REPRODUCTIVE BEHAVIOR AND DISPERAL
IN UMBONIA CRASSICORNIS
(HOMOPTERA: MEMBRACIDAE)

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ABSTRACT

Sibling male Umbonia crassicornis leave aggregations before and disperse further than females. Males leave their natal host tree shortly after leaving the aggregation while sibling females mate and oviposit near their natal host. Under greenhouse conditions sibling females mate before their brothers. Age discrimination in mate choice by females appears to promote outbreeding among siblings.

RESUMEN

Hermanos machos de Umbonia crassicornis dejan su agregación antes y se dispersan más lejos que las hembras. Los machos dejan su árbol hospedero natal al poco tiempo de dejar la agregación, mientras que sus hermanas se aparean y depositan los huevos cerca de su hospedero natal. Bajo condiciones de invernadero, las hembras hermanas se aparean antes que sus hermanos. Discriminación por edad por las hembras en escoger compañeros para aparearse, aparentemente promueve entre las hermanas apareamientos con otros sin parentesco.

Parental care in the Membracidae consists of a composite of female behaviors that promote survival of eggs and offspring. At least 50 species exhibit maternal behaviors (Hinton 1977, Wood 1984) that range from simple egg guarding to active involvement in the maturation of offspring (Wood 1974, 1976a, b, 1977a, 1978, 1979). The degree of parental investment in offspring in some species is modified by mutualistic interaction with ants (Wood 1977a, 1984). Although eusociality is restricted to the Hymenoptera and Isoptera (Wilson 1971, 1975) parental care occurs in a number of unrelated orders (Fickwort 1981). In the Homoptera, only the Membracidae and closely related families (Brown 1976) have parental care.

Female Umbonia crassicornis Amyot and Serville insert eggs into branches or leaf petioles of host plants and make a series of slits in the host below the egg mass before eggs hatch. First instars align themselves along these slits to feed. Offspring and the parent female remain together on the same branch throughout the nymphal stages and for 15 to 20 days as adults. Parent females protect eggs and offspring from predation (Wood 1974, 1976a).

Teneral adults in aggregations are aposeatically colored and are protected from vertebrate predators by a taste factor and cataleptic behavior
The pronotum of teneral adults is light yellow with black strips. As adults mature the dorsal horn becomes heavily sclerotized and loses its aposematic color. The pronotum of both sexes turns dark green as they mature in the aggregation. At this stage, crypsis and physical hardness of the dorsal horn rather than a taste factor provide protection to females (Wood, 1975). Changes in adult color are continuous but the darker coloration in both sexes is evident when individuals are 15 to 20 days old. Females change from light yellow to a dark blue-green. After 30 days in the greenhouse the pronotum of males becomes progressively darker and almost completely black. Black pronotal pigmentation of sibling males occurs after their sisters have mated and deposited eggs. Associated with changes in coloration are changes in how aggregations respond to disturbance. Aggregations of teneral adults can be collected without dispersal by cutting a branch and placing it into a bag. Such aggregations can then be re-established on another branch by placing individuals together. In contrast, aggregations of older individuals (about 10 days old) are more sensitive to disturbance and can not be reaggregated in the same manner as teneral. Movement of the branch in general causes complete dispersal of the aggregation. Although aggregations of mature individuals are more sensitive to disturbance they can be easily observed and counted if care is taken not to move the branch.

*Umbonia crassicornis* is sexually dimorphic with considerable variation within each sex in the size and shape of the pronotum. Mating is preceded by prolonged precopulatory pairing in which males seek out potential mates and remain on the side of the female (Wood 1974). Precopulatory pairing thus is a indicator of male and female sexual activity.

To understand the evolution of parental care in the Membracidae, a clear understanding of reproductive behavior and dispersal is essential. Here we examine these factors as they relate to aggregations of *Umbonia crassicornis*.

**METHODS**

**Field Study Site**—The study site was along U.S. Highway 1 at Key Largo, Florida, and was 146 m long by 76 m. The sides were bordered by roads and a canal. The middle of the site was transected by a road 14 m wide, along each side of the road were trees of *Lysiloma latisiliqua* (L.) Benth (Leguminosae) 5 to 9 m high. Within the study area there were over 350 trees which ranged from 1 to 9 m high. Most trees were estimated to be 5 to 10 years old. Field work reported here was done between 14 December 1977 to 6 January 1978 with periodic sampling through June 1978 and in December 1978.

**Vagility, Mating, and Oviposition**—In December 1977, teneral adults (estimated to be at least 5 days old) in 24 aggregations on 12 host plants distributed throughout the study site were marked with enamel paints and reaggregated on their respective hosts. Aggregations were color-coded so the origin of dispersed individuals could be determined. We recorded the number of individuals remaining in aggregations, the distance marked insects moved from their host, precopulatory and mating pairs, and oviposition. The original host for each aggregation and approximately 150 trees
throughout the study area were examined for marked insects 7 times over a 21 day period (Observations were made between 8:00 am-3:00 pm).

Aggregations and Upon Host Mating—In December 1978 we did the following to determine if mating occurs among aggregations upon a single host. A *L. latisticta* tree approximately 6 m high with a canopy diameter of 5 m was selected. Eight *U. crassicornis* aggregations, which were approximately the same age as indicated by uniformity of their color, were located within 2 m of the ground. Individuals in each aggregation were color-coded with numbered tags glued to the dorsal horn of the pronotum and reaggregated (185 males and 225 females).

Field observations were made between 8:00 a.m. and 2:30 p.m. on consecutive days between 17 and 28 December 1978 with a final count made on 17 January 1979. We recorded the number of solitary individuals, number remaining in aggregations, precopulatory and mating pairs. Males that were black or a darker green than the female or her sibling males were considered older and males a lighter green than the female were considered younger. Insects approximately the same color were considered the same age.

Laboratory Studies—Adults were collected at Key Largo, Florida in December 1978 and released into large cages in a greenhouse in Wilmington, Ohio. Each cage contained several host plants (*Albizia* sp., *Leguminosae*) grown under a 12 h photoperiod. Females mated, deposited eggs and reared offspring to the 5th instar in these cages. Plants with 5th instars were then placed in an environmental chamber (26° C under a 12 h photoperiod). Aggregations were checked daily for new adults which were marked with individually colored numbered tags. When all individuals had molted to adults the plant was returned to a cage. Daily and hourly observations were then made to determine age of individuals involved in the following categories: precopulatory pairs, mating, oviposition and dead. Adult age was measured in days. Greenhouse cages contained individuals from all age classes with overlapping generations to simulate field conditions. Sexual differences in ecdysis to adult stage were determined by considering day one as the day the 1st nymph in an aggregation became adult. The sexes were compared on the basis of the mean day they turned adult. This same experiment was also done with aggregations in the field. Unless stated otherwise, a t-test was used to compare means (P<0.05).

Field Studies

Vagility, Mating and Oviposition—In 1977, 342 females and 341 males were marked and reaggregated on their original host. Of these, 87.8% remained in their reestablished aggregations 1 day later indicating marking and reaggregation had little effect on their behavior. An additional 12 individuals were found outside aggregations raising the recovery to 89.6%. Dispersal from aggregations began to occur about 3 days after aggregations were reaggregated. After 21 days, 23.97% of the females were located. Fifteen were still in their original aggregations, 38 were dispersed solitary individuals, and 34 were found on egg masses. In contrast, after 21 days only 8.5% of the males were recovered off their host and 8 had not left their original aggregations.

Males and females differed in the distance they moved from their host plant. Seventy-one males observed outside their original aggregations moved
on the average $6.73 \pm 8.62$ (S.D.) m while 72 females moved $2.93 \pm 4.98$ (S.D.) m ($t=3.23, df=141, P<0.01$).

After 51 days, 12.6% of the females were found on egg masses. Fourteen females deposited eggs on their original host, 18 on trees 0.2 to 3 m away, and 11 on hosts 5 to 9 m from the natal host tree.

We observed 94 precopulatory pairs over an 11 day period involving marked females with non-siblings. Sixty percent of these took place on the female's natal host. In contrast, we observed 26 marked males in precopulatory pairs with non-siblings with 65.5% of these occurring off their natal host. Eleven sibling precopulatory pairs were observed on the natal host or nearby (1 to 3 m away). In the case of one sibling precopulatory pair, the female mated several days later with a non-sibling. This female deposited eggs two days later on the host on which she mated. One marked male mated with a non-sibling on its natal host. Of 207 precopulatory females observed 13% involved two or more males.

Aggregations and Upon Host Mating—After reaggregation, the number of males and females in aggregations remained high for the first 8 to 4 days. Males left the aggregations first with 44 of 185 remaining at the end of 12 days. Females deserted aggregations more slowly with 110 of 225 remaining after 12 days. Thus earlier male dispersal results in female biased aggregations. In one aggregation, females remained together 7 days after all males dispersed. Several days after reaggregation one aggregation was disturbed by a bird moving among the branches and all insects flew or dropped to the ground.

Sexual differences in the time individuals remained on the host after deserting the aggregation were obtained. The average stay for 71 males was $2.72 \pm 2.2$ (S.D.) days which is significantly shorter than that for 70 females ($4.74 \pm 3.37$ (S.D.) days, $t=4.22, df=139, P<0.05$). Some marked insects left their natal aggregation and became associated with other adult or 5th instar aggregations.

Throughout the 12 days the number of solitary males and females (marked and unmarked) increased on the tree. Black older males outnumbered lighter green males in precopulatory pairs. In 57.0% of 200 precopulatory pairs involving marked females, the unmarked male was darker colored than the females' sibling males. Only 50 (25%) involved partners that were both marked. Seventy-one (35.5%) of precopulatory pairs occurred in aggregations. Of these 71 pairs, 37 involved unmarked males that were darker than marked females or her sibling males. Only 13% of the 200 precopulatory pairs involved siblings and 22 of these occurred within their natal aggregation. Sibling precopulatory pairs tended to be formed as males were leaving the aggregation.

Three of 5 copulations observed during this period involved marked males or females. Unmarked males were darker colored than the marked (or their sibling males) or unmarked females in three copulations. In two others, marked males appeared to be the same color as their unmarked mate. One of these copulations occurred in the male's aggregation with an unmarked female. After 30 days, 21 of the 225 marked females deposited eggs on their natal host and 2 other females were found on egg masses 37 and 46 m away. In contrast, 7 of the marked males were found on their natal host but these were all in their natal aggregation.
**Laboratory Studies**

Ecdysis to Adults—Males in ten laboratory and ten field aggregations molted to adults one day before females (Table 1). This slight intra-aggregation sexual difference in ecdysis does not seem sufficient to restrict sibling mating.

**Table 1. Sexual Differences in Ecdysis to Adults of Umbonia crassicornis. Day One Was the Day the First Nymph Molted Into an Adult in an Aggregation. Comparison Between Males and Females Were Made by a t Test on the Mean Day They Molted. Means Are Expressed with Their Standard Deviation.**

<table>
<thead>
<tr>
<th>Aggregations</th>
<th>Males</th>
<th>N</th>
<th>Females</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field</td>
<td>3.8(a) ± 2.02</td>
<td>196</td>
<td>4.5 ± 1.9</td>
<td>199</td>
</tr>
<tr>
<td>Laboratory</td>
<td>5.0(a) ± 3.7</td>
<td>286</td>
<td>6.1 ± 3.90</td>
<td>328</td>
</tr>
</tbody>
</table>

\(^a\)Significant difference \(P \leq 0.05\).

Precopulatory Pair Formation—The 267 precopulatory pairs observed were assigned to the following classes based on the age (in days) of adult females: 1) male younger than female, 2) male same age as female, and 3) male older than female. Only 22 pairs consisted of males and females the same age while in 80 pairs the male was younger than the female. In the majority (165) of pairs, males were older than females. Thus females attract or are approached by older males \( (\chi^2=116.25, P<0.01, df=2) \) more than by males the same or younger age. Males were 17.6±17.4 (S.D.) days older (\(N=165\)) than the females. In 80 pairs, the males were 11.1±12.0 (S.D.) days younger than the female.

Sibling Mating—The age sibling males entered their first precopulatory pair was with one exception no different from sibling females (Table 2). However, when all precopulatory pairs are considered, sibling males were older than sibling females (Table 2). The difference between mean age of sibling males and females in precopulatory pairs ranged from 2.7 to 18.3 days with a mean of 7.9±5.8 (\(N=6\)) days. Although males and females enter their first precopulatory pair at the same age, overall male precopulatory activity occurs at an older age than in sibling females. The age difference between mating males and females was 16.5±16.1 (\(N=21\)) days. Of 22 matings, eight males were 10.1±10.6 days younger than the female while in 14, males were 20.1±17.8 days older. The eight matings

Sexual differences in vagility and maturation appear to be factors which
TABLE 2. The mean age sibling male and female *Umbonia crassicornis* formed precopulatory pairs under greenhouse conditions. Means were compared with a t test and are expressed with their standard deviations.

<table>
<thead>
<tr>
<th>Sibling Aggregation</th>
<th>% First Precopulatory Pairs</th>
<th>All Precopulatory Pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>N</td>
</tr>
<tr>
<td>1</td>
<td>41.9&lt;sup&gt;a&lt;/sup&gt;, &lt;sup&gt;b&lt;/sup&gt; ± 5.3</td>
<td>(13)</td>
</tr>
<tr>
<td>2</td>
<td>23.0&lt;sup&gt;b&lt;/sup&gt; ± 3.9</td>
<td>(5)</td>
</tr>
<tr>
<td>3</td>
<td>48.9 ± 19.4</td>
<td>(8)</td>
</tr>
<tr>
<td>4</td>
<td>23.9&lt;sup&gt;b&lt;/sup&gt; ± 1.5</td>
<td>(5)</td>
</tr>
<tr>
<td>5</td>
<td>17.9 ± 2.9</td>
<td>(15)</td>
</tr>
<tr>
<td>6</td>
<td>27.7 ± 14.4</td>
<td>(3)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Significant differences between sibling males and females (t test P < 0.05).

<sup>b</sup>Significant differences between age of sibling males first and all precopulatory pairs.
promote outbreeding among sibling *U. crassicornis*. Both factors interact to promote temporal and spatial separation of siblings. Males leave aggregations before females, but remain on the host for several days before they disperse. Once males disperse, they move greater distances than females. Females leave aggregations later and remain on their host longer, but when they disperse they move shorter distances.

A third factor in promoting outbreeding appears to be age discrimination of males by females. On our trees, males younger or the same age outnumbered receptive females. However, older males predominated precopulatory pairs in the field and laboratory. Since males enter their first precopulatory pair at the same age as sibling females, this suggests that females are discriminating among males or that younger males are not as competitive as older males. Whether females discriminate among males of varying ages or sizes and the reproductive consequences remains to be determined. The clumping of females in aggregations and the slow dispersal of unmated females from the natal tree may with further study prove to be a mechanism to attract older dispersing males. Such female aggregations may be necessary if attraction of males is mediated by sex pheromones as in other insect groups.

The mating system of *U. crassicornis* appears to promote outbreeding among siblings. However, low vagility and considerable variation in age when sibling females oviposit appears to provide the potential for mating among close relatives in the next generation. Unless countered by dispersal, populations on isolated trees or small stands of trees could have high coefficients of relatedness. A consequence of low female vagility appears to be increasing treehopper densities on trees over time. Increasing treehopper densities could promote increased predator density which may have directly contributed to the development of female behaviors such as parental care which reduce predation.

References Cited


--. 1977a. Role of parent females and attendant ants in the maturation


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**DEVELOPMENT OF LIRIOMYZA TRIFOLII**

(DIPTERA: AGROMYZIDAE)

**LARVAE ON TOMATO AT CONSTANT TEMPERATURES**

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**ABSTRACT**

The development of *Liriomyza trifolii* (Burgess) larvae was studied at 15.6, 21.1, 26.7, and 32.2°C constant temperatures in excised leaflets of tomato *Lycopersicon esculentum* Mill. cv. ‘Walter’. The relationship between the developmental rate (Y) (as measured by the reciprocal of days required to complete development) and the temperature (X) in Celcius is given by the equation Y = −0.0926 + 0.0118X. The threshold for larval development was predicted by the equation to be 7.8°C. Using this threshold, larval development was predicted to require 85.0°C-days. Under fluctuating greenhouse temperatures, development required 80.7°C-days based upon the 7.8°C threshold.

**RESUMEN**

Se estudió el desarrollo larvario de *Liriomyza trifolii* (Burgess) en hojas de tomate *Lycopersicon esculentum* Mill. variedad ‘Walter’, cortadas individualmente, a temperaturas constantes de 15.6, 21.1, 26.7, y 32.2°C. La relación entre la tasa de desarrollo (Y) (medida por el recíproco de los días requeridos para completar el desarrollo) y la temperatura (X), en grados Celcius, está dada por la ecuación Y = −0.0926 + 0.0118X. En base a esta ecuación, la predicción de la temperatura umbral de desarrollo larvario es de 7.8°C. El desarrollo larvario requeriría 85.0°C días utilizando el umbral antes mencionado. Bajo temperaturas fluctuantes en un invernadero, el desarrollo larvario fue de 80.7°C-días en base al umbral de 7.8°C.

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*Liriomyza* spp. are pests of tomato, celery, and chrysanthemum in Florida. The timing of insecticide applications based upon the results of periodic scouting would be desirable since outbreaks may be induced by the frequent applications of broad spectrum insecticides (Oatman and Kennedy