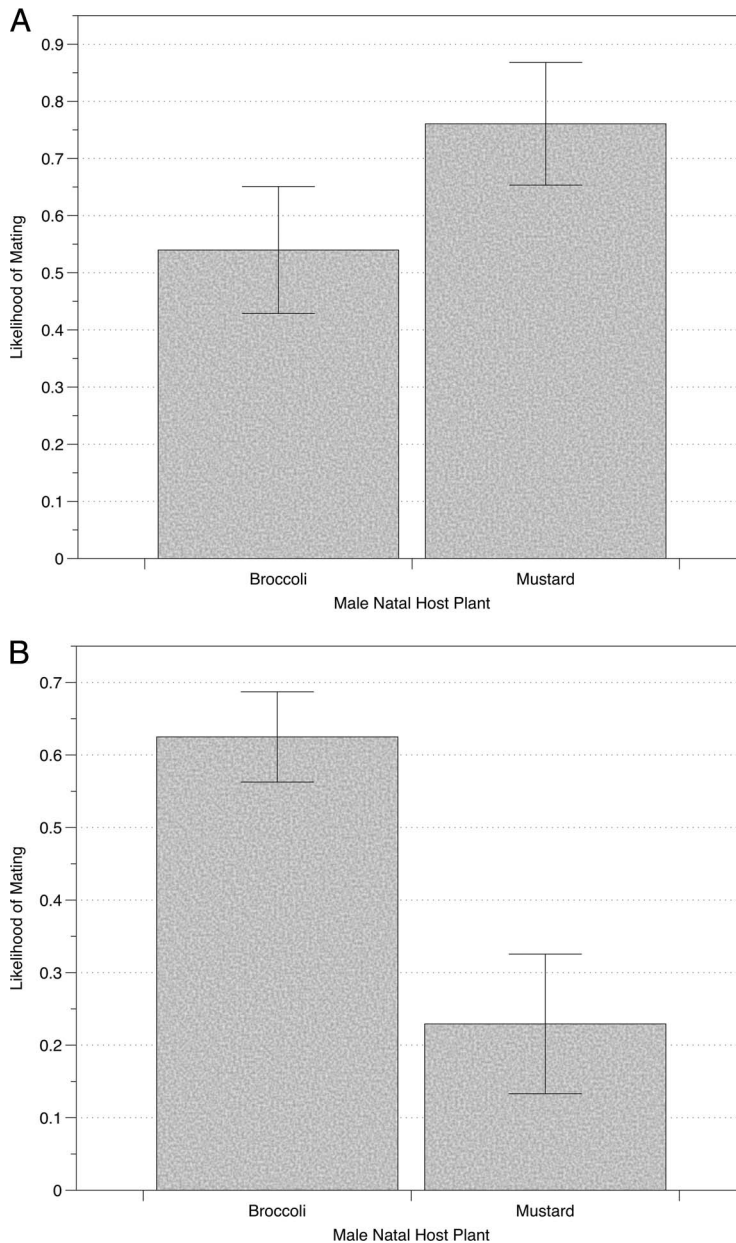

Fig. 3. Likelihood of mating in lab-reared *M. histrionica* based upon encounter host plant environment. Pairs provided mustard as an encounter host plant were more likely to mate during our observation period regardless of the rearing environments of the individuals (*n* = 119). Error bars represent ±SE.

Fig. 4.   The effects of male natal host plant on the likelihood of mating during behavioral trials conducted over different time periods. (**A**) From 28 March 2011 through 20 April 2011, mustard-reared males ($n = 16$) were more likely to mate than broccoli-reared males ($n = 15$). (**B**) From 29 April 2011 through 19 May 2011, broccoli-reared males ($n = 56$) were more likely to mate than mustard-reared males ($n = 31$). Error bars represent ±SE.

demonstrating that environmental variation can affect fitness. In our contact trials for mating success, *M. histrionica* individuals reared on broccoli were more likely to mate than those reared on mustard. However, adults on mustard as an encounter host plant were more likely to mate than those placed on broccoli. In addition, individuals reared on mustard were significantly larger than those reared on broccoli. Consistent with previous work, mustard appears to be a superior host plant for this population. If that is the case, mus-

tard-reared individuals may be larger and in better condition and more likely to be choosy when placed with a potential mate. In our study, the presence of mustard as an encounter host plant corresponded with an increased likelihood of mating. If mustard is a superior host plant, then the presence of this plant during behavioral trials may stimulate individuals to mate because of the availability of a suitable oviposition site. In field studies, higher levels of damage and larger numbers of *M. histrionica* are observed on mustard
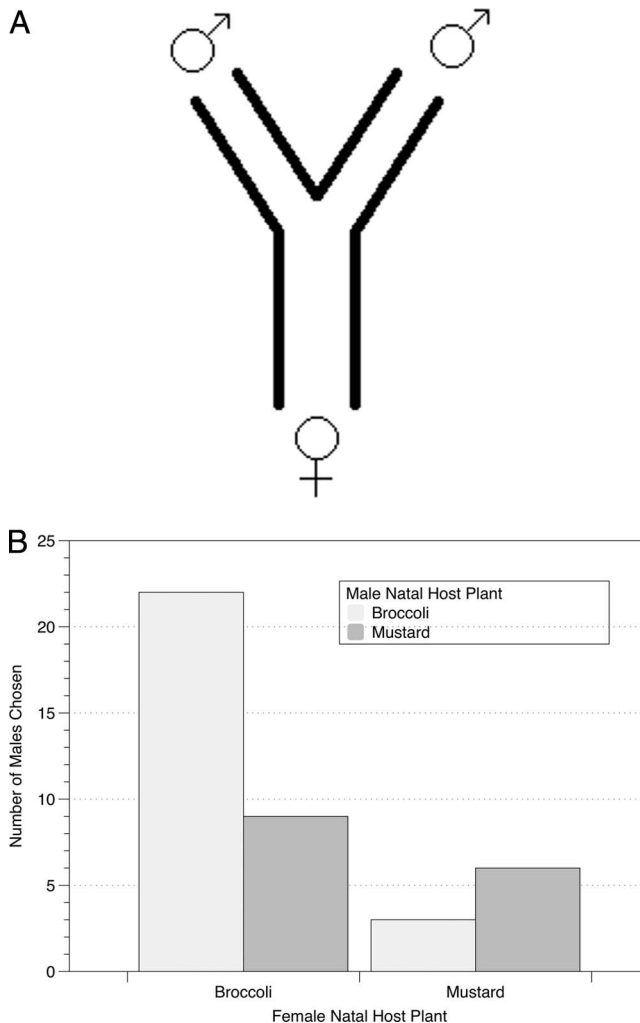
Fig. 5. Sixty trials were conducted with females placed in a Y-tube olfactometer to assess their choice of male based upon chemical cues. In total, 47 females were reared on broccoli and 13 were reared on mustard. (A) Each female was given a choice of a mustard-reared male or a broccoli-reared male in the olfactometer. One male from each rearing environment was placed at separate ends of the Y-tube olfactometer, while the female was placed at the base of the apparatus and allowed to select one of the males based on odor cues. (B) Among females that made a choice based on chemical cues in the olfactometer, females were more likely to choose a male from a similar rearing environment. Twenty of the 60 females used did not make a choice during the observation period.

than on broccoli, suggesting that this species prefers mustard as a food source when both crops are present (Sullivan and Brett 1974, Ludwig and Kok 1998). *M. histrionica* also prefers mustard over collard in field studies (Wallingford et al. 2013), further supporting the suitability of mustard as a preferred host plant for this species under variable field conditions.

When locating a suitable host plant, pentatomids often use chemical cues for long-range communication and vibrational cues at shorter ranges (Millar 2005). The combination of chemical and vibrational cues allows individuals to identify members of their own species and potential mates (McBrien et al. 2002, Moraes et al. 2005). Previous studies have documented chemical signals (Aldrich et al. 1996, Aliabadi et al.

2002, Zahn et al. 2008b) used for defense and aggregation as well as vibrational signals (Čokl et al. 2004, 2007) used during courtship in *M. histrionica.* During close-range courtship, individuals are likely exposed to both chemical and vibrational cues. Both types of cues may be affected by the host plants available during natal development or during the reproductive adult life stage.

Some insect species sequester chemicals from their host plants and incorporate these into their sex pheromones or precursors (Reddy and Guerrero 2004). Although several chemical cues are likely produced by *M. histrionica*, this species possesses a reduced metathoracic gland, suggesting that it may obtain significant chemical components for production of

semiochemicals from the cruciferous plants on which it feeds (Aldrich 1988a, Aldrich et al. 1996). *M. histrionica* has been shown to sequester chemicals, including mustard oil glycosides that are characteristic of the plant species used as a food source (Aliabadi et al. 2002). For example, *M. histrionica* collected from cabbage possess volatile compounds typically found in cabbage (Aldrich et al. 1996).

In addition, the metabolic products derived from the hydrolysis of sequestered glucosinolates vary and are dependent upon the host plant species on which an insect feeds (Halkier and Gershenzon 2006). As a result, feeding on various plants may result in the sequestration and hydrolysis of a variety of plant-specific compounds (e.g., glucosinolates from Brassicaceae) that are used differentially during courtship by individuals. For example, crucifers contain both a free form of mustard oil as well as a glucosidal combination (Bonnemaison 1965). The volatiles produced by these plants can also shift in response to the oviposition and feeding behaviors of *M. histrionica* (Conti et al. 2008). Therefore, both the variation in natal host plants available and their current volatile production can affect the sequestration of different compounds by *M. histrionica* and potentially the compounds released by these insects.

The sequestration of host plant chemicals is observed in other insect orders as well and may impact mating preferences and success in these systems. For example, the cuticular hydrocarbons of the mustard leaf beetle, *Phaedon cochleariae* (F.) (Coleoptera: Chrysomelidae), are dependent upon the cruciferous host plant variety on which an individual feeds; the differing cuticular hydrocarbon profiles in this species result in males preferring to mate with females reared on the same plant species (Geiselhardt et al. 2012).

In our assays of female preferences to male odor cues, female *M. histrionica* placed in an olfactometer significantly preferred chemical cues from males reared on the same host plant type as the female when given a choice between males reared on two different plant varieties (i.e., broccoli or mustard). This suggests that males were producing chemical cues that were dependent in composition on their natal host plant. If *M. histrionica* sequesters chemical precursors for its pheromones from the natal host plant, then adult-released chemical cues would likely differ in composition. The metabolic products of the sequestered compounds likely depend upon the volatile profile of the host plant and may be incorporated into the insect's own chemical profile. Additionally, these sequestered compounds may play a role in the cuticular hydrocarbon signature of these individuals (Geiselhardt et al. 2012). Any change in an individual's cuticular hydrocarbons may be important during the antennation portion of the courtship sequence, in which the male repeatedly antennates the female. Therefore, if cuticular hydrocarbons were affected by natal host plants, these changes could have affected the mating success of these individuals during our contact trials. Ultimately, host plant-specific cues such as these could lead to assortative mating

and potentially ecological speciation within a population (Malausa et al. 2005).

In addition to chemical cues, *M. histrionica* uses vibrational cues during encounters with potential mates (Čokl et al. 2004). Vibrational cues are typically numerous during courtship in *M. histrionica* (W.L.H-H., unpublished data). Differences in acoustic or vibrational cues because of the host plant may affect mate choice in insects that use these signals for mate attraction and courtship. For example, when males of the variable field cricket, *Gryllus lineaticeps* Stål (Orthoptera: Gryllidae), eat a high quality diet they produce calls that are more attractive to potential mates (Wagner and Hoback 1999). These vibrational cues, which may differ based on the host plant, may help explain the variation in mating success during contact trials that we observed in this study.

In addition to changes in chemical or vibrational cues important in mate selection, host plant variation may lead to temporal isolation that can affect mate choice. For example, in *Enchenopa binotata* Say (Homoptera: Membracidae), sympatric species are found on six different host plants. Temporal variation in mating was likely involved in the speciation process for this group as the timing of copulation differs by day or time of day for each host plant (Wood and Guttman 1982). In *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), temporal variation in mating behavior is the most important factor in the isolation of strains from corn and rice (Pashley et al. 1992). Females feeding on corn were more likely to mate during the first two-thirds of the night, while those feeding on rice mated during the last one-thirds of the night (Pashley et al. 1992). Because of the wide range of host plants used by *M. histrionica* throughout the year, differing temporal availability of host plants may lead to changes in sexual selection in this species.

Species may prefer different host plants during the year because of variation in host plant quality and phenology as well as the spatial arrangement of available host plants (Reeves et al. 2010). For example, we found that date affected the likelihood of mating during our behavioral trials, suggesting that time of year is important for mating success in *M. histrionica.* In particular, the effects of the male's natal host plant on mating success varied during our trials through an interaction effect with date. In addition, the rearing and behavioral trials for the current study were conducted with available plant parts, which often included reproductive structures for broccoli but not for mustard. Therefore, the plant structures used here may have affected behavior, although they reflected the seasonal availability of the plants. Thus, reproductive structures are a potential confounding variable with plant variety in this study. However, our plant structures mimic those found in the field during the time period of this study; thus, our results reflect behaviors under biologically relevant and realistic conditions.

Variation in host plants can affect mate choice and even result in assortative mating, which can be a first step in the process of speciation. For example, in *S.*

frugiperda, females select males as mates from the same strain they fed upon ≈85% of the time (Pashley et al. 1992). Pheromonal differences are one possible explanation for differences in mate choice in some populations but are likely not an effective isolating mechanism in all species. In *Ostrinia nubialis* (Hübner) (Lepidoptera: Crambidae), the host plant of the females significantly affects the composition of the pheromones they produce, a possible factor in assortative mating (Thomas et al. 2003).

Additional studies could further elucidate the mechanisms resulting in the differences in mating success and the olfactory preferences of female *M. histrionica.* Environmental conditions can affect both the choosiness of individuals in mate choice and the accuracy with which they can discriminate signals (Jennions and Petrie 1997). Future studies of *M. histrionica* in the field could determine preferred host plants for this species in landscapes including different potential suitable host plants and also determine whether choosiness in mate choice is affected by the encounter host plant.

Although we found that natal and encounter host plants significantly affected mating success, we do not yet know whether this is a result of differences in one or more male-produced cues used during courtship. For example, the effects of the natal host plant on the chemical compounds comprising cuticular hydrocarbons and male pheromones need to be studied to identify potential differences in the chemical cues produced. Collection of headspace volatiles and characterization of the chemicals associated with individuals feeding on different host plants would provide information necessary to determine a potential mechanism by which the host plant may affect chemical cues produced by this species. These compounds could then be compared with those found in the host plants.

In addition, vibrational cues and color could be studied further to determine their potential roles in mating success and preferences in *M. histrionica.* Recordings of vibrational cues could be gathered to determine conclusively whether the natal host plant affects the signal properties of vibrational cues in this species. In addition, although we examined the relative proportions of color on *M. histrionica* in the current study, differences were also noted in the hue of orange observed on these bugs. Future directions could include intensity or hue in analyses of host plant effects. Finally, further studies could determine the effects that the natal host plant may have on condition, thereby affecting mate choice behaviors in both males and females.

Here, we examined the effects of natal and encounter host plant environments on mating success and also the effects of the natal host plant on female preference of chemical cues. Our results suggest that both natal host plant and encounter host plant environment significantly affect mating success and preferences. In addition, we found that the natal host plant significantly affected body size, but not proportions of color, in *M. histrionica.* These results, in conjunction with the additional research suggested here, could help explain a method by which subpopulations of herbivorous insects can become reproductively isolated because of differences in host plant preferences and the resulting effects on mating behavior. This could be an important mechanism for sympatric speciation. Although much work in this area remains to be done, the data provided here demonstrate that environmental variation in host plant availability and phenology can play a significant role in the mating behavior of an herbivorous insect. As environmental variation is experienced by all organisms at different scales both spatially and temporally, additional research should be performed to identify the impacts this variation has on sexual selection and resulting implications for evolution.

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