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## COVER PHOTOGRAPH

*Hemaris* sp. (Lepidoptera: Sphingidae) at Phlox flowers.  
Photograph by Eugene Kenaga.

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## EXTRACTING ADDITIONAL INFORMATION FROM BIOTIC INDEX SAMPLES

Richard A. Lillie<sup>1</sup> and Roger A. Schlesser<sup>2</sup>

### ABSTRACT

Macroinvertebrates were collected from a small midwestern stream over a 3-year period as part of a non-point source pollution study. Temporal and spatial variability in standard biotic index values (BIs) were computed and compared with variability expressed by a series of additional community measurements, including the mean tolerance value of all taxa present in a sample, irrespective of the numerical abundance of individual taxa. The mean tolerance value exhibited lower spatial and temporal variability than the standard BI; therefore, mean tolerance values may be useful in estimating a stream's long-term ambient water quality and its recovery potential. Computations of additional BI metrics are easily accomplished with no additional lab work required, and comparisons of mean tolerance values with standard BIs should aid investigators in interpreting changes in water quality.

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Macroinvertebrates are an important component of the rapid bioassessment protocols for water quality assessment presented by the U.S. Environmental Protection Agency (Plafkin et al. 1989). The recommended protocols include several indices that are based on species richness, diversity, or community composition of benthic macroinvertebrates. The Hilsenhoff Biotic Index (HBI)(Hilsenhoff 1977, 1982, 1987), a modification of Chutter's (1972) biotic index, has proven particularly popular and reliable in detecting impacts of organic pollution on water quality. Essentially, the HBI represents the average pollution tolerance of a randomly-selected subset of more than 100 macroinvertebrate organisms (arthropods) collected from riffles or runs in a particular river or stream. The HBI, or modification thereof, is a principal method of rapid bioassessment protocols II and III of the U.S. EPA (Plafkin et al. 1989). Rapid bioassessment protocol III requires macroinvertebrates be identified to either genus or species level (where possible). The degree of environmental degradation at a site is based on relative comparison with complementary data from a nearby reference site (Plafkin et al. 1989). If reference data are lacking, replication provides an estimate of variability in HBI values, thereby permitting statistical comparisons among other stations or dates. Because this level of analysis is labor intensive, it is desirable to extract as much information as possible from the resultant data. In this paper, we present a method to extract supplemental information from HBI samples without requiring that additional labwork be performed. A new index, repre-

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senting the mean pollution tolerance value of all taxa present in an HBI sample, irrespective of the number of individuals represented by each taxon, offers promise as a complement to the HBI. The mean tolerance value is compared with the standard HBI using data collected over a 3-yr period from a small southwestern Wisconsin stream.

## METHODS

Rattlesnake Creek is a medium-sized, warmwater stream located in southwestern Wisconsin with a recent history of fishkills (Mason et al. 1991). Periodic episodes of depressed dissolved oxygen concentrations during summer rainstorms have been documented in Rattlesnake Creek (Graczyk and Sonzogni 1991), and these storm-related events are believed to have had an adverse impact on stream biota (Graczyk 1993a). This paper is based on benthic surveys conducted over a 3 yr period during an intensive non-point source pollution survey of Rattlesnake Creek (Graczyk 1993a). The hydrologic regime during the period that macroinvertebrate surveys were conducted was relatively stable, coinciding with a period of extreme drought. No major run-off events or extended periods of depressed dissolved oxygen concentrations were observed.

Benthic samples were collected by two independent teams of investigators using different sampling strategies. One team collected three replicates from a riffle adjacent to a United States Geological Survey (USGS) gaging station on six dates—fall 1987, spring 1988, fall 1988, spring 1989, fall 1989, and spring 1990. These samples were intended to correspond with water quality data collected by automated monitoring equipment at the gaging station. Another team collected benthic samples from six riffle sites on three dates—fall 1987, spring 1988, and fall 1989. The latter set of samples, spaced at irregular intervals, was intended to monitor water quality in stream reaches of Rattlesnake Creek concurrent with fisheries investigations. Both teams collected field samples in accordance with standard kick-net procedures (Hilsenhoff 1987). Macroinvertebrate samples were preserved in 95% ethanol and returned to the laboratory for processing. Samples collected by the first team were processed at the University of Wisconsin-Stevens Point, and samples collected by the second team were processed by the WDNR. Both sets of samples were processed following procedures established by Hilsenhoff (1987); chironomids were identified to genus only. Standard biotic index values were computed for all data sets based on the number and corresponding tolerance value of all individuals present in a random subsample of at least 100 individuals (Hilsenhoff 1987). These values are commonly referred to as Hilsenhoff Biotic Index values (HBIs). Additionally, the mean tolerance value of each HBI data set was computed as follows:

$$\text{Mean Tolerance Value} = \text{SUM } t_i / T$$

where  $t_i$  represents the assigned pollution tolerance value for each taxon, and  $T$  represents the number of taxa in the sample.

The mean tolerance value gives equal weight to each taxon in a sample irrespective of its numerical abundance in the sample and, therefore, rare taxa are more important in calculating the mean tolerance value than in calculating the HBI, which is dependent upon the numerically dominant taxa. In streams of poor water quality, the mean tolerance value places increased emphasis on the intolerant forms, which generally are less abundant than tolerant forms in organically enriched streams. The patterns exhibited by HBI and mean toler-

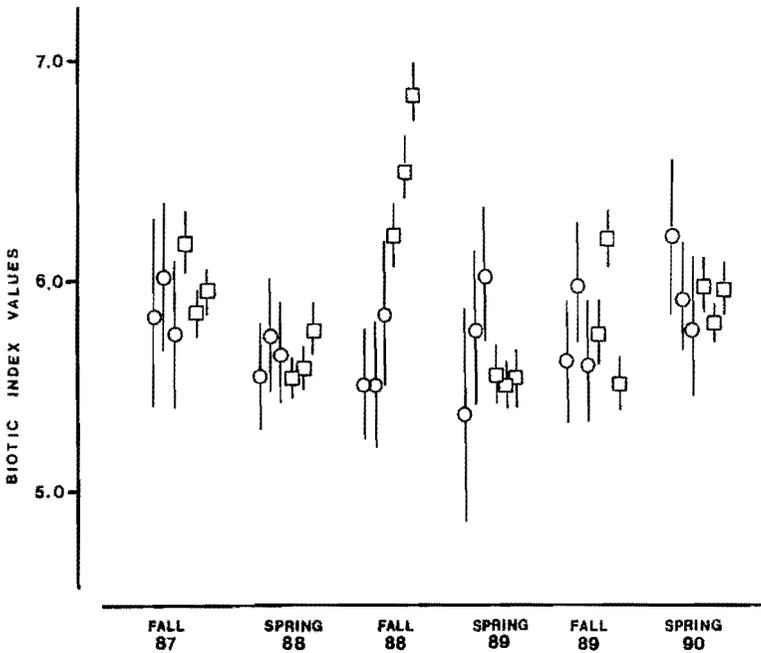


Figure 1. Temporal variations in biotic index values (squares represent HBIs, circles represent mean tolerance values) at the USGS gaging station (3 replicates each date). Vertical lines represent  $\pm 1$  SE based on distribution of pollution tolerance values of individual taxa or all organisms in each sample.

ance value data were examined visually to identify outliers and irregularities in distribution.

## RESULTS AND DISCUSSION

The period of macroinvertebrate sampling on Rattlesnake Creek, October 1987 to May 1989, coincided with a severe drought in the upper Midwest. Both hydrologic and sediment loadings were much reduced. Dissolved oxygen concentrations never dropped below 1 mg/L in Rattlesnake Creek during this period (Graczyk 1993b). Other biological measurements, including total taxa richness, Ephemeroptera-Plecoptera-Trichoptera taxa richness, and abundances indicated either stable or steadily improving water quality (Lillie and Schlessler 1993). Biotic index values also were quite stable, except for high HBIs displayed in the fall 1988 samples (Fig. 1). This abrupt increase in HBIs, which suggested that a decline in water quality had occurred, was not accompanied by a corresponding increase in mean tolerance values. HBIs were substantially higher than corresponding mean tolerance values by an average 0.90 units. All samples were collected within the recommended time window for sampling warmwater streams (Hilsenhoff 1988), so no seasonal adjust-

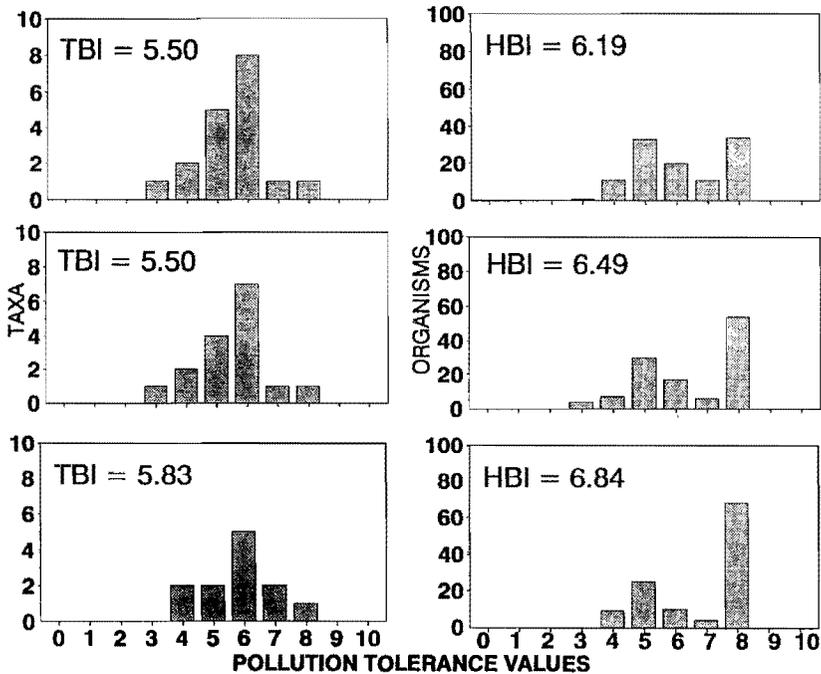


Figure 2. Histograms illustrating the distribution of pollution tolerance values among taxa (mean tolerance values or TBIs, left-hand set) and individuals (HBIs, right-hand set) comprising fall 1988 biotic index samples.

ments of the data were warranted. Closer examination of the data revealed large numbers of the isopod *Caecidotea intermedia* (Forbes) (= *Asellus intermedius* per Jass and Klausmeier 1990) were dominant on this date in all 3 replicates (Fig. 2). *Caecidotea intermedia*, with a tolerance value of 8, had a major influence on the HBI. However, *C. intermedia* was the only taxon in the samples with a tolerance value of 8; the mean tolerance values were dominated by taxa with tolerance values of 5 and 6. Consequently, mean tolerance values were substantially lower than HBIs on this date. HBIs and mean tolerance values (means of the 3 replicates) were not statistically different on the remaining 5 dates. Excluding the fall 1988 data, the average difference between matching sample HBIs and mean tolerance values was  $\pm 0.19$  units ( $N=15$ ). The average discrepancy among dates was  $\pm 0.09$  units, with a net bias of  $-0.03$  units for the 5 dates (i.e. mean tolerance values were slightly higher than HBIs by an average of 0.03 units).

The question arises, therefore, as to which measurement more closely represents true water quality conditions. Most biologists would agree that the occurrence of large numbers of isopods in a sample is indicative of generally poor water quality. However, the high degree of skewedness exhibited in the pattern of tolerance values in the HBI (Fig. 2), combined with lower HBIs in spring 1988 and 1989 samples, and stability or improvements in other water

quality measures in Rattlesnake Creek during the same time period (Lillie and Schlessler 1993), suggest that the fall 1988 HBI values were unduly influenced by the large numbers of *C. intermedia* present in the sample. Additionally, HBIs from concurrent studies of three nearby Wisconsin streams did not exhibit similar rises during the fall of 1988 (Lillie and Schlessler 1993). This seems to rule out any seasonal or climatic influence on the fall 1988 data in Rattlesnake Creek. Without knowledge of other water quality data, biologists likely would have concluded, perhaps wrongly, that water quality declined from spring to fall 1988 in Rattlesnake Creek. Conversely, perhaps the HBI is more sensitive to certain forms of organic pollution than are other measured water quality indicators, and water quality of Rattlesnake Creek did indeed experience some form of event between spring 1988 and fall 1988. Certainly, the high abundance of isopods in the fall 1988 samples should signify something. Perhaps the increase in isopod abundance reflected some change in physical habitat rather than a change in water quality (i.e. Lenat 1988). If so, the mean tolerance value was not responsive to the change. Under the circumstances, it appears that biologists should examine the patterns displayed by tolerance values in HBI samples for skewedness or other abnormalities in distribution and, if detected, consider the corresponding mean tolerance value as more representative of long-term water quality. Similarly, a bimodal distribution pattern of tolerance values may suggest a confluence of two streams of differing water quality or influences of side tributaries. We do not suggest that the mean tolerance value be used in lieu of, or as a substitute for, the HBI, but rather that the mean tolerance value should be used in conjunction with existing HBI data in the interpretation of water quality.

**Spatial Comparisons:** Another example of the possible utility of mean tolerance values is described using data to examine spatial trends in Rattlesnake Creek (Fig. 3). Trends exhibited by mean tolerance values and HBIs were generally similar to one another on each date. However, mean tolerance values were substantially lower than corresponding HBIs on two of three dates. Mean tolerance values were an average of 0.92 and 0.70 units lower than corresponding HBIs during fall 1987 and spring 1988, respectively. Differences between mean tolerance values and HBIs were relatively consistent among all six sampling sites on these two dates. We can offer no explanation for these deviations, other than to note that tolerance value patterns of HBIs were highly skewed towards individuals with high tolerance values.

Mean tolerance values were similar to HBIs during fall 1989 (average discrepancy  $\pm$  0.28 units; average or net bias, mean tolerance values were 0.10 units lower than HBIs;  $N=6$ ). The maximum discrepancy occurred at site F where the mean tolerance value was 0.78 units lower than the HBI. The occurrence of large numbers of the isopod *Caecidotea intermedia* was again the cause for the disparity. In comparison with the histograms exhibited on the other two sampling dates, the fall 1989 HBI patterns exhibited less skewedness. The greater similarity between mean tolerance values and HBIs in the fall 1989 may indicate greater instream stability associated with the prolonged drought that continued throughout the study period.

Again, there is some question as to which attribute more closely represents true water quality. The average of the six mean tolerance values in this data set (Fig. 3) compares more closely with the average of the three mean tolerance values at the gaging station (compare with data in Fig. 1), than does the average HBIs between the two data sets compare. The two data sets were collected within 4 to 13 days of one another. During a four-day period in fall 87, the HBI increased by 0.42 units and the mean tolerance value decreased by 0.41 units at site F (the site closest to the USGS gaging station). HBIs increased substantially at the same site during 12-13 day spans in spring 88 and fall 89 (+1.25 and + 1.13 units, respectively). The average daily rate of

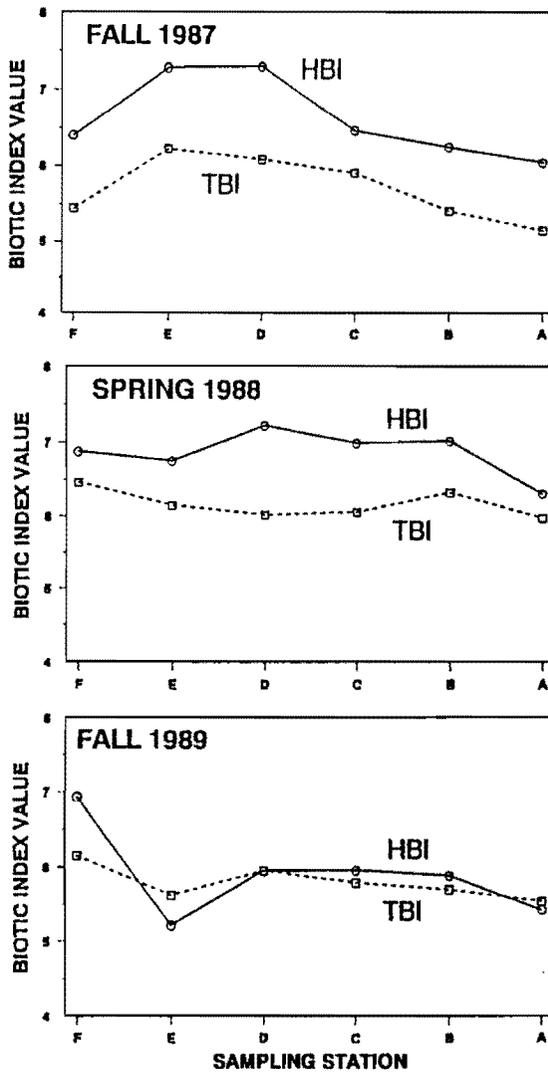


Figure 3. Comparison of spatial trends in biotic index values (HBIs) and mean tolerance values (TBIs) in Rattlesnake Creek on three sampling dates. Sampling stations are ordered from upstream (Site F) to downstream (Site A).

change in HBIs (+ 0.09–0.10 units/day) was similar on all three dates. The rate of change in mean tolerance values was smaller but inconsistent. Therefore, in our opinion, the mean tolerance values depicted in Figure 3 were more representative of true water quality conditions in fall 1987 and spring 1988 samples than HBIs. Clements (1991) suggested that because the number of taxa present at a given site may be less variable than abundance of individual taxa, numbers of taxa may have some advantages in monitoring invertebrate communities. The mean tolerance value supports this suggestion. Furthermore, it has been suggested that the disappearance of intolerant taxa may be more significant than changes in tolerant forms (Fausch et al. 1990). Tolerant taxa generally have a wider distribution ranges than intolerant forms. Although a tolerant taxa, with a tolerance value of 8 for example, may be present in abundant numbers, that same taxa may occur in waters with water quality equivalent to 5 or 6. The fact that several less tolerant taxa also are present at a site may be more indicative of the true water quality than the presence of one tolerant form with a wide range in pollution tolerance. Therefore, the mean tolerance values associated with biotic index samples may be a useful accessory metric in interpreting changes in water quality.

### CONCLUSIONS

A companion metric to the standard HBI, the mean tolerance value, exhibits less temporal variability than the HBI. The mean tolerance value should be used in conjunction with the HBI to evaluate changes in community structure resulting from organic pollution. The mean tolerance value is not presented as a substitute for the HBI but, rather, is offered as a companion metric. The mean tolerance value gives equal weight to rare and dominant taxa and, consequently, may be less susceptible to short-term changes than the HBI. Thus, the mean tolerance value may have some advantages in long-term trend detection.

Some sudden, short-term changes in HBIs were observed in this study. Large population fluctuations in certain relatively ubiquitous taxa with assigned high pollution tolerance values may have had undue influence on HBIs. We suggest that some consideration be given to modifying assigned tolerance values of *Caecidotea intermedia* similar to that provided for *Simulium vittatum* (Hilsenhoff 1987).

Examination of the histogram patterns depicted by HBI data may prove useful in pollution studies. Bimodal patterns (i.e. many tolerant and intolerant taxa present with few intermediate taxa) may indicate junctions between streams of vastly different water quality. The extent and direction of skewness in the patterns may provide clues as to the stability or biotic integrity of an invertebrate community at a particular site. The width of the distribution pattern, as measured by standard measures of variability (i.e. standard deviation, standard error, and coefficient of variation) may also provide useful information. In cases where replication of samples is lacking or not affordable, these conventional statistical measures may provide some indication of the representativeness of a particular set of biotic index data.

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PARASITISM, ADULT EMERGENCE, SEX RATIO, AND SIZE OF *APHIDIUS COLEMANI* (HYMENOPTERA: APHIDIIDAE) ON SEVERAL APHID SPECIESN. C. Elliott,<sup>1</sup> B. W. French, J. D. Burd, S. D. Kindler, and D. K. Reed

## ABSTRACT

*Aphidius colemani* Viereck parasitizes several economically important aphid pests of small grain crops including the greenbug, *Schizaphis graminum* and the Russian wheat aphid, *Diuraphis noxia*. The ability of *A. colemani* to switch from *S. graminum* to several species of aphids common to agricultural and associated non-agricultural ecosystems in the Great Plains, and the effects of host-change on several biological parameters that influence population growth rate were determined. Female *A. colemani* parasitized and developed to adulthood in nine of 14 aphid species to which they were exposed in the laboratory. All small grain feeding aphids except *Sipha flava* were parasitized. Two sunflower feeding species (*Aphis nerii* and *A. helianthi*) and two crucifer feeding species (*Lipaphis erysimi* and *Brevicoryne brassicae*) were parasitized, as was the cotton aphid, *Aphis gossypii*. The average percentage of aphids parasitized differed significantly among host aphid species, as did the percentage of parasitoids surviving from the mummy to the adult stage and the time required for immature development. The sex ratio of adults that eclosed from the various hosts did not differ significantly among species. Dry weights of adult parasitoids differed significantly among host species. Adults from *S. graminum* weighed most (0.054 mg) while those emerging from *A. helianthi* weighed least (0.020 mg). Results are discussed in terms of strategies for classical biological control of aphid pests of cereals.

*Aphidius colemani* Viereck is widely distributed in Asia, southern Europe, Africa, South America, and Australia, and broadly oligophagous on Aphididae (Stary 1975). Although its host range differs geographically (Stary 1975), *A. colemani* is known to parasitize several economically important aphid pests of cereals, including the greenbug, *Schizaphis graminum* (Ron-dani) and the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Stary 1975, Aalbersberg et al. 1988). Although *A. colemani* is an important parasitoid of several aphid pests of cereals, it appears unable to maintain pest aphid populations below the economically damaging levels (Aalbersberg 1988, Gerding et al. 1989, Prinsloo 1990).

Even though published information yields no evidence that establishment of *A. colemani* in the Great Plains of the United States would, by itself, result in effective biological control of *D. noxia*, *S. graminum*, or other aphid pests of cereals, the parasitoid could contribute to multilateral control (c.f. Stary 1972). In the multilateral control concept, the interaction among natural enemy communities in an agricultural landscape is optimized to reduce popu-

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lations of target pests in crops. For aphids like *D. noxia* and *S. graminum*, whose populations are ephemeral in space and time, generalist natural enemies that can persist in reservoirs at times when target pests are unavailable may play an important role in biological control. Alternate hosts may also play an important role during the process of establishing natural enemies in classical biological control programs by providing reservoirs for natural enemies, or by providing alternate hosts on which natural enemies could be released at times when the target pest is unavailable (Eikenbary and Rogers 1974).

Some polyphagous aphidiids show reluctance to switch to alternate hosts in the laboratory, and exhibit phenotypic differences among subpopulations associated with different hosts in the field, thus suggesting the existence of specialized host races (Powell and Li 1983, Cameron et al. 1984, Nemeček and Stary 1983). Thus, our objective was to determine the ability of *A. colemani* to switch from a particular host, *S. graminum* to several species of aphids common to agricultural and associated non-agricultural ecosystems in the Great Plains, and to determine the effects of such host-change on several biological parameters that may influence the population growth rate of the parasitoid.

## MATERIALS AND METHODS

The *A. colemani* colony used in this study was obtained by D. K. Reed and K. S. Pike from Argentina in September, 1990. The parasitoid had been maintained in laboratory culture on *S. graminum* for approximately 12 generations when the study was initiated.

Mated female *A. colemani* reared from *S. graminum* were exposed to nymphs of 14 aphid species for 24-h to determine if they would successfully parasitize the aphids when they had no previous exposure to them. A laboratory colony of each aphid species was established from aphids collected from plants in the field during 1991, or obtained from R. W. Kieckhefer, USDA, ARS, Brookings, South Dakota (*Rhopalosiphum padi* [L.], *S. graminum*, and *R. maidis* [Fitch]) or B. W. Cartwright, Oklahoma State University, Lane, Oklahoma (*B. brassicae* L.). Aphids were maintained in the laboratory on the host plant species from which they were originally obtained or on a suitable alternative species (Table 1). Seedling plants of the species used to maintain an aphid colony were also used as experimental plants.

A replicate of the experiment for each of the 14 aphid species was established by transferring 50 1st-3rd instar nymphs of that species from the laboratory colony to an aphid-free host plant growing in a 10-cm diameter plastic pot. Aphids were allowed to settle for 4 h at which time four mated female *A. colemani* were introduced into the cage. The caged plant was then placed in a growth chamber maintained at 16:8 h (L:D) and 22°C ( $\pm 0.5^\circ\text{C}$ ). After 24 hours the adult parasitoids were removed and the caged plant was returned to the growth chamber. The plant was watered every 1-2 days, and inspected each day for the presence of mummies. Mummies that formed were removed, placed in plastic petri dishes (4-cm diam. by 1.4 cm height), and returned to the growth chamber. All mummies that formed during the three days following formation of the first mummy were weighed as a group on a Mettler AE-240 balance. Mummies were checked each day to determine the number of adults that eclosed during the previous 24 hr. A plant was discarded after one month whether or not mummies formed.

Three or four replicates were established for each of the 14 aphid species. *Schizaphis graminum* was included as one of the 14 species to allow comparison of parasitization of this species, on which *A. colemani* had been reared for

Table 1. Aphid species used in studies of host-change by *Aphidius colemani* and the host plant species used for colony maintenance and in the experiment.

Aphid Species/Common Name	Laboratory Host Plant/Common name
<i>Diuraphis noxia</i> (Mordvilko) Russian wheat aphid	<i>Hordeum vulgare</i> – barley
<i>Schizaphis graminum</i> (Rondani) greenbug	<i>Hordeum vulgare</i>
<i>Rhopalosiphum padi</i> (L.) bird cherry-oat aphid	<i>Hordeum vulgare</i>
<i>Rhopalosiphum maidis</i> (Fitch) corn leaf aphid	<i>Hordeum vulgare</i>
<i>Sipha flava</i> (Forbes) yellow sugarcane aphid	<i>Hordeum vulgare</i>
<i>Aphis helianthi</i> Monell	<i>Helianthus annuus</i> – common sunflower
<i>Aphis nerii</i> Boyer de Fonscolombe Oleander aphid	<i>Helianthus annuus</i>
<i>Dactynotus helianthicola</i> Olive	<i>Helianthus annuus</i>
<i>Dactynotus</i> spp.	<i>Helianthus annuus</i>
<i>Therioaphis trifolii</i> (Monell) clover aphid	<i>Trifolium pratense</i> – red clover
<i>Acyrtosiphon pisum</i> (Harris) pea aphid	<i>Vicia faba</i> -faba bean
<i>Aphis gossypii</i> Glover cotton aphid	<i>Gossypium hirsutum</i> – cotton
<i>Brevicoryne brassicae</i> (L.) cabbage aphid	<i>Brassica oleracea</i> – cabbage
<i>Lipaphis erysimi</i> (Kaltenbach) turnip aphid	<i>Brassica napus</i> – canola

several generations, with that of species to which it had not been exposed. Six variables were measured for each replicate: the proportion of aphids parasitized during 24 hr (proportion of mummies formed); the proportion of individuals surviving from the mummy stage to adulthood; the sex ratio of eclosed adults (proportion female); the median number of days required from parasitization to adult eclosion; and average adult dry weight. Parasitoids were allowed to air dry at room temperature for three months prior to weighing. Adult dry weights were measured by pooling individuals of a particular sex from a replicate and weighing them on a Mettler UM-3 balance. Average adult dry weight was estimated by taking the weighted average (weighted by the number of individuals of each sex) of the male and female weights. Analysis of variance and the least significant difference test were used to compare means of the variables across aphid species. The arcsine transformation was applied to proportional data prior to conducting analysis of variance.

Table 2. The proportion of aphids parasitized during 24-h (proportion of mummies formed), proportion of individuals surviving from the mummy stage to adulthood, sex ratio of eclosed adults (proportion female), median number of days required from parasitization to adult eclosion, average dry weight per adult for 14 aphid species exposed to mated female *Aphidius colemani* for 24 hours as nymphs.

Aphid Species	Median Days	Proportion Parasitized	Proportion Surviving	Proportion Female	Adult Dry Weight (mg)
<i>D. noxia</i>	15.0 (0.00) <sup>a</sup>	0.71 (0.20) <sup>b</sup>	0.96 (0.037) <sup>d</sup>	0.53 (0.213) <sup>a</sup>	0.029 (0.0012) <sup>bc</sup>
<i>R. maidis</i>	15.0 (0.58) <sup>a</sup>	0.51 (0.013) <sup>ab</sup>	0.73 (0.082) <sup>bcd</sup>	0.28 (0.147) <sup>a</sup>	0.029 (0.0036) <sup>bc</sup>
<i>S. graminum</i>	13.3 (0.33) <sup>a</sup>	0.96 (0.042) <sup>c</sup>	0.95 (0.025) <sup>d</sup>	0.64 (0.157) <sup>a</sup>	0.054 (0.0017) <sup>f</sup>
<i>R. padi</i>	14.7 (0.67) <sup>a</sup>	0.81 (0.064) <sup>bc</sup>	0.86 (0.070) <sup>cd</sup>	0.80 (0.054) <sup>a</sup>	0.036 (0.0013) <sup>cde</sup>
<i>S. flava</i>	—	—	—	—	—
<i>A. pisum</i>	—	—	—	—	—
<i>T. trifolii</i>	—	—	—	—	—
<i>D. helianthicola</i>	—	—	—	—	—
<i>Dactynous</i> sp.	—	—	—	—	—
<i>A. helianthi</i>	20.0 (0.58) <sup>b</sup>	0.51 (0.079) <sup>ab</sup>	0.40 (0.046) <sup>b</sup>	0.69 (0.173) <sup>a</sup>	0.020 (0.0025) <sup>a</sup>
<i>A. nerii</i>	15.7 (1.11) <sup>a</sup>	0.17 (0.040) <sup>a</sup>	0.56 (0.179) <sup>bc</sup>	0.87 (0.125) <sup>a</sup>	0.026 (0.0039) <sup>ab</sup>
<i>L. erysimi</i>	15.0 (0.57) <sup>a</sup>	0.94 (0.063) <sup>c</sup>	0.93 (0.041) <sup>d</sup>	0.63 (0.147) <sup>a</sup>	0.037 (0.0015) <sup>de</sup>
<i>A. gossypii</i>	13.3 (0.33) <sup>a</sup>	0.64 (0.111) <sup>b</sup>	0.96 (0.023) <sup>d</sup>	0.65 (0.089) <sup>a</sup>	0.029 (0.0017) <sup>bcd</sup>
<i>B. brassicae</i>	13.0 (0.05) <sup>a</sup>	0.25 (0.059) <sup>a</sup>	0.05 (0.059) <sup>a</sup>	0.90 (0.050) <sup>a</sup>	0.045 (0.0020) <sup>ef</sup>

Means within columns followed by the same letter are not significantly different ( $P > 0.05$ )

## RESULTS AND DISCUSSION

Female *A. colemani* parasitized and developed to adulthood in nine of 14 aphid species to which they were exposed (Table 2). All small grain feeding aphids except *Sipha flava* (Forbes) were parasitized. Two sunflower feeding species (*Aphis nerii* Boyer de Fonscolombe and *A. helianthi* Monell) and two crucifer feeding species (*Lipaphis erysimi* [Kaltenbach] and *Brevicoryne brassicae* [L.]) were parasitized, as was the cotton aphid, *Aphis gossypii* Glover. Neither of the legume feeding species was successfully parasitized.

The average percentage of aphids parasitized differed significantly among host aphid species ( $F=9.08$ ;  $df=8, 19$ ;  $P=0.0001$ ) and ranged from a low of 17% for *A. nerii* to a high of 96% for *S. graminum*. The percentage of parasitoids surviving from the mummy to the adult stage differed significantly among host species ( $F=8.43$ ;  $df=8, 19$ ;  $P=0.0001$ ). Survival was highest for *D. noxia*, *S. graminum*, and *L. erysimi*, and lowest for *B. brassicae*. The sex ratio of adults that emerged from the various hosts did not differ significantly among species. Development times from oviposition to adult emergence ranged from 13.3 days for *A. colemani* parasitizing *S. graminum* and *A. gossypii*, to 20.0 days for *A. helianthi*. Differences in developmental times were significant ( $F=8.35$ ;  $df=8, 19$ ;  $P=0.0001$ ). Dry weights of adult parasitoids differed significantly among host species ( $F=15.15$ ;  $df=7, 18$ ;  $P=0.0001$ ). Adults that emerged from *S. graminum* weighed most (0.054 mg) while those emerging from *A. helianthi* weighed least (0.020 mg).

Body size is positively correlated with fecundity in many aphidiid species (Hofsvang 1991). Our results suggest that *A. colemani* population growth rate may vary when associated with populations of different host species due to variation in adult size (and presumably fecundity), survival to adulthood, and immature development rate; these three factors are well known for their influence on population growth rate (Birch 1948).

Several authors have observed a reluctance by polyphagous aphid parasitoids reared on a particular host in the laboratory to adapt to an alternate host to which it was exposed in no-choice tests (Powell and Li 1983, Cameron et al. 1984, Nemeč and Stary 1983). We found no evidence to suggest that inability to rapidly accept new hosts will limit *A. colemani* in exploiting alternate hosts in the field. *Aphidius colemani* appeared to more efficiently parasitize *S. graminum*, the species on which it was reared for several generations prior to the experiment, than several other hosts to which it was exposed. However, the parasitoid readily accepted several known alternate hosts (Mackauer and Stary 1967, Stary 1975). Species that were not successfully parasitized had not previously been recorded as hosts of *A. colemani*. *Aphis helianthi* and *L. erysimi*, two species not included on host lists (Mackauer and Stary 1967, Stary 1975), were also parasitized. Whether or not these species serve as hosts in the field depends on behavioral considerations such as the parasitoids propensity to locate the appropriate habitat, locate the aphids food plant within that habitat, and locate aphids on the plant. Our study does not address these behavioral considerations but indicated a lack of physiological barriers to successful parasitization. Choice tests and field studies would be required to provide such information.

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SELECTIVE POD ABORTION BY *BAPTISIA LEUCANTHA* (FABACEAE)  
AS AFFECTED BY A CURCULIONID SEED PREDATOR,  
*APION ROSTRUM* (COLEOPTERA)

Chris E. Petersen<sup>1</sup> and Jo Ann Sleboda

ABSTRACT

The effect of a seed predator, *Apion rostrum* (Coleoptera: Curculionidae), on selective pod abortion from *Baptisia leucantha* (Fabaceae) was investigated in a restored tallgrass prairie plot. Weevil densities in and undamaged seed contents of attached and detached pods were compared over four occasions during the summer of 1993. Detached pods had similar to lower counts of weevils/pod and fewer seeds/pod than attached pods. Weevil density in pods appears only important in promoting pod abortion through effects on seed number/pod as pods having fewer seeds are selectively aborted.

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Selective abortion of damaged fruits has been explained as a mechanism by which a plant can cease investment in fruits that are unlikely to contribute to plant fitness (Janzen 1969, Stephenson 1981). Fruits possessing fewer seeds or which are infested by predator-transmitted fungi are those abscised (Janzen 1969, Sallabanks and Courtney 1992). Thus, predispersal seed predation can lead to additional seed mortality through effects on fruit abortion (Boucher and Sork 1979, Janzen 1969, Phillips 1941). In the following study, pod abortion by the legume *Baptisia leucantha* as affected by the seed predator *Apion rostrum* Say (Coleoptera: Curculionidae) was examined in a restored tallgrass prairie located in northeastern Illinois. *Baptisia leucantha* is known to suffer higher rates of pod abortion when infested by *A. rostrum* (Petersen 1990). However, it has not been shown how the presence of the weevil causes abortion and if pod abortion is selective. The objective of this study was to test the prediction that *A. rostrum* affects selective abortion of pods.

*B. leucantha* is a widely distributed prairie native of the Midwest (Larisey 1940). The species, like other members of the lupine genus, contains a number of alkaloids (Cranmer and Turner 1967) which have been used to explain the lack of consumers feeding on it (Frost 1945). *A. rostrum* is the only known consumer of the wild indigo's tissues in the prairie plot under study. In northeastern Illinois, a seasonal cycle of growth by the perennial begins with new above-ground emergence as the ground thaws during spring. Flowering occurs from May to June with *Bombus fervidus* and *B. bimaculatus* being the major pollinators. New flowers appear as indeterminate racemes elongate. Racemes usually number one or two per plant, but may number as high as fourteen. By late June, flowering has ceased and pollinated flowers have transformed into inflated pods. Pods typically initiate 30 to 38 seeds. Many of the pods are aborted as they ripen with rates of pod loss greater among plants infested by

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*A. rostrum*. Racemes may bear over 200 mature pods. Seeds are dispersed as the ripened pods dehisce during autumn.

Over-wintering weevils oviposit into sealed developing pods during June (Petersen 1989). Eggs are inserted individually, although as many as twelve eggs have been found within a pod. A single weevil may consume over five seeds as it develops, and in pods with four or more weevils, it is not uncommon for all of the seeds to have been eaten. Pupation occurs during July as surviving seeds begin to harden and turn from green to a golden color. Adults disperse as the ripened pods dehisce.

## MATERIALS AND METHODS

The study site was the 0.06 ha restored tallgrass prairie located on the northeastern corner of the College of DuPage campus. The college is located in largely residential DuPage County, Illinois. Restoration of the plot began in the early 1970s. Big bluestem (*Andropogon gerardi*) and Indian grass (*Sorghastrum nutans*) dominate the site which is burned annually, usually in the fall. Approximately 150 *B. leucantha* populate the site.

Eighty *B. leucantha* were randomly selected for study as pods began to form during June, 1993. These plants were further randomly subdivided into four groups of 20 plants each. The four groups were sampled sequentially during the summer to examine how sampling time could effect measured outcomes. The first group was sampled on 24 June as pods began to inflate and with the appearance of *A. rostrum* eggs and larvae. The second group was sampled on 11 July as pods fully inflated and when larval weevils composed the majority life stage. Sampling on 28 July coincided with the maturation of the weevils. The final sampling was conducted on 17 August as pods ripened.

Samplings consisted of counting pods along racemes and then removing five pods from each raceme of a plant whenever possible: the most proximal pod, the most distal pod, and three spaced in between. If a raceme had fewer than five pods, then all were sampled. Pods were measured for maximum width between lines of dehiscence and for length. These measurements plus first nodal diameters of plants and racemes provided parameters of pod and plant growth, possible factors useful to understanding the impact of weevil seed predation on pod abortion during a phase of pod development. Counts of weevils and undamaged seeds were taken from each pod.

Detached pods lacking visible damage were assumed to have been aborted. Only those having similar appearance in color and stage of development to and which were still sealed as attached pods were sampled beneath each plant. This discrimination among fallen pods was intended to insure the sampling of newly aborted pods, thus limiting the possibility that decomposition affected outcomes. During the entire sampling period attached pods were green to greenish black. Detached pods turn black within two days.

A distribution-free randomization method (Potvin and Roff 1993) was used where necessary to compare grand mean counts of undamaged seeds/pod and of weevils/pod (counts/pod/plant). The probability (P) of obtaining the observed absolute difference between means among 5000 simulated permutations was used to compute significance. Standard error (SE) measurements of P's were computed as  $\sqrt{P(1-P)/N}$ , where N was the number of permutations (i.e., 5000).

Table 1. Mean counts (mean  $\pm$  s) from *Baptisia leucantha* of pods/plant, first nodal diameters of plants, and first nodal diameters of racemes/plant according to sampling date during 1993.

Date	Plant number	Pods/plant	First nodal plant diam.	First nodal raceme diam.
24 June	20	38.9 $\pm$ 31.0	13.8 $\pm$ 3.1	4.9 $\pm$ 0.9
11 July	20	6.8 $\pm$ 7.5	14.5 $\pm$ 2.8	4.7 $\pm$ 0.7
28 July	20	5.1 $\pm$ 7.5	14.7 $\pm$ 3.5	4.4 $\pm$ 0.9
17 August	20	2.0 $\pm$ 4.1	14.3 $\pm$ 2.9	5.2 $\pm$ 1.2

## RESULTS AND DISCUSSION

The mean counts of pods/plant progressively decreased through the study period with a large drop occurring between 24 June and 11 July (Table 1). Grand mean counts of seeds/pod also reflected this decrease through time in both pods still attached and those detached (Table 2). *Baptisia leucantha* may be most sensitive to aborting pods during the earlier stages of seed development as younger seeds of plants in general are known to produce auxins, gibberellins, and cytokinins that control the mobilization of nutrients into and the maintenance of fruits (Bidwell 1974, Street and Opik 1984). Except for the 24 June sample, differences in grand mean counts of seeds/pod between attached and detached pods were significant (all  $P < 0.001$ ; all  $SE < 0.001$ ).

Trends in weevil development according to sampling date were similar between attached and detached pods, although lagging in pace among the former (Table 3). The greater preponderance of larvae in detached pods during June may explain the lower grand mean counts of seeds/pod. However for a given sampling date, grand mean counts of *A. rostrum*/pod were always higher for attached pods than detached pods, and significantly so for the 11 July ( $P = 0.021$ ;  $SE < 0.001$ ) and 21 July ( $P = 0.011$ ;  $SE < 0.001$ ) samples. Although additional oviposition in pods having more seeds could be advantageous to the weevil by supporting the development of more offspring, such an ability to distinguish among pods has not been shown in *A. rostrum*. The cause of the difference in grand mean counts of weevils/pod remains unknown. Dispersal from aborted pods cannot explain this difference as aborted pods were sealed. Remnants of dead weevils were not apparent.

First nodal diameters of plants and racemes showed little if any change during the course of the experiment (Table 1). By the middle of July, pods had reached full dimensions (Table 4). Changes in size dimensions of detached pods showed a similar pattern over time and were comparable to those of those attached.

Significantly lower grand mean counts of seeds/pod among detached pods provide evidence of selective pod abortion in *B. leucantha*. The affect of weevil

Table 2. Grand mean counts of seeds/pod and weevils/pod ( $\bar{x}$  counts/pod/plant  $\pm$  s [number of plants]) within attached and detached pods of *Baptisia leucantha* according to sampling date during 1993.

Date	Seeds/pod		<i>Apion rostrum</i> /pod	
	Attached	Detached	Attached	Detached
24 June	26.4 $\pm$ 6.4(20)	24.4 $\pm$ 4.0(15)	1.6 $\pm$ 1.5(20)	1.5 $\pm$ 1.2(15)
11 July	11.6 $\pm$ 5.3(17)	2.7 $\pm$ 2.1(19)	4.4 $\pm$ 1.8(17)	3.4 $\pm$ 0.9(19)
21 July	4.2 $\pm$ 2.6(15)	0.1 $\pm$ 0.5(19)	3.8 $\pm$ 1.6(15)	2.3 $\pm$ 1.6(19)
17 August	1.1 $\pm$ 0.9 (7)	0 $\pm$ 0 (10)	3.4 $\pm$ 1.7 (7)	2.7 $\pm$ 2.4(10)

Table 3. Frequencies of *Apion rostrum* ( $\bar{x}$  frequency/pod/plant  $\pm$  s) in various life stages according to time of sample and type of pod attachment.

Sampling date and type of pod attachment	<i>Apion rostrum</i> life stage				n
	Egg	Larva	Pupa	Adult	
24 June					
Attached	0.87 $\pm$ 0.12	0.13 $\pm$ 0.12	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	18
Detached	0.63 $\pm$ 0.28	0.37 $\pm$ 0.28	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	13
11 July					
Attached	0.12 $\pm$ 0.33	0.53 $\pm$ 0.32	0.35 $\pm$ 0.28	0.00 $\pm$ 0.01	17
Detached	0.00 $\pm$ 0.01	0.65 $\pm$ 0.16	0.35 $\pm$ 0.16	0.00 $\pm$ 0.01	19
28 July					
Attached	0.0 $\pm$ 0.0	0.03 $\pm$ 0.06	0.28 $\pm$ 0.23	0.69 $\pm$ 0.24	15
Detached	0.0 $\pm$ 0.0	0.09 $\pm$ 0.17	0.14 $\pm$ 0.19	0.77 $\pm$ 0.32	17
17 August					
Attached	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.01 $\pm$ 0.02	0.99 $\pm$ 0.02	7
Detached	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.01	1.0 $\pm$ 0.0	8

seed predation on abortion is less clear as grand mean counts of *A. rostrum*/pod were lower in detached pods. Earlier studies done over multiple years (Petersen 1989, 1990) have consistently found greater pod losses among plants having high pod densities of the weevil in comparison to plants less infested. However, even plants having low weevil densities suffered substantial pod losses leading to the conclusion that predispersal seed predation is only one of a number of factors affecting pod abortion in *B. leucantha*. Selective abortion may thus be a generalized response to the disposal of pods having few seeds. In particular, *A. rostrum* may promote the abortion of pods already having a marginal number of seeds by reducing seed content. *Baptisia leucantha* which have higher pod infestations should be expected to have more of these "marginal" pods to abort. Moreover, if pods are preferentially aborted because of low seed number, then pods with few seeds should be aborted regardless of weevil densities within them. Such a prediction could be tested in future studies among plants where weevil infestations are reduced or absent.

The pollination study of Haddock and Chaplin (1982) provides additional insight into reproductive investment strategies of *B. leucantha*. Haddock and Chaplin concluded that prolific flowering by *B. leucantha* can result in higher rates of pollination success and seed production than the congener, *B. leucophaea*, but at an increased risk of seed loss to seed predators. During years of favorable environmental conditions, including low seed predator activity, *B. leucantha* may gain the benefits of its extent of reproductive investment. Contrarily, during less than favorable years, the species could minimize losses in investments through selective pod abortion. By this means

Table 4. Grand mean pod lengths and widths ( $\bar{x}$  mm/pod/plant  $\pm$  s [number of plants]) for attached and detached pods of *Baptisia leucantha* according to sampling date during 1993.

Date	Length		Width	
	Attached	Detached	Attached	Detached
24 June	15.5 $\pm$ 4.2(20)	16.0 $\pm$ 4.5(15)	5.1 $\pm$ 1.9(20)	5.3 $\pm$ 2.8(15)
11 July	29.5 $\pm$ 3.7(17)	27.0 $\pm$ 2.1(19)	12.5 $\pm$ 2.3(17)	11.7 $\pm$ 1.8(19)
21 July	27.2 $\pm$ 2.5(15)	25.9 $\pm$ 2.9(19)	12.0 $\pm$ 2.5(15)	11.9 $\pm$ 1.8(19)
17 August	28.6 $\pm$ 4.2 (7)	27.7 $\pm$ 3.3(10)	11.0 $\pm$ 1.5 (7)	11.4 $\pm$ 1.9(10)

*B. leucantha* might optimize reproductive effort over its perennial existence. In turn, as a predispersal seed predator and one of the few consumers of *B. leucantha*, *A. rostrum* would have an exclusive and a fairly productive nutritional resource.

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CRYPTOPYGUS BIPUNCTATUS (COLLEMBOLA: ISOTOMIDAE) IN NORTH AMERICA, AND *C. POSTEROCULATUS* N. COMB.

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ABSTRACT

Specimens of *Cryptopygus bipunctatus* are reported and described from North America (Michigan) for the first time. The species is easily recognized by its lack of color, one pair of ocelli on black eyespots, and one pair of ventral manubrial setae. Michigan and European specimens are very similar. A very similar Polish species, *Isotomina posteroculata*, is transferred to *Cryptopygus*.

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*Cryptopygus bipunctatus* (Axelson) (= *Isotoma bipunctata* Axelson) is widely distributed in Europe (Stach 1947, Gisin 1960), but usually has not been considered part of the North American fauna. Hammer (1938) reported *I. bipunctata* from east Greenland, but Agrell (1939) considered her specimens to be *I. notabilis pallida* Agrell. Mills (1939) reported specimens from Manitoba, but Christiansen and Bellinger (1980) believed they probably were *I. notabilis* Schäffer or *I. ekmani* Fjellberg. Dallai (1969) transferred *I. bipunctata* to *Cryptopygus* Willem. In 1972, Michigan specimens identified as *C. bipunctatus* were collected during surveys of Collembola around wastewater treatment sites. Because this taxon has not been reliably described or reported from North America, a detailed description is given of the Michigan specimens, which were compared to European specimens.

MATERIALS AND METHODS

Michigan specimens were extracted with Tullgren funnels from soil collected from grassy areas at the Belding Sewage Treatment Facility, Ionia County, Michigan, then permanently mounted on slides. For comparison, specimens collected in Europe were solicited from several individuals and institutions. All drawings were made with the aid of a drawing tube. In the description, we refer to thoracic and abdominal segments as TH I, TH II, TH III, ABD I, ABD II, ABD III, ABD IV, and for the final two, fused segments, ABD V+VI. Setae in the posterior, transverse row of each segment are designated as p1, p2, etc., where p1 is the seta closest to the dorsomedian line.

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*Cryptopygus bipunctatus* (Axelson)

- Cryptopygus bipunctatus* Dallai, 1969. Redia 51:238.  
 = *Isotoma bipunctata* Axelson, 1903. Acta Soc. Fauna Flora Fenn. 25:9.  
 = *Proisotoma (Isotomina) bipunctata* Gisin, 1943. Rev. Suisse Zool. 50:162.  
 = *Proisotomodes bipunctata* Bagnall, 1949. Ann. Mag. Nat. Hist. 12:84.  
 = *Parisotoma bipunctata* Hazelton and Glennie, 1953. British Caving (C. D. H. Collingford, ed.):273.  
 = *Isotomina bipunctata* Gisin, 1960. Collembolenfauna Europas:200.

Dallai (1969) transferred *Isotomina bipunctata* to *Cryptopygus* on the basis of the synonymization of *Isotomina* Börner and *Cryptopygus* by Massoud and Rapoport (1967), but did not take into account the other combinations proposed for this species over the years. A brief exposition of its history is warranted.

The taxon described as *Isotoma bipunctata* frequently has been shifted among several genera, due to its unusual morphological features. Axelson (1903) differentiated *I. bipunctata* from other *Isotoma* spp. on the basis of one pair of ocelli on pigmented spots and simple body setae. Other characteristics given by Axelson and important to placement of the species are unguis without teeth, tibiotarsus without clavate tenent hairs, tenaculum corpus with one seta, and two mucronal teeth. Stach (1947), thoroughly redescribing the species, found that the fifth and sixth abdominal segments were fused, the fifth abdominal tergite had one pair of blunt sensilla, and the manubrium possessed one pair of ventrodorsal setae. He considered *I. bipunctata* to be an unusual species for which a new genus eventually would be needed. Gisin (1943) placed the species in *Proisotoma (Isotomina)* and later (1960) in *Isotomina* on the basis of the two ventral manubrial setae, slender dentes, and fused fifth and sixth abdominal segments. Bagnall (1949) established the genus *Proisotomodes*, with *I. bipunctata* as its type and only species. *Proisotomodes* was differentiated by the small size of the body, tenaculum with one seta, manubrium with one pair of ventral setae, and bidentate mucro. Gisin (1960) regarded *Proisotomodes* as a synonym of *Isotomina*. Hazelton and Glennie (1953) listed the species in *Parisotoma* Bagnall, but it is clear from Salmon's discussion (1964) that if *Parisotoma* is a valid genus, it must be restricted to species with 4-6 pairs of eyes. Gisin (1960) considered *Parisotoma* a synonym of *Isotoma*.

Willem (1901) briefly described a new genus and species, *Cryptopygus antarcticus*, separated from other taxa on the basis of the "sixth abdominal segment usually invisible from above, depressed downward by the fifth abdominal segment" (see also Stach 1947). Willem's illustration suggests ankylosed fifth and sixth abdominal segments. Willem also described and illustrated a short furcula with subequal manubrium and dens, and a bidentate mucro. Historically, *Isotomina* Börner 1903 was differentiated from other isotomid taxa by having a partially divided postantennal organ, smooth body setae, fused fifth and sixth abdominal segments, and dens longer than the manubrium. Massoud and Rapoport (1968) considered that both *Cryptopygus* and *Isotomina* had fused fifth and sixth abdominal segments, and thus regarded *Isotomina* as a junior synonym of *Cryptopygus*.

The genus *Cryptopygus* is now defined as Isotomidae with fused fifth and sixth abdominal segments, few ventral manubrial setae, two mucronal teeth, and PAO often constricted or with a median listel (Christiansen and Bellinger 1980). *Isotoma bipunctata* clearly fits this concept of *Cryptopygus*. It is excluded from *Isotoma* because it has only one pair of ventral manubrial setae, not many. The genera *Isotomina* and *Proisotomodes*, to which *I. bipunc-*

*tata* has been referred, are junior synonyms of *Cryptopygus*. The definition of *Parisotoma* as given by Salmon (1964) does not accommodate *I. bipunctata*.

#### DESCRIPTION OF MICHIGAN SPECIMENS

**Color and Size:** White except for black eyespots (Fig. 1). Length = 486–647  $\mu\text{m}$ , mean = 590  $\mu\text{m}$  ( $n = 6$ ).

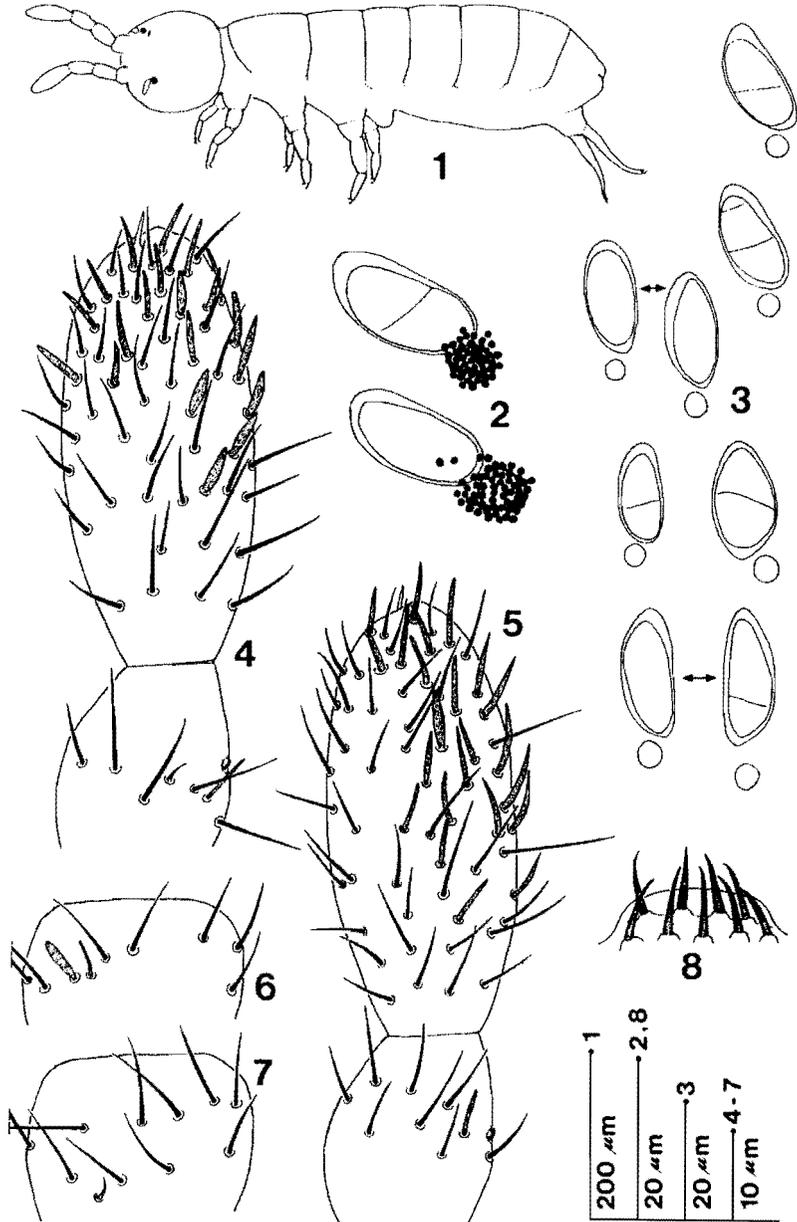
**Head:** Postantennal organ (PAO) oval, length 3.5–5  $\times$  the width of the ocellus, wall irregularly thickened, median listel present or absent (Figs 2, 3). One ocellus on each side of the head, adjacent to the PAO, pigment granules large and distinct, frequently spreading onto PAO (Fig. 2). Antenna slightly longer than length of head, ratio of segments I:II:III:IV as 1:1.5:1.6:2.9. Segment I with short, thorn-like seta dorsally (Fig. 7), one large and one small sensilla ventrally (Fig. 6); segment II without differentiated sensilla; segment III with one thorn-like seta, and sense organ consisting of two small club-shaped sensilla in pits, flanked on each side by a longer sensillum (Figs. 4, 5); segment IV with numerous pointed and blunt sensilla, pin seta simple, bluntly pointed (Figs. 4, 5); subapical pit and sensory rod not seen. Labrum with five subapical and four apical setae, anterior margin smooth (Fig. 8); mandible of typical isotomid form, apically truncated (Fig. 9), with four anterior teeth and large molar region; maxilla with tridentate capitulum and apparently six fringed lamellae (Fig. 9); maxillary outer lobe with trifurcate maxillary palpus, the apical digit the longest, and two basal setae; sublobal plate apically smooth, basally with three seta-like projections (Fig. 9).

**Legs:** Unguis and unguiculus untoothed, pretarsus with one pair of setae, clavate tenent hairs absent. All leg setae smooth and acuminate. Foreleg (Figs. 10, 11) with two long, precoxal setae, coxa without setae; trochanter with two exterior and two interior setae; tibiotarsus with a subapical whorl of seven setae. Mesoleg precoxae I and II with two and six setae, respectively; coxa with nine setae; trochanter with nine setae (Figs. 12, 13); tibiotarsus ventrally with five pairs of setae, dorsally with three longitudinal rows of setae (Figs. 14, 15). Metaleg (Figs. 16, 17) precoxae I and II with four and five setae, respectively; coxa with nine setae, most of them in a transverse row; trochanter with nine setae; femur with many exterior setae, few interior setae; tibiotarsus with four pairs of ventromedian setae.

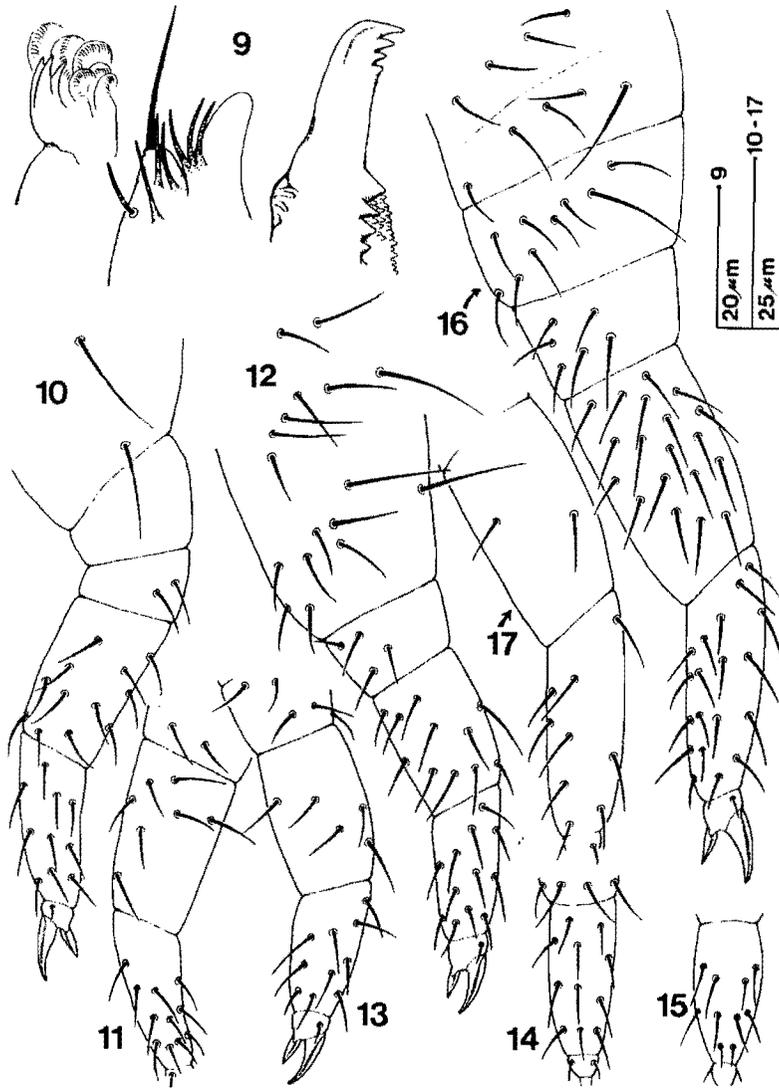
**Abdomen:** Ventral tube with four pairs of lateral setae and one pair of caudal setae (Fig. 21). Each tenaculum ramus with four teeth, tenaculum corpus with one anterior seta. Furcula (Fig. 18) well developed, dens about twice the length of the manubrium; manubrium with 16 pairs of dorsal setae and one pair of ventral setae, apically with two small teeth; dens crenulate, with three rows of setae; subterminal seta extending slightly past furcula terminus; mucro bidentate, apical tooth larger than antepical tooth.

**Chaetotaxy:** All common setae smooth and acuminate (Figs. 19, 20). Seven unpaired dorsomedian setae on head; seta p1 shorter than p2. All body sensilla thin except on ABD V+VI. Each side of TH II tergum with three anteriolateral sensilla; TH III tergum with two posterior sensilla and one anteriolateral sensillum; TH III sternum with two setae. ABD I with one sensillum between p4 and p5, and another between p9 and p10; ABD II with one sensillum between p4 and p5, and another near the lateral margin; ABD III with a sensillum between p4 and p5, and another near the posteriolateral margin; ABD IV with two sensilla, one between p2 and p3, another between p4 and p5; ABD V+VI on each side with one plump laterodorsal sensillum and one thin ventrolateral sensillum.

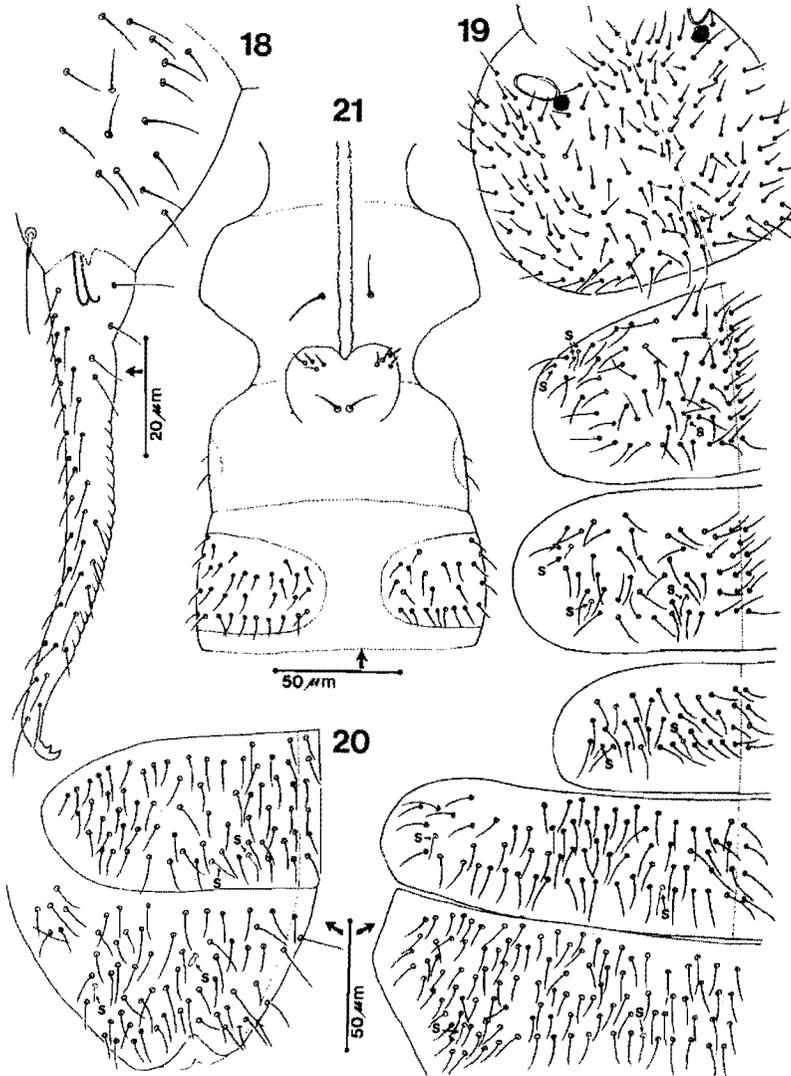
**Collection Data:** Six female and late subadult specimens collected from



Figures 1-8. *Cryptopygus bipunctatus*. 1. Habitus. 2. Postantennal organs (PAO's) and eyespots. 3. Variation in shape of postantennal organ, and location of ocelli. Arrows indicate PAO's from the same specimen. 4. Antennal segments III+IV, exterior view. 5. Antennal segments III+IV, interior view. 6. Antennal segment I, ventral view. 7. Antennal segment I, dorsal view.



Figures 9-17. *Cryptopygus bipunctatus*. 9. Mouthparts (l.-r.): apex of maxilla; maxillary palpus and sublobal plate; apex of mandible. 10. Foreleg, exterior view. 11. Foreleg, interior view. 12. Mesoleg, exterior view. 13. Mesoleg, interior view. 14. Mesotibiotarsus, dorsal view. 15. Mesotibiotarsus, ventral view. 16. Metaleg, exterior view. 17. Metaleg, interior view.



Figures 18–21. *Cryptopygus bipunctatus*. 18. Furcula. 19. Chaetotaxy of head, thorax, and abdominal segments I–III, left side (sensilla indicated by s and arrow). 20. Chaetotaxy of abdominal segments IV–V+VI (sensilla indicated by s and arrow). 21. Venter of metathorax and abdominal segments I–II.

sandy, moist soil at the edge of deciduous secondary forest, Belding Sewage Treatment Facility, Ionia County, Michigan, 25 July 1972, Renate M. Snider and Ernest C. Bernard, collectors.

**Diagnosis:** The combination of one pair of ocelli on black eyespots, one pair of plump sensilla on ABD V+VI, one pair of ventral manubrial setae, and bidentate mucro distinguishes *C. bipunctatus* from most other Collembola. The species described by Stach (1947) as *Isotomina posteroculata* has each ocellus distant from the PAO and has a toothed unguis. Other *Isotoma*-like taxa with only one pair of ocelli have numerous ventral manubrial setae and tridentate or quadridentate mucrones.

**Discussion:** Specimens of European *C. bipunctatus* from Vienna, Austria; Puglia, Italy; Tjømø, Norway; and Budleigh, Salterton, England, were all very similar in structure and sensillar chaetotaxy to the Michigan specimens, and to the description given by Stach (1947).

*Isotomina posteroculata* is so similar to *C. bipunctatus* that the two could be considered the same species. However, the wide separation of the PAO and ocellus, and the toothed unguis, serve to separate the two taxa. Because of the great similarity, *I. posteroculata* is transferred to *Cryptopygus*:

***Cryptopygus posteroculatus* (Stach) n. comb.**

*Isotomina posteroculata* Stach, 1947. Polish Acad. Sci. Lett., p. 278.

ACKNOWLEDGMENTS

We are grateful to Dr. Erhard Christian, Vienna, and Ms. Suzanne Lewis, British Museum (Natural History), for kindly lending us specimens of *C. bipunctatus*, and to Dr. Arne Fjellberg, Tjømø, Norway, for sending freshly collected specimens from Norway. We also thank Dr. Peter Bellinger for his assistance with the literature.

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THE ROBBER FLIES (DIPTERA: ASILIDAE) OF THE ALBANY PINEBUSH<sup>1</sup>Timothy L. McCabe<sup>2</sup> and Christine N. Weber<sup>3</sup>

## ABSTRACT

The Albany Pinebush, a pitch pine-scrub oak sand barrens, was examined for robber flies and the results compared to historical records found in the New York State Museum, Albany. Thirty-six species were recorded of which seventeen were new records. Two species, *Cyrtopogon laphriformis* and *Promachus bastardii*, last recorded in 1914 and 1931, respectively, were not located in the survey.

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Scrub oak-pitch pine (*Quercus ilicifolia*-*Pinus rigida*) barrens occur from Virginia to Maine, but only about 20 large sites exist. Not all of these are sand barrens; a few are ridge-top barrens (Wheeler, 1991). Pitch pine barrens are fire-dependent communities growing on nutrient-poor acid soils. Albany's barrens are near the fork of the Hudson and Mohawk rivers. In early postglacial times, the Hudson-Mohawk valley provided a corridor for Coastal Plain species to reach the Great Lakes (Shapiro, 1971). Albany's pine barrens, therefore, should possess relicts of this post-glacial migration.

Around the turn of the century, the Albany pine barrens were the site of intensive collecting by museum entomologists. A trolley ran from Albany to Karner, N.Y., formerly Centre, N.Y., which is now within the present-day Albany city limits and at the heart of the remaining pine barrens. The Albany pine barrens has been heavily urbanized, and only six of the original 40 square miles of barrens remain. The recent loss of 28 species of Lepidoptera has been documented (McCabe, et. al., 1993). Concern for the preservation of the remaining habitat has led to inventory work.

Scrub oak-pitch pine barrens have remarkable insect diversity (Wheeler, 1991). We recorded 36 species of robber flies from an area of approximately one square mile. By comparison, Bromley (1946) recorded 33 species from the Connecticut township encompassing Stamford, an area of 60 square miles, during a nearly 20-year period. The township took in a much greater and more diverse area than the Albany pine barrens.

Two species known from historical records, *Cyrtopogon laphriformis* Curran and *Promachus bastardii* (Macquart), were last recorded in 1914 and 1931, respectively. They are apparently extirpated. These two species have southeastern distributions. The Albany pine barrens' Lepidoptera that have been extirpated (McCabe, et al., 1993) are evenly split between those that are now found to be more northerly or more southerly in distribution. We believe that the witnessed changes in the fauna result from normal fluctuations in a given

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species' distribution when at the periphery of their range, rather than a warming or cooling event.

Seventeen species of robber flies were collected on Albany's barrens for the first time, based on New York State Museum records, but ten of these were represented by less than six records and may have been missed by earlier collectors. *Cyrtopogon lutatius* (Walker), *Ommatius tibialis* Say, *Proctacanthus rufus* Williston, and *Machimus snowii* (Hine) are common species and thought to be recent colonizers. An introduced European species, *Dioctria baumhaueri* Meigen, is also common. *Cyrtopogon lutatius* (Walker), *Laphria cinerea* (Back), *L. virginica* (Banks), and *Proctacanthus rufus* Williston are all pitch pine ecological associates according to Bromley (1946). The loss of any of these four species would be indicative of a decline in the quality of habitat.

The records presented here are gleaned from the New York State Museum, the Albany Pine Barrens Entomological Project (supported by The Nature Conservancy), and the individual collecting efforts of the authors. All 1992 records were netted, the other recent records were taken by Malaise trap and historical records were presumably netted. The following list gives the earliest to latest dates of capture followed by the oldest to most recent year of capture, including collections through 1992. Females of some *Laphria* were not included because of the lack of identifying characters. Nomenclature follows Wood (1981).

List of the species of Asilidae from the Albany pine barrens.

#### Asilidae Leptogastrinae

*Leptogaster flavipes* Loew. 8 records: 17 June–21 July; 1991–1992.

*Leptogaster glabrata* (Wiedemann). 9 records: 15 June–11 August; 1984–1992.

#### Dasyopogoninae

*Ceraturgus cruciatus* (Say). 3 records: 28 June–19 July; 1931–1991.

*Cyrtopogon falto* (Walker). 48 records: 14 May–5 July; 1912–1992.

*Cyrtopogon laphriiformis* Curran. 1 record: 11 June 1914.

*Cyrtopogon lutatius* (Walker). 32 records: 14 May–7 July; 1982–1992.

*Cyrtopogon marginalis* Loew. 38 records: 12 May–23 June; 1903–1992.

*Dioctria baumhaueri* Meigen. 57 records: 10 June–21 July; 1982–1992. An introduced species first recorded from Boston in 1916 (Bromley, 1946).

*Diogmites basalis* (Walker). 3 records: 20 July–30 August; 1984–1987.

*Diogmites umbrinus* Loew. 1 record: 1 September 1992.

*Holopogon guttulus* (Weidemann). 120 records: 25 May–22 July; 1912–1992.

*Lasiopogon currani* Cole & Wilcox. 21 records: 19 May–4 June; 1912–1992.

*Lasiopogon terricola* (Johnson). 3 records: 18 May–12 June; 1982–1992.

#### Laphriinae

*Atomosia puella* (Wiedemann). 5 records: 20 June–20 August; 1985–1992.

*Cerotainia macrocera* (Say). 3 records: 30 June–20 July; 1985–1986.

*Laphria aktis* McAtee. 4 records: 28 May–23 June; 1983–1992.

*Laphria cinerea* (Back). 3 records: 18 June–2 July; 1902–1985.

*Laphria divisor* (Banks). 3 records: 17 June–16 July; all 1992.

- Laphria flavicollis* Say. 3 records: 3 June–5 July; 1931–1992.  
*Laphria franciscana* Bigot. 7 records: 23 June–7 August; 1991–1992.  
*Laphria index* McAtee. 13 records: 11 June–19 July; 1981–1992.  
*Laphria posticata* Say. 12 records: 11 June–1 August 1992; 1902–1992.  
*Laphria sadales* Walker. 4 records: 25 June–21 July; 1983–1991.  
*Laphria thoracica* Fabricius. 7 records: 9 June–11 July; 1931–1992.  
*Laphria virginica* (Banks). 4 records: 3 June–4 August; 1923–1992.

#### Asilinae

- Asilus erythrocnemius* Hine. 3 records: 13 June–2 July; 1931–1991.  
*Efferia aestuans* (Linnaeus). 20 records; 17 June–22 August; 1907–1992.  
*Machimus notatus* (Wiedemann). 173 records: 13 June–11 August; 1912–1992.  
*Machimus sadyates* (Walker). 6 records: 7 August–28 August; 1985–1991.  
*Machimus snowii* (Hine). 102 records: 16 July–11 September; 1985–1992.  
*Neoitamus flavofemoratus* (Hine). 151 records: 11 June–16 August; 1902–1992.  
*Neoitamus orphne* (Walker). 1 record: 8 June 1981.  
*Ommatius tibialis* Say. 24 records: 24 June–10 August; 1984–1992.  
*Proctacanthus philadelphicus* Macquart. 31 records: 2 July–6 September; 1901–1992.  
*Proctacanthus rufus* Williston. 10 records: 25 June–17 August; 1981–1992.  
*Promachus bastardii* (Macquart). 1 record: 2 July 1931.

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THE MAYFLY FAMILY BEHNINGIIDAE (EPHEMEROPTERA:  
EPHEMEROIDEA): KEYS TO THE RECENT SPECIES  
WITH A CATALOG OF THE FAMILY

Michael D. Hubbard<sup>1</sup>

ABSTRACT

Keys to the known Recent species of the mayfly family Behningiidae are presented. Also included is a catalog of references to the genera and species of the Behningiidae, along with indications of described stages and geographical distributions.

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The mayfly family Behningiidae is one of the smallest families of the Ephemeroptera. It comprises only four genera: the three Recent genera *Behningia* Motaş & Băcesco, *Dolania* Edmunds & Traver, and *Protobehningia* Tshernova, and the Jurassic fossil genus *Archaeobehningia* Tshernova. To date there are only seven described species in the family.

Although McCafferty (1991) recently elevated the Behningiidae to its own superfamily, he presented little data (McCafferty 1979, McCafferty & Edmunds 1976) to support his rationale and his arguments therefore remain unconvincing. I still consider the family to belong in the Ephemeroidea, and accordingly, following standard practice among mayfly workers, I have left it placed therein.

Keys to the known stages of the nymphs and imagoes of the Recent species of the Behningiidae are presented.

The catalog is intended to be a comprehensive, but certainly not exhaustive, listing of references in the scientific literature to all known species of the Behningiidae. Included with each species are indications of the geographic distributions listed in the scientific literature. Listed with the references to taxonomic papers are indications of the stage described or figured. Only selected taxonomic references are given for each genus.

This paper is one in a continuing series of catalogs of the Ephemeroptera (c.f. Hubbard & Pescador 1978, Hubbard & Peters 1978, Hubbard 1979, 1982a, 1982b, 1986, 1987, 1990, Hubbard & Savage 1981, Hubbard, Dominguez & Pescador 1992).

**Family Behningiidae Tshernova, 1938**  
Behningiidae Tshernova, 1938, 1938:131.

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**Genus *Archaeobehningia* Tshernova**

*Archaeobehningia* Tshernova, 1977, 1977:94; Soldán, 1979, 72:636; Kaludina, 1980, 178:229; Tshernova, 1980, 178:33; Landa & Soldán, 1985, 4:99; Hubbard, 1987, 129:61; Peters & Gillies, 1991, p:211.

Type-species: *Archaeobehningia edmundsi* Tshernova, original designation.

***Archaeobehningia edmundsi* Tshernova**

*Archaeobehningia edmundsi* Tshernova, 1977, 1977:95, fig. 2, pl. 10 fig. 2 (nymph); Sinitshenkova, 1985, 211:22; Hubbard, 1987, 129:62; Peters & Gillies, 1991, p:211.

*Archaeobehningia* [sic] *edmundsi*; Sinitshenkova, 1984, p:63.

Distribution: Jurassic of Russian Transbaikal (fossil).

**Genus *Behningia* Lestage**

*Behningia* Lestage, 1930, 69:436; Tshernova, 1938, 1938:131; Lestage, 1938, 78:315; Tshernova, 1940, 1:130; Bertrand, 1954, p:254; Edmunds & Traver, 1959, 52:46; Tshernova & Bajkova, 1960, 39:415; Landa, 1969, 18:295; McCafferty, 1975, 101:451; Soldán, 1979, 72:636; Landa & Soldán, 1985, 4:99; Peters & Peters, 1986, 69:246; Tshernova et al. 1986, 1:111; Peters & Gillies, 1991, p:211.

Type-species: *Behningia ulmeri* Lestage, monotypy.

***Behningia lestagei* Motaş & Băcesco**

*Behningia lestagei* Motaş & Băcesco, 1937, 24:27, fig. 1-2 (nymph); Lestage, 1938, 78:315 (nymph); Motaş & Băcesco, 1940, 26:78, figs. 1-4, pl. 1 (nymph); Demoulin, 1952, 28(21):1; Demoulin, 1955, 91:207; Keffermüller, 1957, 7:254; Edmunds & Traver, 1959, 52:46, fig. 13-23 (nymph); Poprawska, 1960, 4:160; Tshernova & Bajkova, 1960, 39:410; Keffermüller, 1963, 12:323; Brodsky, 1974, 53:296, fig. 1g (adult); Koss & Edmunds, 1974, 55:324, pl. 12 fig. 138-139 (egg); Peters & Peters, 1977, 62:409; Tshernova, 1977, 1977:95; Soldán, 1979, 72:636; Puthz, 1978, 2:263; Fink, Soldán, Peters & Peters, 1991, 69:1083.

[?] *Behningia lestagei*; Bertrand, 1954, p:254, fig. 123 (nymph).

*Behningia lestagei* ?; Keffermüller, 1959, 19(5):8, pl. 4-7, 9-12 (male, female, nymph); Keffermüller, 1960, 19(8):6; Peters & Peters, 1986, 69:245.

*Behningia ulmeri*; Landa, 1969, 18:295, pl. 28 (male, female, nymph).

*Behningia ulmeri* [partim]; Kluge, 1989, pl. 5 fig.3-4 (nymph).

Distribution: Moldavia, Poland, Czechoslovakia, Romania.

***Behningia tshernovae* Edmunds & Traver**

*Behningia ulmeri* (?); Tshernova, 1938, 1938:132, fig. 1-4 (male).

*Behningia ulmeri* [partim]; Tshernova, 1940, 1:133; Kluge, 1989, pl. 5 fig.3-4 (nymph).

*Behningia ulmeri* ?; Demoulin, 1952, 28(21):1, fig. 5 (male); Tshernova, 1952, 3:248, figs. 20-24 (nymph); Tshernova, 1958, 37:73.

*Behningia ulmeri*; Bertrand, 1954, p:254, fig. 124 (male).

*Behningia tshernovae* Edmunds & Traver, 1959, 52:47, fig. 23-30 (male, nymph); Landa, 1969, 18:297; Peters & Peters, 1977, 62:409; Tshernova,

1977, 1977:95; Tiunova, 1986, p:21; Tshernova et al. 1986, 1:111, fig. 48(1-4) (male).

Distribution: Eastern Russia.

#### *Behningia ulmeri* Lestage

"Nov. gen., nov. sp. ?" Behning, 1924, 1:252, fig. 33-34 (nymph).

"Merkwürdige Ephemeriden-Nymphe" Ulmer, 1924, 7:3, fig. 1-6 (nymph).

*Behningia ulmeri* Lestage, 1930, 69:436; Motaş & Băcesco, 1937, 24:25 (nymph); Lestage, 1938, 78:315 (nymph); Motaş & Băcesco, 1940, 26:78 (nymph); Demoulin, 1952, 28(21):1; Demoulin, 1955, 91:207; Keffermüller, 1957, 7:254; Edmunds & Traver, 1959, 52:46, fig. 22; Tshernova & Bajkova, 1960, 39:410; Peters & Peters, 1977, 62:410; Tshernova, 1977, 1977:95; Soldán, 1979, 72:636; Puthz, 1978, 2:263; Peters & Gillies, 1991, fig. 9, 12-13 (male).

*Behningia ulmeri* [partim]; Tshernova, 1940, 1:133; Kluge, 1989, pl. 5 fig.3-4 (nymph).

*Behningia ulmeri* ?; Klyutschareva, 1963, Zoologicheskii Zhurnal 42:1604.

[not] *Behningia ulmeri*; Tshernova, 1938, 1938:132, fig. 1-4; Bertrand, 1954, p:254, fig. 124 (male); Bertrand, 1954, p:254; Landa, 1969, 18:295, pl. 28 (male, female, nymph).

[not] *Behningia ulmeri* ?; Demoulin, 1952, 28(21):1, fig. 5 (male); Tshernova, 1952, 3:248, figs. 20-24 (nymph); Tshernova, 1958, 37:73.

Distribution: Russia.

#### Genus *Dolania* Edmunds & Traver

*Dolania* Edmunds & Traver, 1959, 52:46; Tshernova & Bajkova, 1960, 39:415; McCafferty, 1975, 101:451; Edmunds, Jensen & Berner, 1976, p:274; Berner, 1977, 22(1):48; Peters & Peters, 1977, 62:409; Landa & Soldán, 1985, S4:99; Berner & Pescador, 1988, p:259; Peters & Gillies, 1991, p:211.

Type-species: *Dolania americana* Edmunds & Traver, original designation.

#### *Dolania americana* Edmunds & Traver

*Dolania americana* Edmunds & Traver, 1959, 52:46, figs. 1-16, 31-32 (nymph); Tshernova & Bajkova, 1960, 39:414; Edmunds, 1962, 12(5):17; Schneider, 1966, 29:205; Peters & Jones, 1973, p:246; Koss & Edmunds, 1974, 55, pl. 12 fig. 140-141 (egg); McCafferty, 1975, 101:451, fig. 1 (nymph); Edmunds, Jensen & Berner, 1976, p:276, fig. 42, 197, 202, 204, 424 (male, female, nymph); Berner, 1977, 22(1):48; Peters & Peters, 1977, 62:409; Tshernova, 1977, 1977:95; Soldán, 1979, 72:636, fig. 1-15 (male, female, nymph); Tsui & Hubbard, 1979, 67:119; Finn & Herlong, 1980, 91:102; Harvey, Vannote & Sweeney, 1980, p:211; Dakin & Felder, 1981, 64:454; Peters, 1982, 6:28; Sweeney & Vannote, 1982, 36:811; Basha & Pescador, 1984, p:205; Benke et al., 1984, 54:43; Fink, 1986, p:1; Peters & Peters, 1986, 69:245, fig. 1-3 (male, female); Peters, Peters & Fink, 1987, 65:3177; Berner & Pescador, 1988, p:259, pl. 14, fig. 14 (male, female, nymph, egg); Fink & Yasui, 1988, 17:448, fig. 1-9 (sperm); Peters & Peters, 1988, 97(5):8, 3 figs (male); Kluge, 1989, pl. 5 fig. 2 (nymph); Jacobs, 1990, 101:219; Fink, Soldán, Peters & Peters, 1991, 69:1083, fig. 3a-g, 6a-j, 7a-d (nymph); Peters & Gillies, 1991, p: fig. 8, 10-11 (male); Sweeney & Funk, 1991, 13:17; Peters & Peters, (in press).

Distribution: United States (Florida, Georgia, Louisiana, North Carolina, South Carolina, Wisconsin-Minnesota).

***Dolania* sp.**

*Dolania* sp. nov.; Sweeney & Funk, 1991, 13:18.

Distribution: United States (Alabama).

**Genus *Protobehningia* Tshernova**

*Protobehningia* Tshernova in Tshernova & Bajkova, 1960, 39:411; Peters & Peters, 1977, 62:410; Soldán, 1979, 72:636; Landa & Soldán, 1985, 4:99; Tshernova et al., 1986, 1:111; Peters & Peters, 1986, 69:246; Peters & Gillies, 1991, p:207.

Type-species: *Protobehningia asiatica* Tshernova, original designation.

***Protobehningia asiatica* Tshernova**

*Protobehningia asiatica* Tshernova in Tshernova & Bajkova, 1960, 39:413, fig. 1-3 (nymph); Peters & Peters, 1977, 62:410; Tshernova, 1977, 1977:95; Tiunova, 1986, p:21; Tshernova et al., 1986, 1:111; Kluge, 1989, pl. 5 fig. 1 (nymph); Peters & Gillies, 1991, p:207, fig. 7 (nymph).

Distribution: Far Eastern Russia.

***Protobehningia merga* Peters & Gillies**

*Protobehningia merga* Peters & Gillies, 1991, p:208, fig. A, 1-6 (male, nymphal exuviae).

Distribution: Thailand.

**Key to the imagos of Behningiidae**

(portions adapted from Peters & Gillies 1991)

1. Vein CuA of fore wings not forked; length of penes  $3/5$  to  $4/5$  length of abdomen . . . . . *Protobehningia* (*Protobehningia merga*)
- Vein CuA of fore wings forked; length of penes  $1/4$  length of abdomen or less . . . . . 2
- 2(1). Longitudinal veins form geminate pairs in fore wings; length of forceps nearly as long as length of penes . . . . . *Behningia*, 3
- Longitudinal veins evenly spaced in fore wings; length of forceps  $1/2$  length of penes. . . . . *Dolania americana*
- 3(2). One longitudinal intercalary vein in fork of  $CuA_1$  of fore wings (see Edmunds and Traver, 1959, fig. 24) . . . . . 4
- Two longitudinal intercalary veins in fork of  $CuA_1$  of fore wings . . . . . *Behningia ulmeri*
- 4(3). Intercalary reticulations along hind margin of fore wings . . . . . *Behningia lestagei*
- No intercalary reticulations along hind margin of fore wings . . . . . *Behningia tshernovae*

### Key to the nymphs of Behningiidae

1. Tarsi of fore legs fused to tibiae; tibiae of hind legs not reduced . . . . . *Protobehningia*, 5
- Tarsi of fore legs not fused to tibiae; tibiae of hind legs reduced . . . . . 2
- 2(1). Labial palp III less than 4/5 length of palp II; galea-lacina of maxilla ovoid . . . . . *Behningia*, 3
- Labial palp III subequal to longer than palp II; galea-lacinea of maxilla not ovoid. . . . . *Dolania americana*
- 3(2). Labial palp II at least 2/3 as long as palp III . . . . . *Behningia ulmeri*
- Labial palp II less than 2/3 as long as palp III . . . . . 4
- 4(3). Labial palp I subequal in length to palp III; labial palp I more than twice as long as broad . . . . . *Behningia tshernovae*
- Labial palp I about 1 3/20 length of palp III; labial palp I less than twice as long as broad. . . . . *Behningia lestagei*
- 5(1). Glossae and paraglossae with few (<5) long stout setae on ventral surface . . . . . *Protobehningia asiatica*
- Glossae and paraglossae with more than 20 long stout setae on ventral surface . . . . . *Protobehningia merga*

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EFFECTS OF ASCORBIC ACID DEFICIENCIES ON LARVAE OF *LYMANTRIA DISPAR* (LEPIDOPTERA: LYMANTRIIDAE)Richard L. Lindroth<sup>1</sup> and Anthony P. Weiss<sup>2</sup>

## ABSTRACT

We assessed the effects of ascorbic acid and total vitamin deficiencies on growth, food processing efficiencies and survival of larval gypsy moths. Artificial diet lacking ascorbic acid did not alter performance of fourth instars, whereas diet lacking a total vitamin mix marginally reduced growth. All vitamin deficient diets substantially reduced survival of fourth-fifth instars. Mortality occurred primarily during molting periods, providing further evidence of the putative role of ascorbic acid in cuticle formation.

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That insects require dietary sources of water-soluble and fat-soluble vitamins is well-established, although the specific roles of such compounds, and their importance in insect nutritional ecology, are not. Such is particularly true for folivores of woody plants. Although the low nutrient content of tree foliage (relative to herbaceous foliage, Mattson and Scriber 1987) would suggest that vitamin deficiencies may be particularly important for tree-feeders, empirical studies with such insects are exceedingly few.

The role of ascorbic acid (vitamin C) in the nutritional ecology of the gypsy moth, *Lymantria dispar* L., is of interest for several reasons. First, ascorbic acid deficiencies have been implicated in predisposing gypsy moth larvae to one of their most important natural enemies, gypsy moth nuclear polyhedrosis virus (Lindroth et al. 1991). Second, ascorbic acid and other antioxidants may play important roles in the biological activation/deactivation of plant phenolics (Appel 1993, Felton and Duffey 1992), the dominant allelochemicals of preferred gypsy moth hosts. Third, procedures for mass-rearing of gypsy moths on artificial diets can be fully optimized only as the roles of particular dietary constituents are elucidated. At the time this study was conducted, ascorbic acid deficiency was under consideration as a contributor to Abnormal Performance Syndrome (APS, Odell 1990), which upon occasion interrupted rearing activities at USDA laboratories responsible for large-scale production of gypsy moth eggs and larvae.

Here we report the consequences of both ascorbic acid and total vitamin deficiencies on performance of larval gypsy moths. We addressed not only affects on growth and survival, but also proximate effects on food consumption and processing efficiencies.

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Table 1. Composition of test diets (% wet weight).

Component	HiVit+Asc	HiVit-Asc	+Asc	NoVit
Wheat germ	2.00	2.00	2.00	2.00
Casein (vitamin-free)	2.00	2.00	2.00	2.00
Cellulose (alphacel)	9.40	9.87	9.86	10.33
Mineral mix (Wesson's)	0.74	0.74	0.74	0.74
Sorbic acid	0.19	0.19	0.19	0.19
Vitamin mix <sup>a</sup>	0.93	0.46	—	—
Ascorbic acid	(0.47) <sup>b</sup>	—	0.47	—
Agar	1.39	1.39	1.39	1.39
Water (distilled)	83.36	83.36	83.36	83.36

<sup>a</sup>Hoffmann-LaRoche No. 26862 for HiVit+Asc; same minus ascorbic acid for HiVit-Asc.

<sup>b</sup>This value is included in the preceding column value for vitamin mix.

## MATERIALS AND METHODS

We obtained gypsy moth egg masses from the Beneficial Insects Research Laboratory (USDA), Newark, Delaware. Larvae were reared in groups of 40–50 for the first three stadia; all rearing was conducted in a Percival® environmental chamber at 25°C with a 15:9 L:D photoperiod.

Artificial diets were modifications of the control diet described by Lindroth et al. (1991), which itself is a low wheat germ modification of the standard Bell diet (ODell 1985). We prepared four diets (Tables 1,2). The first contained the standard high concentrations of all vitamins, including ascorbic acid. The second was identical, with the exception that it contained no ascorbic acid. The third contained the standard amount of ascorbic acid but no additional vitamins. The fourth contained no supplemental vitamins. For ease of presentation these four diets will henceforth be referred to as HiVit+Asc, HiVit-Asc, +Asc, and NoVit, respectively. The HiVit+Asc and +Asc diets contained ascorbic acid at a concentration of 0.47% (fresh weight), a value at the upper end of the range of ascorbic acid concentrations in angiosperm foliage (mean of 0.16%, Jones and Hughes 1983). Diet mixtures were autoclaved to inhibit subsequent growth of mold; vitamins were added after diets were cooled to below 70°C. All insects were reared on the HiVit+Asc diet for stadia 1–3.

We performed two types of bioassays to assess the effects of ascorbic acid

Table 2. Composition of vitamin mix formulation.

Component	%
Vitamin A	3.39
Vitamin E	0.80
Vitamin B12	0.04
Vitamin B2	0.05
d-Pantothenic acid	0.10
Choline chloride	10.02
Folic Acid	0.02
Ascorbic Acid	50.10
Thiamin	0.02
Pyridoxine	0.02
Biotin	0.02
Niacin	0.10
Inositol	2.00
Dextrose	33.09

Table 3. Dietary effects on nutritional indices of fourth stadium gypsy moths (mean  $\pm$  1 S.E.)\*\*

Diet	Duration (days)	RGR (mg/mg/day)	RCR (mg/mg/day)
HiVit+Asc	5.7 $\pm$ 0.2 <sup>a</sup>	0.21 $\pm$ 0.01 <sup>a</sup>	1.81 $\pm$ 0.05 <sup>a</sup>
HiVit-Asc	5.5 $\pm$ 0.3 <sup>a</sup>	0.20 $\pm$ 0.00 <sup>ab</sup>	1.77 $\pm$ 0.10 <sup>a</sup>
+Asc	5.0 $\pm$ 0.2 <sup>a</sup>	0.20 $\pm$ 0.00 <sup>ab</sup>	1.93 $\pm$ 0.05 <sup>a</sup>
NoVit	5.5 $\pm$ 0.2 <sup>a</sup>	0.18 $\pm$ 0.01 <sup>b</sup>	1.99 $\pm$ 0.08 <sup>a</sup>
P-value	0.197	0.029	0.105

Diet	AD (%)	ECD (%)	ECI (%)
HiVit+Asc	21.1 $\pm$ 0.9 <sup>a</sup>	56.4 $\pm$ 4.3 <sup>a</sup>	11.5 $\pm$ 0.3 <sup>a</sup>
HiVit-Asc	19.5 $\pm$ 2.5 <sup>a</sup>	63.6 $\pm$ 9.0 <sup>a</sup>	11.1 $\pm$ 0.6 <sup>a</sup>
+Asc	17.6 $\pm$ 1.2 <sup>a</sup>	61.4 $\pm$ 4.0 <sup>a</sup>	10.4 $\pm$ 0.2 <sup>a</sup>
NoVit	13.4 $\pm$ 0.6 <sup>b</sup>	70.2 $\pm$ 4.0 <sup>a</sup>	9.3 $\pm$ 0.3 <sup>b</sup>
P-value	0.005	0.357	0.001

\*\*Within a column, means with different superscripts are significantly different ( $P < 0.05$ ). RGR = relative growth rate, RCR = relative consumption rate, AD = approximate digestibility, ECD = efficiency of conversion of digested food, ECI = efficiency of conversion of ingested food.

and general vitamin deficiencies on gypsy moth performance. Feeding trials with fourth instars were conducted to determine dietary effects on growth and consumption rates and food processing efficiencies. Newly molted fourth instars (80–100 mg) were placed individually into 28 ml plastic cups containing a cube of one of the four test diets. We assayed twelve insects (replicates) per diet. Food was replaced at 2–3 day intervals, or more frequently if needed, until completion of the fourth stadium. Newly molted fifth instars were frozen, then larvae, frass and remaining food were dried (65°C) and weighed. Initial dry weights of larvae and food were estimated using proportional dry weights derived from subsets of larvae and food not used in the experiment. We calculated nutritional indices based on standard formulas (Waldbauer 1968, Scriber 1977). Relative rates of growth and consumption were calculated based on initial rather than mean insect weight (Farrar et al. 1989).

Our second bioassay assessed the effects of vitamin deficiencies on insect survival, development, and pupal weights. Newly molted fourth instar larvae (12–16 per replicate, six replicates per diet) were placed into 600 ml plastic rearing containers and fed one of the four test diets. We recorded survival rates and pupal weights (3–4 days post pupation) until all larvae had either died or pupated.

Results from both bioassays were analyzed by one-way analysis of variance (ANOVA) using SAS statistical software. Treatment means were compared by the Student-Newman-Keuls multiple range test (SAS Institute 1985).

## RESULTS

Performance of fourth instar gypsy moths was largely unaffected by dietary vitamin treatment (Table 3). Development rates (stadium duration) and consumption rates did not differ among treatments. Growth rates of larvae fed the NoVit diet were 14% lower than those of larvae fed the HiVit+Asc

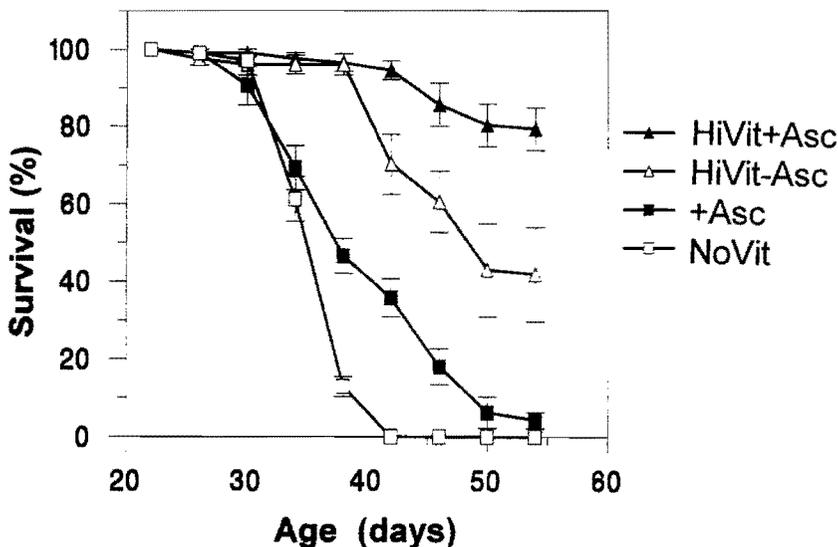


Figure 1. Survival of fourth and fifth instar gypsy moths on control and vitamin deficient diets. Vertical lines indicate  $\pm 1$  S.E.

diet, but not significantly lower than those of larvae on other vitamin deficient diets. Larvae on the NoVit diet also exhibited reduced food processing efficiency; approximate digestibility decreased 36% relative to that of insects on the HiVit+Asc diet.

In contrast to results from the fourth instar feeding studies, we found striking effects of vitamin deficiencies on mortality of fourth/fifth instars (Fig. 1). Elimination of ascorbic acid from a high vitamin diet reduced survival rate from 79 to 42%. Only 4% of larvae fed the +Asc diet survived through pupation, whereas none of the larvae on the NoVit diet survived through pupation. Moreover, mortality occurred earlier for insects on the NoVit diet than for those on the +Asc diet, and earlier for larvae fed the +Asc diet than for those fed the HiVit-Asc diet. Many of the insects reared on the NoVit diet died in the molt to the fifth stadium. Most mortality for insects fed the HiVit-Asc diet occurred during the metamorphic molt (larva to pupa). Interestingly, development times and pupal weights were not negatively affected for the fraction of insects fed the HiVit-Asc diet that successfully pupated (Table 4).

## DISCUSSION

In general, vitamin deficient diets did not markedly alter growth and developmental rates of gypsy moth larvae. The single exception was the NoVit diet, but even those effects were marginal. In an earlier study with the HiVit+Asc and NoVit diets, the latter caused a 27% reduction in growth due to a decrease in the efficiency of conversion of digested food (ECD) (Lindroth et al. 1991). Growth of other lepidopteran species appears to be more sensitive to ascorbic acid deficiency than what was exhibited by gypsy moth larvae.

Table 4. Dietary effects on development times and pupal weights of gypsy moths (mean  $\pm$  1 S.E.) $\dagger$ 

Diet	Duration (days)		Weight (mg)	
	Males	Females	Males	Females
HiVit+Asc	37.3 $\pm$ 0.2 <sup>a</sup>	42.5 $\pm$ 0.4 <sup>a</sup>	541 $\pm$ 10 <sup>a</sup>	1559 $\pm$ 47 <sup>a</sup>
HiVit-Asc	38.9 $\pm$ 0.3 <sup>a</sup>	42.9 $\pm$ 0.3 <sup>a</sup>	550 $\pm$ 12 <sup>a</sup>	1298 $\pm$ 35 <sup>a</sup>
P-Value	0.064	0.863	0.827	0.192

$\dagger$ Within a column, means bearing different superscripts are significantly different ( $P < 0.05$ ).

$\ddagger$ Poor survival of larvae on the +Asc and NoVit diets precluded incorporation into this table.

Shao et al. (1993) reported greatly reduced growth and 0% survival (to pupation) of *Manduca sexta* Joh. larvae reared on artificial diets lacking ascorbic acid. Navon et al. (1985) found that within 72 hours following ascorbic acid deprivation, consumption rates increased and growth rates decreased in *M. sexta* and *Spodoptera littoralis* (Boisduval).

The most pronounced effect of ascorbic acid (and total vitamin) deficiency in our study was on larval mortality. This result was also observed by Lindroth et al. (1991), who found that vitamin-deficient larvae succumbed to NPV infection. Such was not the case in this study, as microscopic examination revealed no polyhedral inclusion bodies.

Mortality occurred primarily during periods of molting. Elevated mortality during the molt is consistent with results of other studies with lepidoptera (Navon 1978, Kramer and Seib 1982). This phenomenon has been attributed to the putative role of ascorbic acid in cuticle formation, particularly in collagenesis and control of diphenoloxidase activity (Navon 1978, Navon et al. 1985). Rapid onset of ascorbic acid deficiency symptoms in actively feeding *M. sexta* and *S. littoralis* larvae, however, led Navon et al. (1985) to investigate other mechanisms of action. They concluded that debility may be linked to disruption of ion and water transport processes.

That ascorbic acid plays multiple roles in insect biochemistry/physiology is becoming increasingly clear. The sensitivity of different biochemical/physiological processes to ascorbic acid deficiency, however, appears to differ among insect species. Unlike the results of Navon et al. (1985) for *M. sexta* and *S. littoralis*, only molting processes appear to be highly susceptible to ascorbic acid deficiency in gypsy moth larvae.

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SWARMING AND MATING IN *Aedes PROVOCANS*  
(DIPTERA: CULICIDAE)

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ABSTRACT

Male *Aedes provocans* formed canopy-level linear swarms in association with prominent trees along hedgerows or convex prominences along woodlot margins. Males oriented along the east-west or north-south axis of the swarm site and flew continuously in alternating directions along the longitudinal axis of the swarm. Swarming began shortly before (mean = -0.78 crep) and ended after sunset (mean = 0.81 crep). The time of onset of swarming was more variable than the time of cessation; on 3 of 5 occasions, swarming stopped abruptly at 0.94 crep, about 2 minutes before the end of civil twilight. Swarming began 4 d after the onset of emergence of the adults and persisted for 3 weeks, but copulations were observed for only the first 6 d. In-flight mating always took place after sunset, many minutes after the onset of swarming. On average, copulation lasted 9.9 s.

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In most species of Diptera, males aggregate at species-specific times in species-specific arenas, and there fly, hover, or perch, and respond to females that enter the arena by pursuing and capturing them (Downes 1969); mating is initiated and often completed in flight. Among the *Aedes* mosquitoes the aggregation is usually a lek-like swarm (inter alia: Frohne and Frohne 1952; Nikolaeva 1976; Reisen et al. 1977), but the swarming sites and behaviors of most species remain undescribed or poorly known. Swarming is the critical species-isolating mechanism (Downes 1969) and may provide a mechanism for sexual selection via scramble-competition polygyny or even female choice (Thornhill and Alcock 1983). An understanding of the multi-species communities of mosquitoes that are common in many parts of the world could be enhanced by knowledge of the swarming habits of the constituent species.

*Aedes provocans* (Walker) is among the first of the snow-melt *Aedes* to emerge in eastern Ontario (Wood et al. 1979, Gadawski and Smith 1992). The species provides a convenient model for the field study of mosquito behaviors: emergence is highly synchronous and occurs over a narrow time window; the species is abundant (Gadawski and Smith 1992); and, as compared to most snowmelt *Aedes*, the adults are unusually easy to identify (Owen 1937). Here we present observations of swarming and mating of *Ae. provocans* through an entire season.

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## MATERIALS AND METHODS

Field studies were conducted near Read, Ontario (44°18'N, 77°10'W; UTM: 18TUE271072; ca. 20 km NE of Belleville) in May-June 1978. The study area (Fig. 1) provided a diversity of habitats, including hayfields, pasture, fields abandoned since 1975, hedgerows and mature deciduous forest (predominantly *Acer rubrum* and *A. saccharinum*) with abundant, temporary, snowmelt pools. Both nectar and blood sources were abundant and nearby (Gadawski and Smith 1992; Smith and Gadawski 1994).

Emergence traps (Hayton 1979) were used to ascertain dates of adult emergence. Three traps were placed on woodland pools in late April before adults had emerged; sites with different degrees of canopy closure were selected to ensure that the range of emergence dates in the study area would be well represented.

Host-seeking females were captured at human bait throughout the adult flight season. For capture and dissection methods, see Gadawski and Smith (1992).

Swarming behavior was studied with the naked eye and with the aid of 8× binoculars. Copulation times were measured with a digital stopwatch. Air temperatures at the conclusion of swarming were measured with a shaded thermistor at 1 m. Males were captured from swarms with a standard insect net and identified using Wood et al. (1979). The height of swarming males was measured with an optical range finder aimed at trees immediately adjacent to and at the elevation of the swarms. Times of sunset and the duration of civil twilight were computed by The Floppy Almanac (Carroll 1991); corrections for local altitude, refraction and parallax were deemed unimportant biologically and were not made. Because the time of sunset advances rapidly from day to day in the spring, times of swarming and mating are given in crep units (Nielsen 1963) as well as real time (EDT); 1 crep unit is equal to the duration of civil twilight, with negative values indicating times prior to sunset. As a point of reference—on 18 May, the day that mating was first observed, sunset is at 2032 h; civil twilight lasts 34 min, ending at 2106 h.

Means for copulation times were examined by a 2-tailed t test and variances by a 2-tailed F test. The maximal probability of a type-1 error was set at 0.05. Error terms are standard errors.

## RESULTS

Male *Ae. provocans* emerged over the 7-d period from 14 to 21 May, peaking on 16 May; females emerged over the 5-d period from 16 to 21 May, peaking on 19 May (Fig. 2). Swarming males were first seen on 18 May, 4 d after male emergence had begun (Fig. 2) and males continued to swarm, in diminishing numbers, until 7 June (Fig. 2), for a total swarming duration of 21 d. However, copulations were observed for only the first 6 d (18–23 May) of the swarming period (Fig. 2). Uninseminated females were encountered in the population until 27 May, 6 d after the last detected female emergence and 4 d after the last observed copulation in swarms (Fig. 2). Host-seeking females were encountered over a 38-d period, from 16 May, 2 d before the first swarming, until 23 June (Fig. 2). Thus, male swarms were present for a little more than half the period of time that females were on the wing but copulations were observed for only a small proportion of that time (Fig. 2).

In the evening of 18 May, the first pleasant evening since the beginning of emergence, males of *Ae. provocans* were found in a single, large swarm at site 1 (Fig. 1) along the southern boundary of a woodlot, about 50 m south of the nearest larval habitats. The swarm was situated at about 15.5 m, about 1 m



Figure 1. Aerial photograph, taken in late summer in the year of the study, showing swarm sites (arrows) used by male *Aedes provocans*. Numbered sites are discussed in the text. Larval habitats were in both the north and south woodlots.

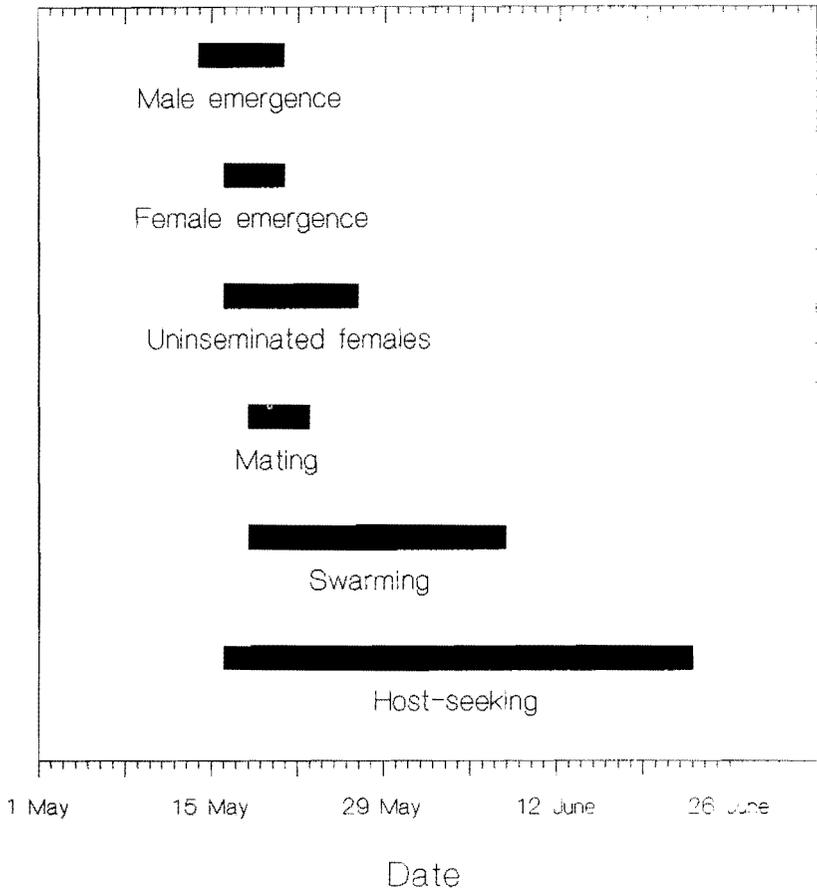


Figure 2. The duration of major events in the life history of adult *Aedes provocans*. The period shown for uninseminated females includes females taken during the emergence period, swept from resting sites and while host seeking at man.

below the forest canopy and 1-2 m out (south) from the forest margin. The long axis of the swarm was parallel to the ground and extended from east to west, bending slightly along the convex margin of the woodlot. The swarm measured 20 m long by 1 m wide by about 1 m deep and we estimated a density of several hundred males per cubic meter, so that the swarm comprised at least several thousand individuals. The noise of the swarm was audible from a considerable distance. Swarming began at 2020 h (-0.35 crep) (Table 1) under a cloudless sky with almost no wind. As light intensity declined, the elevation of the swarm decreased slightly; at 2038 h (0.18 crep) the swarm was at about 12 m.

Two additional swarms appeared about 2040 h (0.24 crep) at sites 2 and 3 (Fig. 1), each also associated with convex prominences of the woodlot bound-

Table 1. Time of initiation, termination and duration of swarming and mating in *Aedes provocans*.

Date	Swarming <sup>a</sup>			Temp. (°C) <sup>b</sup>
	Beginning	Ending	Duration (h)	
18 May	-0.35	0.94	0.73	13.3
19 May	-0.66	0.77	0.83	19.8
20 May	-0.83	0.46 <sup>c</sup>	0.75	15.3
21 May	-1.29	0.94	1.30	14.3
23 May	-	0.94	-	18.0

Date	Mating <sup>a</sup>			Temp. (°C) <sup>b</sup>
	Beginning	Ending	Duration (h)	
18 May	-	-	-	13.3
19 May	-	-	-	19.8
20 May	-	-	-	15.3
21 May	0.43	0.69	0.15	14.3
23 May	0.23	0.83	0.35	18.0

<sup>a</sup>Times of beginning and ending of swarming and mating are given in crep units.

<sup>b</sup>Air temperature at 1 m at the end of the swarming period.

<sup>c</sup>Heavy rain falling at this time.

ary. The height, orientation and behavior of the males in these swarms was identical to those of the males swarming at site 1. Males did not swarm along the concave sections of the forest edge (Fig. 1). Cessation of swarming was abrupt. A slight reduction in the density of swarming males at site 1 was evident at 2058 h (0.76 crep) and the remaining males had moved closer to the trees. One minute later (2059; 0.79 crep) the reduction in density was marked; only scattered individuals remained at 2104 (0.94 crep). In total, then, males swarmed for slightly less than 45 minutes at a temperature of about 13°C (Table 1).

Flights of males within the swarm were along the east-west axis. Males flew toward the western sky in a leisurely, dance-like fashion, with up-and-down bobbing, then turned abruptly and flew east at a faster pace, turned and resumed a westward flight. Individual males pursued flight paths that were shorter (8-10 m) than the length of the swarm.

On 19 May, swarming began at 2010 h (-0.66 crep) at sites 1 and 2; no males swarmed at site 3. In addition, swarms were found at two sites (site 4 and 5, Fig. 2) along a fence row about 100 m to the east of the original swarm sites. At these sites male *Ae. provocans* swarmed contemporaneously with the males at sites 1 and 2 but their orientation was quite different. Males at sites 4 and 5 swarmed along a north-south axis on the western margin of the hedge-row, again near the summit of the adjacent trees: males at site 4 swarmed at 9.5 m in a swarm about 5×1×1 m in size and those at site 5 at 16 m in a swarm 20×1×1 m in size. In these sites, the slow dance was performed toward the south and the fast return flight toward the north. On this second evening of swarming, males began swarming earlier and ended earlier so that the total duration of swarming (0.83 h) was only slightly longer than that of the previous evening (Table 1).

On 20 May observations were restricted to sites 1-3. Swarming had not yet begun at 2000 h (-0.97 crep); light rain was falling and there was a gusty, light, west wind. Swarming began abruptly at 2005 (-0.83 crep) at both sites 1 and 2 but, again, males did not swarm at site 3. The density of males in the swarm increased rapidly, reaching a maximum about 2010 (-0.69 crep). At

2013 h the swarm was dispersed by a strong gust of wind, driving some males to within 2 m of the ground where a net sample was taken; all 30 males haphazardly selected from the sample were *Ae. provocans*. The males regrouped following this wind disturbance and resumed swarming near the canopy, to be disrupted by wind several more times. Swarming ended abruptly at 2050 h (0.46 crep) in heavy rain.

On 21 May, additional swarm sites were discovered along the hedgerows (Fig. 1); elevation of these swarms was often lower owing to the reduced height of the trees but males were always oriented along the long axis of the site (east-west at site 6 and north-south at the 4 other sites) and were associated with prominent trees or copses along the hedgerows. Observations at site 1 at 2030 h (-0.14 crep) and at site 6 at 2041 h (0.17 crep) revealed small groups of males moving across the open meadows from the south at an elevation of 2-4 m and then entering the high swarms. Swarming ceased at 2108 h (0.94 crep), yielding a swarming period of 1.3 h (Table 1).

On 23 May, observations of the relatively low swarm at site 6 permitted more detailed inspection of male behavior. The males flew 4-5 m above the ground in a swarm subdivided into 2 portions, each about half the length of the swarm (about 8 m). A male would fly back and forth about 10 times within about half the swarm length, would then traverse the entire length of the swarm, and then repeat the entire pattern. Movement during the shorter flights was characterized by periodic bursts of speed so that a male might fly 2-3 m at a slower speed and then 1-2 m at a faster speed. The longer flight through the entire swarm was at the lower speed. Males turned and accelerated independently of one another. Swarming again ended abruptly at 0.94 crep (Table 1). 60 vouchers collected on 2 occasions from this swarm were all *Ae. provocans* (59 males, 1 female).

Over the first few days of swarming, the time of onset of swarming was more variable than the time at which swarming ended (Table 1). On 3 of 5 occasions, swarming ceased abruptly at 0.94 crep; illumination at this time (Nielsen 1963) would be about 5 lux. Inclement weather, as on 20 May, caused swarming to end much earlier (Table 1).

Observations on 27, 28 and 31 May showed that swarming continued to occur at all sites except 3, 4 and 5 but the abundance of swarming males was markedly reduced. By 2 June, the swarm at site 6 was reduced to a few scattered males and there were no swarms at sites 8-11. By 4 June, only small numbers of males could be found swarming at sites 1, 2 and 6 and after 7 June, no swarming males could be found at any site.

Copulations were seen frequently during the first 6 d of swarming (Fig. 1), and detailed observations were made on two occasions at site 6. On 21 May, copulation began at 2050 h (0.43 crep), 15 min after sunset and well after the beginning of swarming. Pairing was usually initiated within the swarm but occasionally first contact was made 1-2 m outside the swarm. After initial contact, the pair moved out of the swarm, flying horizontally or downward. Mating was completed in flight; the mean copulation time was  $12.3 \pm 2.37$  s (range 5-29;  $n=12$ ). After separation, the male rejoined the swarm but the female left the swarm site, either flying across the meadow or into adjacent vegetation. A copulation was observed every several seconds until 2059 h (0.69 crep) when all mating activity stopped abruptly. A reduction in swarm density was evident at 2104 (0.83 crep) and swarming ceased at 2108 (0.94 crep). On 23 May, mating began at 2045 (0.23 crep), 8 min after sunset, and continued until 2106 (0.83 crep). Swarming ceased at 2110 (0.94 crep). The mean copulation time was  $7.7 \pm 1.14$  s (range 2-16;  $n=13$ ). The variance of copulation times was large and on 21 May was possibly greater than that on 23 May ( $F_{11,12}=3.99$ ,  $p=0.025$ ) but the mean copulation times were not different ( $t_{23}=1.79$ ,  $p=0.087$ ). The pooled mean copulation time was 9.9 s ( $n=25$ ).

## DISCUSSION

The spring of 1978 was cool and the emergence dates of *Ae. provocans* observed in this study were somewhat later than indicated by the historical data in James et al. (1969) and by observations in the years since 1978 (Smith and Gadawski 1994); however, the durations of the emergence periods were similar over that period. Thus, the relative durations of demographic events observed in this study are probably typical but the calendar references are later than is usual for *Ae. provocans* in eastern Ontario.

There are only a few reports of the swarming of *Ae. provocans* in the literature, one questionable and the others very brief. Dyar (1923) described small "swarms" of *Ae. provocans*, about 50 males in each, drifting from a woods over a meadow in Warroad, MN on 21 May 1922. It is not clear from the description that these were really swarming males; the observation is similar to the behavior we observed, coincidentally on the same day in 1978, when males moving across the meadow subsequently joined active swarms. Perhaps what both Dyar and we witnessed was pre-swarming dispersal of males from day-time resting sites; certainly, males were commonly encountered during the day resting in vegetation both in the woods and in vegetation along the hedgerows. Maw (1961) described the swarm site of *Ae. provocans* as being defined by the electrostatic potential of the air space and hypothesized that steep electrical gradients are necessary to direct individuals into well-defined flyways. That hypothesis has not been tested and is not supported by our observations of male *Ae. provocans* swarming in a variety of directions always with reference to prominent visual markers. James et al. (1969) reported "diffuse swarms at margins of woods, with a definite circulating form similar to that described by Downes (1958) for *Aedes hexodontus*", an observation that, in part, is similar to our findings. And Wood et al. (1979) stated that they had observed males swarming after sunset in clearings in the forest, at about 5 m above the ground. Although we commonly encountered males of *Ae. provocans* swarming at that height, the swarms we observed were associated with edges (forest margins or hedgerows) and not with forest clearings, and invariably began before sunset. None of these papers provided detailed information about location and duration of the swarms on either a diel or phenological basis, and only Maw (1961) related the swarming activity to mating (2 copulations were seen over 2 years).

Swarming in *Ae. provocans* began on 18 May, 4 d after emergence had begun. Swarming may have been delayed by weather until that time but it is perhaps noteworthy that, at the temperatures near the emergence sites, males of *Ae. provocans* require about 4 d to complete hypopygial rotation (Smith and Gadawski 1994). As well, time will be needed between emergence and first swarming to obtain a nectar meal (Smith and Gadawski 1994). It is unlikely, therefore, that swarming would have begun much before 18 May even if weather conditions had been permissive. Fedorova (1988) found that swarming in *Ae. communis* (De Geer) began on the 5th day after emergence.

Our observations of crepuscular swarming in *Ae. provocans* are in agreement with the periodicities noted for most swarming mosquitoes (Nielsen and Greve 1950; Haddow and Corbet 1961; Corbet 1964). It seems clear that light intensity around the time of sunset is an important regulating or releasing stimulus for swarming (Nielsen and Nielsen 1962). The important role of light intensity is supported by our observations of *Ae. provocans* ceasing hovering at exactly the same time (0.94 crep) on 3 of the evenings on which matings were seen (Table 1). The light intensity at this time (about 5 lux) is similar to the low light intensities at which *Ae. cantans* (Meigen) (Nielsen and Greve 1950) and *Anopheles freeborni* Aitken (Yuval and Bouskila 1993) ceased swarming (7 and 0.5 lux, respectively). Dawn swarming of *Ae. provocans* was

not observed; perhaps early-morning temperatures in May are usually too low to permit sustained flight.

Commonly, mosquito swarms keep station and are situated in relation to a visually distinct marker—a treetop, roadway, patch of lichen or moss, margin of a pool, tip of a branch, and so forth (Downes 1958). *Aedes provocans* always swarmed at near tree-top level, adjacent to trees at the margins of woods or in hedgerows. The specific nature of the marker is not known but is likely to be the light-dark edge provided by trees against sky. The height above ground varied from swarm to swarm, depending on the site, but the height below the top margin of the adjacent trees was much less variable. Clearly, males of *Ae. provocans* “measure” swarming height from the top down and not from the bottom up; this is additional evidence that the marker is not ground-based. Maw (1961) observed swarms of *Ae. provocans* at an elevation of only 0.5 m flying continuously in a clockwise direction; however, details of the vegetation in the site in which the swarms formed are not given other than that it was a “small glade” in a plantation of red, white and jack pine; the ages and heights of the trees and the dimensions of the glade are not given.

Many workers (e.g. Nielsen and Greve 1950; Haddow and Corbet 1961; Downes 1969) have reported that swarming mosquitoes maintain an upwind orientation. Downes (1969) further reported that the morphology of the swarms of *Ae. hexodontus* Dyar changed as wind velocities changed; in low-wind conditions, the swarms were vertical columns, becoming progressively elongated as wind speeds increased. In striking contrast to these observations, we observed males of *Ae. provocans* orienting not with respect to wind but to the linear axis of the assembly site, and we observed males under both low- and moderate-wind situations. Males did orient to the brighter portion of the sky (west in east-west swarms and south in north-south swarms) but they flew actively in both directions within the swarm, slowly toward the brighter sky and more rapidly toward the darker sky, in striking contrast to the pattern described by Downes (1969) for *Ae. hexodontus*, in which the males flew upwind and then drifted backwards. Reisen et al. (1977) also reported that the swarms of *Anopheles*, *Culex* and *Aedes* mosquitoes in Pakistan adopted a wide variety of swarming directions. It may be that the dynamics of orientation in mosquito swarms are a function of size and position (i.e. elevation) of the marker. The purpose of the within-swarm flights and the significance of species differences in such flights are unknown.

The swarms of *Ae. provocans* are clearly mating stations. We frequently observed mating in swarms but in several years of study of *Ae. provocans* we have seen no copulations in any other situation. Most mating in *Ae. provocans* took place in the first few days of swarming. However, we encountered unseminated females in the host-seeking population for several days after we last saw mating in swarms, so some low level of mating activity may have continued for the duration of the swarming period. Fedorova (1988) found a similar pattern in *Ae. communis*, in which 80% of the females were inseminated on the third to fourth day of adult life. The emergence period in *Ae. provocans* is brief and matings were restricted to a subset of the swarming period, a pattern also reported by Yuval and Bouskila (1993), who observed mating in *Anopheles freeborni* to be most common 10–20 min after swarming had begun; in *An. freeborni*, the time of mating coincides with the maximal swarm size and a reduced risk from predation. We did not observe predation events in the swarms of *Ae. provocans* but there was a progressive increase in the size of swarms over time so females may be delaying an approach to the swarm until the swarm contains large numbers of males. The in-copula time of *Ae. provocans* (9.9 s) was brief in comparison to the copulation times reported for *Anopheles culicifacies* Giles (15.6–33.6 s) and *Culex pipiens fatigans* Wiedemann (19.7–33.0 s) by Reisen et al. (1977) but much longer than the

copulation times reported for *Mansonia fuscopennata* (Theobald) (1-3 s) (Corbet 1964).

Relative to both the temporal and seasonal durations of swarming, copulation in *Ae. provocans* is a rare event. This is probably a not-uncommon situation in many species and it is perhaps not surprising therefore that some early workers, on observing swarms without seeing copulations, questioned the functional role of swarming (Nielsen and Greve 1950). However, the high energetic costs of swarming, its almost universal occurrence, and the now-frequent correlation of swarming with mating, make it clear that mating in most *Aedes* species takes place in swarms (Downes 1969). In general, the frequency of observed mating is low in landmark-based mating systems such as those used by *Aedes* mosquitoes (Thornhill and Alcock 1983). For species such as *Ae. provocans* in which emergence is highly synchronized and occurs over a brief time period, it would be very easy to conclude that swarming was not associated with mating if the first few days of swarming activity were not sampled intensively.

Differential mating success among swarming male mosquitoes has rarely been examined. Yuval et al. (1993) found that swarming males of *Anopheles freeborni* were larger than the resting population, suggesting that some males never swarm at all. As well, early-swarming males were smaller than later-swarming males and most matings took place 10-20 minutes after swarming had begun. It is conceivable that the delay of mating seen in *Ae. provocans*, in which mating also took place late in the swarming period, may be related to differential male mating success. Such possibilities are currently under investigation.

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