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Sexual Dimorphism, Deactivation of Plant Defense, and Attraction of Conspecifics in the Four-Eyed Red Milkweed Beetle (*Tetraopes tetrophthalmus*)

E. J. Craig · M. B. Goldman · A. A. Agrawal

Abstract Herbivorous insects frequently exhibit sexual dimorphism in body size and a variety of other traits. Such differences often lead to distinct behaviors, which may present themselves in insect responses to conspecifics, plant defenses, and feeding. Based on a previous study of a congeneric species, we hypothesized that sexual dimorphism may yield differences in how the host-specific red milkweed beetle *Tetraopes tetrophthalmus* (Coleoptera: Cerambycidae) deactivates milkweed defenses, a behavior in which beetles cut latex-delivering veins prior to feeding. We also predicted that beetles would display differences in their subsequent feeding patterns and attraction of conspecifics. Although beetles were size dimorphic (females were larger than males), we did not find consistent differences in the rates of vein cutting or initiation of feeding between males and females. Females did, however, cut more milkweed veins per leaf, and attracted more conspecifics than males. Sex differences in size and other traits were thus associated with differential attraction, but not strongly associated with the overall deactivation of plant defense.

Introduction

Sexual dimorphism is the variability in traits between males and females of a species, including body size, pheromone production, and feeding behavior (Gontijo 2013; Mori et al. 2017; Brzozowski et al. 2020). Dimorphism is common in herbivorous insects, and often reflects sex differences in mate attraction and tolerance of certain stresses, such as avoiding predation or harsh abiotic conditions (Verrell et al. 2001; Gontijo 2013; Vinterstare et al. 2021). Here, we focus on two prominent examples of dimorphic behaviors: the attraction of conspecifics and deactivation of plant defense. Insects utilize a variety of cues, including pheromones produced by other insects, plant volatiles, and other visual or auditory signals to locate and aggregate near conspecifics (Reisenman et al. 2000; Bengtsson 2008; Brzozowski et al. 2020). In this study, we define behaviors which attract conspecifics, and may lead to mating or aggregation, as *attraction*. Secondly, herbivorous insects often display adaptive feeding behaviors to avoid plant defenses, including aggressive attack, leaf clipping, and vein cutting (Boone et al. 2011; Dussourd 2017). This, too, may reflect underlying sex differences. For example, research has revealed that, when available, male milkweed beetles feed opportunistically on plants which have

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been previously damaged by female conspecifics (Gontijo 2013). This finding suggested the novel hypothesis that seemingly unrelated traits and behaviors, such as sexual dimorphism, deactivation of plant defense, and attraction, may interact.

In this study, we use latex production as a model plant defense to investigate sexual dimorphism in defense deactivation in the red milkweed beetle, *Tetraopes tetrophthalmus* (Coleoptera: Cerambycidae) (Fig. 1). Latex runs through the veins of about 8–10% of flowering plant species (Agrawal and Konno 2009). Although it presents no primary function for plants, latex flows from damaged tissues and acts as a physical and chemical barrier against chewing insects (Agrawal and Konno 2009). In response, many insects display "vein cutting" behaviors, in which they sever or puncture either the midrib or veins of leaves prior to feeding. We define vein cutting as a single puncture to the midrib or a distal vein. This serves to drain and depressurize latex to distal parts of the leaf, enabling safer feeding and up to 92% lower latex intake (Dussourd 1999). Insects often preferentially feed on pre-damaged leaves over leaves that have not been previously punctured (Dussourd and Eisner 1987; Gontijo 2013). This finding has implications for insect aggregation and raises the question of whether plant damage and feeding may also facilitate attraction of conspecifics. Accordingly, here we measure sex differences in morphology, associated defense deactivation and feeding, and whether the sexes differentially attract conspecifics.

Fig. 1 Two red milkweed beetles (*Tetraopes tetrophthalmus*) interacting on a common milkweed leaf. Note the droplet of latex and several vein cuts above the droplet (indicated by arrows) leading to feeding damage. Photo by A.A. Agrawal

The common milkweed, *Asclepias syriaca*, contains latex that acts as a defense against *T. tetrophthalmus* in eastern North America (Dailey et al. 1978; Agrawal 2004). *Tetraopes tetrophthalmus* is size dimorphic; like many insect species, females tend to be larger than males in terms of size and mass (Mori et al. 2017). Previous research has documented sex differences in vein cutting behaviors of a closely related species, *T. femoratus*, with females cutting veins more frequently and earlier than males, and males opportunistically feeding on the female-damaged leaves (Gontijo 2013). Indeed, using cut milkweed stems, Gontijo (2013) concluded that, while females disproportionately cut leaf veins, both male and female beetles preferentially fed and mated on damaged leaves. Observations of *T. tetrophthalmus* have indicated that they also display vein cutting behavior (Dussourd and Eisner 1987), although previous research had not addressed sex differences (Agrawal and Konno 2009). Additionally, *T. tetrophthalmus* has been observed to aggregate on milkweed leaves in small groups (Lawrence 1982). We were thus interested in extending the results of Gontijo (2013) to behavior of *T. tetrophthalmus* and further studying the relationship between defense deactivation and attraction of conspecifics.

We conducted a series of field experiments over two years to measure vein cutting and attraction patterns of male and female *T. tetrophthalmus* with relation to sexual dimorphism, initiation of feeding, and mating. Specifically, we addressed the following questions: (1) Are there sex differences in the timing and amount of vein cutting in *T. tetrophthalmus*, and are these differences driven by body size? (2) Are there sex differences in the attraction of conspecifics? And (3) Is any differential attraction of conspecifics related to the amount of feeding or vein cutting?

Materials and Methods

Study Site

We conducted a series of experiments at two field sites surrounding Ithaca, NY. The first site was a relatively isolated hayfield, containing several discrete patches of milkweed, including several hundred plants in total (42.45302° N, 76.428° W). All *T. tetrophthalmus* were collected from this field site, and

Experiment 1 (Trials 1 and 2) and Experiment 2 were conducted here. The second field site (Experiment 1, Trials 3 and 4) was an older field with fewer, smaller, isolated milkweed patches (around 200 stems each; 42.4302° N, 76.42518° W). This second site was selected because it did not have any *T. tetrophthalmus* nor did the plants have any existing beetle damage. We conducted Experiment 1 (Trials 1, 3, and 4) and Experiment 2 between 15 and 23 July 2022 and Experiment 1, Trial 2 between 3 and 5 July 2023.

Experiment 1 - Sexual Dimorphism in Feeding, Vein Cutting, and Attraction (When Alone)

Trial 1

We sexed twenty-two mating pairs of *T. tetrophthalmus* and separated each beetle into individual 30 ml plastic containers, measuring their length, width, and mandible width using digital calipers. The beetles were left overnight in their cups with one milkweed leaf each. The following morning, each beetle was enclosed on a single milkweed leaf at Site 1 (one beetle per plant) using a mesh bag enclosure (KUPPO brand drawstring pouches made from synthetic organza); the enclosed leaf was young (upper third of the plant) but fully developed. We took a census of each beetle at four times: 12:30, 13:30, 16:30, and 11:30 the following morning. At each census, we recorded the number of vein cuts per leaf, whether feeding had occurred, and the sex and number of colonizing beetles present on each plant. Beetles were then put back into their individual plastic cups, frozen overnight, and freeze dried. The freeze-dried beetles were weighed to find dry mass.

Trial 2

We collected 26 mating pairs of *T. tetrophthalmus*, separating and measuring them following the procedure in Trial 1. Individuals were enclosed in mesh bags the day after collection between 11:30 and 12:10. We conducted five circuits of data collection, recording if feeding had taken place and the number of vein cuts (measured as paired mandible cuts on vein). Data was collected at the following times: 12:13, 13:13, 14:07, 15:38, and 11:10 the next morning. On the last circuit, we also recorded the total number of veins that had been cut per leaf.

A second round was deployed between $12:23 - 12:56$, again using 26 mating pairs collected the previous day. We collected observations in four circuits, at 13:30, 14:30, 15:30, and 9:30 the following day. We measured if feeding occurred, the number of vein cuts, and the number of veins that had been cut.

Trial 3

We enclosed a single *A. syriaca* leaf from each of 80 stems using a mesh bag, and gave each bag one of four possible treatments: a female beetle ($n = 20$), a male beetle ($n = 20$), no beetle and manual vein cutting (forceps used to puncture the midrib, with paired punctures each at three points in the bottom, middle, and top thirds of the leaf; $n = 20$), or no beetle and no vein cutting ($n = 20$). We collected 180 *T. tetrophthalmus*, 90 male and 90 female, from Site 1 and left them with food in 6 plastic containers overnight. The following morning at 9:00 the 180 beetles were released near the center of the milkweed patch containing the 80 mesh bags. We took census data at 9:30, 11:00, 12:30, 16:30, and 9:30 the following morning, taking note of the presence of vein cutting and feeding inside the mesh bag, and number, sex, and location of other colonizing beetles present on each of the bagged plants.

Trial 4

We repeated Trial 3 for a set of 75 plants (split between the three treatments above, without the manual vein cutting treatment) and 210 beetles (half male, half female) were released. For this trial, we released the beetles at 9:30, and collected census data at 11:30, 16:30, and 9:30 the next morning, collecting the same data as Trial 3.

Experiment 2 – Sexual Dimorphism in Feeding and Vein Cutting (When Paired)

We collected forty-two mating pairs of *T. tetrophthalmus*, and males and females were placed in 30 ml cups of two to three beetles, separated by sex. We observed the beetles periodically following collection to ensure that no mating occurred (i.e., that the beetles were sexed correctly). Beetles were left in the containers and deprived of food overnight ($n = 37$ pairs); five pairs of beetles died overnight, and these were replaced in the morning with new beetles which

were starved for two hours prior to experimentation. We chose two size dimorphic individuals, with a large female and a smaller male, to place in a mesh enclosure on a single milkweed leaf and observed for one hour. We recorded the following observations: time and sex of first beetle to cut a vein, time and sex of first beetle to feed, male/female feeding place (intact leaf or leaf previously damaged by other beetle), time of first mating (and whether this occurred before or after feeding), and whether males fed before or after mating.

Statistical Analysis

Fisher's Exact tests and logistic regressions were used to analyze sex differences in the initiation of vein cutting and feeding for Experiment 1, Trials 1 and 2. We also used a MANOVA of four traits to compare sizes of male and female beetles (and subsequent principal components analysis to generate size-related PC axes). For Experiment 2, we used chi-squared tests to compare sex differences in the timing of vein cutting and feeding. Experiment 1, Trials 3 and 4 were analyzed using generalized linear models with a zero-inflated Poisson distribution. All analyses were conducted using JMP pro V.14.

Results

Sexual Dimorphism in Feeding and Vein Cutting (When Alone): Experiment 1 – Trials 1, 2, and 4

During Trial 1, Male and female beetles fed on milkweed leaves and cut veins at approximately equal rates. At the first census, 1 h after initiating the experiment, 40% of beetles had fed and 26% had cut veins on the leaf. Females and males showed nearly identical probabilities of each behavior ($n = 42$, Fisher's Exact test, $p = 1$ for each behavior). By 24 h after initiating the trial, 93% had fed and 60% had cut veins, but again there was no difference between the sexes ($n = 42$, Fisher's Exact test, $p = 1$ for each behavior). Size differences between the sexes did not appear to affect the probability of vein cutting and feeding, although males and females were size dimorphic (MANOVA including length, width, mandible width, and dry mass: exact $F_{4,36} = 5.06$, $p = 0.002$). All measured size components were significantly different

themselves: females weighed 35% more, were 10% longer, 5% wider, and had mandibles that were 11% wider than males (all Ps < 0.01). Using PCA, a single principal component explained 72% of the variation in our four size measures. Neither this PC nor mandible width was predictive of feeding or vein cutting in the initial census ($n = 42$, logistic regression, PC1: feeding: $\chi^2 = 0.65$, $p = 0.42$; vein cutting $\chi^2 = 0.03$, $p = 0.86$; mandible width: feeding $\chi^2 = 1.38$, $p = 0.24$; vein cutting $\chi^2 = 0.46$, $p = 0.50$) or after 24 h (PC1: feeding $\chi^2 = 0.18$, $p = 0.68$; vein cutting $\chi^2 = 0.84$, $p = 0.36$; mandible width: feeding $\chi^2 = 0$, $p = 0.97$; vein cutting $\chi^2 = 2.12$, $p = 0.15$).

We used the setup of additional experiments (Trials 2 and 4) to address the same question of sexual dimorphism in vein cutting. For Trial 2, male and female beetles showed no difference in number of vein cuts ($F_{1,98} = 0.56$, $p = 0.455$), although larger beetles made fewer vein cuts (size PC1 $F_{1,98} = 7.03$, $p = 0.009$), and sexes were again dimorphic in size (MANOVA exact $F_{3,99} = 21.41$, $p < 0.001$). Nonetheless, in Trial 2, females did puncture 55% more veins after 24 h compared to males (mean ± SE, females 4.21 ± 3.45, males 2.72 ± 0.44; $F_{1,98} = 4.39$, $p = 0.039$). In Trial 4 after 24 h, beetles made substantially more vein cuts than in Trial 1 (range 0–25, mean 8.6, compared to a mean of 1.2 vein cuts in Trial 1), and females made 65% more vein cuts than males (females 10.68 ± 1.70

males 6.48 ± 1.19; $F_{1,48} = 4.08$, $p = 0.049$). We did not measure beetle size in this trial. Thus, although evidence for size-related dimorphism is abundant in this system, we only detected marginal differences in vein cutting between the sexes.

The Role of Sexual Dimorphism and Leaf Damage in Attracting Conspecifics: Experiment 1 – Trials 3 and 4

In a natural population, our 135 treated stems counted 68 female and 68 male *T. tetrophthalmus* summed across all census times. We found significantly higher average colonization (or retention) on stems with a caged female beetle than on stems with a male beetle or on controls (ZI Poisson glm, Wald $\chi^2 = 10.02$, $p = 0.007$; pairwise comparisons, control-female $p = 0.085$, control-male $p = 0.12$, female-male $p = 0.003$) (Fig. 2). These pairwise comparisons were similar when we separately considered male vs. female colonizers, as the only significant difference was that females attracted more beetles than males.

Sexual Dimorphism in Feeding and Vein Cutting (When Paired): Experiment 2

Paired male and female beetles showed comparable timing of vein cutting and feeding when introduced
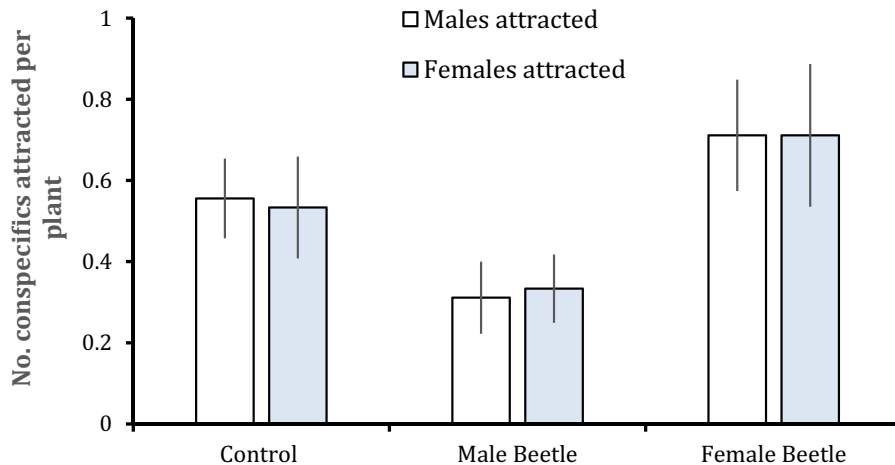

Fig. 2 Number of male and female *Tetraopes tetrophthalmus* attracted to milkweed leaves caged with a male, female, or no beetle (control) of the same species. Data shown are combined from Trials 3 and 4 of Experiment 1. The manual vein cutting treatment was only included in the third trial and is not shown here (no difference in beetles attracted to controls vs. manual vein cutting treatment, $P > 0.2$). Although means ± SE are shown, data were analyzed assuming a zero-inflated Poisson distribution

together to a milkweed leaf in the field. In 15 of the 29 pairs that showed vein cutting (total $n = 42$ pairs), the female beetle cut the first vein ($\chi^2 = 0.034$, $p = 0.853$) and 12 of 26 pairs had a female beetle feeding first ($\chi^2 = 0.154$, $p = 0.695$). Mating occurred in 13 pairs, and of these, 11 mated before feeding or vein cutting.

Discussion

The Role of Sexual Dimorphism in Attraction of Conspecifics

Our strongest result is that caged female beetles were more attractive to both male and female conspecifics in the field compared to male beetles. This differential attraction may be linked to a variety of factors, at both short or long ranges. Here, we define short-range as within a radius of three meters from a given plant, and long-range as longer distances; given our study sites for Experiment 1, Trials 3 and 4, our plants may have been colonized by beetles using either type of signaling. Previous research has indicated that many beetles do not use long-range signaling from either pheromones or sound production (Alexander 1957; Reagel et al. 2002; Brzozowski et al. 2020). Nonetheless, these may be important at short distances or for maintaining an aggregation once it is formed. Despite their lack of long-range signaling, *T. tetrophthalmus* do tend to form moderately sized, often sex-biased groups (Reagel et al. 2002; Matter 2009). This may be due to differential movement patterns and durations of stay for male and female beetles: male beetles tend to travel more frequently and for longer distances than females (Lawrence 1982). Males appear to land arbitrarily on plants but stay for longer durations on plants already occupied by females than on plants with other males or no other beetles (Reagel et al. 2002). This preference for occupied plants may explain the formation of aggregations, regardless of whether the beetles themselves have a mechanism for attracting conspecifics. Finally, cuticular hydrocarbons may play a role in differential aggregation. These pheromones are found predominantly in females and are thought to facilitate short-range formation and maintenance of groups in several species of insects (Blomquist and Bagnéres 2010). Although there is little data on the presence of cuticular hydrocarbons in female *T. tetrophthalmus*, the role of these

compounds in other longhorn beetles suggests that they may have contributed to differential attraction in our study (Silliman 2014).

Physical features of milkweed flowers may also yield differential attraction to certain plants. Plants with large inflorescences tend to attract beetles more than non-flowering plants or plants with small inflorescences. Furthermore, there is a positive correlation between plant height and size and number of umbels per plant with density of beetle aggregation (Reagel et al. 2002; Agrawal 2004). Though we expect the effects of plant characteristics to be minimal due to the randomization of our treatments, it is nonetheless possible that these factors may have been involved. More likely, plant damage may have been a contributor to differential aggregation. Given Gontijo's (2013) findings, which had employed cut milkweed stems, we had expected damaged plants to be more attractive to beetles. Although we found no difference in vein cutting and feeding frequency for male versus female beetles, female vein cutting did tend to be more extensive, making cuts to more individual veins per leaf than males. This widespread vein cutting could serve as a visual cue for conspecifics, indicating the presence of a food source or potential mates. In this way, increased cutting of veins in females may provide an alternative explanation for the dimorphic attractiveness of female over male beetles. Previous work had not documented a link between these two phenomena, and the interaction of these two findings is a potential direction for further research.

The Role of Sexual Dimorphism in Feeding and Vein Cutting

We had predicted that, following Gontijo's (2013) work, females would broadly cut veins more than males (or at least more quickly), and that this may be related to dimorphism in size. After repeated experimentation on wild caught beetles over two years, however, we found that dimorphism in this behavior is not common in *T. tetrophthalmus* despite differences in size. Although closely related, *T. tetrophthalmus* and *T. femoratus* tend to occupy different regions of North America (Rice 1998). Here, we studied *T. tetrophthalmus* in central New York state, while *T. femoratus* were observed in Washington state by Gontijo (2013); it is thus possible that these distant populations evolved different behavior with regard

to male and female vein cutting. Furthermore, small size is not a barrier to vein cutting in other species of insects. *Danaus gilippus* larvae, for example, cut veins less frequently as they grow; similarly, *Theroa zethus* caterpillars utilize acid secretions to enable vein cutting even at small sizes (Ferreira and Rodrigues 2015; Dussourd 2015). In monarchs, caterpillars cut veins throughout development, but in different patterns as they grow (Agrawal 2017). These findings are consistent with our result and suggest that size may not be a strong predictor of vein cutting in many systems. As noted earlier, we did find that, while total vein cutting rates were comparable, females tended to make cuts in more individual veins per leaf than did males. This approach may be more effective in deactivating latex over an entire leaf, despite similar rates of the behavior overall.

Although we generally found little evidence of dimorphism in vein cutting behaviors, we did note that for one out of three measured timepoints of Experiment 1 - Trial 4, female beetles made significantly more vein cuts than males. This finding occurred 24 h after the start of the trial and was the census in which we observed the highest overall vein cutting rates for both males and females. Although our analysis of dimorphism comes from an average of vein cutting rates from males and females, we noted that for this trial, a few female beetles had made particularly high numbers of vein cuts. Given this finding, and the results of our other experiments, we conclude that this datapoint is likely an outlier based on a few individuals and not reflective of species-level sexual dimorphism in vein cutting behavior. A second limitation of our experiment comes from the timing of our data collection. We observed each plant during discrete censuses across 24 h, with several hours between each circuit. It is thus possible that differences in timing of vein cutting across long time periods may not have been captured. Nonetheless, our observations of timing of vein cutting and feeding at shorter timeframes have indicated that there is not a strong difference between males and females in this regard.

Our findings have demonstrated that sexual dimorphism is an important driver of some differential behaviors in *T. tetrophthalmus*. While we provide empirical evidence of differences in attraction and veins cut, we also note that some predicted differences in vein cutting and feeding were not present. Future work studying this, as well as the broader mechanisms of beetle aggregation, is needed to fully understand the results we report here.

Conclusion

We studied common milkweed (*A. syriaca*) and its insect specialist beetle *T. tetrophthalmus* as a model to understand plant-insect interactions and sexual dimorphism of adaptive behaviors, including vein cutting and attraction of conspecifics. Existing literature on a related species, *T. femoratus*, had suggested that beetles are dimorphic in both size and vein cutting frequency. While we did not find strong evidence for sex-specific differences in vein cutting in *T. tetrophthalmus*, we note that female beetles were larger in size, more attractive to male and female conspecifics, and made cuts to more veins per leaf than males. The latter two findings are novel observations, and we propose here that extensive vein cutting may serve as a visual cue to facilitate differential attraction. These findings raise interesting questions regarding the evolution of behavior in closely related beetle species, the significance and interaction of differential vein cutting and attraction, and the broader mechanisms of coevolution between milkweed and its herbivores. Our work highlights the complexity of sexual dimorphism in this system.

Data Availability All data from this study will be accessible after publication from: https://doi.org/10.6084/m9.figshare.25037171.

Declarations

The authors have no financial or non-financial interests to disclose.

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