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**COVER PHOTOGRAPH**

*Oecanthus nigricornis* F. Walker (Orthoptera: Gryllidae).
Photograph taken by Eugene Kenaga
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EFFECTS OF ASPEN PHENOLIC GLYCOSIDES ON GYPSY MOTH (LEPIDOPTERA: LYMANTRIIDAE) SUSCEPTIBILITY TO BACILLUS THURINGIENSIS

Gavin E. Arteel and Richard L. Lindroth

ABSTRACT

Performance of the gypsy moth, *Lymantria dispar*, on quaking aspen, *Populus tremuloides*, is strongly affected by foliar concentrations of phenolic glycosides. Because the microbial insecticide *Bacillus thuringiensis* is widely used against gypsy moths and has a mode of action similar to that of phenolic glycosides, we investigated the combined effects of the two toxins on gypsy moth larvae. The experimental design was a 2 x 2 factorial: two levels (0, +) of phenolic glycosides for each of two levels (0, +) of *B. thuringiensis*. The toxins were incorporated into artificial diets and bioassayed against first and fourth instars. *Bacillus thuringiensis* and phenolic glycosides negatively and additively affected larval survival, growth and development times. Both agents slightly reduced consumption rates. In addition, *B. thuringiensis* reduced diet digestibility whereas phenolic glycosides decreased the efficiency with which food was converted to biomass. These results suggest that the efficacy of *B. thuringiensis* applications in aspen forests is likely to be affected by the allelochemical composition of foliage.

The western leading edge of the range of the gypsy moth, *Lymantria dispar* L., is now passing through the Great Lakes states. In Michigan, defoliation increased nearly 10-fold from 1988 to 1991, with over 600,000 acres affected in 1991 (F. Sapio, Michigan Dept. Natural Resources, pers. comm.). Widespread defoliation has not yet occurred in Wisconsin, but gypsy moth populations are now established in the eastern part of the state and control programs are underway.

Establishment of the gypsy moth in the Great Lakes region is of concern for many reasons, notable among them being its impact on the aspen resource. Quaking aspen (*Populus tremuloides*) and bigtooth aspen (*P. grandidentata*) are preferred food plants of the gypsy moth (Lechowicz and Maufette 1986). Unlike northeastern forests, aspens are a dominant component of forests in the Great Lakes area; Wisconsin alone has over 3 million acres of the aspen forest type (Spencer et al. 1990). Moreover, aspen is harvested extensively for production of a variety of pulpwood and plywood commodities (Maass et al. 1990). Extensive defoliation of aspen forests is also of concern because of potential impact on outdoor recreational activities in this area.

Although considered a preferred host, quaking aspen is not uniformly susceptible to defoliation by the gypsy moth. Clonal differences in foliar defensive chemistry are great, and have been implicated as one cause of this...

*Bacillus thuringiensis* subspecies *kurstaki* (strain HD-1) is widely used in commercial formulations for control of the gypsy moth. The mode of action of *B. thuringiensis* also involves formation of gut lesions. Endotoxins produced by *B. thuringiensis* are activated in insect guts by proteases, whereupon they bind to brush-border membrane vesicles. Resulting lesions cause lysis of the gut epithelium and death due to septicemia and starvation (Li et al. 1991).

The purpose of this study was to evaluate the combined effects of aspen phenolic glycosides and *B. thuringiensis* on gypsy moth performance. Because the two toxins have similar modes of action, we predicted they would exert additive or synergistic effects when administered together. If such results are found, then differential effects of *B. thuringiensis* are likely to occur for gypsy moths feeding on aspen clones of widely varying defensive chemistry.

**MATERIALS AND METHODS**

Our feeding experiments were designed as 2 x 2 factorials, with two levels (0, +) of phenolic glycosides for each of two levels (0, +) of *B. thuringiensis*. Gypsy moth larvae used in the experiments were obtained from egg masses provided by the Otis Methods Development Center, Otis Air National Guard Base, MA.

Artificial diets. The four artificial diets used in this study were adapted from the standard high wheat germ formulation of ODell et al. (1985). Methyl paraben, a diet preservative, was not used so diets were autoclaved to inhibit growth of mold. Vitamins, *B. thuringiensis* and phenolic glycosides were incorporated after diets had cooled to 45-50°C. The *B. thuringiensis* product used was Foray 48B (Novo Nordisk Bioindustrials, Danbury, CT). Phenolic glycosides were semi-purified from quaking aspen foliage by the extraction and fractionation procedure of Lindroth et al. (1986). Analysis by HPLC indicated that 90% of the crude preparation consisted of the phenolic glycosides salicortin and tremulacin.

Because we were interested in potential interactive effects between *B. thuringiensis* and phenolic glycosides, each toxin was incorporated at a level less than that causing substantial mortality. Based on preliminary experiments, we selected 100 and 500 IU/ml diet as appropriate concentrations for first and fourth instar gypsy moths, respectively. Phenolic glycosides were incorporated at 2% diet wet weight.

**Bioassays.** We conducted two types of bioassays, first instar survival trials and fourth instar feeding trials, to assess effects of *B. thuringiensis* and phenolic glycosides on gypsy moth performance. For each bioassay, larvae from individual egg masses were distributed across treatments to equalize potential maternal or genetic effects (Rossiter et al. 1990). Larvae were maintained at 25°C, with a 15:9 light-dark cycle.

For survival trials, each of ten replicates per treatment consisted of 15
newly hatched larvae placed into 28 ml plastic rearing cups containing a cube of experimental diet. Insects were provided with diets containing *B. thuringiensis* for only 48 hours, in order to mimic the short-lived viability of the pathogen under field conditions. Afterwards these larvae were switched to corresponding diets without *B. thuringiensis* (i.e., the control and phenolic glycoside diets). All food was replaced at 2–3 day intervals to maintain freshness. We checked rearing containers three times a day for dead larvae or new second instars. We calculated survival rates as the proportion of larvae that survived the first larval stadium, and development times as the time elapsed from onset of a trial to the time at which half of the living larvae molted into the second stadium.

We conducted fourth instar feeding trials in order to measure standard nutritional indices of larval performance. Larvae were reared on control diet through the third stadium. As newly molted fourth instars, larvae were assigned to one of the four experimental diets (10 replicates per treatment). Each replicate consisted of a single larva in a 28 ml plastic cup containing an experimental diet. As for the survival trials, diets containing *B. thuringiensis* were provided for only 48 hours. All diets were replaced at 1–2 day intervals as required. At the end of each trial, we froze the larva, then dried (50°C) and weighed the larva, frass and uneaten food. Dry weights of larvae at the onset of the trials were estimated based on proportional dry weights of a sample of 10 newly molted fourth instars. We calculated nutritional indices on the basis of dry weights, using standard formulas (Waldbauer 1968, Scriber 1977) for relative growth rate (RGR), relative consumption rate (RCR), approximate digestibility (AD), efficiency of conversion of digested food (ECD), and efficiency of conversion of ingested food (ECI).

We analyzed results from the bioassays by two-way analysis of variance (ANOVA), using SAS statistical software. Nutritional indices varied little between male and female larvae, so data from both sexes were pooled prior to analysis.

**RESULTS AND DISCUSSION**

First instar performance was reduced by both *B. thuringiensis* and phenolic glycosides (Fig. 1). Survival rates decreased 11% in the presence of *B. thuringiensis*, 24% in the presence of phenolic glycosides, and 34% in the presence of both, indicating a simple additive effect. First instar development times were prolonged 40% by *B. thuringiensis* and 27% by phenolic glycosides. The combined effect of both toxins on development time was somewhat less than additive, as indicated by the nearly significant *B. thuringiensis* x phenolic glycoside interaction term.

Fourth instar development times and growth rates were also significantly affected by the dietary toxins (Table 1). In both cases the effects of *B. thuringiensis* and phenolic glycosides were additive. For example, relative growth rates of larvae were reduced 33, 24 and 52% on the *B. thuringiensis*, phenolic glycoside and *B. thuringiensis* plus phenolic glycoside diets, respectively.

Effects of the experimental diets on larval growth can be attributed to changes in consumption rates and digestion and conversion efficiencies (Table 1). That both toxins independently reduced food consumption by larvae is indicated by the fact that the main effects of *B. thuringiensis* and phenolic glycosides were significant, whereas their interaction was not. *Bacillus thuringiensis* decreased the ability of larvae to digest diets (ADs) but phenolic glycosides did not; moreover, the negative effect of *B. thuringiensis* on AD values was ameliorated in the presence of phenolic glycosides. In contrast, phenolic
glycosides reduced the efficiency with which larvae converted digested food into biomass (ECD values) but *B. thuringiensis* did not. Finally, because ECI is the mathematical product of AD and ECD, it follows that this parameter was significantly reduced by both *B. thuringiensis* and phenolic glycosides, and that the reduction due to *B. thuringiensis* was less pronounced in the presence of phenolic glycosides.

Results from this study illustrate that both aspen phenolic glycosides and dietary *B. thuringiensis* negatively affect the performance of gypsy moth larvae. The effects of these toxins are, however, primarily additive rather than synergistic in nature. This additive effect is consistent with the mode of action of both toxins, which appears to involve the formation of degenerative lesions in larval gut epithelia. The modes of action of the compounds are not
Table 1.—Effects of *B. thuringiensis* and phenolic glycosides on nutritional indices of fourth instar gypsy moths (X ± 1 SE).

<table>
<thead>
<tr>
<th>Diet</th>
<th>Development RGR (mg/mg/day⁻¹)</th>
<th>RCR (mg/mg/day⁻¹)</th>
<th>AD (%)</th>
<th>ECD (%)</th>
<th>ECI (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>5.4±0.1</td>
<td>0.21±0.1</td>
<td>0.56±0.2</td>
<td>52.7±0.1</td>
<td>71.9±3.3</td>
</tr>
<tr>
<td><em>B. thuringiensis</em></td>
<td>7.2±0.4</td>
<td>0.14±0.1</td>
<td>0.62±0.2</td>
<td>39.9±2.2</td>
<td>70.5±4.9</td>
</tr>
<tr>
<td>Phenolic glycoside</td>
<td>7.1±0.6</td>
<td>0.16±0.1</td>
<td>0.54±0.2</td>
<td>47.4±0.8</td>
<td>59.7±2.2</td>
</tr>
<tr>
<td><em>B. thuringiensis</em> + phenolic glycoside</td>
<td>10.0±0.5</td>
<td>0.10±0.1</td>
<td>0.42±0.3</td>
<td>44.4±3.0</td>
<td>55.9±5.5</td>
</tr>
</tbody>
</table>

P values:

*B. thuringiensis* <.001 <.001 .002 <.001 .520 <.001
Phenolic glycoside <.001 <.001 .022 .868 .003 <.001
Interaction .200 .747 .120 .029 .763 .051

entirely similar, however, because *B. thuringiensis* suppressed ADs whereas phenolic glycosides reduced ECDs.

Few studies have investigated the effects of specific plant allelochemicals on the efficacy of *B. thuringiensis* as an insecticidal agent, and results have differed for various compounds. Trumble et al. (1991) found that psoralens and *B. thuringiensis* had an additive effect in prolonging development time in *Spodoptera exigua*. Krischik et al. (1988) showed that the alkaloid nicotine inhibited the toxicity of *B. thuringiensis* against *Manduca sexta*, whereas the flavonoid rutin had no effect. Felton and Dahlman (1984) found that effects of *B. thuringiensis* on *M. sexta* were enhanced by the nonprotein amino acid L-canavanine. The authors suggest that these results may be due to the combined effects of both *B. thuringiensis* and L-canavanine on gut permeability and function, biological activity similar to that which we have proposed for the action of *B. thuringiensis* and phenolic glycosides on the gypsy moth.

Gypsy moth performance on aspen is strongly and inversely correlated with phenolic glycoside concentrations (Hemming and Lindroth, unpubl. data) and these concentrations vary by over an order of magnitude among aspen clones (Lindroth et al. 1987b, Hemming and Lindroth, unpubl. data). Given that phenolic glycosides and *B. thuringiensis* have additive effects on gypsy moths, it follows that the efficacy of *B. thuringiensis* applications in aspen forest types may be influenced by the chemical composition of foliage. Future research will address that possibility.

ACKNOWLEDGMENTS

We thank Novo Nordisk Bioindustrials for the gift of Foray 48B. This research was supported by USDA Competitive Grant 91–37302–6294 and by the College of Agricultural and Life Sciences (Hatch Project 3211), University of Wisconsin, Madison.

LITERATURE CITED


Felton, G. W., and D. L. Dahlman. 1984. Allelochemical induced stress: effects of L-


ABSTRACT

Third instar hop vine borer (Hydraecia immanis) and potato stem borer (H. micacea) are new pest species on corn in the Midwest. Early instar larvae feed on small-stemmed grasses, and later instar larvae switch to broad-leaved hosts to complete development. In order to assess potential suitability of various weeds of corn fields, larvae were reared on seven selected broad-leaved plants for 16-18 days under greenhouse conditions to determine their feeding behavior and performance. Domestic plants included hop (Humulus lupulus) and potato (Solanum tuberosum); weed species included curly dock (Rumex crispus), redroot pigweed (Amaranthus retroflexus), lambsquarters (Chenopodium album), common ragweed (Ambrosia artemisiifolia) and giant ragweed (A. trifida). Larvae of both species survived best on corn, hop, and curly dock. While potato was an excellent host for the potato stem borer H. micacea, survival was poor for the hop vine borer, H. immanis. Red root pigweed, common ragweed, giant ragweed and lambsquarters were poor hosts for both moth species. While the potato stem borer, H. micacea, larvae were able to grow well and gain weight rapidly on several hosts, the hop stem borer, H. immanis, grew well only on hops. Larval feeding behavior and size, as well as plant phenology, stem thickness, and growth form, are all critical determinants as to whether or not a particular plant species can serve as a final host on which H. immanis and H. micacea can complete development.

Both the hop vine borer, Hydraecia immanis (Gueneé), and the potato stem borer, H. micacea Esper, belong to a small genus of noctuid moths whose members inhabit the temperate/boreal interface zones of the Nearctic and feed by boring into various herbaceous plants (Forbes 1954). The hop vine borer is native to North America and the potato stem borer was introduced from Europe into New Brunswick during the early 1900's (Gibson 1908, Brittain 1918). Neither species was considered an agricultural pest in North America until the mid-1970's when populations suddenly rose to damaging levels in corn fields across the Great Lakes region of the U.S. and Canada (Giebink et al. 1984).

Although related and very similar in appearance, the geographic origins and reported host ranges of these species are quite different. The hop vine borer (HVB) is a native North American insect previously associated only
with hops (*Humulus lupulus*) and considered to be only a minor pest on that crop (Bethune 1873, Comstock 1883, Howard 1897, Sanderson 1902). Long considered a grass/hops specialist, this insect has successfully switched to corn, (*Zea mays*) with some local populations in Michigan, Iowa, Minnesota, Illinois, Wisconsin and New York causing significant economic damage (Hawley 1918, Giebink 1983, Giebink et al. 1984, Scriber and Hainze 1987).

The potato stem borer (PSB) is thought to be introduced from Europe (Brittain 1918), where it is widely distributed throughout all northern and central portions of that continent (Gibson 1908) as well as Scandinavia, Siberia and Japan. Accidentally introduced into Nova Scotia and New Brunswick in the early 1900's (McIntosh 1899, Gibson 1908), it has since become an occasional pest in North America on a variety of cultivated plants including corn, rhubarb (*Rheum rhaponticum*) and potatoes (*Solanum tuberosum*) (Jobin 1963, Deedat and Ellis 1983). The PSB is presumed to be much more polyphagous than HVB.

During late summer, the females of both species oviposit within the leaf sheaths of grasses. Eggs overwinter and hatch the following spring (Deedat and Ellis 1983, Giebink et al. 1984). Initially, larvae feed within grass stems, but eventually outgrow them and disperse to plants which have thicker above- and below-ground stems. During this active host-seeking period, early season crop plants such as corn may be attacked. Therefore, the importance of these stalk borers as pests is closely related to the composition of suitable weed populations in and around commercial crops. Both *Hydraecia* species typically complete their larval development and pupate below the soil surface (Hawley 1918, Zwolfer 1962, Jobin 1963, Giebink 1983, Deedat and Ellis 1983, Deedat et al. 1983, Giebink et al. 1984).

Although a number of plant hosts have been reported for *H. immanis* (Giebink 1983, Tietz 1972, Hawley 1918) and *H. micacea* larvae (Deedat 1980, Brittain 1918, Gueneé 1852, Nordstrom et al. 1941, 1974, Seppanen 1970, West 1984, Zwolfer 1962), relatively little is known about their feeding behavior, survival, and growth performance across a range of potential weed hosts commonly found in plant communities in and around Midwestern corn fields. This study represents an analysis of the relative suitabilities of selected broad-leaved plants (which differ in phenology, stem thickness, growth form, and root system). This information is critical to understand the potential for continued geographic spread, local population densities, and phenological damage periods for HVB and PSB to susceptible crop plants in the northeast and north central states.

**MATERIALS AND METHODS**

These host suitability studies consisted of seven thick-stemmed broad-leaved plants as no-choice treatments (two domestic and five midwestern wild or “weed” species) for each insect, with each host replicated five times for each insect species. The study, which was completely randomized and conducted under greenhouse conditions, was repeated twice.

Domestic plants included hop (*Humulus lupulus*) and potato (*Solanum tuberosum*); weed species included curly dock (*Rumex crispus*), redroot pigweed (*Amaranthus retroflexus*), lambsquarters (*Chenopodium album*), common ragweed (*Ambrosia artemisiifolia*) and giant ragweed (*A. trifida*). At the beginning of the study, plants were 56–63 days old. All of these "wide-stem" plants ranged from 4–9 mm in diameter.

Seeds for these plants were obtained from either wild plants or F & J Seed Service, P.O. Box 82, Woodstock, IL 60098. These were planted directly into
plastic pots (21 cm diam. × 20 cm ht.) filled with autoclaved soil (equal parts compost, field soil, and sand), grown under Metalarc® high-intensity lamps (15L : 9D photoperiod), watered as necessary and fertilized every two weeks. Temperatures ranged from 14°C (early morning) to 30°C (late afternoon).

Larvae used in these studies were obtained from eggs deposited by one-generation laboratory-reared females on grasses in the greenhouse during late June through July the previous season. After remaining in the greenhouse for 3–4 weeks, these eggs were removed from the plants, chilled (5.6°C) for 8 or more weeks, and incubated at 21°C to promote egg hatch. Upon hatching, larvae were reared to the third instar on a modified navy bean diet (Shorey and Hale 1965) in the manner described by Giebink et al. (1985).

To ensure that introduced larvae did not escape from the test pot, a combination of screen cylinders and Teflon® coatings were used on each pot. The Teflon® coating (Phillips and Burkholder 1981), applied in a 3 cm band to the inside of the pot rim with a cotton-tipped applicator, prevented any larvae from crawling directly out of the pot; the screen cylinders (18 cm diam. × 50 or 80 cm ht.) kept all foliage directly above the pots, thereby preventing escapes via overhanging foliage.

At dusk, five larvae were introduced into each pot (i.e., 25 larvae per host treatment). Third instar larvae were used because it is this stage that typically disperses from grasses to seek out suitable thick-stemmed hosts (Giebink, pers. obs.). After the larvae had fed for 16 to 18 days, all plants were gently uprooted, placed in labeled plastic bags, refrigerated, and later examined for damage and dissected for larvae. Three larval parameters (survival, instar, and weight) were measured.

Using temperatures recorded by hygrothermographs placed at opposite ends of the study bench, centigrade degree-day accumulations (CDD’s) were calculated with the sine-wave method (Allen 1976) and developmental thresholds (Giebink et al. 1985) of 4.9 (HVB) and 6.8°C (PSB). CDDs accumulated during these feeding periods were ca. 260 for HVB and 230 for PSB, or 13–16 CDDs per day, on average. Data were analyzed using SAS GLM procedures (SAS 1988).

RESULTS AND DISCUSSION

Larvae of both species survived most successfully on corn, followed closely by hop and curly dock (Table 1). While potato plants were excellent for the PSB, HVB survival on potato plants was poor (only 4%, Table 1). Lambsquarters, common ragweed, giant ragweed and redroot pigweed were generally poor hosts for both moth species with larval survival less than 20% (Table 1). Larvae of both species initiated feeding on all plant species except lambsquarters.

HVB larvae grew very fast on hop compared to all other broad-leaved plant species tested. On hops, HVB larvae attained weights 4–5x greater than those on corn and curly dock and 10x those of surviving larvae on potato, both ragweed species, pigweed and lambsquarters (Table 1). This supports the theory that the HVB does in fact appear physiologically better adapted for survival and growth on its preferred host rather than other plants in the cornfield community.

In contrast, PSB appears to grow rapidly on several hosts (including corn, curly dock, potato and hop; Table 1). Growth rates on redroot pigweed and giant ragweed is less than that observed on the four previously mentioned hosts, but still was enough to produce pupae (although smaller) at about the same time as the best four hosts (see developmental index, Table 1).
Table 1. — A comparison of the larval growth of hop vine borer and potato stem borer larvae reared on broadleaf plants in the greenhouse.

<table>
<thead>
<tr>
<th>Grass species</th>
<th>% Larval survival(^1)</th>
<th>Developmental index(^2,3)</th>
<th>Larval weight (mg)(^4)</th>
<th>Total no. surviving larvae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hop Vine Borer(^3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corn</td>
<td>52.0 ± 12.0a</td>
<td>4.9 ± 0.1ab</td>
<td>82.4 ± 7.8 b</td>
<td>13</td>
</tr>
<tr>
<td>Hop</td>
<td>44.0 ± 7.5ab</td>
<td>6.4 ± 0.2a</td>
<td>465.8 ± 75.0a</td>
<td>11</td>
</tr>
<tr>
<td>Curly dock</td>
<td>30.0 ± 6.1abc</td>
<td>4.7 ± 0.3ab</td>
<td>106.4 ± 27.5 b</td>
<td>15</td>
</tr>
<tr>
<td>Common ragweed</td>
<td>16.0 ± 6.5 bcd</td>
<td>4.0 ± 0.2 b</td>
<td>23.8 ± 5.6 b</td>
<td>8</td>
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<tr>
<td>Redroot pigweed</td>
<td>14.0 ± 3.0 bcd</td>
<td>4.4 ± 0.2 b</td>
<td>37.5 ± 37.5 b</td>
<td>7</td>
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<tr>
<td>Giant ragweed</td>
<td>10.0 ± 3.3 cd</td>
<td>4.3 ± 0.2 b</td>
<td>31.3 ± 5.5 b</td>
<td>5</td>
</tr>
<tr>
<td>Potato</td>
<td>4.0 ± 2.7 cd</td>
<td>4.5 ± 0.5 b</td>
<td>50.8 ± 24.4 b</td>
<td>2</td>
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<tr>
<td>Lambsquarters</td>
<td>0 d</td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Potato Stem Borer(^4)</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Corn</td>
<td>56.0 ± 7.5a</td>
<td>6.0 ± 0.0ab</td>
<td>483.2 ± 50.5a</td>
<td>14</td>
</tr>
<tr>
<td>Curly dock</td>
<td>40.0 ± 7.3a</td>
<td>6.3 ± 0.2a</td>
<td>390.5 ± 32.9ab</td>
<td>20</td>
</tr>
<tr>
<td>Potato</td>
<td>36.0 ± 7.5a</td>
<td>6.9 ± 0.1a</td>
<td>554.4 ± 37.3a</td>
<td>9</td>
</tr>
<tr>
<td>Hop</td>
<td>28.0 ± 4.9a</td>
<td>6.6 ± 0.2a</td>
<td>392.6 ± 14.0a</td>
<td>7</td>
</tr>
<tr>
<td>Redroot pigweed</td>
<td>6.0 ± 3.0 b</td>
<td>5.0 ± 0.0 b</td>
<td>128.3 ± 3.4 b</td>
<td>3</td>
</tr>
<tr>
<td>Giant ragweed</td>
<td>2.0 ± 2.0 b</td>
<td>7.0 ± 0.0a</td>
<td>168.0 ± 0.0 b</td>
<td>1</td>
</tr>
<tr>
<td>Common ragweed</td>
<td>0 b</td>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>Lambsquarters</td>
<td>0 b</td>
<td></td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

1 Means followed by the same letter within a column are not significantly different (P < 0.05; Scheffe arc sin sq. rt (%1100) transformation). Values are combined overall results of both spring and fall experiments. For HVB, values are averages of 10 replications of 5 larvae each for all treatments except hops (spring only) and corn (fall only) which are averages of 5 replications; for PSB, values are averages of 10 replications of 5 larvae each for all treatments except hops, potatoes (spring only) and corn (fall only).  
2 For calculations of the developmental index, a numerical assignment was made for each stage (e.g., 1–6 = larval instars and 7 = pupa, with molting larvae assigned the mean value of the two instars).  
3 Values are averages of the number of replications (10 or less) with surviving larvae (i.e., replications with no surviving larvae were excluded from the calculations; means followed by the same number within a column are not significantly different (P < 0.05; Scheffe's test).  
4 After feeding for 16–18 days on 8-week-old plants, centigrade degree day (CDD) accumulations were 260 and 230 for hop vine borer and potato stem borer, respectively. Data are presented as a mean ± SE.

The normal feeding behavior of HVB and PSB larvae is to feed initially on small-stemmed grasses, then switch to larger small-stemmed grasses or broad-leaved plants. Without these grasses the survival of larvae to the third instar would be much less successful (Hawley 1918, Giebink et al. 1984). Our study standardized the rearing conditions for the first three larvae instars in order to analyze the importance of differential suitability of the final hosts for these two stalk-boring species. It is important to realize that the early instar feeding on grasses will also vary according to their differential suitability (Giebink et al. in prep.). We still do not know if previous hosts (for early instars) differentially affect survival or growth performance on subsequent broadleaved hosts and corn.

Among other things, phenology, larval feeding behavior, and stem size are all critical determinants as to whether or not a plant species can serve as host for these *Hydraecia* spp. When HVB and PSB larvae begin feeding in late April, very few host plants are available. This temporal isolation, in itself, drastically limits the number of potential host plants. Typically, the only available hosts are early developing perennials including grasses (Giebink et
Once feeding has been initiated on a particular plant host, feeding behavior and larval size usually dictate how long feeding on a particular plant continues. Feeding behavior of *Hydraecia* sp. larvae proceeds in two steps. Initially, larvae feed above-ground within grass stems. But by the fourth instar they outgrow these stems, with the majority feeding either within or beside stems/roots of the secondary host below the soil surface. This behavior differs considerably from other stalk borers, such as *Papaipema nebris* Gue-née, which feed exclusively within the host above the soil surface and may even pupate within it (Alvarado 1985, Decker 1931).

Most primary hosts (grasses), however, have neither the stem thickness nor root mass to sustain larval development beyond the third or fourth instar. Consequently, larvae are often forced to disperse to other available hosts that have these characteristics (e.g., corn, hops, or potatoes). Such interplant movement is often, but not always, necessary; a number of perennial grass species (primarily sedges, reeds and several aquatic grasses) in marsh or swamp habitats have thick, fleshy culms, rhizomes, or underground roots capable of sustaining *H. micacea* larvae to pupation.

As with the grass hosts, the known wild broad-leaved hosts of these stalk borers are also exclusively perennials. For PSB, most of these hosts inhabit swampy or marshy areas. They include several members of the iris family and several docks (buckwheat family) as well as hops. For the stenophagous HVB hosts include *Silphium* spp., *Lupinus microcarpus* (Tietz 1972), and of course, *Humulus lupulus*. Known as rosinweed, *Silphium* spp. comprise a group of ca. 20 species of coarse perennial herbs (e.g., compass plant, cup plant, and prairie dock) native to eastern North America. *Lupinus microcarpus*, a member of the lupine family, resides in western North America.

As frequent residents of marsh habitats, the polyphagous PSB has been reported feeding on a wide variety of these wild plants in Europe (Seppanen 1970, Zwolfer 1962) and Canada (Jobin 1963). In Wisconsin, thus far PSB has only been reported on quackgrass (*Agropyron repens*), reed canary grass (*Phalaris arundinacea*), and corn—usually adjacent to marshy, low lying habitats. However, over 200 sedge species inhabit the state (Fassett 1976) and the possibility exists that endemic PSB populations are already established on these plants.

Both HVB and PSB, particularly HVB, exhibit many characteristics associated with "K" specialists: both are univoltine; both have relatively long larval periods; both depend on relatively reliable resources (e.g., perennials or continuous corn); and the sedentary females oviposit close to the pupation site. As such, the composition of the plant community has important implications with regard to cultural controls such as crop rotation (Southwood 1977). For these reasons, and in view of our findings with broad-leaved hosts, crop rotation should be able to locally eliminate HVB and perhaps even the generalized PSB larvae from corn fields, except perhaps along field edges near swampy or marshy areas.

**ACKNOWLEDGMENTS**

This research was supported by the Colleges of Agriculture of the University of Wisconsin, Madison (Hatch Project 5134) and Michigan State University (MAES Projects #16448072 and 8051), Regional Research Projects NC-180 and NC-205 and in part by the “Agroecology” LTER Project at Kellogg Biological Station (NSF-BSR-02332). We are grateful for assistance from Phil Pellitteri and Jeffrey Beehler.
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EFFECTS OF NEIGHBORING NECTAR-PRODUCING PLANTS ON POPULATIONS OF PEST LEPIDOPTERA AND THEIR PARASITOIDS IN BROCCOLI PLANTINGS

J. Z. Zhao¹, ², G. S. Ayers¹, E. J. Grafius¹ and F. W. Stehr¹

ABSTRACT

Eggs and larvae of the imported cabbageworm, Pieris rapae, were much more abundant in broccoli interplanted with nectar-producing plants than in broccoli monoculture. More diamondback moth larvae, Plutella xylostella, occurred in broccoli interplanted with or adjacent to nectar-producing plants than in broccoli monoculture. Density of cabbage looper larvae, Trichoplusia ni, was similar among the three types of broccoli plantings. For Cotesia rubecula, established in Michigan after introduction from Yugoslavia, pupae were more numerous in broccoli interplanted with nectar-producing plants than in other plots. High parasitism rates of diamondback moth, mainly by Diadegma insulare, were observed in every plot, but there were no differences in parasitism of diamondback moth between the treatments. Results indicate that the interactions between pests, parasitoids and nectar-producing plants are complex and may be different for each species.

Diversification of agricultural crops often lowers pest populations. In a summary of 198 herbivore species in 150 published studies, 53% of these species were less abundant in more diversified agroecosystems and only 18% were more abundant (Risch et al. 1983). Herbivore movement patterns related to host-finding may be more important than the activities of natural enemies in explaining the reduction of monophagous pest populations in diverse annual systems (Risch 1981, Risch et al. 1983). Floral nectar is an important source of nutrition to both adult Lepidoptera and Hymenoptera biocontrol agents (Kevan and Baker 1984). Understanding how the abundance of pest Lepidoptera and their parasitoids in crops are affected by neighboring nectar-producing plants is valuable for the design and manipulation of pest management systems.

Pest Lepidoptera, especially the imported cabbageworm, Pieris rapae (L.), diamondback moth, Plutella xylostella (L.), and cabbage looper, Trichoplusia ni (Hübner), are key insect pests in crucifers (cabbage, broccoli, etc.) in North America (Harcourt 1963) and have wide distribution in other regions. Previous studies have reported that some herbs neighboring cabbage may be attractive to imported cabbageworm adults, resulting in higher damage to cabbage (Latheef and Irwin 1979). Population densities of diamondback moth in polycultures are often lower than in monocultures of crucifers (Buranday

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and Raros 1973, Taleker et al. 1986). In Hawaii, monospecific cabbage plots had greater densities of diamondback moth larvae and lower parasitism compared with plots of cabbage interplanted with tomato (Bach and Tabashnik 1990).

Bee forage plots, including nectar-producing plants in 34 genera, were planted in 1989 at the Michigan State University Entomology Research Farm, East Lansing, Michigan (Ayers, unpublished data). The objective of our study was to evaluate the effects of some of these nectar-producing plants interplanted with or adjacent to broccoli on densities of the major Lepidoptera pests of broccoli, i.e. imported cabbageworm, diamondback moth, and cabbage looper. A second objective was to measure the effects of nectar-producing plants on parasitism of imported cabbageworm by *Cotesia rubecula* (Marshall) (Braconidae), and of diamondback moth larvae by *Diadegma insulare* (Cresson) (Ichneumonidae) and *Microplitis plutellae* Muesebeck (Ichneu­monidae). *C. rubecula* is a solitary parasitoid that attacks early instar imported cabbageworms. It generally kills the cabbageworm by the third or fourth instar and forms a white cocoon. A related species, *Cotesia* (*Apanteles*) *glomeratus*, also attacks imported cabbageworms, but does not kill the larvae until they are mature, after significant amounts of feeding and foliar damage has occurred. *D. insulare* is a very common parasitoid of diamondback moth in the U.S. and Canada (Harcourt ). *M. plutellae* is much more rare (Idris and Grafius 1992).

**MATERIALS AND METHODS**

**Field plot experiment.** A plot containing nectar-producing plants in 34 genera was planted in 1989 (20 rows and 2.4 m between rows). Anise hyssop, *Agastache foeniculum*, was among the most prolific nectar producers in this plot. Broccoli seedlings were started in the greenhouse and transplanted to the field on 9 July 1991.

Treatments were: (1) broccoli interplanted between the anise hyssop rows in the nectar-producing plant plot; (2) broccoli adjacent to the the nectar-producing plant plot; (3) broccoli monoculture about 120 m east of the the nectar-producing plant plot. Treatment (1) was one row of broccoli (24 plants and 15 m long) between two of the nectar-producing plant rows. Treatments (2) and (3) were 30 m long and four rows wide. Plant spacing was 0.6 m between plants within rows and 1 m between rows. The numbers of pest Lepidoptera and their parasitoids were counted weekly on 10–20 broccoli plants in each treatment from 30 July to 3 September 1991. Only the middle two rows of broccoli plants in treatments (2) and (3) were sampled.

**Diamondback moth larvae release.** Because field diamondback moth populations were low, 120 second and third instar diamondback moth from a laboratory culture (reared on broccoli leaves) were released on 15 July 1991 on 12 marked broccoli plants in treatments (1) and (3) to investigate diamondback moth parasitism rates. Larvae, parasitized and non-parasitized pupae were collected on 21 August, 1991. The larvae were reared in the laboratory until pupation. Parasitized pupae were kept in petri dishes until emergence of adult parasitoids for identification.

**Data analysis.** Since the nectar-producing plants were originally planted in a single block for bee forage research, the treatments were not spatially replicated and could not be statistically compared. Parasitism rates of diamondback moth were calculated as the number of parasitized pupae divided by the total number of parasitized and unparasitized pupae per plant. Differences in parasitism rates based on diamondback moth larvae released
were analyzed using a t test (Zar 1974). Precise parasitism rates of imported cabbageworm by *C. rubecula* could not be calculated because *C. rubecula* pupates on the plants but imported cabbageworm larvae prefer to pupate off the host plants (Harcourt 1963). A relative parasitism rate of imported cabbageworm was calculated as the season-long totals of parasitized pupae divided by the season-long totals of large ICW larvae (fourth and fifth instar) plus parasitized pupae per plant. The parasitoids of the cabbage looper were not investigated.

RESULTS AND DISCUSSION

**Lepidoptera pest abundance.** The effects of nectar-producing plants on pest abundance were different for imported cabbageworm, diamondback moth, and cabbage looper. Imported cabbageworm eggs and larvae were much more abundant in broccoli interplanted with nectar-producing plants than in broccoli adjacent to nectar-producing plants or broccoli monoculture (Fig. 1a & b, Table 1). Only a few imported cabbageworm pupae were found during the season in the three broccoli plots because the larvae leave the broccoli plants to pupate.

There were generally more diamondback moth larvae in broccoli interplanted or adjacent to nectar-producing plants than in broccoli monoculture (Fig. 1c). However, the density of diamondback moth pupae in broccoli interplanted with nectar-producing plants was much lower than in broccoli adjacent to nectar-producing plants or monoculture (Table 1).

The season-long total of cabbage looper larvae was similar between the three plots (Table 1), although the density was higher on 20–27 August in broccoli plants interplanted with nectar-producing plants (Fig. 1d).

Most adult Lepidoptera feed extensively on floral nectar (Kevan and Baker 1984), so the attractiveness of nectar-producing plants to imported cabbageworm butterflies and diamondback moths may be an important reason for more eggs and larvae in broccoli interplanted with nectar-producing plants than in broccoli monoculture. Imported cabbageworm butterflies were seen visiting the nectar-producing plants as well as the broccoli. Diamondback moths were observed only on the broccoli. Cabbage looper females were apparently not attracted to nectar-producing plants and may not rely as much on them for food.

**Parasitism of imported cabbageworms and diamondback moth larvae.** No unparasitized imported cabbageworm pupae were found in broccoli monoculture or interplanted with nectar-producing plants. The relative parasitism rates of imported cabbageworm by *C. rubecula* were 39.9%, 22.2%, or 26.2% in broccoli interplanted with nectar-producing plants, adjacent to nectar-producing plants or broccoli monoculture, respectively. The number of *C. rubecula* pupae was much higher in broccoli interplanted with nectar-producing plants than in other plots (Table 1). It is evident that *C. rubecula* has been established in Michigan after introduction from Yugoslavia in 1985. This is the only known establishment site of *C. rubecula* in the eastern U.S. (initially provided by Dr. B. Puttler, U.S.D.A. Biocontrol Laboratory, Columbia MO; current address, University of Missouri, Columbia, MO).

_Diadegma insulare_ is the major parasitoid of diamondback moth in Michigan (Idris and Grafius 1992). Only _D. insulare_ was found on 21 August in this study. However, in the broccoli monoculture on 7 August, the parasitism of diamondback moth was 68.2% by _D. insulare_ and 31.8% by _M. plutellae_, indicating that the latter could also be an important parasitoid of diamondback moth in early August in Michigan. High parasitism rates of diamondback
Figure 1. Population abundance of imported cabbageworm, diamondback moth and cabbage looper in broccoli as affected by proximity to nectar-producing plants.
Table 1.—Numbers of imported cabbageworm eggs, larvae, pupae and parasitized pupae; diamondback moth larvae, pupae and parasitized pupae; and cabbage looper larvae in broccoli as affected by nectar-producing plants.

Table 2.—Parasitism of diamondback moth after larvae were released in broccoli interplanted with nectar-producing plants or as a monoculture.
ACKNOWLEDGMENTS

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LITERATURE CITED


FACTORS INFLUENCING OVIPOSITION IN *Aedes triseriatus* (DIPTERA: CULICIDAE)

Jeffrey Beehler¹,³, Sharon Lohr² and Gene DeFoliart¹

ABSTRACT

Five factors associated with natural oviposition sites were tested for their attractancy to ovipositing *Aedes triseriatus*, including dyed oviposition water, presence of decaying organic matter, a dark oviposition container, water in which conspecific larvae have been reared to the 4th instar and the presence of eggs on the balsa wood oviposition substrate. A replicated fractional factorial design was used to examine the effects of the above factors on oviposition behavior in laboratory experiments. Regression analysis showed dyed oviposition water and eggs on the oviposition substrate to be statistically significant attractants for ovipositing *A. triseriatus* females. The attraction to dyed oviposition water indicated that dyed water in oviposition traps may greatly increase their competitiveness with naturally occurring oviposition sites.

*Aedes triseriatus* (Say) is a common woodland mosquito in the upper midwestern United States. It breeds primarily in treeholes, although other containers such as discarded tires may also be used as oviposition sites. This species is the vector of La Crosse encephalitis virus (DeFoliart et al. 1986) and thus, there is much interest in monitoring its presence. Unfortunately, *A. triseriatus* responds poorly to light traps (Craig 1983), and since it breeds in containers, it is not subject to sampling by dipper. To detect its presence, Loor and DeFoliart (1969) adapted the ovitrap previously used for monitoring *Aedes aegypti* (Linn.) during the Pan American Health Organization *A. aegypti* eradication program. The trap consists of a water-filled, black-painted, 400 ml beverage can containing a balsa paddle (Novak and Peloquin 1981) which serves as an artificial oviposition site.

A number of physical and biological factors have been suggested as oviposition attractants for *Aedes triseriatus*. Physical factors which influence *A. triseriatus* oviposition include the orientation of the opening of the oviposition container, texture and coloring of the container walls, and the optical density of the oviposition water (Wilton 1968). Novak and Peloquin (1981) used dark oviposition containers when determining if egg counts differed in relation to the oviposition substrate provided in the ovitrap. They found balsa substrates to be best suited for use.

A biological factor reported as an oviposition attractant for *A. triseriatus* is the presence of decaying organic matter in the oviposition water (Wilton

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Decaying organic matter has often been reported as an oviposition attractant with other *Aedes* and *Culex* species (e.g. Kramer and Mulla 1979, Hazard et al. 1967). Hazard et al. (1967) also found that the volatiles produced from the bacteria associated with organic infusions induced oviposition.

Egg pheromones have been reported as oviposition attractants in *Culex tarsalis* Coquillett and *Culex pipiens* (Linn.) (Osgood 1971, Dadd and Klienjan 1974). These volatiles induce oviposition when eggs of conspecifics are present. Another volatile attractant is the larval factor (LF), which is produced by 4th instar conspecifics and is present in larval holding water. Bentley et al. (1976) showed that LF was present in the holding water of 4th instar *A. triseriatus*. The LF was also shown to be present in the volatile fraction of holding water. By treating water with kaolin, McDaniel et al. (1979) showed that LF was not associated with waste products or larval gut bacteria. LF attractive to conspecifics has also been reported in *A. aegypti*, *A. atropalpus* (Coquillett), *A. togoi* (Theobald), *A. communis* (DeGeer), *Culex quinquefasciatus* Say and *Culiseta incidunt* (Thomson) (Soman and Rueben 1970, Bentley et al. 1976, Mair 1984, Mair and Langis 1985, Trimble and Wellington 1980, Wilmot et al. 1987).

The objective of this study was to test 5 reported oviposition attractants in the laboratory to determine if there are simple ways of increasing ovitrap efficiency. The 5 factors: (1) dyed oviposition water, (2) presence of decaying organic matter, (3) presence of a dark oviposition container, (4) presence of eggs on the oviposition substrate, and (5) presence of conspecific LF were compared using a replicated fractional factorial design.

**MATERIALS AND METHODS**

A replicated 2^5-2 (Resolution III) fractional factorial design was used to analyze the effects of factors that may influence the oviposition behavior of *A. triseriatus*. A standard design matrix and generators were used in the experimental design (Box et al. 1978). Each of the factors examined could be coded as present (+) or absent (-). A third replicate using a "fold-over" design (Box et al. 1978) was used to clarify the effect of the presence of decaying organic matter from interactions with other factors. Six experimental blocks were used. Each block represented a group of 4 oviposition cups within a single replication placed in an individual cage.

Fractional methods have 3 main advantages. First, they allow the comparison of a number of factors in a small number of experimental trials. Second, fractional designs allow the estimation of two-factor interactions. For example, if the combination of LF and decaying organic matter are important factors in inducing oviposition when present in tandem this interaction can be quantitatively considered. Third, fractional designs allow the use of small experimental blocks.

The first factor, dyed oviposition water, was produced by using 3 drops of red odorless vegetable dye and 3 drops of odorless green dye in 150 ml of distilled water. Water containing organic matter was produced for this study by placing 3 g of shredded, dried white oak (*Quercus alba*) leaves in 950 ml of distilled water 5 days before the beginning of the selection trial. This infusion was stored at 26°C until the trial. A darkened oviposition container was made by encircling the normally gray oviposition container with black construction paper. Balsa wood strips, 2.5 x 7.6 cm, with 40-100 *A. triseriatus* eggs/strip were kept at 3°C until the start of the experiments. Balsa wood strips without eggs were soaked for 24 hours and then stored at 3°C with the strips positive for eggs. The LF, water in which *A. triseriatus* larvae had been reared...
at least to the 4th instar, was provided by the water in which the experimental mosquitoes were reared. Larvae were reared in pans with a density of approximately 15 larvae per 150 ml of distilled water. Ground Tetramin™ tropical fish food was supplied ad libitum as a larval food source. When pupation began, pupae were removed and the water was stored at 3°C until the start of the assay. Particulate matter was removed by passing the water through filter paper (Whatman #1, Qualitative) prior to the start of the experiments.

Approximately 100 one-to two-day old female A. triseriatus were placed in a cage (1 m³) with approximately 150 males. The mosquitoes were kept at 26 ± 2°C in an insectary with a photoperiod of 14L:10D including a 1 hr evening twilight period. Humidity was maintained at approximately 90%. Mosquitoes were allowed 5 days in which to swarm and mate during which they were provided a 5% sucrose solution. After 5 days, females were fed on an anesthetized mouse (University of Wisconsin-Madison animal welfare assurance #A1457). The following day 30 blood-engorged females were placed in each of 2 separate cages (1 m³).

Plastic dental cups (6.5 cm diam) were used as oviposition containers. Inserted into each container was a 2.5 x 7.6 cm piece of balsa wood held in place by a #20 binder clip. Cups were placed near the cage corners and treatments were assigned randomly within each cage.

Each container held 150 ml of water. If the design matrix called for LF in the water, then 75 ml of LF water was placed in the cup along with 75 ml of distilled water (− for organic matter) or 75 ml of oak infusion water (+ for organic matter). Distilled water (75 ml) was added to a container negative for LF and either distilled or oak infusion was added to bring the volume up to 150 ml per cup. After the cups were filled, vegetable dyes were added to cups positive for dyed oviposition water.

Blood-engorged females were left in the cages for 6 days, with access to a 5% sucrose solution. Cages were maintained at the environmental regime described above. The balsa strips were then removed and the number of eggs counted. The number of eggs on the strips positive for eggs at the start of the bioassay were subtracted to determine the number of eggs deposited during the study period. Data were analyzed using multiple regression. Since the measured response was an egg count, the square root of the eggs laid was used as the dependent variable in the regression. The square root transformation was used because it stabilizes the variance in count data. For this data, the square root transformation was also close to the Box-Cox estimate (Box and Cox 1964) of an appropriate transformation.

RESULTS AND DISCUSSION

A total of 2,367 eggs were laid in the first replicate, 1,958 in the second and 3,529 in the third. Clearly the strongest attractant for ovipositing A. triseriatus in this study was dyed oviposition water. Of 7,854 eggs laid, 6,959 (89%) were deposited in containers containing dyed water (Table 1).

Regression analysis was performed to clarify the effects of the different factors on oviposition behavior. The regression coefficients for the final model, along with their standard errors and P-values can be found in Table 2. The $R^2$ for this regression was 0.92. This analysis confirmed that dyed oviposition water had the greatest effect on oviposition (P<0.00001). Beehler and DePoliart (1990) showed in a field study that oviposition traps which contained dyed oviposition water collected up to 4 times as many A. triseriatus eggs as traps containing water without dye. The presence of eggs on the oviposition substrate also increased oviposition (P<0.001). Sixty-nine percent
Table 1.—The effect of 5 factors on the oviposition behavior of *A. triseriatus*.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Percent of Total Eggs Deposited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dyed water</td>
<td>89%</td>
</tr>
<tr>
<td>Decaying oak leaves</td>
<td>31%</td>
</tr>
<tr>
<td>Darkened container</td>
<td>47%</td>
</tr>
<tr>
<td>Eggs on oviposition substrate</td>
<td>69%</td>
</tr>
<tr>
<td>Larval factor</td>
<td>41%</td>
</tr>
</tbody>
</table>

1Factors in fractional factorial designs are not presented singly against other factors, but are presented in combination. Therefore percentages will not total 100%.

of the eggs laid were in oviposition cups which had eggs on the oviposition substrate. This increase in oviposition could be caused by an egg pheromone or some other factor associated with *A. triseriatus* eggs which is consistent with the findings of Osgood (1971) and Dadd and Klienjan (1974) in *Culex*. This result contradicts that of Kitron et al. (1989) who, in field studies found that the presence of eggs on the oviposition substrate decreased the oviposition of *A. triseriatus*.

The presence of decaying organic matter (*P*<0.001) and LF (*P*<0.05) also affected oviposition. Both factors have negative regression coefficients. The negative effects of organic matter and LF do not necessarily imply that they deter oviposition compared to distilled water. These two results merely reflect the great attractiveness of dyed oviposition water. Given a choice between dyed water with no organic matter and water with decaying organic matter and no dye, mosquitoes prefer the former. When comparisons were made within experimental blocks, water with decaying organic matter did prove attractive compared to distilled water. Within each block (an individual cage) there is not true statistical independence between treatments, and dyed oviposition water is such a strong oviposition attractant that fair comparisons for water with decaying organic matter and LF cannot be made using this design as these factors are not both present (+) and absent (−) within a block with the other factors held constant. In this study attractiveness of LF to ovipositing *A. triseriatus* would be confounded with the effect of bacteria and their metabolites present in the larval rearing pans. McDaniel et al. (1976) showed that there was a strong interaction between container color and the presence of LF. A dark oviposition container had no effect on oviposition in this analysis.

Table 2.—Multiple regression coefficients (√*x* transformed data), standard errors and significant *P*-values for factors assayed for *A. triseriatus* oviposition attraction.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Coefficient + Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>15.2 ± 0.7****</td>
</tr>
<tr>
<td>Dyed oviposition water</td>
<td>8.5 ± 0.8****</td>
</tr>
<tr>
<td>Decaying oak leaves</td>
<td>−2.5 ± 0.7**</td>
</tr>
<tr>
<td>Dark oviposition container</td>
<td>−0.04 ± 0.7</td>
</tr>
<tr>
<td>Conspecific eggs on substrate</td>
<td>3.0 ± 0.7***</td>
</tr>
<tr>
<td>Larval factor</td>
<td>−1.6 ± 0.7*</td>
</tr>
<tr>
<td>Interaction between dye and organic matter</td>
<td>−3.6 ± 0.7***</td>
</tr>
<tr>
<td>Interaction between dye and eggs on substrate</td>
<td>−2.2 ± 0.7**</td>
</tr>
</tbody>
</table>

* *P* < 0.05  
** *P* < 0.01  
*** *P* < 0.001  
**** *P* < 0.0001
Again, the extreme attractiveness of the dyed oviposition water within each block make comparisons of this interaction with a distilled water control difficult.

In most previous studies the hypothesized attractants were compared singly to a distilled water control. This study is unique in that possible attractants were compared directly with each other. Thus, these data give an indication of which oviposition attractants will perform well when competing with other naturally occurring factors, rather than distilled water controls. The extremely significant attraction to dyed oviposition water indicates that is a very important factor in selection of oviposition sites by *A. triseriatus*, especially in conjunction with the presence of eggs on the oviposition substrate.

Wilton (1968) examined six environmental variables using an overlapping fractional factorial design. He concluded that a horizontal opening, rough-textured and dark colored walls, and a dark background were important oviposition attractants for *A. triseriatus*. He also suggested that water of high optical density and decaying organic matter were strong oviposition attractants. All containers used in our studies had horizontal openings. The balsa wood oviposition substrate was light in color and had a consistent texture between treatments. The container walls were uniform in color making comparisons with the containers of Wilton impossible. The attractiveness of dyed oviposition water to ovipositing females is consistent with the results of Wilton (1968).

Our results indicated that dying the oviposition water dark when sampling for *A. triseriatus* could greatly improve trap competitiveness with naturally occurring oviposition sites. These results also suggest the presence of an *A. triseriatus* egg factor which is attractive to ovipositing females.

ACKNOWLEDGMENTS

We thank Joyce Gibbons for her technical assistance during the course of this study. Dr. Kinley Larntz, Department of Applied Statistics, University of Minnesota kindly provided assistance in data analysis.

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ECOLOGICAL OBSERVATIONS ON PREDATORY COCCINELLIDAE (COLEOPTERA) IN SOUTHWESTERN MICHIGAN

K. M. Maredia¹, S. H. Gage¹, D. A. Landis² and T. M. Wirth¹

ABSTRACT

Ecological observations on habitat utilization by thirteen species of predatory Coccinellidae were made at a southern Michigan site during 1989 and 1990. Most of species were common during both years and used both agricultural and uncultivated habitats. Coccinella septempunctata and Coleomegilla maculata, were the most abundant in agricultural crops (alfalfa, maize, soybean and triticale), whereas Adalia bipunctata and Cycloneda munda, were the most abundant in deciduous and bushy habitats.

Biological control of insect pests is gaining increasing importance as issues such as environmental and health safety and long term sustainability become more and more critical. The importance of lady beetles as regulators of pests has been recognized since the late 19th century, when the cottony cushion scale outbreak in California, which threatened the citrus industry was controlled by the introduced vedalia beetle, Rodolia cardinalis Mulsant, (van den Bosch 1982).

There are over 400 species of Coccinellidae in North America with a wide range of life histories (Gordon 1985). The majority thrive in diverse habitats and are predators of soft-bodied insects (aphids, scale insects, mealybugs and others). Apart from feeding on Homoptera, some prey on early instars of Lepidoptera and Coleoptera (Hodek 1967). Some species are both pollenophagous and insectivorous. Both adults and larvae consume similar prey and can be found together when their prey is abundant. Lady beetles most often overwinter as adults in non-crop areas (field edges, old field-woodlot edges).

This paper presents ecological observations made on 13 species of Coccinellidae in southwestern Michigan during 1989 and 1990. Emphasis is placed on differences in habitat utilization by different species.

MATERIALS AND METHODS

Observations were made at Michigan State University's Kellogg Biological Station (KBS), Hickory Corners, Kalamazoo County, Michigan. A total of 880 ha are within the contiguous station holdings. Approximately 400 ha are devoted to agricultural research and production; 240 ha are in various stages of native succession, and the remaining 240 ha are in woodlots and plantation forests.

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Observations were made from May to October, 1989 and March to October, 1990 using yellow sticky traps, sweep net samples and visual counts. The habitats sampled represent the entire KBS area, including cereal crops (wheat *Triticum* sp., triticale X *Triticosecale*, and oat *Avena* sp.), field crops (maize *Zea mays*, soybean *Glycine max*), early successions, grasses, apple *Malus* sp. orchard, *Populus* plantations, deciduous trees, shrubs and bushes. The early successions was a abandoned crop field (after plowing in spring 1989) primarily consisting annual and biannual weeds. Alfalfa, early successions, deciduous and apple orchard habitats were sampled weekly during both years, and wheat, triticale, soybean, maize and *Populus* were sampled either of the two years depending on the availability of the habitat. Sample size in specific habitats depended on the number of patches available in the landscape.

Yellow sticky traps: Adult coccinellids were sampled weekly using double sided yellow sticky traps (22.5 cm x 14.0 cm, unbaited Pherocon, Zocon, Palo Alto, CA) that were changed every two weeks. Varying numbers of traps were set up in all habitats depending on the size of the habitat patch (5 traps/ha).

Sweep samples: Adults and larvae were collected weekly from different habitats using a standard sweep net (37.5 cm diameter). Samples were collected from alfalfa, wheat, triticale, soybean, succession and grassy habitats. Fifty sweeps were made in each habitat each week. Each sample was put in a paper bag, labelled and brought to the laboratory where number of coccinellid larvae and adults were recorded.

Visual observations: Observations of adults were made in *Populus* and maize. This consisted of individual plant examinations or counts of insects in a given time. During 1989, in the *Populus* plantation (4-months old trees), an outbreak of brown aphids *Chaitophorus* sp., occurred in late July. Weekly visual examination of *Populus* trees (minimum of 50 trees sampled) from 8 to 30 August documented coccinellid adults and aphid incidence. During 1990, coccinellid adult counts were made weekly in maize fields for 2 min from 6 July to 30 August.

**OBSERVATIONS**

Thirteen species of coccinellids were observed during the two year survey. Of these 13 species, *Coccinella septempunctata* L., *Coleomegilla maculata lengi* Timberlake, *Adalia bipunctata* (L.), *Hippodamia convergens* Guérin-Meneville, *Hippodamia parenthesis* (Say), *Cycloneda munda* (Say), *Chilocorus stigma* (Say) and *Brachiacantha ursina* (Fab.) were commonly observed, and *Coccinella trifaciata perplexa* Mulsant, *Hyperaspis undulata* (Say), *Coccinella novemnotata* Herbst, *Hippodamia tredecimpunctata tibialis* (Say) and *Anatis labiculata* (Say) were occasionally observed. The mean number of adults of eight commonly observed coccinellid species in different habitats is shown in the Table 1. The relative abundance of these eight species in different habitats is expressed in percentages (Table 2).

*Coccinella septempunctata* is a Palearctic species which has recently been established in several regions of the United States (Angalet et al. 1979, Obrycki et al. 1987, Schaefer et al. 1987). In recent years this species has become established in Michigan (USDA 1990). It was introduced for control of several aphids. It is widely distributed in Eurasia and preys upon several aphid species in a variety of agroecosystems (Hodek 1973, Honek 1985).

*Coccinella septempunctata* was one of the most abundant coccinellids in agricultural crops during both years (Tables 1 & 2). It used wheat, triticale, oat, alfalfa, maize, soybean, *Populus*, horse weed *Conyza canadensis*, walnut
Table 1. — Mean number of adult Coccinellidae for varying time period in different habitats.

<table>
<thead>
<tr>
<th>Species</th>
<th>Alfalfa</th>
<th>Wheat</th>
<th>Triticale</th>
<th>Soybean</th>
<th>Maize</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1989 (N = 238)</td>
<td>1990 (N = 158)</td>
<td>1989 (N = 8)</td>
<td>1990 (N = 120)</td>
<td>1990 (N = 120)</td>
</tr>
<tr>
<td></td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
</tr>
<tr>
<td>C. septempunctata</td>
<td>0.45 ± 0.05</td>
<td>0.91 ± 0.16</td>
<td>5.63 ± 0.31</td>
<td>0.35 ± 0.15</td>
<td>0.18 ± 0.04</td>
</tr>
<tr>
<td>C. maculata</td>
<td>0.66 ± 0.06</td>
<td>0.74 ± 0.11</td>
<td>2.63 ± 0.39</td>
<td>0.85 ± 0.20</td>
<td>0.13 ± 0.04</td>
</tr>
<tr>
<td>A. bipunctata</td>
<td>0.03 ± 0.01</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>H. parenthesis</td>
<td>0.03 ± 0.01</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>H. convergens</td>
<td>0.19 ± 0.03</td>
<td>0.02 ± 0.01</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>C. munda</td>
<td>0.42 ± 0.05</td>
<td>0.02 ± 0.01</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>C. stigma</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>B. ursina</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
</tbody>
</table>

Mean based on 50 sweeps collected weekly from 17 alfalfa fields in 1989 (5 July to October 18) and from 8 alfalfa fields in 1990 (24 April to 16 October).

Mean based on 50 sweeps collected weekly from 2 fields from 21 June to 26 July.

Mean based on 50 sweeps collected weekly from 1 field from 24 April to 16 October.

Mean based on 50 sweeps collected weekly from 12 fields from 12 June to 30 August.

Mean based on 2 minute observations made weekly in each of 12 fields from 6 July to 30 August.

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Table 1. — Continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Early succession</th>
<th>Deciduous</th>
<th>Apple orchard</th>
<th>Populus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
<td>Mean ± SEM</td>
</tr>
<tr>
<td>C. septempunctata</td>
<td>0.22 ± 0.03</td>
<td>1.04 ± 0.20</td>
<td>0.12 ± 0.05</td>
<td>0.02 ± 0.01</td>
</tr>
<tr>
<td>C. maculata</td>
<td>1.44 ± 0.10</td>
<td>0.08 ± 0.04</td>
<td>0.05 ± 0.02</td>
<td>0.08 ± 0.02</td>
</tr>
<tr>
<td>A. bipunctata</td>
<td>0.00 ± 0.00</td>
<td>0.03 ± 0.02</td>
<td>0.08 ± 0.03</td>
<td>0.25 ± 0.06</td>
</tr>
<tr>
<td>H. parenthesis</td>
<td>0.00 ± 0.00</td>
<td>0.08 ± 0.04</td>
<td>0.00 ± 0.00</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>H. convergens</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>C. munda</td>
<td>0.00 ± 0.00</td>
<td>0.18 ± 0.05</td>
<td>2.62 ± 0.81</td>
<td>0.32 ± 0.13</td>
</tr>
<tr>
<td>C. stigma</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.09 ± 0.03</td>
<td>0.28 ± 0.07</td>
</tr>
<tr>
<td>B. ursina</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
<td>0.13 ± 0.05</td>
<td>0.09 ± 0.02</td>
</tr>
</tbody>
</table>

Mean based on 50 sweeps collected weekly in 1989 (21 June to 30 August) and in 1990 (30 May to 30 August).

Mean based on weekly yellow sticky trap catch in 1989 (5 July to 18 October) and in 1990 (15 March to 16 October).

Mean based on weekly yellow sticky trap catch in 1989 (14 June to 7 August) and in 1990 (3 May to 13 September).

Mean per tree based on visual observations made on 50-100 trees in 1989 (8-30 August).
Table 2. — Relative abundance (%) of adults of different species of Coccinellidae in different habitats at KBS.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>C. septempunctata</td>
<td>25</td>
<td>52</td>
<td>63</td>
<td>29</td>
<td>56</td>
<td>21</td>
<td>13</td>
<td>74</td>
<td>4</td>
<td>3</td>
<td>18</td>
<td>18</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. maculata</td>
<td>37</td>
<td>42</td>
<td>30</td>
<td>71</td>
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<td>79</td>
<td>87</td>
<td>6</td>
<td>2</td>
<td>8</td>
<td>6</td>
<td>18</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. bipunctata</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>29</td>
<td>63</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>H. parenthesis</td>
<td>2</td>
<td>3</td>
<td>7</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
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</tr>
<tr>
<td>H. convergens</td>
<td>11</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. munda</td>
<td>23</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
<td>84</td>
<td>30</td>
<td>47</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. stigma</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>26</td>
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<td>B. ursina</td>
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<td>0</td>
<td>0</td>
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</tr>
</tbody>
</table>

*Juglans nigra,* apple orchard, early success and grassy habitats. It was observed in almost every habitat during both years. Habitat preference of *C. septempunctata* depended upon availability of prey and disturbance (alfalfa cutting and wheat harvesting). During 1989, adults were abundant in wheat and alfalfa in May and June. Both larvae and adults were present in these habitats in June. The preference changed to walnut in mid-July and to *Populus* in late July when aphids built up there. During 1990 adults were abundant in alfalfa and triticale in May and June. Both larvae and adults were present in these habitats in June. The preference changed to succession habitats when aphids built up on horse weed in mid-July. The abundant food supply on horse weed stimulated oviposition and induced a second generation. Both annual and perennial habitats were important in supporting this predator. During the two years of observations *C. septempunctata* used aphid species *Acythosiphon pisum* (Harris) and *Theroaphis maculata* (Buckton) in alfalfa, *Chaitophorus* sp. in *Populus*, *Trioxys pallidas* (Haliday) in walnut, *Uroleucon* sp. in horse weed, *Rhopalosiphum maidis* (Fitch) in maize and *Macrosiphum avenae* (Fab.) in wheat as a food source. Our observations indicate that there are one to two generations per year depending upon food supply and weather.

*Coleomegilla maculata lengi* is a native coccinellid widely distributed east of the Rocky Mountains (Gordon 1985). It is polyphagous (Hodek 1973), feeding on aphids and other prey (certain Lepidoptera eggs and larvae) (Conrad 1959, Warren and Tadic 1967, Groden 1989), and pollen from a variety of plants (Putman 1964).

*Coleomegilla maculata lengi* was also one of the most abundant coccinellids in agricultural crops during 1989 and 1990 (Tables 1 & 2). It was associated with many habitats including wheat, triticale, oat, maize, alfalfa and dandelion *Taraxacum officinalis,* with low numbers in *Populus,* horse weed and early succession. During May and early June, it was abundant on dandelion in alfalfa. Dandelion pollen rather than insect prey appeared to be the primary reason for high numbers. During late June and mid-July adults and larvae were seen mainly in wheat; adults moved to maize in mid-July when maize started flowering. Both adults and larvae were seen in maize. In late August adults moved to alfalfa fields. Alfalfa at this time had a high number of aphids, primarily pea aphids *Acythosiphon pisum* (Harris). Both larvae and adults were seen in alfalfa. *Coleomegilla maculata lengi* started moving out of alfalfa fields after mid-September, even though aphids were still present in high numbers. At this time high numbers were observed on the edges of alfalfa fields in habitats that included weeds, grasses, shrubs, bushes and deciduous trees. This may represent movement toward overwintering sites.

*Hippodamia convergens* is by far the most abundant and widespread
species of Hippodamia in North America (Gordon 1985). It is mainly aphidophagous and seems to be mainly associated with alfalfa. In 1989, this species appeared late in the season (mid-August to mid-September). It was abundant in 1989, but during 1990 was observed in very low numbers. During 1989, it responded to late season brown aphid build-up and both larvae and adults were found in high numbers in young Populus plantations.

*Adalia bipunctata* is a widespread polymorphic species generally found in tree habitats (Hodek 1973). It is specially beneficial in orchards and groves where it is the most important coccinellid predator (Smith 1958, Putman 1964, Hodek 1973). We observed *A. bipunctata* adults in selected deciduous habitats with low numbers in alfalfa, early succession and maize. *Adalia bipunctata* was one of the most abundant species in managed deciduous habitats such as apple orchard and *Populus* (Tables 1 & 2). In 1989, both adults and larvae were found in high numbers in young *Populus* plantations where there was brown aphid build-up in August. During 1990 high numbers were found in apple orchard in early June. As many as 21 adults were trapped on a single yellow sticky trap in June.

*Cycloneda munda* is a widespread coccinellid in the eastern United States and primarily feeds on aphids (Gordon 1985). It was also one of the most abundant coccinellids in deciduous habitats although it also occurred in horse weed, alfalfa, maize and *Populus*. During 1989, it was found there until mid-August. As many as 67 adults were trapped on a single yellow sticky panel in bushy habitat over a week period in early August. After mid-August there was a sharp decline in their numbers in deciduous habitats which coincided with their first appearance in alfalfa fields. In late August 1989, adults were observed feeding on brown aphids on *Populus*. During 1990, this species responded to aphid (*Uroleucon* sp.), build-up in horse weed in late July and was in high numbers. It was also seen in low numbers on maize during late August in both years.

*Hippodamia parenthesis* is a widespread nearctic aphidophagous coccinellid (Gordon 1985) found in a variety of grassy habitats and agroecosystems. We mainly observed this species in grassy and successional habitats, with low numbers in alfalfa and wheat. During August 1990, a high concentration of *H. parenthesis* larvae and adults were found in a grassy habitat mainly composed of *Agropyron repens, Andropogon virginicus, Bromus inermis* and *Phleum pratense*. As many as 15 adults were found in 50 sweeps. It also responded to aphid (*Uroleucon* sp.) build-up in horse weed in late July, 1990, and was in high numbers in horse weed during the time of aphid infestations.

*Brachiacantha ursina, Hyperaspis undulata, Chilocorus stigma* and *Anatis labiculata* were mainly found in deciduous habitats, and were not observed in crop fields. The *Hippodamia tredecimpunctata tibialis, Coccinella trifaciata perplexa* and *Coccinella novemnotata* were observed occasionally in low numbers in succession areas.

The two-year survey indicated that *C. septempunctata* and Coleomegilla maculata lengi seem to be generalized predators but tended to prefer agricultural crop plants and were the most abundant coccinellids in agricultural crops. *Adalia bipunctata* and *Cycloneda munda* were the most abundant species in deciduous and bushy habitats, however; *A. bipunctata* preferred managed deciduous habitats (apple orchard, *Populus*), whereas *C. munda* preferred the unmanaged deciduous and bushy habitats, but switched to field crops when the prey was available. *Hippodamia convergens* preferred alfalfa and *H. parenthesis* preferred the grassy habitats. *Chilocorus stigma* and *Brachiacantha ursina* preferred unmanaged deciduous habitats and were not observed in field crops.

*Coccinella septempunctata* has recently become established in Michigan and observations show that it has become one of the dominant species in
agricultural crops. Long term ecological observations are needed to see if the patterns of habitat utilization by different species are changing over time. If *C. septempunctata* becomes increasingly dominant, then further studies will be required to investigate any negative effects it may have on the native coccinellids, specifically on *Coleomegilla maculata lengi*, a dominant species in agricultural crops.

ACKNOWLEDGMENTS

This research was made possible with funding from the National Science Foundation (BSR89–06618) and the National Science Foundation LTER Program in Agricultural Ecology at Michigan State University (BSR87–02332). Aspects of this study were also partially supported by a grant from Rackham Foundation. Aphid species were identified by the Systematic Entomology Laboratory (Manya B. Stoetzel), ARS USDA, Beltsville, Maryland 20705.

LITERATURE CITED


EPIGEAL AND FLIGHT ACTIVITY OF COLEOPTERA IN A COMMERCIAL
RASPBERRY PLANTATION AND ADJACENT SITES IN SOUTHERN QUEBEC
(CANADA): INTRODUCTION AND NITIDULIDAE

Claire Levesque and Gilles-Yvon Levesque¹

ABSTRACT

We studied the epigeal and flight activity of Coleoptera in a commercial raspberry plantation and adjacent sites in southern Quebec, from 1987-1989. In this first paper, we present the results for the Nitidulidae. Pitfall traps yielded 521 beetles representing 15 species; Glischrochilus quadrisignatus represented 86% of catches in raspberry rows (old and young plants), and Epuraea spp. were the most abundant nitidulids in a woods-field boundary and in a pine woods. Nitidulids in flight interception traps comprised 2179 individuals of 28 species; Meligethes nigrescens was the most abundant species in open sites around the raspberry plantation, while Epuraea avara and E. ovata were common in the boundary and pine woods. Species composition in the boundary was quite variable in the relative abundance of species flying either in open sites or in wooded sites. We studied the seasonal activity of Colopterus truncatus, E. avara, E. ovata, G. fasciatus, G. quadrisignatus, M. nigrescens, and some other minor species. We suspect that during their mating period, overwintered adults of M. nigrescens could play a role in raspberry pollinization.

Red raspberry, Rubus idaeus, is cultivated in most of the temperate regions of the world (Gordon et al. 1990), however, few workers have studied the beetle fauna in raspberry plantations. Forty years ago, Hill (1952) recorded 137 species of insects on cultivated raspberries in Scotland, including 51 beetle species. More recently, Kieffer et al. (1983) reported at least 62 insect and spider families on the foliage during red raspberry harvest in the states of Washington and Oregon; the lathridiid beetle Melanophthalma americana (Mann.) constituted 26% of the total catches whereas the strawberry root weevil (Otiorhynchus ovatus [L.]) and lady beetles (Coccinella spp.) were the most common beetles contaminating mechanically harvested berries. In the 1984-1985 growing season, 42 arthropod species were associated with raspberry in Chilean Metropolitan Region (Guilleminot and Apablaza 1986); among the 9 beetle species monitored, the weevil Naupactus xanthographus (Germar) was a major pest while Stethorus sp. (Coccinellidae) and Oligota pygmaea Solier (Staphylinidae) were predators of the mite Tetranychus urticae Koch. In Canada, Campbell et al. (1989) reported about 40 beetle species known to attack wild and cultivated red raspberry.

Although many arthropods are found in red raspberry plantations, only a few cause yield loss or reduction in fruit quality. Current knowledge on pest

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monitoring and forecasting of pest intensity on red raspberry in the United Kingdom was recently reviewed by Gordon et al. (1990). The introduction and development of an IPM system in cane fruit will be studied in the future because consumers demand fruits largely free from pesticide residues. It should also be noted that predators, microbial-based compounds, natural plant products and insect behavior-modifying compounds (semiochemicals) are either available or being developed for pest control in many small fruits. However, very little research has been done to assess their effectiveness in raspberry crops (Gordon et al. 1990).

The development of an IPM program requires the knowledge of the most abundant insect species and their seasonal fluctuations in crops and adjacent sites. The aim of the present work was to evaluate the variations of the epigean beetle community in a red raspberry plantation in southern Quebec (Canada). Over a three-year period (1987-1989), we determined: (1) the composition and abundance of the epigean adult beetle fauna of young and old raspberry plants, in a boundary of the plantation and in an adjacent wooded site; (2) the seasonal activity of the most abundant species; (3) the potential role of adjacent sites (boundary and wooded site) as refugia for injurious insects and as an overwintering site; (4) the flight period and dispersal activity of the beetles between the raspberry plantation and adjacent sites.

Nearly 60,000 adult beetles were caught during the study. Here, we present results only for the sap beetles or Nitidulidae. Most nitidulid species are saprophagous or mycetophagous, as they use decaying fruits, fermenting materials, carrion, and decaying fungi, but a few species are predaceous or even phytophagous (Campbell et al. 1989). Some species are of economic importance in some North American raspberry fields, such as the picnic beetle, Glischrochilus quadrisignatus (Say), and the strawberry sap beetle, Stelidota geminata (Say) (Campbell et al. 1989, Miller and Williams 1982). However, commonly found in woodlots, sap beetles can be vectors of forest pathogens causing wood rots (Peng and Williams 1990).

STUDY SITES

The beetles were collected in a commercial monocultural raspberry farm at Johnville, near Sherbrooke, in southern Quebec. This farm was surrounded by a hay field and a railroad on its northern boundary and by wooded sites dominated by eastern white pine (Pinus strobus) on other sides (Fig. 1). In the studied raspberry plantation (about 7 ha, on sandy soil), the cultivars were Boyne, Carnival, Killarney and Latham but we sampled only in the Boyne cultivar. Table 1 presents periods of flower and fruit development during this study. The water from a farm pond was used to irrigate the raspberry plantation. The grower applied chemical fertilizer, many chemical pesticide sprays, fructocane cutting after harvest, and regular mowing between raspberry rows. During the present study, there were no corn, strawberry or other raspberry plantations surrounding the area.

The epigean beetle fauna was sampled with pitfall traps in the following sites: (1) a raspberry row planted in 1978 (old plants), (2) a raspberry row planted in 1985 (young plants), (3) a woods-field boundary (boundary), (4) a wooded site dominated by eastern white pine (pine woods) (Fig. 1).

In addition, we studied flying beetles with interception traps in four sites: (1) an open site near the center of the plantation (A), about 20 m from old plants, (2) an open site near the pond (B), about 5 m from young raspberry plants, (3) a woods-field boundary (C), and (4) a pine woods (D) (Fig. 1). These
traps were not located between rows of raspberry plants because of grower's activities and public access during harvest.

In the plantation, the most abundant plants between raspberry rows were grasses (Gramineae), dandelion (Taraxacum officinale), clovers (Trifolium spp.), vetch (Vicia cracca) and common milkweed (Asclepias syriaca). Plant species in uncultivated areas, in addition to the aforementioned plants, were sedges (Carex spp.), buttercup (Ranunculus acris), goldenrods (Solidago spp.), hawkweeds (Hieracium spp.), ox-eye daisy (Chrysanthemum leucanthemum) and plantains (Plantago spp.). Some poplars (Populus spp.) and willows (Salix

<table>
<thead>
<tr>
<th>Plant Stages</th>
<th>1987</th>
<th>1988</th>
<th>1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floral buds</td>
<td>May 27 – June 14</td>
<td>May 22 – July 3</td>
<td>May 21 – June 25</td>
</tr>
<tr>
<td>Flowers</td>
<td>June 7 – June 28</td>
<td>June 12 – July 10</td>
<td>June 11 – July 2</td>
</tr>
<tr>
<td>Green or pink fruits</td>
<td>June 21 – August 9</td>
<td>June 19 – August 7</td>
<td>June 21 – August 6</td>
</tr>
<tr>
<td>Ripe fruits</td>
<td>July 8 – August 19</td>
<td>July 10 – August 21</td>
<td>July 9 – August 13</td>
</tr>
<tr>
<td>Decaying fruits</td>
<td>July 26 – August 30</td>
<td>July 17 – August 28</td>
<td>July 23 – August 20</td>
</tr>
</tbody>
</table>
spp.) were present in the open site near the pond and along the brook. The boundary vegetation was diversified with wild raspberry (*Rubus idaeus*), wild strawberry (*Fragaria virginiana*), choke cherry (*Prunus virginiana*), meadowsweet (*Spirea latifolia*), small maples (*Acer spp.*), willows (*Salix spp.*), poplars (*Populus spp.*), fir (*Abies balsamea*), spruces (*Picea spp.*), and wild lily-of-the-valley (*Maianthemum canadense*). In the pine woods, the vegetation was very sparse; the grower selectively cut some of the large pine trees and in 1988 and 1989 we observed the presence of wild raspberry around a few pitfall traps, but not around the flight trap D.

**MATERIALS AND METHODS**

We used pitfall traps for ground surface-active beetles and flight interception traps for beetles flying close to the ground. These methods are widely used even if catch number is influenced by factors such as population density, locomotor activity (walking or flying) and behavior of the animals (Adis 1979, Alm et al. 1989, Baars 1979, Chapman and Kinghorn 1955, Chénier and Philogène 1989, Desender 1986, Franke et al. 1988, Halsall and Wratten 1988, Hocking and Hudson 1974, Morrill et al. 1990, Scheller 1984, Turnbow and Franklin 1980).

Pitfall traps consisted of glass jam jars (450 ml, 6.5 cm diameter at the top) partially filled with 100 ml of 4% formalin. In the plantation, traps were inserted into the soil beneath the canopy as close to the cane of raspberry plants as possible. Collection of very small beetles was made easier with a piece of white plastic inserted under the jar. A plywood cover (20 by 20 cm) was placed 2.5 cm above the trap to avoid flooding the trap, excessive formalin evaporation and capture of flying beetles. The cover also furnishes a shelter for some beetle species before the raspberry canopy has fully developed. In each site, a row of twenty traps (5 m apart) was set from the beginning of May through the end of October and traps were emptied weekly.

Flight interception traps were modified from the large-area “window” trap design promoted by Peck and Davies (1980). Each consisted of a gray 1.5 mm mesh window screen (1.22 m height, 1.52 m width, about 1.85 m² of surface) fastened to a wooden frame. The frame itself was suspended by two lateral triangular wooden supports (1.83 m at the base, 1.25 m height), 2-4 cm over a set of two galvanized metal pans (25 by 61 cm at the top, 7.5 cm deep) which were placed directly on the ground. The insects were caught in the pans partially filled with 2% formalin into which a few drops of detergent were added. To increase resistance of these traps to strong winds, small boulders and plastic garbage bags partially filled with sand were put on the bases of lateral supports. We also placed small boulders on each side of the pans to prevent tampering by mammals. The pan interior was painted white to make collection of very small beetles easier and also to reduce formalin evaporation. The frame and the two lateral supports were painted green.

We installed one flight trap in each site (Fig. 1) but in the pine woods (D), the trap was operated in 1988 and 1989 only. The catching-surface of traps was perpendicular to dominant western winds in the two open sites and parallel to raspberry rows in the boundary and pine woods. Like the pitfall traps, the flight traps were set from May through October. Samples were collected twice a week and the formalin solution was replaced at each collection. The trap counts from individual sampling periods were combined on a weekly basis. Very few insects flew on days with substantial precipitation or strong winds.

In all traps, formalin was used as a killing and preserving agent as well as
to prevent escape and predation, in spite of its potential selective effect as repellent or attractant to some beetle species (Adis 1979). Otherwise, we did not use a special bait to catch a particular species or family.

The climatic data were compiled by the Canadian Atmospheric Environment Service of the Sherbrooke Airport (45°26'N, 71°41'W, 241.0 m a.s.l.) which is 8 km away from the studied raspberry plantation and at a similar elevation. The degree-days (base: 5°C) were cumulated from 1 April through 31 October; the annual counts were 1692 in 1987, 1682 in 1988 and 1748 in 1989 while the annual normal (1951-1980) was 1580 degree-days.

Because data did not meet the criteria for parametric testing, non-parametric tests were performed. We used the Renkonen's percent similarity (PS) that is simple to calculate and comparable to more complex indices (Huhta 1979, Wolda 1981). Percent similarity is calculated as follows:

$$\text{PS} = \Sigma \min(x_i, y_i)$$

where $x_i$ and $y_i$ are the percentages representing species “i” in the two annual collections. In addition, when we captured at least ten species in two sites, we calculated the Spearman’s coefficient of rank correlation ($r_{sc}$) corrected for tied observations (Cancela da Fonseca 1968). The $\rho$ nullity was tested against $\rho > 0$ with table of the coefficient of correlation (Jolicoeur 1991) since we were interested in the similarity between beetle faunae. In cases where the number of beetles captured by a method was low (< 50 individuals/site/year), we did not use any test.

RESULTS AND DISCUSSION

Relative abundance of nitidulid catches. We captured a total of 2700 Nitidulidae representing 29 species. Pitfall trapping resulted in the catch of 521 beetles of 15 species (Table 2). Total catches of nitidulid species in flight traps comprised 2179 individuals representing 28 species (Table 3).

In raspberry rows (old and young plants), *Glischrochilus quadrisignatus* and *G. fasciatus* (Oliv.) represented 86% and 8.7% of total catches in pitfall traps respectively (Table 2). A few adults of *G. quadrisignatus* were also collected in the boundary, but most of the species active at the ground surface in the boundary and pine woods belonged to the genus *Epuraea* (Table 2).

The pollen beetle *Meligethes nigrescens* Stephens was the most abundant species caught in flight traps near the raspberry plantation, particularly in the two open sites (65% of total catches in site A, 80% in site B) (Table 3). In flight traps A, B and C, we also captured many adults of *Carpophilus brachypterus* (Say), *Colopterus truncatus* (Randall), *G. fasciatus* and *G. quadrisignatus* (Table 3). However, the species of *Epuraea*, chiefly *E. avara* (Randall) and *E. ovata* Horn, represented 46% of total catches in the flight trap at the boundary and 81% in the pine woods (Table 3).

Flying nitidulids in open sites (A and B) were rather similar over the two years in a site (A or B) or between these two sites for one year (Table 4). We obtained a similarity of 75 to 82% for site A, 79 to 91% for site B, and 70 to 89% between sites A and B; the Spearman's coefficient was always significant ($P < 0.05$) for all comparisons. Species variations in flying nitidulids in the pine woods were of little importance between the years 1988 and 1989 (PS = 73%, $r_{sc} = 0.86$); the species composition was very different from that of the two open sites (PS = 2 to 6% only) (Table 4). However, the species composition at the boundary was quite variable during the three study years (PS = 50% for two years in site C), because of variations in the relative abundance of species flying either in open sites or in wooded sites (Table 4).
Table 2.—Total catches of nitidulid species in pitfall traps (1987–1989).

<table>
<thead>
<tr>
<th>Species</th>
<th>Old Plants</th>
<th>Young Plants</th>
<th>Boundary Woods</th>
<th>Pine Woods</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
<td>N</td>
</tr>
<tr>
<td><strong>Carpophilus brachypterus (Say)</strong></td>
<td>7</td>
<td>3.3</td>
<td>3</td>
<td>1.3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Colopterus truncatus (Randall)</strong></td>
<td>6</td>
<td>2.9</td>
<td>3</td>
<td>1.3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Epuraea avara (Randall)</strong></td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>9.5</td>
<td>10</td>
</tr>
<tr>
<td><strong>Epuraea labilis Er.</strong></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2.4</td>
<td>0</td>
</tr>
<tr>
<td><strong>Epuraea ovata Horn</strong></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>Epuraea parsonsi Connell</strong></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2.4</td>
<td>1</td>
</tr>
<tr>
<td><strong>Epuraea planulata Er.</strong></td>
<td>1</td>
<td>0.5</td>
<td>0</td>
<td>4.9</td>
<td>23</td>
</tr>
<tr>
<td><strong>Epuraea sp. 1</strong></td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>19.0</td>
<td>2</td>
</tr>
<tr>
<td><strong>Glischrochilus fasciatus (Oliv.)</strong></td>
<td>13</td>
<td>6.2</td>
<td>25</td>
<td>11.0</td>
<td>1</td>
</tr>
<tr>
<td><strong>Glischrochilus quadrisignatus (Say)</strong></td>
<td>180</td>
<td>86.1</td>
<td>196</td>
<td>86.3</td>
<td>9</td>
</tr>
<tr>
<td><strong>Glischrochilus siepmanni W.J. Brown</strong></td>
<td>1</td>
<td>0.5</td>
<td>0</td>
<td>1</td>
<td>2.4</td>
</tr>
<tr>
<td><strong>Glischrochilus vittatus (Say)</strong></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2.4</td>
<td>0</td>
</tr>
<tr>
<td><strong>Heterhelus pennatus (Murray)</strong></td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>4.8</td>
<td>0</td>
</tr>
<tr>
<td><strong>Omosita colon (L.)</strong></td>
<td>1</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>209</td>
<td>100.0</td>
<td>227</td>
<td>99.9</td>
<td>42</td>
</tr>
</tbody>
</table>

Number of species 7 4 11 8 15

Glischrochilus fasciatus and G. quadrisignatus are generally considered to be secondary pests in raspberry plantations because adults feed on injuries inflicted by other insects or diseased berries (Campbell et al. 1989). According to Parsons (1967), several species of *Epuraea* (including *E. avara*) have been reared from fungi causing pine diseases over much of northern United States and Canada whereas *E. ovata* occurs under beech bark and in fungus (Parsons 1943). Larvae and adults of *Meligethes nigrescens* are known to feed on the pollen of various flowers, but not on raspberry pollen (Easton 1955, Connell 1956). In Oregon it is a pest of Dutch clover (*Trifolium pratense*) and hairy vetch (*Vicia* sp.), in Pennsylvania it has been injurious to muskmelon (*Cucumis melo*), while in Quebec it is sometimes numerous on clover (*Trifolium spp.*) (Campbell et al. 1989). Although *M. nigrescens* is a very common species throughout Europe (Easton 1955), Hill (1952) did not record this insect on cultivated raspberries in Scotland, but he reported the fairly common presence of *M. aeneus* (Fab.) and *M. viridescens* (Fab.); these two species probably did more good than harm to the raspberry plants, in that they helped in pollination. However, the pollen beetle *M. aeneus* is a major pest on oil-seed rape throughout most of Europe (Nielsen and Axelsen 1988).

Seasonal activity of most abundant species. In three years, we captured adults of *G. quadrisignatus* in pitfall and flight traps from May through September, particularly between mid-May and mid-June (Fig. 2); 23 tenerals were trapped between 15 May and 9 August. At the boundary, eight of nine adults captured in pitfall traps were active in May while 16 of 23 adults captured in flight trap C were active in mid-July and August. We also observed a few adults on ripe fruits in the plantation sporadically. Our interpretation of these facts is as follows: (1) The adults overwintered in the sites around the plantation, principally in uncultivated areas. (2) When the temperature first began to rise, overwintered beetles flew towards the raspberry plantation where the reproduction occurred. (3) The new generation fed on ripe and decaying fruits without leaving the plantation except to feed on berries of wild plants in the boundary area. (4) We suspect the presence of only one extended period of reproduction each year or two generations of this species in
Table 3.—Total catches of nitidulid species in flight traps (1987-1989).

<table>
<thead>
<tr>
<th>Species</th>
<th>Open Site Near Center</th>
<th>Open Site Near Pond</th>
<th>Boundary</th>
<th>Pine Woodsa</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachypterolus pulicarius (L.)</td>
<td>1 0.1</td>
<td>1 0.1</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Brachypterus urticae (Fab.)</td>
<td>0 0</td>
<td>0</td>
<td>1 0.4</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Carpophilus brachypterus (Say)</td>
<td>36 4.8</td>
<td>34 3.7</td>
<td>12 4.7</td>
<td>0</td>
<td>82</td>
</tr>
<tr>
<td>Carpophilus marginellus Mots.</td>
<td>5 0.7</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Colopterus truncatus (Randall)</td>
<td>31 4.1</td>
<td>33 3.6</td>
<td>17 6.7</td>
<td>0</td>
<td>81</td>
</tr>
<tr>
<td>Conotelus obscurus Er.</td>
<td>27 3.6</td>
<td>23 2.5</td>
<td>3 1.2</td>
<td>0</td>
<td>53</td>
</tr>
<tr>
<td>Cryptarcha ampla Er.</td>
<td>0 0</td>
<td>1 0.4</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Cryptarcha concinna Melsh.</td>
<td>0 0</td>
<td>1 0.4</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Epuraea aestiva (L.)</td>
<td>1 0.1</td>
<td>0</td>
<td>3 1.2</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Epuraea acara (Randall)</td>
<td>2 0.3</td>
<td>5 0.5</td>
<td>76 29.9</td>
<td>56 21.3</td>
<td>139</td>
</tr>
<tr>
<td>Epuraea labilis Er.</td>
<td>8 1.1</td>
<td>7 0.8</td>
<td>7 2.8</td>
<td>1 0.4</td>
<td>23</td>
</tr>
<tr>
<td>Epuraea ovata Horn</td>
<td>1 0.1</td>
<td>0.1</td>
<td>9 3.5</td>
<td>119 45.2</td>
<td>130</td>
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<tr>
<td>Epuraea parsonsi Connell</td>
<td>0 0</td>
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<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Epuraea planulata Er.</td>
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<td>0</td>
<td>6 2.4</td>
<td>7 2.7</td>
<td>14</td>
</tr>
<tr>
<td>Epuraea rufula (Say)</td>
<td>0 0</td>
<td>2 0.8</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Epuraea sp. 2</td>
<td>2 0.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Epuraea truncatella Mann.</td>
<td>0 0</td>
<td>12 4.7</td>
<td>29 11.0</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>Glischrochilus fasciatus (Oliv.)</td>
<td>39 5.2</td>
<td>24 2.6</td>
<td>6 2.4</td>
<td>1 0.4</td>
<td>70</td>
</tr>
<tr>
<td>Glischrochilus quadrisignatus (Say)</td>
<td>88 11.7</td>
<td>33 3.6</td>
<td>23 9.1</td>
<td>1 0.4</td>
<td>145</td>
</tr>
<tr>
<td>Glischrochilus sanguinolentus (Oliv.)</td>
<td>0 0</td>
<td>8 3.2</td>
<td>26 9.9</td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Glischrochilus siepmanni W.J. Brown</td>
<td>1 0.1</td>
<td>0.5</td>
<td>9 3.5</td>
<td>3 1.1</td>
<td>18</td>
</tr>
<tr>
<td>Glischrochilus vittatus (Say)</td>
<td>0 0</td>
<td>0</td>
<td>6 2.4</td>
<td>12 4.6</td>
<td>18</td>
</tr>
<tr>
<td>Heterhelus pennatus (Murray)</td>
<td>2 0.3</td>
<td>1 0.1</td>
<td>3 1.2</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Lobiopa undulata (Say)</td>
<td>1 0.1</td>
<td>3 0.3</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Meligethes nigrescens Stephens</td>
<td>489 65.2</td>
<td>727 79.7</td>
<td>42 16.5</td>
<td>7 2.7</td>
<td>1265</td>
</tr>
<tr>
<td>Nitidula bipunctata L.</td>
<td>1 0.1</td>
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<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Nitidula rufipes (L.)</td>
<td>1 0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Omosita colon (L.)</td>
<td>13 1.7</td>
<td>15 1.6</td>
<td>6 2.4</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Total</td>
<td>750 99.8</td>
<td>912 99.7</td>
<td>254 100.2</td>
<td>263 100.1</td>
<td>2179</td>
</tr>
<tr>
<td>Number of species</td>
<td>20</td>
<td>14</td>
<td>22</td>
<td>12</td>
<td>28</td>
</tr>
</tbody>
</table>

*not sampled in 1987.

Note: G. sanguinolentus include the two subspecies G. s. sanguinolentus (Oliv.) and G. s. rubromaculatus (Reitter).

Some years at Johnville. Our results agreed partially with previous observations on the biology of this species (Campbell et al. 1989). At 21.1-29.4°C, the life cycle (egg to adult) averaged 31-36 days and the new adults remained in the soil for an average of 11.2 days before emerging (Foott and Timmins 1979). Emergence began on 15 June in southwestern Ontario and peaked from mid-July to early August (Foott and Timmins 1977). *Glischrochilus quadrisignatus* is univoltine in southwestern Ontario and bivoltine in the United States (Campbell et al. 1989). Luckmann (1963) suspected that in some locations, particularly in late September or October, conditions could be favorable for a sufficient length of time to initiate oviposition. According to Peng and Williams (1990), hibernation is unnecessary for oviposition in *G. quadrisignatus* because these beetles can produce eggs when suitable food and favorable environmental conditions are available. Although photoperiod was not considered in this study, it may limit the production of a second generation alone or in combination with other factors (Luckmann 1963). The effects of photoperiod on the larval development and possibly on larval hibernation are uncer-
Table 4. — Percent of similarity (PS, upper part of the oblique line) and Spearman's coefficient of rank correlation ($r_s$, lower part) for Nitidulidae captured with flight traps.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>Near Center (A)</th>
<th>Near Pond (B)</th>
<th>Boundary (C)</th>
<th>Pine Woods (D)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* 0.1 ≤ $p < 0.05$

** 0.001 ≤ $p < 0.01$

*** $p < 0.001$
tain. It is possible that a part of the population hibernates in the larval stage in the soil of the raspberry field and mature to the adult stage by May. Alm et al. (1989) hung baited flight traps in crabapple trees (Malus sp.) in Ohio; they caught beetles, using fruit volatiles as bait, from 29 May to 5 September with a peak of captures in July. According to the same authors, adults of *Glischrochilus quadrisignatus* were also attracted to butyl acetate and propyl proprionate. Our observations on the flight of the new generation were probably linked to the absence of bait in traps and not to summer temperatures.

Adults of *M. nigrescens* flew from early May to the end of October (Fig. 3). Flight activity began in May when at least 100 degree-days above 5°C were accumulated. The first peak of captures occurred in late May and June, in part...
during the period of raspberry flowering (Fig. 3). During this period of maximal activity in May-June (1987-1989), we captured 873 males and only 143 females (6.1 $\delta : 1 \varphi$). If males and females flew at the same height, it was then the mating period. From mid-July to late August, we observed a small increase in activity (Fig. 3); males and females were almost in the same proportions (1.2 $\delta : 1 \varphi$) during this second period which was probably linked with emergence of new adults since we captured a teneral female on 24 July 1988. In 1989, the flowering periods were, respectively, 21 May-7 June for dandelion, 25 June-6 August for vetch, and 25 June-27 August for clover. We believe that overwintered adults moved to the raspberry plantation and fed on dande-
lion and raspberry pollens during the mating period, that the larvae fed on vetch and clover pollens, and that the new adults fed also on clover pollen and could move progressively to new food sources (such as goldenrod pollen) near the plantation before hibernation. Where adults of this species feed on raspberry pollen, we are uncertain of their effectiveness as pollinators or if there might be competition with bees for the pollen of raspberry or other plant species in the plantation. No damage associated with this species has ever been detected. According to Parsons (1943), this species occurs in April-July in North America. In Delaware, adults were common on the flowers of *Brassica* sp., *Cornus* sp. and *Magnolia macrophylla* from 15 April to 17 May; they were also collected occasionally on the Rosaceae flowers (*Prunus* spp., *Malus* spp.) from 18 April to 1 May (Connell 1956). In Europe, the pollen beetle *M. aeneus* has one annual generation with two larval stages and pupate in the soil (Nielsen and Axelsen 1988). In England, overwintered beetles mate from mid-May until the emergence of new generation adults; these did not mate before hibernating, since pollen is probably their main food (Williams and Free 1978).

In 1989, adults of *Colopterus truncatus* (30 ♀♂, 19 ♂♂) flew from mid-May to early October and the peak captures occurred in June-July (Fig. 4). Apparently, they overwintered as adults. According to Parsons (1943), this species occurs mainly in April-July. In Wisconsin, McMullen and Shenefelt (1961) collected this species in pitfall traps baited with banana: the adults were active in May and chiefly in September-October.

In 1987–1989, adults of *E. avara* (89 ♀♂, 50 ♂♂) flew from early May to early August and occasionally again in September; peak captures occurred in May-June (Fig. 4). In May 1987, we captured 13 adults (5 ♀, 5 ♂♂) in pitfall traps. Overwintering by these adults was probable. According to Parsons (1943), this species occurs in May-August, chiefly in June. In Wisconsin, banana bait pitfall trapping resulted in the catch of adults mainly in May-June (McMullen and Shenefelt 1961).

In 1988–1989, adults of *E. ovata* (62 ♀♂, 67 ♂♂) flew from early May to mid-August (Fig. 4). In 1988, the first peak of catches occurred in May and is possibly linked to the activity of overwintering beetles (Fig. 4). We also observed a small increase of activity in July, possibly due to the emergence of new adults although we did not capture tenerals. According to Parsons (1943), this species occurs in May-September, chiefly in June.

In 1989, we collected 31 ♀♀ and 20 ♂♂ of *G. fasciatus* in unbaited flight traps, mainly in May (Fig. 4). In 1987–1989, 34 ♀♀ and 5 ♂♂ were caught in pitfall traps, chiefly in May. We suspect that: (1) the adults overwintered in uncultivated areas around the plantation, and (2) when the temperature first began to rise, overwintered beetles flew to the raspberry plantation where reproduction probably occurred. Because of the absence of bait in traps, we could not prove that the new generation fed on ripe and decaying raspberries. *Glischrochilus fasciatus* was apparently univoltine at Johnville. According to Parsons (1943), this species may be collected from April to October, but mainly in April and May. In Wisconsin, in banana bait pitfall traps, adults were very abundant in May-June and again in September-October; nevertheless, *G. fasciatus* tends to show a small increase of activity in mid-summer, indicating perhaps two generations (McMullen and Shenefelt 1961). According to Peng and Williams (1990), hibernation is unnecessary for oviposition of *G. fasciatus* because these beetles can produce eggs when suitable food is available and environmental conditions are favorable.

**Seasonal activity of some other species.** During the three years of this study (1987–1989), one or two periods of flight activity were observed in *Carpophilus brachypterus* (Say), *E. labilis* Er., *E. planulata* Er., *E. truncatella* Mann., *G. sanguinolentus rubromaculatus* (Reitter), *G. sanguinolentus san-
guinolentus (Oliv.), G. siepmanni W.J.Brown, G. vittatus (Say) and Omosita colon (L.) (Table 5). The peak of captures occurred generally in May-June although adults of E. truncatella flew mainly in October. In addition, we captured adults of C. brachypterus, E. planulata and E. truncatella in pitfall traps chiefly in May-June. We also collected one teneral of G. siepmanni in a pitfall trap in September 1987. For these nine taxa, adult overwintering and spring reproduction were probable. However, larval hibernation was possible in Conotelus obscurus Er. because adults flew during summer, chiefly in July-August (Table 5). Our results generally agreed with previous observations on the biology of these ten species (Parsons 1943, Connell 1956, Peng and Williams 1990). In Delaware, larvae of C. obscurus were common on the
Table 5.—Seasonal abundance and number of females and males of some nitidulid species (1987-1989).

<table>
<thead>
<tr>
<th>Species</th>
<th>Traps</th>
<th>M</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
<th><strong>F : M</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Carpophilus brachypterus</td>
<td>Flight</td>
<td>41</td>
<td>16</td>
<td>7</td>
<td>12</td>
<td>6</td>
<td>58</td>
<td>29 : 1</td>
</tr>
<tr>
<td>Carpophilus brachypterus</td>
<td>Pitfall</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>58</td>
<td>29</td>
<td>10</td>
<td>0 : 0</td>
</tr>
<tr>
<td>Conotelus obscurus</td>
<td>Flight</td>
<td>2</td>
<td>2</td>
<td>16</td>
<td>33</td>
<td>2</td>
<td>31</td>
<td>22 : 1</td>
</tr>
<tr>
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<td>Pitfall</td>
<td>2</td>
<td>2</td>
<td>16</td>
<td>33</td>
<td>2</td>
<td>31</td>
<td>22 : 1</td>
</tr>
<tr>
<td>Eupreaa labilis</td>
<td>Flight</td>
<td>6</td>
<td>9</td>
<td>7</td>
<td>1</td>
<td>8</td>
<td>3</td>
<td>14 : 1</td>
</tr>
<tr>
<td>Eupreaa planulata</td>
<td>Flight</td>
<td>11</td>
<td>3</td>
<td>8</td>
<td>1</td>
<td>5</td>
<td>5</td>
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<tr>
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<td>12</td>
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<td>1</td>
<td>21</td>
<td>1</td>
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<td>6 : 1</td>
</tr>
<tr>
<td>Eupreaa truncatella</td>
<td>Flight</td>
<td>10</td>
<td>2</td>
<td>1</td>
<td>28</td>
<td>23</td>
<td>18</td>
<td>18 : 6</td>
</tr>
<tr>
<td>Eupreaa truncatella</td>
<td>Pitfall</td>
<td>9</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>9</td>
<td>5</td>
<td>18 : 6</td>
</tr>
<tr>
<td>Glischrochilus sanguinolentus</td>
<td>Flight</td>
<td>9</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>18</td>
<td>18 : 6</td>
</tr>
<tr>
<td>Glischrochilus sanguinolentus</td>
<td>Flight</td>
<td>8</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>18</td>
<td>18 : 6</td>
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<td>16</td>
<td>2</td>
<td>1</td>
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<td>1</td>
<td>18</td>
<td>18 : 6</td>
</tr>
<tr>
<td>Glischrochilus sanguinolentus</td>
<td>Flight</td>
<td>16</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>18</td>
<td>18 : 6</td>
</tr>
<tr>
<td>Glischrochilus sanguinolentus</td>
<td>Flight</td>
<td>11</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>11</td>
<td>7</td>
<td>11 : 6</td>
</tr>
<tr>
<td>Omosita colon</td>
<td>Flight</td>
<td>26</td>
<td>8</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>18</td>
<td>18 : 6</td>
</tr>
</tbody>
</table>

Flowers of *Hibiscus* sp. from 4 August to 17 September (Connell 1956). In Illinois and New Jersey, adults of *O. colon* were caught in carrion-bait traps from April to November, chiefly in April-July (Johnson 1975, Shubeck et al. 1977).

In flight traps and pitfall traps, we captured more females than males of *Carpophilus brachypterus* (~1.8 : 1 in flight traps and only females in pitfall traps) and *E. truncatella* (~1.5 : 1 for two methods) (Table 5); we have no explanation for these results. We observed that the sex-ratio for trapped adults of *E. planulata* varied with the method, 1 : 1 : 1.8 in flight traps and 3.5 : 1 in pitfall traps; we suspect that the epigeal activity of females was linked to oviposition behavior.

**Suggestions for further studies.** We suggest: (1) the determination of the exact role of *M. nigrescens* in the raspberry pollinization; (2) the effects of the photoperiod, alone or in combination with the temperature, on the life cycle of nitidulid species, particularly in *G. quadrisignatus*; and (3) an examination of factors influencing the sex-ratio of some species at flight traps (e.g. type and height of traps, use and type of preserving agent (formol or other), or the absence of bait in traps).

**ACKNOWLEDGMENTS**

We thank Dr. Roger N. Williams (OARDC, Ohio State University, Wooster, Ohio) who read and commented on a first draft of this manuscript. We are grateful to two anonymous reviewers for their useful comments. We appreciated the help of Mrs. Jean McNamara (Centre for Land and Biological Resources Research, Agriculture Canada, Ottawa, Ontario) for identifications and confirmations of species collected in this study; voucher specimens of some species are deposited in the Canadian National Collection. We thank Mrs. Louise Jodoin for making linguistic improvements. Also, we wish to thank Mr. Michel Couture and Mrs. Lucie Labrecque, proprietors of "La Framboisiere de l'Estrie, Enr." at Johnville (Quebec). This study was partially supported by the Fonds F.C.A.R. (Quebec).
LITERATURE CITED


COMPARATIVE ASPECTS OF MATING BEHAVIOR PATTERNS IN SIX SPECIES OF STINK BUGS (HETEROPTERA: PENTATOMIDAE)

Lee C. Drickamer and J. E. McPherson

ABSTRACT

Mating sequences were analyzed for six species of stink bugs using videotapes. The results consisted of qualitative descriptions of the precopulatory activities of the pairs and quantitative analyses of the number and direction of mating sequences, including the latency to and duration of copulatory lock. It was possible to quantitatively characterize each of the six species tested. In addition, certain infrequent behavior patterns, e.g., head butts, were observed for some species and not others. The results extend the previous information on mating activities in stink bugs, particularly for Euschistus. We interpret our findings with regard to reproductive strategies in different species of stink bugs, and consider the use of behavior as a taxonomic tool.

Locating mates and mating behavior are critical aspects of insect behavioral biology; these issues have been emphasized, both in general theoretical terms and studied in particular species (Matthews and Matthews 1978, Thornhill and Alcock 1983). Sexual behavior patterns have been investigated in several North American species. Descriptions of all or portions of mating sequences are available for Murgantia histrionica (Hahn) (Lanigan and Barrows 1977), Cosmopepla bimaculata (Thomas) (Fish and Alcock 1973, Olsen 1910), Nezara viridula (L.) (Harris and Todd 1980, Mitchell and Mau 1969), Brochymena sulcata Van Duzee (Ruckes 1938), B. quadripustulata (Fabricius) (Gamboa and Alcock 1973), and Euschistus conspersus Uhler (Alcock 1971). Attractant pheromones have been identified in some species (Aldrich 1988) and it has been hypothesized that, at least in N. viridula, the pheromone operates over a relatively long distance followed by touching behavior (Harris et al. 1982). Furthermore, in N. viridula, a sophisticated auditory communication system may act as an intermediate step between the pheromone and touch mode (Harris et al. 1982). In all of the species tested, a precopulatory mating sequence is carried out while the members of the prospective pair are in close proximity to one another.

Although stink bugs share elements of their mating activities, inter- and intraspecific variation exist in courtship. The most frequent elements include males using their antennae to palpate various parts of the female; making head contact with the female, involving simple touching contact, head butts and attempts to lift the rear of the female abdomen; and the male turning so that the partners face in opposite directions (the end-to-end copulatory position; Gamboa and Alcock 1973). Several reports concern the pattern of the sequence as the male palpates and makes contact with the female (Alcock

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1971, Gamboa and Alcock 1973, Lanigan and Barrows 1977), the latency to
copulatory linkage (Alcock 1971, Harris and Todd 1980, Lanigan and Barrows
1977), and the duration of the linkage (Fish and Alcock 1973, Harris and Todd

Some elements of the mating and copulatory sequence could be important
cues for species recognition and other elements may be related to species­
specific mating strategies. The major purpose of this paper is to describe the
mating sequences for six sympatric species of stink bugs from southern Illi­
nois, five from the same genus. Our results suggest that differences in court­
ship patterns could serve as aids for species recognition, and add to existing
information on mating sequences in stink bugs.

Our findings also are relevant to the potential use of behavior as a taxo­
nomic tool as has been attempted previously for various mammals (Bekoff et
al. 1975, Dewsbury 1972), and the bird orders Pelicaniformes (Van Tets 1965)
and Anseriformes (Lorenz 1972), as well as for several insects (e.g. wasps
[Evans 1966] and ants [Wilson 1971]). The possible benefits from a cross­
fertilization between ethology and phylogenetic systematics are apparent
from recent work on fish (McLennan et al. 1988).

MATERIALS AND METHODS

We observed six species of stink bugs: *Euschistus icterus* (L.), *E. politus*
Uhler, *E. servus* (Say), *E. tristigmus* (Say), *E. variolarius* (Palisot de
Beauvois), and *Thyanta custator accerra* McAtee. All were reared under labo­
ratory conditions from wild stocks taken from the La Rue – Pine Hills Ecologi­
cal Area of the Shawnee National Forest, southern Illinois. The various stocks
were reared according to the procedures developed by McPherson and
Mohlenbrock (1976). Field-collected parents were kept in Mason jars in incu­
bators maintained at 23 ± 1°C and a 16L:8D photoperiod. Each jar contained a
ircular piece of filter paper covering the bottom, and beans or carrots served
as food. Strips of paper towel were added to each jar to increase the area for
footing and excrement absorption. Several 3 cm x 5 cm strips of cheesecloth
were placed in each jar to serve as oviposition sites. Each jar was closed with a
screen mesh top, a disc of paper toweling, and the ring of the two-piece jar lid.

Cheesecloth with attached egg clusters was removed and placed in Petri
dishes on moist filter paper and maintained under the same ambient condi­
tions as the parents. First instars (a nonfeeding stage) were maintained in the
same Petri dishes. Second through fifth instars were reared in Mason jars in a
fashion similar to that described for maintaining adults. Upon reaching
adults, the bugs were separated by sex and maintained in separate Mason jars
until used in mating tests. We tested the mating sequences of the stink bugs
about two weeks after they emerged as adults because previous observations
(unpublished data) indicated they are prepared to mate by two weeks after the
final molt.

We used a Panasonic Digital 5000 camera system with a zoom lens and a
Panasonic AG-6010s VHS tape deck to videotape mating activities of stink
bugs. Playback was done on a Sony 40 cm color monitor. The tape deck
permitted us to view tapes in slow motion or to stop the tape to make a record
of the time. The camera system was equipped with a continuous timer display,
reading to the nearest second.

The videotaping session involved placing either 2 males and 2 females or 3
males and 3 females of a designated species into a 250 ml beaker (5 cm in diam,
7.5 cm deep) closed with a Petri dish lid. Each beaker contained a piece of
cheesecloth taped to the rear wall as seen on the television monitor and, in
many instances, several beans were added to the bottom of the container. Two observation chambers were placed side-by-side and filmed simultaneously. Most stink bug activity occurred on either the cheesecloth or the beans. In a few instances (n < 5 cases for all species combined), the bugs' locations made it impossible to accurately record the mating and copulatory sequence completely. In these instances, we discarded the data from our sample.

Animals were placed into the observation chambers for approximately 24 hours. A standard 2-hour videotape cassette was used with the machine set to record every 12th frame, thus permitting us to tape 24 hours of activity with a single tape. Preliminary data from the tapes indicated that recording every 12th frame was sufficient to obtain an accurate record of the behavior sequences.

Based on preliminary observations of videotapes, we recorded the following dependent variables associated with mating activities and copulation: (1) number of mating sequences, defined as a series of antennal palpations of the female by the male, followed by or in conjunction with head contact by the male to the thorax, abdomen and rear of the female, culminating in an attempt by the male to turn around and achieve intromission; (2) the orientation of the male with respect to the female during courtship, with the male initiating contact with the female's head (or tip of abdomen) and moving to the tip of her abdomen (or head); (3) latency from initial contact via antennation until intromission was achieved; and (4) duration of copulation. In addition, we noted behavior patterns for each species. Our results consist of quantitative observations that we have analyzed statistically, using Chi-square and ANOVA (Sokal and Rohlf, 1983), and qualitative descriptions of behavior patterns for each species.

RESULTS

Analysis of the videotapes provided an opportunity to describe the mating sequences for the six species. After initial contact between members of a pair, the general pattern involved a series of antennal palpations of the female by the male; antennal contact occurred with the head, thorax and abdomen of the female, and varied according to species. The direction of palpation of the female's body from either head to abdomen or abdomen to head also varied. Antennal palpation was followed by, or occurred in conjunction with, head contact by the male with some or all of the three body regions of the female; here also the direction of the sequence of contacts was from head to rear or vice versa. The final stages of the sequence involved the male turning his body 180° so that the rear of his abdomen was in contact with the rear of her abdomen in the pattern characteristic of the Pentatomoidea; at this point the male attempted intromission. Differences occurred among species in the number of times the male completed the entire sequence from palpation to attempted intromission. In addition, there were other species differences in the courtship sequence, including head butts of the female by the male, and variations when the male turned around to assume the end-to-end copulatory position. In the latter instance, some males completed the turn with their body remaining in contact with the female, sliding the rear of their body along the thorax and abdomen of the female until genital-to-genital contact occurred while for other males, there was little or no contact between the partners.

Quantitative analyses, using Chi-square contingency tests as the basis for generating expected values, revealed significant differences among species for both the number of mating sequences that occurred before copulation ($X^2 = 25.52; \text{ d.f.} = 5; p < 0.001; \text{ Table 1}$) and the direction of the sequence ($X^2 =$
Table 1.—Numbers (A) of mating and copulation sequences and (B) direction of the mating sequence for pairs of stink bugs of six species.a

(A) Mating Sequences

<table>
<thead>
<tr>
<th>Species (sample size = # pairs)</th>
<th>Number of Pairs Exhibiting 1 or 2+ Mating Sequences Before Copulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euschistus ictericu (11)</td>
<td>3 (5.6)</td>
</tr>
<tr>
<td>Euschistus politus (16)</td>
<td>16 (9.4)</td>
</tr>
<tr>
<td>Euschistus sericus (11)</td>
<td>9 (6.5)</td>
</tr>
<tr>
<td>Euschistus tristigmus (19)</td>
<td>4 (11.2)</td>
</tr>
<tr>
<td>Euschistus variolarius (14)</td>
<td>9 (8.2)</td>
</tr>
<tr>
<td>Thyanta custator accerra (9)</td>
<td>6 (5.3)</td>
</tr>
</tbody>
</table>

(B) Direction of Mating Sequence

<table>
<thead>
<tr>
<th>Species (sample size = # pairs)</th>
<th>Head-to-rear</th>
<th>Rear-to-head</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euschistus ictericu (11)</td>
<td>10 (8.5)</td>
<td>1 (2.5)</td>
</tr>
<tr>
<td>Euschistus politus (16)</td>
<td>16 (12.4)</td>
<td>0 (3.6)</td>
</tr>
<tr>
<td>Euschistus sericus (11)</td>
<td>11 (8.5)</td>
<td>0 (2.5)</td>
</tr>
<tr>
<td>Euschistus tristigmus (19)</td>
<td>11 (14.7)</td>
<td>8 (4.3)</td>
</tr>
<tr>
<td>Euschistus variolarius (14)</td>
<td>13 (10.8)</td>
<td>1 (3.2)</td>
</tr>
<tr>
<td>Thyanta custator accerra (9)</td>
<td>1 (7.0)</td>
<td>8 (2.0)</td>
</tr>
</tbody>
</table>

aFor each dependent measure, the expected values from a contingency Chi-square test are given in parentheses.

Latencies to copulatory linkage varied significantly across the six species ($F = 9.85; d.f. = 5, 74; p < 0.001; Table 2$). E. politus, E. variolarius, and T. c. accerra, which did not differ from each other in latency to copulation, all achieved linkage more rapidly than the other three species; the latter three also did not differ from one another. There were also significant differences in the duration of the copulatory linkage ($F = 8.88; d.f. = 5, 74; p < 0.001; Table 2$).

Table 2.—Latency (sec) to establishment of copulatory linkage and duration (min) of the copulatory linkage in six species of stink bugs.a

<table>
<thead>
<tr>
<th>Species (sample size = # pairs)</th>
<th>Latency (sec)</th>
<th>Duration (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euschistus ictericu (11)</td>
<td>271.5 (46.0)B</td>
<td>741.4 (176.0)C</td>
</tr>
<tr>
<td>Euschistus politus (16)</td>
<td>90.6 (16.3)A</td>
<td>84.8 (17.0)A</td>
</tr>
<tr>
<td>Euschistus sericus (11)</td>
<td>348.8 (43.1)B</td>
<td>538.1 (104.9)BC</td>
</tr>
<tr>
<td>Euschistus tristigmus (19)</td>
<td>252.2 (33.3)B</td>
<td>589.7 (56.1)BC</td>
</tr>
<tr>
<td>Euschistus variolarius (14)</td>
<td>119.2 (24.4)A</td>
<td>407.4 (48.2)B</td>
</tr>
<tr>
<td>Thyanta custator accerra (9)</td>
<td>117.8 (23.8)A</td>
<td>683.7 (77.9)C</td>
</tr>
</tbody>
</table>

aValues are presented as means ± 1 S.E.M. Means in each vertical column not marked with the same superscript letter are significantly different at the 0.02 level using Tukey’s w-procedure.
There was an overlapping pattern of statistically significant differences; *E. politus* had a shorter duration than any of the other species. *E. ictericus* and *T. c. accerra* both remained in the copulatory linkage longer than *E. variolarius*. *E. servus* and *E. tristigmus* were intermediate in copulation duration.

For *E. politus*, the precopulatory mating sequence involved a rapid set of antenodal palpations starting from the head of the female and progressing toward the rear of the abdomen. The single sequence usually involved male antenodal and head contact only with the sides and rear of the female’s abdomen; no contact was made with the head or thorax of the female. Near the end of the palpation and head contact phase, males often made distinct head butts to the sides and rear of the female’s abdomen. In the process the male would back away and then rapidly move toward and slightly underneath the female, lifting her posterior off the substrate. Then the male would turn and achieve intromission without making contact with the female while turning; males were almost always successful on their first attempt. Mating sequences were short and the duration of the copulatory linkage was brief (Table 2).

*Euschistus tristigmus* varied considerably in palpation and head contact; the sequence was both head-to-rear and vice versa depending on the individual mating. There was more antenodal palpation of the female’s head by the male than in any other species examined. This first phase involved palpation and head contact with the female’s head, thorax and abdomen. Just prior to turning around, the male generally used his head to push the rear of the female’s abdomen upward. Most males then turned slowly, out of contact with the female, and attempted intromission. However, three males remained in contact with the female during the turning phase, sliding the rear of their abdomen along the side of the female until achieving the end-to-end position. Most, but not all, sequences involved two or more complete cycles involving antenonation, head contact and turning prior to achieving successful intromission. Sequences were relatively long and the duration of the copulatory linkage approached those of longest duration among the species tested (Table 2).

In *E. ictericus*, all but one sequence involved a pattern of antenodal palpation and head contact that was initiated at the head region of the female and progressed to the rear. The antenonation was directed at the head, thorax and abdomen of the female, but head contact occurred only with the latter two body regions. Males turned to attempt intromission without making contact with females. A majority of males engaged in two or more complete sequences before achieving intromission. The mating sequence was relatively long, and duration of the copulatory linkage was one of the longest among the six species we examined (Table 2).

For *E. variolarius*, all of the antenodal palpation and head contact portions of the precopulatory mating sequence began, with one exception, at the head region and progressed to the rear of the abdomen. There was a great deal of variation with regard to where male palpation and head contact occurred on the female’s head, thorax and abdomen with no clear pattern. Two of the males exhibited head butting of the female similar to that seen in *E. politus* (i.e., only along the abdomen). Only one complete mating sequence occurred for each pair. The male turned to achieve intromission without maintaining contact with the female. Overall, mating sequences were short and the duration of the copulatory linkage was intermediate relative to the other species (Table 2).

Most male *E. servus*, performed only one mating sequence before intromission; most but not all made both antenodal palpation and head contact with all three body regions of the female. We observed more palpation of the thorax than in the other species. In three pairs, the male lifted the rear of the female’s abdomen as seen in *E. tristigmus*. The overall mating sequence for this species was quite long, including lengthy bouts of palpation. Duration of
the copulatory linkage was intermediate relative to the species examined (Table 2).

For *T. c. accerra*, there was a single mating sequence for a majority of the pairs. With one exception, males started their antennal palpation and head contact with the rear of the female's abdomen and progressed toward the head. The male's antennal and head contact with the head, thorax and abdomen of the female varied more in these pairs than in any of the *Euschistus* species examined. Some males made antennal and head contact with all three regions of the female's body, but others made antennal contact with all three regions and head contact with only one or two regions, etc. One male exhibited head butts similar to those recorded for several of the other species. All of the males except one turned to attempt intromission without remaining in contact with the female; the exceptional male slid the rear of his abdomen along the outer edge of the female's thorax and abdomen as he turned. The mating sequence was short, but the duration of the copulatory linkage was among the longest of the species we tested (Table 2).

**DISCUSSION**

Three conclusions emerge from our study: (1) Mating behavior patterns of the six sympatric stink bug species are each unique in some aspect or combination of aspects. Thus, it is possible that the behavior patterns could be part of a set of cues used for species recognition. (2) Several features of the mating patterns suggest that different general mating strategies exist in stink bugs. (3) Behavior patterns could be used to distinguish species when the total set of behavior patterns is examined, but not when any one feature of the mating sequence is used.

Our observations corroborated many of the mating behavior patterns reported by previous investigators examining pentatomid reproductive behavior. We agree with Alcock (1971) that the mating sequences in this group are diverse; however, we did note some similarities. For example, in none of the species we examined did males arrive at the copulatory position by climbing over the female nor did males ever occupy any type of male-above position. In all cases, males turned 180° to arrive at the end-to-end copulatory position.

If only the three precopulatory aspects of the mating sequence for the six species examined are considered, it is possible to distinguish all six from one another. They differ in the number of sequences, the direction along the female's body of the male's antennal palpations and head contact, and the total time from initiation of the sequence to copulatory linkage (Table 3).

<table>
<thead>
<tr>
<th>Species</th>
<th>No. Sequences</th>
<th>Direction</th>
<th>Latency to Lock</th>
<th>Duration of Lock</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Euschistus politus</em></td>
<td>1</td>
<td>head to rear</td>
<td>short</td>
<td>short</td>
</tr>
<tr>
<td><em>Euschistus tristigmus</em></td>
<td>2+</td>
<td>both</td>
<td>long</td>
<td>intermediate/long</td>
</tr>
<tr>
<td><em>Euschistus ictericus</em></td>
<td>2+</td>
<td>head to rear</td>
<td>long</td>
<td>long</td>
</tr>
<tr>
<td><em>Euschistus variolarius</em></td>
<td>1</td>
<td>head to rear</td>
<td>short</td>
<td>intermediate</td>
</tr>
<tr>
<td><em>Euschistus servus</em></td>
<td>1</td>
<td>head to rear</td>
<td>long</td>
<td>intermediate/long</td>
</tr>
<tr>
<td><em>Thyanta custator accerra</em></td>
<td>1</td>
<td>rear to head</td>
<td>short</td>
<td>long</td>
</tr>
</tbody>
</table>
son and Mohlenbrock 1976), it may be important for females to discriminate male conspecifics from heterospecific males to avoid unnecessary copulations and gamete wastage. Quantitative data plus additional qualitative differences noted in some species, e.g., head butts, or total amount of antennal palpation, suggest that such discriminations are possible for all six species. Apparently, no previous studies have dealt with as large a number of sympatric species; our data suggest that additional studies of this sort are needed.

The rapid mating sequences of *E. politus* contrast with those of the other *Euschistus* species we examined (Table 3). The short duration of the precopulatory mating sequence coupled with brief copulatory linkages suggests that, for this species, the mating strategy involves multiple copulations by both males and females. For *E. variolarius* and *T. c. accerra* the mating sequences were also of short duration, but the copulatory linkages were intermediate or long. In these latter two species, and certainly in the other three species of *Euschistus*, the long copulatory linkage might be a type of mate guarding.

The data we collected exhibit enough variation in behavior among the five *Euschistus* species, and between them and *T. c. accerra*, to warrant investigation of additional taxa with the ultimate goal of a cladistic analysis. Further understanding of the evolutionary relationships within the Pentatomidae, and between this family and other groups of bugs, could be gained by such an approach.

Lastly, we must note that mating sequences in stink bugs, which we studied primarily from the perspective of the males' actions, involve response by the females as well. In many stink bug species, a receptive female will lift her abdomen at the appropriate point in the mating sequence, which is necessary before the male turns around and attempts aedeagal insertion (e.g., Alcock 1971, Fish and Alcock 1973, Vangeison and McPherson 1975, Youther and McPherson 1975). We observed similar behavior in females of several of the species we tested. An unreceptive female will not lift her abdomen (e.g., Cuda and McPherson 1976, Youther and McPherson 1975) and may actually kick the male (Youther and McPherson 1975). When the sexes interact behaviorally, some reciprocal stimulation could lead to acceptance (or rejection) of the male by the female and a successful copulation (or no copulation). Though likely part of mate location or mate choice, the calling recorded for *N. viridula* (Harris et al. 1982) could also involve reciprocal stimulation between the sexes. These sorts of phenomena have been reported for a variety of insects (Thornhill and Alcock 1983), although the proximate details of physiological changes for each member of the mating pair have not been studied in detail.

ACKNOWLEDGMENTS

We thank Heather Rice and Stephen Taylor for assistance with maintaining the stink bugs and Heather Rice for helping analyze the videotapes. This research was supported in part by funds from the College of Science at Southern Illinois University at Carbondale. We are grateful to the U. S. Forest Service (Harrisburg, IL) for permission to obtain stink bugs from the La Rue—Pine Hills Ecological Area. We also thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.
LITERATURE CITED


CARNIVORY IN ADULT FEMALE EUMENID WASPS (HYMENOPTERA: VESPIDAE: EUMENINAE) AND ITS EFFECT ON EGG PRODUCTION

Charles F. Chilcutt1,2, and David P. Cowan1

ABSTRACT

Seventy captive adult female wasps of the eumenid genera Ancistrocerus and Euodynerus were observed to feed on multiple prey items. It was shown experimentally that E. foraminatus females that fed on prey had significantly larger egg volumes than adult wasps deprived of prey.

Most wasp larvae feed on arthropod prey provided for them by their parents (Spradbery 1973), but the basic food of adult wasps is presumed to be carbohydrates obtained from the nectar of flowers or honeydew of homopterous insects (Evans 1966a, 1966b; Spradbery 1973; Iwata 1976). Frequent observations of adult predatory wasps eating sugary solutions has led to the assumption by many researchers, that wasps acquire enough protein as larvae so that as adults they do not need high protein food (Hunt 1991). Nectar contains but a limited amount of protein (Hunt et al. 1982) and the amount of pollen consumed by predatory vespids is too low to be important for nourishment (Hunt et al. 1991).

Feeding by adult wasps on prey has been observed many times and Evans (1966b) divided these behaviors into 3 categories: (1) imbibing blood from the sting puncture; (2) malaxating prey, defined here as chewing prey then feeding on blood from the wound before provisioning it for the young; and (3) malaxating prey specifically for adults and not using it as provisions, referred to as hypermalaxation. Our observations are similar to hypermalaxation, but we observed entire prey being consumed including flesh, along with instances of hypermalaxation.

Many families of parasitoid wasps are known to feed from puncture wounds (Askew 1971). Those families of wasps known to malaxate their prey include the parasitoid Bethylidae (Finlayson 1950) and the predators, Pompilidae (Evans and West-Eberhard 1970), Sphecidae (Leclercq 1959), and the solitary Vespidae (Eumeninae) (Malyshev 1968). Hypermalaxation has been described in the bethylids (Finlayson 1950), tiphids (Burdick and Wasbauer 1959), pompilids (Evans and Yoshimoto 1962), sphecids (Lin 1978), and eumenids (Rau 1945).

Three main hypotheses have been proposed to explain why adult wasps feed on prey: (1) a source of fluids (Lin 1978) especially during flower (nectar) scarcity (Evans and West-Eberhard 1970); (2) to quiet struggling prey (i.e. Spradbery 1973); and (3) it has no function, but is a displacement activity.
exhibited by confused wasps unable to nest (Huber 1961). A fourth possibility, that female predatory wasps require proteinacious prey for egg development (Spradbery 1973) has not been tested. Evans (1966a) stated that many sphecid wasps feed on prey only under special conditions, but there is little evidence that it occurs regularly. Hunt (1991) reiterated this generally accepted opinion by stating that reports of prey-feeding by adult wasps is "fragmented and largely anecdotal", and continues "that nectar, nectar-like liquids, and body fluids of prey or carrion are the typical, and nearly exclusive, sources of adult nourishment". Several workers have argued that adult wasps are not morphologically adapted to eating solid food. Imms (1957) suggested that the mandibles of adult wasps were adapted for nest building rather than for a trophic function, Spradbery (1973) believed that adult wasps are restricted to a liquid diet by the narrowing of the esophagus in the cervical region, and Hunt (1991) emphasized the distensible crop and restrictive proventriculus. Because the prey of solitary wasps is usually widely scattered, frequent observations of predatory events in nature are unlikely and we believe that carnivory in predatory wasps has been overlooked as a source of protein for ovarian development. In this study we report on adult female carnivory in captive eumenid wasps and its relationship with egg development.

MATERIALS AND METHODS

A total of 71 adult female wasps of the eumenid genera Ancistrocerus and Euodynerus were observed nesting in captivity from 1989 to 1991. While nesting, all of these adult females were observed feeding on multiple prey items. To study the effects of adult female carnivory on ovarian development, 20 females of Euodynerus foraminatus (Saussure) were maintained in one gallon jars (two wasps per jar). Each was provided with water and a honey solution (to replace the nectar they would normally obtain at flowers). All females were mated to control for possible effects on egg maturation found in other insect species (De Wilde 1964).

One group of 10 females was given spruce budworm (Choristoneura fumiferana Clemens) caterpillars and observed the first day to ensure that each consumed the prey. Following this, they were provided with an abundance of prey (more than they could eat). A second group of 10 females was not given caterpillars. Starting 3 days after the first caterpillars were provided, one wasp from each group was dissected daily for 10 days. The length and diameter of the 2 largest eggs (one terminal oocyte from each of the paired ovaries) were measured using a dissecting microscope and ocular micrometer. Oocyte volume was approximated by multiplying the length by the square of the diameter \( V = Ld^2 \). Significance for all statistical tests was set at \( p < 0.05 \). During dissection, the crop and ventriculus of each wasp was also dissected and examined for content. The head widths (an indicator of size in wasps) of the 20 \( E. foraminatus \) were measured using a dissecting microscope and ocular micrometer.

RESULTS

The average total egg volume (the 2 largest eggs) for the group given prey (0.809 \( \text{mm}^3 \)) was significantly greater than for the group denied prey (0.330 \( \text{mm}^3 \)) \( (t = 3.75, p < 0.001) \). The average largest egg volume for the experimental group (0.520 \( \text{mm}^3 \)) was significantly greater than for the control (0.255 \( \text{mm}^3 \)) \( (t = 3.32, p < 0.005) \). The average smallest egg volume for the experimental
group (0.289 mm$^3$) was significantly greater than for the control (0.075 mm$^3$) ($t=3.45$, $p<0.005$). The average head width of the group fed on prey (3.28mm) and the group denied prey (3.25mm) were not significantly different ($t=0.268$, $p>0.1$). This was important, because Larsson (1990) and O’Neill (1985) found strong correlations between head size and egg size in sphecid wasps.

All wasps fed on the sugar solutions provided, but none showed any interest in the cups containing pollen. The crops of dissected wasps were found to be distended with sugar solution. When we dissected wasp ventriculi, we found no fragments of prey, although the ventriculi did take on the darker color of prey tissues after wasp feeding.

We estimate that individual wasps ate from 6 to 18 caterpillars after being given access to prey. Due to difficulties of observation, it seems likely that the high end of the range is closest to the actual number of prey eaten. There was a distinct period before nesting began, when the wasps each ate approximately 4 caterpillars. After nesting and provisioning began, however, all females were observed eating prey at various times which we could not correlate with any phase of the nesting cycle. When wasps were deprived of prey (twice, each time for one week) nest cavities were partitioned and closed with mud, but no eggs were found. Because eumenids oviposit before provisioning, cells with only eggs might be expected if the presence of prey were not needed to stimulate ovarian development (through feeding).

Prey captured and fed upon by adult females were not always stung first. Individuals of *E. foraminatus* were more likely to chew through the prey’s cervical area to kill it, and then devour the rest of the prey without a struggle. Feeding always began on the last abdominal segment and lasted from 2 to 15 min. Larger caterpillars were often only partly eaten and discarded, while smaller prey were devoured leaving only the head capsule. While eating prey, a wasp holds the caterpillar by the abdomen with her forelegs and curls her abdomen under the prey in a position similar to stinging. This position made it difficult to discern whether wasps were just holding prey or stinging it. Smaller prey were less likely to be stung because of difficulties involved in locating the normal sting region and the ease of subduing a small victim by biting it.

**DISCUSSION**

Our observations of prey-feeding by adult eumenids contradict the view that adult wasps feed to acquire fluids on dry days (Lin 1978). Our wasps were always provided with an ample supply of water, yet still fed on prey. The idea that adult feeding behavior is a response to flower nectar scarcity (Evans and West-Eberhard 1970) is contradicted by our observations of distended crops (filled with sugar solution) found in females dissected during the period we observed prey-feeding. This indicates that the absence of nectar is not what stimulates prey-feeding. Nor was there any indication that eating prey was a displacement activity exhibited by wasps in response to novel or confusing situations. Rather, it is a normal necessary activity associated with egg development. Our results are in line with numerous studies of parasitoid Hymenoptera that require maturation feeding on hosts (prey) for full egg development (DeWilde 1964). Flanders (1942) explained that in many species of Hymenoptera larval nutrition is insufficient for egg development to proceed in the adult without further feeding, adding that these adult females habitually feed on the body fluids of their hosts prior to oviposition. Our measurements of eggs for wasps which did not feed on prey (some eggs almost as large as those of prey-fed wasps) indicate that vitellogenesis begins in eumenid females in the
absence of prey or protein sources other than those acquired as larvae. Prey-feeding is essential to maturation of more than one egg (wasps not fed prey as adults had only one developing egg) and possibly even for maturation of the first egg. This condition is similar to that described by Flanders (1935) for the Pteromalidae and found in several dipteran species (Clements 1963).

Until now research on the effects of prey-feeding on ovarian development had not been carried out for solitary predatory wasps. The many reports of prey-feeding (on the body fluids) by adult female Sphecidae (Evans 1966a), eumenids (Iwata 1953), and pompillids (Rau 1945) have not been correlated with ovarian development. It is likely that these many anecdotal reports of predatory solitary wasps feeding on prey are involved with egg maturation. It also seems likely that more intensive studies of predatory behavior will reveal prey feeding to be a regular part of female activities and not something brought on by adverse conditions (i.e. lack of water).

Total mastication of prey as we observed for eumenids has been observed for social species. Rau (1945) described workers of Polistes spp. thoroughly pulping caterpillar prey in their jaws so that it could be swallowed. Chapman (1963) found Vespula pennsylvanica (Saussure) feeding on swarming reproductive ants. Wasps were observed “dozens of times” capturing ants and landing to chew their prey, while no prey was seen to be carried back to the nest. Examinations of the ventriculi of 20 wasps failed to reveal any ant fragments, implying that only body fluids were ingested. Unlike the soft, thinly sclerotized lepidopterans fed on by eumenids, the heavily sclerotized ant cuticle would be difficult to digest. This, along with the need for adult wasps (with a narrowed esophagus) to finely chew their food, probably is related to why no fragments were found. Chapman (1963) described the wasps biting off the heads of their ant prey and “preferring” to feed on the abdomen rather than the thorax, behaviors we described earlier for E. foraminatus. This behavior has also been described by Ross (1983) for Vespula spp. which assume the same posture we described for solitary vespids feeding on prey, enclosing “the struggling prey with the ventral surface of the gaster, the legs, and the mouthparts”. Gillaspy (1979) gave descriptions of Polistes spp. returning to the nest with no apparent load with dissected crops containing a “thin gruel of protein food with recognizable insect parts”.

Among vespids, the transition from solitary to social life has also involved the transition from feeding larvae intact prey items to feeding young completely masticated prey meat. Our results indicate that the complete chewing of prey was likely well established among the solitary ancestors (as a preadaptation) of the living social species.

LITERATURE CITED


IXODES DENTATUS (ACARI: IXODIDAE) IN MICHIGAN: FIRST STATE RECORDS AND OCCURRENCE ON A HUMAN

Edward D. Walker¹, Melvin L. Poplar², and Howard L. Russell³

ABSTRACT

An *Ixodes dentatus* adult female was taken from a cottontail rabbit in Kalamazoo County, and a nymph from a child in Berrien County, in 1992 in Michigan. These findings represent the first records of *I. dentatus* in the state, and document an unusual parasitization of a human being by this species of tick.

*Ixodes dentatus* Marx is distributed in the eastern U.S., mainly occurring in coastal states, but it has been reported from several inland states as well, including Indiana and Ohio (Cooley and Kohls 1945, Clifford et al. 1961, Keirans and Clifford 1978, Kollars 1992). There are no previous records of this tick from Michigan. *Ixodes dentatus* normally parasitizes cottontail rabbits (*Sylvilagus floridanus*). It has also been found on several species of passerine birds, woodchucks, a white-footed mouse, and Norway rats (op. cit.). In this note, we report the presence of *I. dentatus* in Michigan, and document parasitism of a human being.

On May 15, 1992, in Kalamazoo County, a pet dog flushed a young cottontail rabbit from a hole. The dog’s owner, a county health department sanitarian, noticed a tick on the rabbit and submitted it to the Michigan Department of Public Health (MDPH) for identification. We identified the tick as an adult, female *I. dentatus*. On June 15, 1992, parents in Berrien County, Michigan noticed a tick embedded in their child’s head, between the ear and hairline. They submitted the tick to the state health department, via their county health department, for identification. We identified the tick as an *I. dentatus* nymph. The tick was not bloodfed.

*Ixodes dentatus* has not previously been identified from among 4,462 tick identification records compiled by the MDPH since 1968. These records include tick submissions from the public for identification by the MDPH; the Parasitology Laboratory, Michigan State University Veterinary Clinic; and the insect diagnostic service at the Department of Entomology, Michigan State University. Thus, our observations may represent new state distribution records for *I. dentatus*. Indeed, these two records in the southwestern part of the state may indicate that *I. dentatus* has recently become established in Michigan. Alternatively, *I. dentatus* may be endemic in the state, but has not previously been documented simply owing to a lack of surveys.

Experimentally, *I. dentatus* is a competent vector of *Borrelia burgdorferi*,

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the spirochete that causes Lyme disease (Telford and Spielman 1989a). This spirochete has been isolated from I. dentatus in Connecticut, Massachusetts, and Virginia (Anderson et al. 1989, Telford and Spielman 1989b, Levine et al. 1991), suggesting that B. burgdorferi may be maintained in a zoonotic cycle involving I. dentatus and rabbits, separate from the well-documented cycle involving Peromyscus mice and Ixodes dammini Spielman, Clifford, Piesman, and Corwin (Lane et al. 1991). Although we do not suspect that I. dentatus currently is an enzootic vector of the Lyme disease spirochete in Michigan, its presence along with I. dammini and B. burgdorferi in the state (Strand et al. 1992; E.D. Walker and M.L. Poplar, unpublished data) intimates that it may have some future role. Whether I. dentatus could transmit B. burgdorferi to humans depends upon whether this tick ever bites people. The frequency of this event is apparently very low (Anderson et al. 1989; R.A. Restifo, Vector-Borne Disease Unit, Ohio Department of Health, personal communication). Our observation of I. dentatus parasitizing a human documents this rare event in Michigan.

ACKNOWLEDGMENTS

We are grateful to J.E. Keirans, curator of the National Tick Collection, Georgia Southern University, for confirming the I. dentatus identifications. The nymph was deposited with that collection, specimen number RML 120803.

LITERATURE CITED


The two new records of Odonata reported here for Wisconsin are northwestern range extensions for each species.

The genus *Gomphaeschna* Selys contains two species, *antilope* (Hagen) and *furcillata* (Say), the distributions of which are limited to eastern North America. *Gomphaeschna antilope* ranges from New Jersey west to Ohio and south to Louisiana and Florida (Needham and Westfall 1955). *Gomphaeschna furcillata* is similarly distributed in the south, but ranges further north, to Nova Scotia and Maine eastward, and to Michigan westward.

I collected two males of *G. furcillata* in Sawyer County, northern WI, 10 June 1992. They were flying over a ditch along a gravel road in an alder swamp, close to Hwy. 70, just east of Draper (2 mi. W of Thornapple River bridge on Hwy. 70). To my knowledge, this species has not been reported to occur in WI. Several other males were seen near the ditch and also along Hwy. 70 E of the Thornapple River. I also netted a male of *Somatochlora franklini* (Selys) over the gravel road, a northern species rarely recorded in the state. This locality is approximately 650 km (over 400 mi.) NW of the nearest MI record for *G. furcillata*—the Detroit River, Wayne County, based on a single female (Gloyd 1940). Kormondy (1958) suggested that this species might not have an established population in MI, and indeed no other specimens have been recorded there. I think that the WI population, however, might be resident, because it is unlikely that this many individuals would stray to one remote location.

Dunkle (1977) found nymphs of both *Gomphaeschna* species in a dense cypress swamp in Florida, clinging to the underside of small, barkless logs. He also reported that D. L. Nye collected a nymph of *G. furcillata* in a “cedar” swamp in Delaware, and found exuviae 0.6 m above the water on herbaceous plants, 18 April 1972. In Hardin County, Tennessee, I collected 16 exuviae of *G. furcillata* 0.6–4.6 m above the water on trunks of tupelo gum and cypress, with no understory, 1 April 1986. The habitat at the WI locality appears to be dense alder swamp, perhaps near or in hardwood canopy, although I did not search for nymphs. Observations of *G. furcillata* to date indicate that densely wooded, shallow swamp is the primary habitat requirement, the type of vegetation being of less or little importance.

The second new record for WI is *Anax longipes* Hagen, which I observed flying over a pond along Hwy. 152, 3 mi. east of Wautoma, Waushara County. A male was seen on 27 June 1978, and a male seen again on 4 July 1978. Although I was unable to collect a specimen, this species is unmistakable because of its unique character combination of large size, green thorax and red abdomen. This record extends the range northward, as it has been reported for IN and IL, but not MI or MN (Needham and Westfall 1955). Hilsenhoff (1981)

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1 1949 Hickory Ave., Florence, AL 35630.
intended to include *A. longipes* as a species which might occur in WI, but it was mistakenly listed as occurring in the state.

**LITERATURE CITED**


OCCURRENCE OF *ULULODES QUADRIMACULATA* (NEUROPTERA: ASCALAPHIDAE) IN MICHIGAN

Douglas R. Spencer

ABSTRACT

The first published record of the owlfly, *Ululodes quadrimaculata* from Michigan is reported. Other verified distribution records from Michigan are listed along with published accounts of the species in the Great Lakes region.

The owlflies (Ascalaphidae) represent an interesting and rarely collected insect group in the northern United States. They are characterized as having long, knobbed antennae as in the Rhopalocera Lepidoptera, and with a body and wing structure resembling certain Odonata.

On 18 July 1987, I collected a single male specimen of *Ululodes quadrimaculata* (Say) at UV light at 240 Bull Run Road, south of Fowlerville, Livingston County, Michigan. This area is located near the middle branch of the Red Cedar River which has extensive wetlands adjacent to wooded upland and field biomes. Subsequent collecting at this locality has not produced additional specimens.

I examined the entomological collections at the University of Michigan (UM) and Michigan State University (MSU) for additional specimens of *U. quadrimaculata*. Only two specimens were found: MICHIGAN: Kalamazoo Co., Gull Lake Biological Station, 11 July 1961, Coll: Roland L. Fischer. (MSU); Washtenaw Co., University of Michigan Botanical Gardens, 1 August 1967, Coll: Tim Newcomb. (UMMZ)

Shetlar (1977) listed several additional counties in Michigan where *U. quadrimaculata* had been collected: Barry, Berrien, Ottawa, and Wexford. Specimens from these areas could not be verified, and are presumed lost.

Other published reports of this species from the Great Lakes region include Indiana (Lawson and McCafferty 1984) and Ontario (Garland and Marshall 1980). This report is the first published record of Ascalaphidae from Michigan. The specimen of *U. quadrimaculata* from Livingston County is deposited in my collection.

ACKNOWLEDGMENTS

I appreciate the support of Mark O'Brien, the University of Michigan, Museum of Zoology, in permitting examination of the Ascalaphidae in the UMMZ, obtaining Dr. Shetlar's dissertation, and pursuing additional information. I also acknowledge Dr. Fred Stehr, Michigan State University, for permitting me to check their collections for Michigan specimens. Dr. Norman

1 240 Bull Run Road, Fowlerville, MI 48836.
Penny, California Academy of Science, San Francisco, California, sent me his publications on the Ascalaphidae and reviewed an earlier version of this manuscript. I am also grateful for his encouragement and consultation on this fascinating group of insects.

LITERATURE CITED


BOOK REVIEW

THE OWLET MOTHS OF OHIO, ORDER LEPIDOPTERA FAMILY NOCTUIDAE, by Roy W. Rings, Eric Metzler, Fred J. Arnold, and David H. Harris. 1992. Published by College of Biological Sciences, The Ohio State University, in Cooperation with Ohio Department of Natural Resources, Division of Wildlife and the Ohio Lepidopterists, Columbus, Ohio 43210. VI + 219 pp., 9 text figures, 8 color plates, 8 black and white plates. Soft cover, 8.5 x 11 in. (21.6 x 27.9 cm), ISSN 0078-3994, $20.00 U.S.

The authors are to be commended for producing an extremely useful and thoroughly complete compilation of this fascinating but frequently ignored group of Lepidoptera. It is, without a doubt, the finest state systematic checklist that this reviewer has previously read and one that will probably not be exceeded in the near future. This monograph, a systematic checklist of the owlet moths (Noctuidae) of Ohio, is the second monograph to present the lepidopterological results of a cooperative effort among the Ohio Biological Survey, the Ohio Lepidopterists, and the Ohio Department of Natural History. It follows a very comprehensive survey of the state's butterfly fauna, "Butterflies and Skippers of Ohio", by David C. Iftner, John A. Shuey, and John V. Calhoun.

The first 22 pages are devoted to an introduction, nomenclature and systematics, collection and preparation of specimens, identification, development biology, conservation, and a systematic checklist of the owlet moths of Ohio. The annotated checklist, which makes up the bulk of the text, covers 708 species of Ohio's noctuids in a systematic checklist that provides nomenclature current through 1991. The annotated checklist cites references to illustrations of the species, status as to relative abundance (i.e. endangered, threatened, special concern, etc.), lists the species' known larval host plants, presents historical information as to earliest and latest year of record, depicts distributional ('dot') maps for each species, and uses horizontal graphs to indicate the seasonal flight pattern. In presenting each species' account, the format is easy to use because the family, genus and species names are printed in bold type; Hodges and McDunnough checklist numbers and plate numbers (if illustrated) are also in bold print. Remarks are presented with many species which provide identification tips (a useful addition) and other useful and interesting information.

Following the annotated checklist are sections on owlet moths that qualify for special attention in Ohio, descriptions of special habitats, moths considered as migrants and a hypothetical checklist of moths in Ohio, species excluded from the checklist (due to previous erroneous data and/or identification), host plants and list of host plant names and substrates with reference to Hodges' checklist numbers, and a glossary of terms.

The appendices includes regional lepidopterists' societies, Ohio county abbreviation code, literature cited, useful publications in the study of Noctuidae and an index to owlet moths via Hodges' checklist numbers. The 8
black and white plates include 3 plates that show a selected number of eggs of Amphipyrrinae, Cuculliiinae, Hadentinae and Noctuinae. The remaining black and white plates depict mature larvae of 30 species of Catocalinae, Acronictinae, Amphipyrrinae, Cuculliiinae, Hadentinae and Noctuinae. The eight colored plates illustrate 238 species of owlet moths, including species that have never been illustrated in color, i.e. Herminiinae, Hypeninae, Sarrothripinae, Rivulinae, Hypenodinae and Nolinae. Also illustrated are species that are very similar in appearance and are shown next to each other to allow easy comparison. These plates illustrate 324 specimens.

The illustrated specimens are shown at life size and represent immaculate and properly prepared specimens; however, not all of the illustrated specimens were collected in Ohio. It is assumed the authors wished to depict the most accurate and easily identified specimens to further assist users, and to encourage more study of Ohio's noctuid fauna. The colors are accurate and should be of tremendous help to all users of this checklist.

The authors encourage the conservation of all species, particularly those classified as endangered and threatened, under the section "Conservation of Owlet Moths" (p. 10). They give the impression of comparing noctuids to butterflies with the comment "the collector should examine netted specimens and immediately release those of inferior quality, ones with tattered wings and/or missing appendages or runts." Those of us who regularly collect noctuids using UV lights with vertical sheets and UV or bait traps cannot readily make this distinction of specimen quality until the specimen is immobilized in a killing jar. Even females cannot always be easily determined at a lighted sheet, or in a bait trap, until a closer examination is made using forceps or a binocular microscope. One could easily read into this section that all trapping of noctuids (one of the best methods of sampling moths) should be discouraged.

As stated before, this annotated checklist is the most comprehensive and the best organized treatment of a state's noctuid fauna seen to date. Avocational lepidopterists, biologists, zoogeographers, conservationists and ecologists, whether Ohio residents or not, will find this publication a valuable addition to their library. The $20.00 price is certainly reasonable. It is very encouraging to see a reasonably priced, high-quality treatment of U.S. Lepidoptera as compared to the proliferation of very expensive and little used books featuring exotic Lepidoptera. Lastly, this new book should stimulate lepidopterists to add more species and distributional data to Ohio's noctuid fauna.

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Papers dealing with any aspect of entomology will be considered for publication in The Great Lakes Entomologist. Appropriate subjects are those of interest to professional and amateur entomologists in the North Central States and Canada, as well as general papers and revisions directed to a larger audience while retaining an interest to readers in our geographic area.

All manuscripts are refereed by two reviewers, except for short notes, which are reviewed at the discretion of the Editor. Manuscripts must be typed, double-spaced, with 1" margins on 8 1/2 x 11" or equivalent size paper, and submitted in triplicate. Please underline only those words that are to be italicized. Use subheadings sparingly. Footnotes (except for author’s addresses, which must be on the title page, and treated as a footnote), legends, and captions of illustrations should be typed on separate sheets of paper. Titles should be concise, identifying the order and family discussed. The author of each species must be given fully at least once in the text, but not in the title or abstract. If a common name is used for a species or group, it should be in accordance with the common names published by the Entomological Society of America. The format for references must follow that used in previous issues of The Great Lakes Entomologist. Literature cited is just that—no unpublished manuscripts or internal memos. Photographs should be glossy finish, and mounted on stiff white cardboard (transparencies are not acceptable). Drawings, charts, graphs, and maps must be scaled to permit proper reduction without loss of detail. Please reduce illustrations or plates to a size no greater than 9 x 12” to permit easier handling. Attach a figure number to the reverse side of each figure and include the authors’ names. Unsuitably mounted photographs or poor figures will be returned to authors for revision.

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All manuscripts for The Great Lakes Entomologist should be sent to the Editor, Mark F. O’Brien, Insect Division, Museum of Zoology, The University of Michigan, Ann Arbor, MI, 48109-1079, USA. Other correspondence should be directed to the Executive Secretary (see inside front cover).