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**COVER PHOTO**

*Hyles lineata* (Lepidoptera:Sphingidae) photographed August 2001, Huron Mountains, Mi. Photo by Mark F. O'Brien.
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COMMENTARY ON AMETROPUS SPECIES (EPHEMEROPTERA: AMETROPODIDAE) IN NORTH AMERICA

W. P. McCafferty¹

ABSTRACT

*Ametropus albrighti* is shown to be a junior subjective synonym of *A. neavei*, n. syn. *Ametropus neavei* sensu lato demonstrates stable structural characteristics with respect to male genitalia and larval morphology, whereas degree of maculation and therefore abdominal patterning varies both among populations and within populations. *Ametropus ammophilus* is distinctive, and the two North American species are apparently allopatric based on known distributions, which are reviewed.

The Holarctic mayfly genus *Ametropus* Albarda was originally discovered in Europe (Albarda 1878) and is now known from Asia and North America as well. Bengtsson (1913) placed this distinctive genus in a separate higher taxon Ametropodidae (originally spelled Ametropidae) where it has resided either at the family or subfamily level ever since. McCafferty (1981) referred to these mayflies as the sand minnow mayflies because of the peculiar adaptations of the larvae for life in sand substrates of rivers (e.g., Soluk and Craig 1988), and workers in general have regarded the group's relationships to be with the pisciform mayflies (e.g., Edmunds et al. 1976, McCafferty 1991).

McDunnough (1928) first discovered the genus in North America. His report was based on a single female adult from Alberta that he described as *Ametropus neavei* McDunnough. Traver (1935) described a second species, *A. albrighti* Traver, based on a series of larvae taken from the San Juan River in extreme northwest New Mexico. Edmunds (1954), Woodbury and Argyle (1963), and Pearson et al. (1968) all referred to additional larval populations of *A. albrighti* from the Green River in northeastern Utah. Newell (1970) listed *A. neavei* from Montana but provided no substantiating locale data (presumably he saw a female adult that matched McDunnough's [1928] description). Allen and Edmunds (1956) listed an unnamed species of *Ametropus* from Oregon, and later Allen and Edmunds (1976) described that species as *A. ammophilus* Allen and Edmunds based on male and female adults and larvae from Oregon, Washington, and western Montana. At the same time, Allen and Edmunds (1976) described the male adult and female subimago of *A. albrighti*, and provided additional records of that species from northwestern Utah, northeastern Colorado, and southwestern Wyoming. Allen and Edmunds (1976) also provided descriptions of the male adult and larva of *A. neavei* for the first time, along with a record of the species from Saskatchewan.

Allen and Edmunds (1976) concluded that *A. neavei* was restricted to Alberta and Saskatchewan; that *A. albrighti* was restricted to the Colorado River Drainage System in Colorado, New Mexico, Utah, and Wyoming; and that *A. ammophilus* was restricted to Oregon, Washington, and areas east to western Montana. Subsequent to the review of the genus *Ametropus* in North America by Allen and Edmunds (1976), however, several additional reports under the various species names were forthcoming. *Ametropus albrighti* was reported from Saskatchewan by Lehmkuhl (1976a) and by Dosdall and Lehmkuhl (1989). *Ametropus ammophilus* was reported from northern California by Allen (1977). *Ametropus neavei* was reported from additional localities in Alberta by Clifford

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and Barton (1979), Barton (1980), and Soluk and Craig (1988); from the upper peninsula of Michigan by Steven and Hilsenhoff (1979); from the Northwest Territories by Cobb et al. (1995); and again from Montana by Waltz et al. (1998).

ANALYSIS OF SPECIES

Ametropus ammophilus is a distinctive species within Ametropus with respect to its much larger size, cleft penes of its male genitalia, and complex abdominal color pattern. These distinctions are accurately reflected in the species treatment and key provided by Allen and Edmunds (1976) and therefore all reports under that name can reasonably be expected to have been applied to the correct species. It is known to range from northern California north through Oregon, Washington and, in the north, east to western Montana, including a first report from Idaho by Lester et al. (2002). It may also occur in Alberta (see below).

My study of materials of Ametropus from north-central and far eastern Montana and re-examination of most of the materials on which Allen and Edmunds (1976) based their review suggested that reports variously assigned to A. albrighti or A. neavei, other than those of the types, may not be reliable. Importantly, the key provided by Allen and Edmunds (1976), and probably used by every worker since that time when faced with identifying Ametropus larvae and adults, is inaccurate based on the actual concepts of the species. This fact was borne out by the examination of specimens used by Allen and Edmunds (1976) in their study. Couplet 2 indicated that A. neavei had abdominal terga 5-7 with inverted T-shaped markings. That statement actually is referable to A. albrighti based on the descriptions and figures provided by Allen and Edmunds (1976) and all prior descriptions. In the same sense, the key statement that abdominal terga 5-7 have triangular shaped markings in A. albrighti would actually have been applicable to A. neavei based on available descriptions at the time. If workers had used the maculation characters as stated in the Allen and Edmunds key, in the absence of further checking of formal descriptions, then identifications certainly could have been, and probably were, confused.

Ostensibly, A. neavei and A. albrighti differed in the intensity of the brown coloration of the mesothorax in the adults, in slight size differences, and in the abdominal tergal patterning. No differences in male genitalia and no larval structural differences (generally the important species characters in many Ephemeroptera species) had been identified, and I have not been able to find any.

My examination of mature larval and adult specimens belonging to populations from northern Saskatchewan to New Mexico demonstrate no reliable size differences that could be correlated with the coloration patterns that Allen and Edmunds assigned to A. albrighti and A. neavei, and certainly the "usually less than 16 mm" (A. albrighti) vs. "usually greater than 17 mm" (A. neavei) could not be applied with any consistency.

Ametropus albrighti adults were thought to have dark brown mesonota, and larvae and adults were thought to have inverted T-shaped markings on middle abdominal terga. Ametropus neavei were thought to have light brown mesonota in the adults and triangular markings on middle abdominal terga in larvae and adults. However, whereas some populations I examined appeared to be consistent with respect to thoracic or abdominal characteristics that had been associated either with A. albrighti or A. neavei, a few populations showed a mixture of shape and degree of abdominal markings or mixture of thoracic color intensity. In addition, most adults with a dark brown thorax, as previously associated with A. albrighti, also possessed well maculated abdominal terga (i.e., extensive triangular markings) as previously associated with A. neavei. The variation found on abdominal tergum 6 of three male adults of the same population from the North Saskatchewan River is shown in Figures 1-3.
It is strongly suggested from this that the difference between an inverted T and the triangle described by Allen and Edmunds is a matter of degree of maculation. The one larva I have from far eastern Montana has tergal patterning that is intermediate between the two extremes (close to Figure 2). Such degrees of maculation are often intraspecifically variable among populations, within populations, or may be influenced by temperature of developmental regime over time (e.g., see McCafferty and Periera 1984).

Allen and Edmunds (1976) also stated that abdominal tergum 2 in *A. albrighti* had an inverted T-shaped marking. In all specimens that would otherwise appear to be *A. albrighti* based on most other characteristics, this tergum always had a variously developed triangular marking, including the larval specimens identified and examined as *A. albrighti* by Allen and Edmunds (1976). The dark brown medial stripe described for tergum 9 of *A. neavei* may or may not be present in individual larvae of the same populations of both of what otherwise would appear to be *A. neavei* or *A. albrighti*.

Based on all of the above, it is apparent that *A. albrighti* and *A. neavei* represent a single North American species that is structurally stable but inconsistently variable with respect to degree of maculation. Therefore, I here place *A. albrighti* as a subjective junior synonym of *A. neavei*, **new synonym**.

This synonymy obviates the potential problems with the assignments of distribution records commented on above. The two now-recognized North American species, *A. ammophilus* and *A. neavei*, are not only easily characterized from each other, but they appear, to a large degree, to be allopatric. *A. ammophilus* has been reported from the Pacific Coast states and Idaho and Montana, as mentioned previously. Although both North American species possibly occur in the Athabasca River region of Alberta (J. M. Webb, pers. comm.), the only other state or province in which they both have been reported to occur is Montana, where they are clearly disjunct. In Montana, the records associated with *A. ammophilus* are from Missoula and Lake Counties (Allen and Edmunds 1976), both in the mountainous western part of that state, whereas the records associated with *A. neavei* are from Custer (Waltz et al. 1998) and Hill Counties (see Material Examined below), from the eastern and central plains area of the state, respectively. In addition to Alberta and central and eastern Montana, *Ametropus neavei* is now known from western Colorado, northern Michigan, northern New Mexico, the Northwest Territories, Saskatchewan, northeastern Utah, and southwestern Wyoming.

Figures 1-3. *Ametropus neavei* male adults, single Saskatchewan population, abdominal tergum 6: Fig. 1, individual variant 1; Fig. 2, individual variant 2; Fig. 3, individual variant 3.
Distributions of certain other mayflies also encompass ranges from New Mexico to Saskatchewan, for example, *Camelobaetidius warreni* (see McCafferty and Randolph 2000) and *Lachlania saskatchewanensis* (see McCafferty et al. 1997). Such patterns are explicable in view of historical biogeography that shows connections between the Pleistocene Saskatchewan, Columbia, and Colorado drainage systems (see Lehmkuhl 1976b). It remains to be seen if *A. neavei* still exists in New Mexico or if it has been recently extirpated as a result of impoundments on the San Juan River (see McCafferty et al. 1997). It would also be important to determine if populations still exist in the Green River in Utah below Flaming Gorge Dam. The somewhat rare western psammophilous species *Analetris eximia* Edmunds of the family Acanthametropodidae has been taken at the same locales as *A. neavei* in Wyoming (at the Black's Fork River [Edmunds and Koss 1972]), the same habitat in Saskatchewan (in the Saskatchewan River [Lehmkuhl 1976b]), the same locale in Alberta (in the Athabasca River [Barton 1980]), and from the same locale in Montana (reported here for the first time from the Milk River, see material examined below).

**MATERIAL EXAMINED**


**ACKNOWLEDGMENTS**

I thank Luke Jacobus (West Lafayette, IN) for illustrations and review of the manuscript and Pat Randolph (West Lafayette, IN) for his review of the manuscript. Research was supported in part by NSF Grant DEB 9901577. The paper has been given Purdue ARP Journal No. 16450.

**LITERATURE CITED**


The nematoceran fly family, Axymyiidae, is recorded from Wisconsin for the first time. A single adult female Axymyia furcata was collected in flight near a dead log along a forested path in south central Wisconsin on 24 April 2000.

Axymyiidae is a small and aberrant family of nematoceran flies, presently known from only five described and one or two undescribed species in the world. European and Asian species include Mesaxymyia kerteszi Duda (eastern Europe), M. stackelbergi Mamaev (eastern Siberia), Protaxymyia melanoptera Mamaev & Krivosheina (Palaearctic), and P. japonica Ishida (Japan). The single described Nearctic species, Axymyia furcata McAtee, was known previously from eastern Canada (Ontario and Quebec) south through the Appalachian Mountains to North Carolina, with isolated records from Minnesota (Krogstad 1959) and Ohio (Foote 1991). According to Wood (1981), one, or possibly two, additional undescribed Nearctic species have been discovered from Alaska and Oregon.

On 24 April 2000, a single adult female of A. furcata was captured flying within three feet of a fallen and strongly fermenting cottonwood (Populus deltoides Bartram) log. The time was between 15:30 and 17:30; the temperature was approximately 65 °F and skies were clear. The collection site, Hemlock Draw, N43° 21' 34", W 89° 56' 54", is a largely mesic forested habitat under care of The Nature Conservancy. It is located in the Baraboo Hills, Sauk County, in south central Wisconsin. A nearby small stream provides ample riparian situations hypothesized to correspond to the larval habitat described by Krogstad (1959; see below). The single specimen of A. furcata upon which this new state record is based is housed in the Insect Research Collection of the Department of Entomology, University of Wisconsin-Madison.

Larvae of A. furcata have been found in moist, water-logged wood that is in continuous contact with standing water or wet, muddy soil (Krogstad 1959, summaries by Wood 1981 and Foote 1991). The abdomen bears pinnately branched anal papillae and a prominent, non-retractile respiratory siphon that is as long as, or longer than, the body. Adults are known to emerge in late April and early May.

The large compound eyes and short antennae and legs suggest a bibionid-like appearance, but axymyiids appear not to be closely related to Bibionidae. Hennig (1973) included this family in his Pachyneuridae, based on the branching of wing veins R_3 and R_5, with the simultaneous unbranched nature of R_4+. It is now hypothesized that this character is plesiomorphic, and as no other characters appear to be supportable as synapomorphies between Axymyiidae and Pachyneuridae, the relationship is in dispute. Mamaev and Krivosheina (1966) proposed a new superfamily, Axymyioida, for the family; this scheme was supported by Wood and Borkent (1989).
LITERATURE CITED


CHECK LIST OF IDENTIFIED LEPIDOPTERA COLLECTED AT MUD LAKE STATE NATURE PRESERVE, WILLIAMS COUNTY, OHIO

Roy W. Rings

ABSTRACT

A total of 696 species of Lepidoptera is reported from the Mud Lake State Nature Preserve, Williams County, Ohio. This preserve is only a few miles from both the Indiana and Michigan state borders. The great biodiversity of moths is reflected in the bog, fen, shrub swamp, and marsh communities bordering the lake. A check list of species summarizes identified collections for 1988, 1992, 1995 and 1996 and includes the Hodges et al (1983) species numbers, the scientific name, and the numbers collected by different collecting methods. The list does not fully represent the Tineoidea and Gelechioidea lepidopteran superfamilies. Melanchra assimilis is a new State record.

This paper documents the species of Lepidoptera collected and identified at Mud Lake Bog State Nature Preserve in 1988, 1992, 1995 and 1996. It is a contribution to the comprehensive, statewide survey of Lepidoptera sponsored by The Ohio Lepidopterists begun in 1985. Our previous contributions to the Ohio survey are lepidopteran check lists of the Stark County Wilderness Center (Rings et al 1987), Atwood Lake Park in Carroll County (Rings and Metzler 1988), Mohican State Park in Ashland County (Rings and Metzler 1989), Fowler Woods in Richland County (Rings and Metzler 1990), and Goll Woods in Fulton County (Rings et al 1991). The late Dr. Sonja E. Teraguchi and Katherine J. Lublin, Cleveland Museum of Natural History, have published six check lists of moths collected in northeastern Ohio (see literature cited). An independent survey of the moths of Funk Bottoms Wildlife Area in parts of Ashland and Wayne counties was reported by Williams et al (1997).

METHODS AND MATERIALS

Description of study site. Mud Lake State Nature Preserve is one of the few remaining glacial kettle lakes in northwest Ohio. The most unusual aspect of the 74-acre preserve is the existence of an alkaline fen on one margin of the lake and a sphagnum bog on the other margin. The vegetation includes swamp birch (Betula pumila), round-leaved sundew (Drosera rotundifolia), small purple-fringed orchid (Platanthera psychodes), hoary willow (Salix candida) and large cranberry (Vaccinium macrocarpon). The marsh, bog, and fen communities are surrounded by mixed shrub swamp and swamp forest. The shrub thickets contain dogwood (Cornus amomum), willows (Salix discolor, S. sericea, S. serissima, and S. amygdaloides) and swamp rose (Rosa palustris). The bog remnant includes several mature tamarack (Larix laricina) as well as red maple (Acer rubrum) and poison sumac (Toxicodendron vernix). The cinquefoil-sedge fern remnant includes shrubby cinquefoil (Potentilla fruticosa), marsh fern (Thelypteris palustris), royal fern (Osmunda regalis), and numerous sedges (Carex spp.) interspersed with zones of broad-leaved cat-tail (Typha latifolia).
Collecting methods. Four techniques were used to recover specimens during this study. (1) Mercury vapor light and collecting sheet: A 600-volt Honda generator powered a 175-watt mercury vapor lamp suspended from a tripod of aluminum conduit pipes at a height of eight feet. A king-sized, white bed sheet was also suspended from the tripod just below the lamp. Moths, attracted to the sheet, were collected in potassium cyanide killing jars which were also charged with chloroform on rolled, paper toweling. (2) Black light traps: Two portable, Ellisco black light traps were operated each collecting night from dusk to dawn. One trap was located at the south edge of the lake and the second at the site where the light-sheet was operated. (3) Bait traps. Two bait traps were operated each collecting night from dusk to dawn. One was located at the edge of the woodland at the west end of the preserve and the other at the east end of the preserve. A sugar line was seldom used because of the lack of suitable trees and the difficulty in walking through the nearly impenetrable ground vegetation. (4) Nets. Conventional aerial nets were employed to capture butterflies and skippers. However comparatively few butterflies were collected since the density and prevalence of goldenrod thickets around the lake impeded walking.

Collection dates. Eight collecting trips were made to Mud Lake from 19 April to 7 September in 1988. In 1992 the Lake was visited 17 times from 1 May to 26 October, in 1995 10 times from 20 June to 13 October and in 1996 12 times from 27 February to 15 October. The access road (P Road) from state route 49 was not often cleared of snow and ice so the earliest collections, from 1988 to 1995, were delayed until April and May and therefore many winter and early spring species were not collected.

RESULTS

Collections of Lepidoptera for 1988, 1992, 1995 and 1996 are summarized in Table 1. The scientific names of most species listed in Table 1 follow Hodges et al. (1983). However, Hodges' check list has been up-dated by more recently published information. The systematics and nomenclature of Lepidoptera are in a dynamic state and are frequently revised. Therefore, changes in Hodges' list are necessary to incorporate newly published information by Brown (1983 & 1986); Hodges (1986); Solis and Mittr (1992); Heppner (1995); Poole (1989); Hardwick (1996); Nielsen et al (1996); Poole and Gentili (1996); and Lafontaine (1998).

Following the scientific name and author are the first and last dates of collection for that species. The numbers following each method of collection are the actual numbers collected for the four years. The status is given only for the endangered species and the rare but not endangered species.

DISCUSSION

A total of 696 species of Lepidoptera was collected and identified at Mud Lake, however, the check list does not fully represent the Tinioidea and Gelechioidea superfamilies because of the difficulty in getting specialists in these superfamilies to determine them. One species of moth collected at Mud Lake was classified as endangered, and eight species rare but not endangered. Rings et al (1992) considered Melanchra assimilis (10295) as endangered and rare since the only known specimens in Ohio are from Mud Lake. This population apparently is at the southern portion of its range in the United States. Catocala gracilis (8847) prior to 1993 was thought to be endangered since it was known only from two acid bogs in Portage County. Since that time I have

3 This information was provided by Eric H. Metzler for The Lepidoptera of Portage County, Ohio that has been submitted for publication as a Research Bulletin of the Ohio Agricultural Research and Development Center, Wooster, Ohio.
collected the species from Ravenna Arsenal also in Portage County and at Mud Lake. The current record extends the range of the species in Ohio and suggests that it may be more widely distributed in bogs than formerly indicated and not qualified for endangered species status.

The eight rare, but not endangered, species were: 8361 Macrochilo louisiana (Forbes), 9059, Capis curvata Grote, 9464 Papaipema cerina (Grote), 9480 Papaipema ptersii Bird, 9965 Xanthia undescribed species near togata, 10406 Lacinipolia olivacea (Morrison), 11064 Pyrrhia exprimens (Walker), and 11074 Heliocheilus paradoxus (Grote).

Table 1. Checklist of the identified lepidoptera collected at Mud Lake

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>HEPIALIDAE - Ghost moths</th>
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<tbody>
<tr>
<td>18</td>
<td>Sthenopis argenteomaculatus (Harris) 14 Jun 1996 MVL 1.</td>
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<tr>
<td>FAMILY</td>
<td>TINEIDAE - Fungus moths</td>
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<td>FAMILY</td>
<td>OECOPHORIDAE - Concealer moths</td>
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<td>FAMILY</td>
<td>PLUTELLIDAE - Diamond-back moths</td>
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<tr>
<td>2366</td>
<td>Plutella xylostella (Linnaeus) 10 May 1992 BLT 1.</td>
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<tr>
<td>FAMILY</td>
<td>YPONOMEUTIDAE - Ermine moths.</td>
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<td>FAMILY</td>
<td>SESIIDAE - Clear-winged moths.</td>
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<td>FAMILY</td>
<td>TORRICIDAE - Leaf-roller moths.</td>
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<tr>
<td>2765</td>
<td>Apotomis decepplana (Kearfott) 28 Jul 1992 BLT 1.</td>
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<td>2768</td>
<td>Apotomis removana (Kearfott) 6 Jul 1992 BLT 1.</td>
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<tr>
<td>2769</td>
<td>Pseudosciaphila duplex (Walsingham) 12 Jun 1988 MVL 1.</td>
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<td>2770</td>
<td>Orthotaenia undulana (Denis &amp; Schiffermüller) 5 Sep 1992 MVL 1.</td>
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<td>2785</td>
<td>Olethreutes atrodenata (Fernald) 22 Aug - 21 Sep 1992 BLT 1, MVL 4.</td>
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<td>2787</td>
<td>Olethreutes connectus (McDunnough) 28 Jul 1992 BLT 1.</td>
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<td>2788</td>
<td>Olethreutes inornatana (Clemens) Jul 30 - 4 Sep 1992 BLT 1, MVL 1.</td>
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<td>2847</td>
<td>Olethreutes glaciata (Möschler) 6 Aug 1992 BLT 3.</td>
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<td>2848</td>
<td>Olethreutes bipartitana (Clemens) 4 Sep 1992 BLT 1.</td>
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<td>2859</td>
<td>Olethreutes cespitana (Hübner) 4 Sep 1992 BLT 1.</td>
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<td>2861</td>
<td>Hedya ochroleucana (Fröhlich) 6 Jul 1992 BLT 1.</td>
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<td>Phaneta radiatana (Walsingham) 2 Jun 1992 BLT 1.</td>
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<td>Phaneta awemeana (Kearfott) 3 Jun 1992 MVL 1.</td>
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<td>Phaneta ochrocephala (Walsingham) 21 Sep 1992 BLT 1.</td>
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<td>2929</td>
<td>Phaneta ochroterminana (Kearfott) 4 Sep 1992 BLT 1.</td>
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<tr>
<td>2936</td>
<td>Phaneta tomonana (Kearfott) 5 Sep 1992 BLT 1.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2998</td>
<td>Phaneta olivacea (Riley) 4 Sep 1992 MVL 1.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3009</td>
<td>Eucosma robinsonana (Grote) 12 Jun 1988 MVL 1.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3116.1</td>
<td>Eucosma similata (Clemens) 3 - 28 Sep 1992 &amp; 1995 BLT 3, MVL 54.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3151</td>
<td>Pelochrista scintillana (Clemens) 3 Sep 1995 MVL 1.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3168</td>
<td>Pelochrista zomonana (Kearfott) 4 - 21 Sep 1992. MVL 1.</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3189 Epiblema obfuscana (Dyar) 3 Jun 1992 MVL 1.
3202 Epiblema atiosana (Clemens) 18 Jul 1995 MVL 1.
3251 Pseudexentera spoliana (Clemens) 10 May 1992 BLT 1.
3263 Gretchena bolliana (Slingerland) 2 Oct 1992 BLT 1.
3268 Gretchena concitatricana (Heinrich) 10 May 1992 MVL 1.
3251 Pseudexentera spoliana (Clemens) 10 May 1992 BLT L
3263 Gretchena bolliana (Slingerland) 2 Oct 1992 BLT 1.
3268 Gretchena concitatricana (Heinrich) 10 May 1992 MVL 1.
3471 Cydia caryana (Fitch) 4 Sep 1992 BLT 1.
3607 Argyrotaenia velutinana (Walker) 4 Sep - 3 Oct 1992 BLT 1, MVL 1.
3607 Argyrotaenia occulta (Freeman) 10 May 1992 MVL 3, BLT 1.
3623 Argyrotaenia quercifolia (Fitch) 28 Jul 1992 MVL 1.
3625 Argyrotaenia mariana (Fernald) 20 Jun 1995 MVL 2.
3632 Choristoneura fumiferana (Clemens) 24 Jul 1992 MVL 1.
3638 Choristoneura fumiferana (Clemens) 24 Jul 1992 MVL 1.
3658 Archips purpurana (Clemens) 28 Sep 1995 MVL 1.
3706 Sparganothis xanthodes (Walker) 6 Jul 1992 BLT 1.
3711 Sparganothis unifasciana (Clemens) 26 Jun - 6 Jul 1992 MVL 2.
3720 Sparganothis reticulatana (Clemens) 5 Sep 1992 MVL 1.
3725 Sparganothis pettitana (Robinson) 6 Jul 1992 MVL 1.
3732 Platynota flavida (Clemens) 5 Sep 1992 BLT 1.

FAMILY PIERIDAE - Whites and sulfur butterflies
4197 Pieris rapae (Linnaeus) 5 Sep 1992 N 2.
4209 Colias philodice philodice (Godart) 5 Sep 1992 N 5.

FAMILY LYCAENIDAE - Gossamer-winged butterflies
4282a Catocala palaestina albaceps (Godart) 28 Jul 1992 MVL 1.

FAMILY NYMPHALIDAE - Brush-footed butterflies
4421 Polygonia comma (Harris) 23 Aug -23 Oct 1992 BT 5.
4433 Aglais milberti milberti (Godart) 5 Sep 1992 N 1.
4437 Vanessa atalanta rubria (Fruhstorfer) 4 Sep - 23 Oct 1992 BT 3, N 1.
4450 Speyeria cybele cybele (Fabricius) 5 Sep 1992 N 2.
4522b Limenitis arthemis arthemis (Fabricius) 23 Aug 1992 BT 1.
4523 Limenitis archippus archippus (Cramer) 5 Sep 1992 N 2.
FAMILY SATYRIDAE - Satyr butterflies
4569 Satyrodes appalachia leeuwi (Gatrelle & Arbogast) 23 Aug 1992 BT 2.

FAMILY LIMACODIDAE - Slug caterpillar moths
4562 Tortricida testacea (Packard) 2 Jun 1992 BLT 1, MVL 2.
4564a Tortricida flexuosa caesonia (Grote) 20 Jun 1995 MVL 1.
4671 Prolimacodes badia (Hubner) 18 Jul 1995 1:VL 2.
4677 Phobetron pithecium (J. E. Smith) 31 Jul 1995 MVL 1.

FAMILY PYRALIDAE - Snout moths.
4755 Synclita obliteralis (Walker) 30 Jul 1995 MVL 2.
4759 Paraponyx maculalis (Clemens) 28, 7 Nov 1992 BLT 1.
4897 Evergestis pallidata (Hufnagel) 4 - 19 Sep 1992 & 1996 BT 1, MVL 1.
4936 Saucrobotys futilalis (Lederer) 3 Jun - 4 Sep 1992 BLT 2.
4958a Anania funebris glomera lis (Walker) 27 Jun 1996 MVL 1.
4962 Hahncappsia marculenta (Grote & Robinson) 6 Aug 1992 MVL 1.
5034 Pyrausta signatalis (Walker) 6 Jul 1992 BLT 2.
5073a Pyrausta niveicilialis (Grote) 6 Jul 1992 MVL 1.
5355 Crambus praefectellus (Zincken) 4 Sep 1992 BLT 1.
Crambus girardellus Clemens 29 May 1988 MVL 1.
Crambus laqueatellus Clemens 27 Jun 1996 MVL 1.
Crambus girardellus Clemens 29 May 1988 MVL 1.
Crambus laqueatellus Clemens 27 Jun 1996 MVL 1.
Crambus laqueatellus Clemens 27 Jun 1996 MVL 1.
Agriphila vulgivagella (Clemens) 19 28 Sep 1995 MVL 9.
Microcrambus elegans (Clemens) 14 Jul - 4 Sep 1992 & 1996 (multiple generations) BLT 14, MVL 8.
Parapediasia teterella (Zincken) 18 Jul 1995 MVL 1.
Acrobasis caryae Grote 4 Sep 1992 BLT 1.
Nephopterix vetustella (Dyar) 6 Jul - 4 Sep 1992 BLT 1, MVL 1.
Acrobasis caryae Grote 4 Sep 1992 BLT 1.
Geina periscelidactyla (Fitch) 27 Jun 1996 MVL 1.
Euthyatira pudens (Guenee) 10 May 1992 BLT 1.
Eumacaria latiferrugata (Walker) 4 Sep 1992 MVL 2.
Semiothisa xanthometata (Walker) 18 May 1996 MVL 1.
Semiothisa ocellinata (Guenee) 3 Sep 1995 MVL 1.
6598 Protoboarmia porcelaria (Gueneé) 31 Jul 1995 MVL 3.
6601 Melanolophia signataria (Walker) 18 May 1996 MVL 2.
6603a Eiston betularia cognataria (Gueneé) 2 Jun - 5 Sep 1992 BLT 2, MVL 10.
6606 Phigalia titea (Cramer) 19 Apr 1996 BLT 2.
6608 Erannis tiliaria (Harris) 29 May 1988 (larvae); 23 Oct 1992 MVL 2.
6610 Lomographa glomeraria (Grote) 7 - 29 May 1988 MVL 3.
6612 Chromolithia garnetaria (Grote) 2 May - 3 Jun 1988 BLT 2.
6617 Euchlaena irraria (Barnes & McDunnough) 29 May 1988 MVL 1.
6631 Cepphis armataria (Herrich-Schäffer) 31 Jul - 16 Aug 1995 MVL 8.
6634 Probole alienaria nyssaria (Gueneé) 10 May 1992 BLT 2, MVL 1.
6638 Plagodis fervidaria (Herrich-Schäffer) 27 Jul 1988 BLT 1.
6639 Plagodis alcoolaria (Gueneé) 7 May - 20 Jun 1988 & 1995 BLT 1, MVL 1.
6641 Lambdina fiscellaria (Gueneé) 20 Oct 1995 MVL 1.
6642 Lambdina fiscellaria (Grote & Robinson) 20 Jun 1996 MVL 6.
6643 Cingilia catenaria (Drury) 3 Oct 1992 MVL 1.
6644 Lambdana fiscellaria (Grote & Robinson) 20 Jun 1996 MVL 6.
6648 Eugonobapta nivosaria (Gueneé) 6 Jul - 4 Sep 1992 BLT 5, MVL 32.


7157 *Scopula vacuminaria* (Morrison) 26 Jun - 6 Jul 1992 BLT 1, MVL 2.


7197 *Eulithis gracilinata* (Guenee) 4 Sep - 3 Oct 1992 BLT 1, BT 2, MVL 2.

7201 *Eulithis testata* (Linnaeus) 14 - 19 Sep 1992 & 1995 BLT 1, MVL 3.


7240 *Coryphista meadii* (Packard) 20 Sep 1996 MVL 2.


7329 *Anticlea vasiliata* (Guenee) 7 - 10 May 1988 & 1992 MVL 17.

7398 *Coryphista meadii* (Packard) 20 Sep 1996 MVL 2.


7445 *Horisme intestinata* (Guenee) 3 Jun 1996 MVL 1.


7474 *Heteropacha rileyana* Harvey 18 May 1996 MVL 1.


FAMILY SATURNIIDAE - Emperor moths.
7758 Actias luna (Linnaeus) 10 May - 18 Jul 1992 BLT 1, MVL 4.

FAMILY SPHINGIDAE - Hawk moths.
7784 Dolba hyloeus (Drury) 18 Jul 1995 MVL 1.
7846 Heterocampa subrotata Harvey 3 Jun 1992 BLT 1.
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7995 Heterocampa biundata Walker 20 Jun 1995 MVL 1.
8006 Schizura badia (Packard) 27 Jun 1996 MVL 1.
8007 Schizura unicornis (J. E. Smith) 29 May - 16 Aug 1988, 1992 & 1995 BLT 1,
MVL 15.
8011 Schizura leptinoides (Grote) 18 Jul 1995 MVL 1.

FAMILY ARCTIIDAE - Tiger moths

MVL 22.
8112 Haploa lecontei (Guérin-Méneville) 31 Jul 1992 MVL 1.
8118 Holometina opella (Grote) 18 Jul 1995 MVL 7.
MVL 23.
8133 Spilosoma latipennis Stretch 26 Jun - 6 Jul 1992 BLT 3.
8169 Apantesis phalerata (Harris) 29 May - 13 Oct 1988 BLT 5, MVL 15.
8211 Lophocampa caryae Harris 3 - 20 Jun 1992 BLT 2, MVL 37.
8231 Cycnia oregonensis (Stretch) 3 Jun 1996 MVL 3.
MVL 105.

FAMILY LYMANTRIIDAE - Tussock moths


FAMILY NOCTUIDAE - Owllet moths

8333 Idia denticulalis (Harvey) 19 Sep 1995 MVL 1.
8340 Zanclognatha litudialis (Hübner) 29 May 1988 BLT 2.
8351 Zanclognatha cruralis (Gueneé) 16 Aug 1995 MVL 2.
8352 Zanclognatha jacchusalis (Walker) 17 Jul - 21 Sep 1988 MVL 5.
8362 Phalaenostola metonalis (Walker) 12 Jun - 5 Sep 1988 BLT 6, MVL 2.
8368 Tetanolita floridana (Smith) 6 Jul-19 Sep 1992 & 1995 BLT 1, MVL 2.
8773 *Catocala epione* (Drury) 12 Aug 1940 (from data base of The Ohio Lepidoperists - collector unknown).
8781 *Catocala judith* Strecker 31 Jul - 20 Sep 1995 MVL 8.
8797 *Catocala subnata* Grote 31 Jul - 23 Oct 1995 BLT 1, BT 1, MVL 5.
8864 *Catocala grynea* (Cramer) 28 Jul - 21 Sep 1992 BLT 2, BT 1, MVL 6.
8876 *Catocala micronympha* Guenee 17 Aug 1996 MVL 1.
8877 *Catocala connubialis* Guenee 18 Jul 1995 MVL 3.
8889 *Ctenoplusia oxygramma* (Geyer) 21 Sep 1992 MVL 2.
8905 *Eosphoropteryx thyatiroides* (Gueneé) 26 Jun 1992 BLT 1.
8907 *Megalographa biloba* (Stephens) 6 Aug - 21 Sep 1992 BLT 2.
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8957 Paectes oculatrix (Gueneé) 14 Jun - 3 Sep 1995 & 1996 MVL 5. Common

8958 Eutelia pulcherrima (Grote) 3 Jun 1992 & 1996 BLT 1, MVL 1.

8970 Baileya ophthalmica (Gueneé) 2 Jun 1992 BLT 2.


8972 Baileya levitans (Smith) 2 Jun - 26 Jul 1992 MVL 2.


8975 Nycteola frigida (Walker) 6 Jul 1992 BLT 1.

8983 Meganola minuscula (Zeller) 7 May 1995 BLT 1.

8983.1 Meganola (Dyar) 21 Sep 1992 MVL 1.

8992 Nycteola lrigidana (Walker) 6 Jul 1992 BLT 1.


9059 Capis curvata Grote 20 Jun 1995 MVL 1. Rare but not endanded.


9066 Leuconycta lepidula (Grote) 2 Jun - 14 Jul 1992 & 1996 BLT 1, MVL 3.

9070 Amyna octo (Gueneé) 4 - 19 Sep 1992 & 1995 MVL 2.


9184 Colocasia flavieornis (Smith) 6 Aug 1992 MVL 1.


9251 Acronicta retardata (Walker) 29 May 1998 MVL 1.
9261 Acronicta impressa (J. E. Smith) 20 Jun 1995 MVL 3.
9285 Polygrammate hebraeicum Hubner 20 Jun 1995 MVL 3.
9308 Apamea cariosa (Gueneé) 28 Jun 1992 MVL 1.
9309 Apamea vulgaris (Grote & Robinson) 20 Jun 1995 MVL 1.
9310 Apamea lignicolora (Gueneé) 3 Jun 1992 MVL 1.
9333 Oligia chlorostigma (Harvey) 6 Jul 1992 MVL 1.
9338 Oligia exhausta (Smith) 19 Jul 1995 MVL 1.
9341 Oligia mactata (Gueneé) 21 Sep - 13 Oct 1992 BT 3, MVL 3.
9346 Papaipema cerina (Grote) 19 Sep - 6 Oct 1995 & 1996 BLT 5. Rare but not endangered.
9351 Papaipema rutila (Gueneé) 3 Oct 1992 MVL 1.
9353 Papaipema pterisii Bird 6 Aug 1988 BLT 1. Rare but not endangered.
9355 Papaipema rutila (Gueneé) 3 Oct 1992 MVL 1.
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9497 Papaipema necopina (Grote) 3 Sep 1995 MVL 2.
9535 Eupsilia tristigmata (Grote) 1 May 1992 BLT 1.
9939 *Eupsilia devia* (Grote) 11 Apr 1996 BT 2.

9961 *Anathix ralla* (Grote and Robinson) 3 Sep 1995 MVL 1.


10048 *Endangered and rare. State record.*

10495 Orthosia hibisci (Gueneé) 19 Apr - 7 May 1988, 1992 & 1996 BLT 7, MVL 47.
10502 Himella intractata (Morrison) 10 May 1992 MVL 1.
10521 Morrisonia confusa (Hubner) 7 - 10 May 1988 & 1992 BLT 11, MVL 3.
10521.1 Morrisonia latex (Gueneé) 6 - 14 Jul 1992 & 1995 MVL 2.
10563 Protorthodes oviduca (Gueneé) 7 May - 3 Jun 1992 & 1996 BLT 1, MVL 17.
10589 Orthodes goodei (Grote) 31 Jul 1995 MVL 1.
10676 Feltia herilis (Grote) 21 Sep - 3 Oct 1992 BLT 3, MVL 1.
10891 Ochropleura implecta (Harris) 7 May - 30 Jul and 6 Aug - 28 Sep 1988, 1992 & 1996 (two generations) BLT 24, BT 1, MVL 47.
10911 Anicia infecta (Ochsenheimer) 30 Jul - 28 Sep 1995 MVL 2.
10926 Spa.elotis clandestina (Harris) 12 - 26 Jun and 6 - 23 Oct 1988, 1992 & 1996 (two generations) BLT 1, BT 1, MVL 47.
10996 Metalepsis saticarum (Walker) 19 Apr 1996 BLT 2, MVL 1.
11010 Heptagrotis phyllophora (Grote) 18 Jul 1995 MVL 1.
11045 Rhynechagrotis anchocelioides (Guenee) 28 Sep 1995 MVL 1.
11064 Pyrrhia exprimens (Walker) 20 Jun 1995 MVL 1. Rare but not endangered.
11072 Heliothis unidentifed species (near phloxiphagus) 30 Jun 1996 MVL 1.

Forbes identified this species as Heliothis lutetitiusc Grote.

111074 Heliocheilus paradoxus (Grote) 28 Jul 1992 MVL 1. Rare but not endangered.
11135 Schinia rivulosa (Guenee) 23 Aug - 21 Sep 1992 MVL 5.
11164 Schinia florida (Guenee) 18 Jul 1995 MVL 1.

Abbreviations: BLT, black light trap; BT, bait trap; MVL, mercury vapor light and sheet; N, net capture; S, sugaring.

ACKNOWLEDGMENTS
Sincere thanks and gratitude are extended to the following taxonomic specialists who identified moths that I could not determine: Eric H. Metzler, Arctiidae, Notodontidae, and Noctuidae; Dr. William E Miller, Olethreutinae; Dr. George Balogh and Dennis Currutt, Pyralidae; Dr. Charles V. Covell, Jr., Geometridae; Reed A. Watkins, Pterophoridae.

LITERATURE CITED


DISTRIBUTION OF TERRESTRIAL ISOPODS (CRUSTACEA: ISOPODA) THROUGHOUT MICHIGAN: EARLY RESULTS

Jennifer L. Stoyenoff

ABSTRACT

Results are reported from the first two years of a multi-year study on the distribution of terrestrial isopods (Crustacea: Isopoda) in Michigan. During the first year of the study (1997), intensive investigations were carried out using pitfall traps in a small area of Midland, MI. The study was resumed in 2001 with opportunistic collection and hand-sorting of litter samples for terrestrial isopods throughout 30 Michigan counties. As a result of this data collection, the species *Haplothalmus danicus*, previously unrecorded in the state, has been located in seven counties, and 83 new county records have been established for eight other terrestrial isopod species in Michigan. In particular, this study adds extensively to distributional knowledge for four species so far: *Hyloniscus riparius*, *Trichoniscus pusillus*, *Oniscus asellus*, and *Armadillidium vulgare*. Another species, *Armadillidium nasatum*, previously reported only inside greenhouses in three somewhat southern locations in the state, was found as clearly well-established outdoor populations in two additional counties further north. Habitat/microhabitat information is presented for all species.

The isopod fauna of Michigan is poorly studied. Much information is lacking on species occurrence and distributions, associations with habitats and microhabitats, and biology and ecology of the organisms. As of 1991, only 12 papers listing any new records for isopod distributions in Michigan had been published, and just two of those had appeared in the preceding 40 years (Snider 1991). The most up-to-date compilation of records from both published literature and museum holdings (Snider 1991) indicated that 11 terrestrial species were known from the state as of 1991, many of these from only a few localities (Table 1).

Of the 83 counties in Michigan, nine counties had no known terrestrial isopod records as of 1991, 36 counties had records of only a single species, and 25 counties had only two or three species reported (Snider 1991). The remaining 13 counties in the state—one with four or five isopod species recorded, one with seven species records, and one with 10 known species—suggest that the other 70 counties are likely not as barren in terms of terrestrial isopod fauna as current records would indicate. More in-depth and current survey work has been sorely needed on this group of organisms.

It is likely that some or all of the numerous terrestrial isopod species occurring in surrounding areas of the Great Lakes region may be found in similar distribution patterns in Michigan as well. For instance, workers in Wisconsin have recorded *Cylisticus convexus* (DeGeer), *Porcellio spinicornis* Say, and *Trachelipus rathkei* (Brandt) from every county in their state (Jass and Klausmeier 1996). It is reasonable to expect that these same species may be widespread in Michigan also. In fact, two of these species had been recorded from numerous localities in the state as of 1991, although they had not yet been found state-wide; the third species, *P. spinicornis*, has been much less known in Michigan. Further investigation is needed to determine which if any species are present state-wide here.

While surrounding areas have many of the same terrestrial isopod species as Michigan, 11 additional species not previously reported from Michigan have

1 Dow Gardens, Midland, MI 48640 (correspondence address) and University of Michigan, School of Natural Resources and Environment, Ann Arbor, MI 48109-1115.
Table 1. Terrestrial isopod species known from Michigan, and the number of counties in which each species had been recorded as of 1991 (data from Snider 1991 with an emendation from Hatchett 1947), as well as after the present survey. There are a total of 83 counties in the state of Michigan.

<table>
<thead>
<tr>
<th>Species</th>
<th>Counties where known in 1991</th>
<th>Counties where known in 2001</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ligidium elrodii Packard</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Haplophthalmus danicus Budde-Lund</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Hyloniscus riparius (C. L. Koch)</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>Trichoniscus pusillus Brandt</td>
<td>2</td>
<td>21</td>
</tr>
<tr>
<td>Oniscus asellus Linnaeus</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>Armadillidium nasatum Budde-Lund</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Armadillidium vulgare (Latreille)</td>
<td>14</td>
<td>36</td>
</tr>
<tr>
<td>Cylisticus convexus (DeGeer)</td>
<td>30</td>
<td>35</td>
</tr>
<tr>
<td>Porcellio scaber Latreille</td>
<td>21</td>
<td>25</td>
</tr>
<tr>
<td>Porcellio spinicornis Say</td>
<td>9</td>
<td>15</td>
</tr>
<tr>
<td>Porcellionides pruinosus (Brandt)</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Trachelipus rathkei (Brandt)</td>
<td>73</td>
<td>73</td>
</tr>
</tbody>
</table>

been found in Ohio, Indiana, Illinois, Wisconsin, or southern Ontario (Table 2) (see also Jass and Klausmeier 2001, 1990). Many of these additional species potentially reside in Michigan, but may simply be unknown from the state due to lack of collecting efforts.

Isopods often are present at high densities in suitable ecosystems (Stoyenoff, unpubl. data; Oliver and Meechan 1993, Sutton 1972). These organisms are involved in decomposition and nutrient cycling processes (Zimmer and Topp 1999, 1998; Van Wensem et al. 1993, Coûteaux et al. 1991, Hassall et al. 1987, Hassall and Sutton 1978, Hassall 1977) and also serve as a food source for other organisms (Sutton 1972). Knowing which terrestrial isopod species are present and what their patterns of distribution are across the state will form a basis of knowledge for additional study on the biology and ecology of these organisms.

**MATERIALS AND METHODS**

Isopod collections began in 1997 with an intensive investigation carried out using pitfall traps on lands owned by the Dow Gardens in Midland, Michigan, USA (latitude 43° 62’ N, longitude 84° 25’ W). The Dow Gardens is composed of a complex of landscape beds and turf areas under varying levels of management, patchworked with largely unmanaged woodlots and floodplain ecosystems. During a two-week period which began on 14 July 1997, 242 unbaited pitfall traps were operated in a variety of ecosystem types located throughout these lands.

Each pitfall trap consisted of two clear plastic cups nested together. The inner 414 ml cup was 9.5 cm tall and 9 cm in diameter. The outer 473 ml cup was 11 cm tall and 9.5 cm in diameter. This diameter was just enough larger than that of the inner cup to ensure that when the cups were nested together,
Table 2. Terrestrial isopod species not reported in Michigan as of 1991 but reported from surrounding areas (Ohio, Indiana, Illinois, Wisconsin, or southern Ontario).

<table>
<thead>
<tr>
<th>Species</th>
<th>Location reported and reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ligidium hypnorum (Cuvier)</td>
<td>Ontario (Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Ligidium longicaudatum Stoller</td>
<td>Ontario (Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Androniscus dentiger Verhoeff</td>
<td>Ontario (Van Name 1940, Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Haplothalmus danicus Budde-Lund</td>
<td>Indiana (Richardson 1905, Eberly 1953); Ohio (Keeney 1990); Ontario (Walker 1927, Judd 1965, Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Miktoniscus barri Vandel</td>
<td>Indiana (Vandel 1965, Schultz 1976)</td>
</tr>
<tr>
<td>Miktoniscus medcofi (Van Name)</td>
<td>Illinois (Van Name 1940); Indiana (Schultz 1976); Ohio (Muchmore 1964, Schultz 1976); Wisconsin (Jass and Klausmeier 1996)</td>
</tr>
<tr>
<td>Trichoniscus pygmaeus Sars</td>
<td>Illinois (Van Name 1940); Ohio (Hobbs and Flynn 1981); Ontario (Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Philoscia muscorum (Scopoli)</td>
<td>Ontario (Belaoussoff et al. 1998)</td>
</tr>
<tr>
<td>Trichorhina tomentosa Budde-Lund</td>
<td>Ohio (Keeney 1990)</td>
</tr>
<tr>
<td>Venezillo parvus (Budde-Lund)</td>
<td>Ohio (Keeney 1990)</td>
</tr>
<tr>
<td>Porcellio laevis Latreille</td>
<td>Ohio (Richardson 1905, Van Name 1936); Ontario (Thompson 1932, Hatch 1947, Belaoussoff et al. 1998)</td>
</tr>
</tbody>
</table>

the rims fit snugly and level with one another. These nested cups were installed so that their rims were level with the ground surface. The inner cup contained an ethyl alcohol solution as a killing agent and was the cup used for sample collection. The outer cup served as a sleeve lining the hole which allowed the inner cup to be easily removed and replaced during collection of contents without further disturbance of the soil surrounding the hole. Each pitfall trap was shielded by a 15 by 15 cm plywood rain cover supported by three 15 cm long legs that staked into the ground.

In 2001, the study was resumed with opportunistic collection and hand-sorting of litter samples for terrestrial isopods throughout 30 Michigan counties. Meander surveys in each county were structured to include a variety of areas with likely habitat, such as riverine ecosystems, meadows, agricultural areas, and areas of different forest cover types. During all meander surveys, litter was hand sorted for isopods in the field, and refuges such as rocks, tree root flares, stumps, and downed woody debris were examined (Sutton 1972). This type of targeted search covering specific microhabitats was a more efficient means of encountering isopods than is a sampling scheme such as collecting at fixed intervals along a
transect. In addition, litter and soil samples were often collected for later hand sorting in the laboratory. Specimens collected in the field, along with the samples of soil and litter, were held alive in plastic bags on ice. They were transported back to the laboratory in Midland, MI, where isopods were removed by hand and field identifications confirmed.

Specimens were determined using keys in Muchmore (1990). I also consulted keys in Belaoussoff et al. (1998) and Hatchett (1947), as well as species descriptions in Jass and Klausmeier (1996). Classification follows Oliver and Meechan (1993), who combined the classification system of Bowman and Abele (1982) with emendations from Holdich et al. (1984). Materials from this study were preserved in 70% ethyl alcohol in glass vials with double-seal lids. Voucher specimens are deposited at Michigan State University, East Lansing, MI.

RESULTS

Distribution maps incorporating known county records prior to 1991 along with the new county records determined in this study are shown in Figs. 1-7. Included for purposes of comparison and completeness are distribution maps for three species known from the state of Michigan, but for which no new records have been found to date in this survey.

Order Isopoda

Suborder Oniscidea

Section Synocheeta

Superfamily Trichoniscoidea

Family Trichoniscidae

**Haplothalmus danicus** Budde-Lund. NEW MICHIGAN RECORD. Species identification was verified by Richard J. Snider, Dept. of Zoology, Michigan State University, East Lansing, MI. (Fig. 1a). MICHIGAN collection records: Bay Co., Maple Leaf Golf Course, T16N/R4E/S33, 09/11/01, edge of drainage ditch. Crawford Co., T28N/R4W/S35, 08/08/01, mixed woody and grassy litter in very wet soil on the banks of the Au Sable River; very high numbers of this species were present in this area. Huron Co., T15N/R9E/S8, 08/18/01, in and under wood and leaf litter on soil that varied from sandy to heavy clay along the Sebewaing River. Manistee Co., T21N/R14W/S8, 08/11/01, very wet soil near Pine Creek. *Midland Co.*, Dow Gardens, Midland, 07/24/97 – 07/30/97, taken in pitfall traps in several ecosystem types: seasonally flooded lowland deciduous woodlot areas in the Sebewaing Creek floodplain; beds of ostrich ferns; beds of spreading junipers; and shady beds with complex vegetation structure dominated by deciduous overstory trees and including shrub and weedy ground cover layers. Saginaw Co., Oakwood Cemetery, T12N/R4E/S30, 09/24/01, in a large pile of coarse woody debris mixed with maple leaves and other deciduous leaf litter in a woodlot area. *Wexford Co.*, T23N/R12W/S11, 08/12/01, grass and sedge litter in very wet, organic soil near banks of Manistee River.

**Hyloniscus riparius** (C. L. Koch). (Fig. 1b). MICHIGAN collection records: *Genesee Co.*, Captain’s Club Golf Course, T6N/R7E/S36, 09/27/01, in very moist leaf litter by the side of a small stream. *Huron Co.*, T15N/R9E/S8, 08/18/01, in and under wood and leaf litter in soils that varied from sandy to heavy clay along the Sebewaing River. *Isabella Co.*, Viet’s Woods, Mount Pleasant, 07/24/01, in wet, heavy clay soil in a large depressional area. *Jackson Co.*, T28S/R2E/S11, 11/04/01, woody litter and leaf litter by the side of a drainage ditch. *Kent Co.*, Rockford, 10/19/01, small patch of trees including walnut and small box elders in an urban area next to a factory parking lot, with a small drainage ditch down a steep slope of 4-5 m: isopods were inside walnut shells, woody debris, leaf litter, under cinder blocks, and in miscellaneous trash items left at the site. *Leelanau Co.*, T28N/R11W/S28, 08/11/01, in damp leaf litter along an
Figure 1. Michigan distribution of isopod species in the family Trichoniscidae: a) *Haplophthalmus danicus* Budde-Lund, b) *Hyloniscus riparius* (C. L. Koch), and c) *Trichoniscus pusillus* Brandt.

Unnamed creek in a small woodlot. **Midland Co.,** Dow Gardens, Midland, 07/21/97 – 07/30/97, taken in pitfall traps in several ecosystem types: seasonally flooded lowland deciduous woodlot areas in the Snake Creek floodplain; upland deciduous woodlot areas; areas of non-irrigated, low maintenance turf; beds of ostrich ferns; beds of spreading junipers; bed of annual flowers; beds of dense, creeping or trailing ground cover of various species commonly used in landscaping; large beds of needle mulch under groups of many pine trees; smaller oblongs of needle mulch surrounded by turf under pairs of trees; small circles of needle mulch surrounded by turf under individual pine trees; shady beds with complex vegetation structure dominated by deciduous overstory trees and including shrub and
weedy ground cover layers; and shady beds with complex vegetation structure dominated by coniferous overstory trees and including ericaceous and other shrubs with a weedy ground cover layer. They were particularly abundant in lowland woodlot areas, beds of junipers, and large beds of needle mulch under groups of pine trees. **Oceana Co.**, T16N/R17W/S10, 08/12/01, damp organic material on flats along the north branch of the Pentwater River. **Saginaw Co.**, T11N/R6E/S27, 09/10/01, under stones and logs and in leaf litter on the banks of the Cass River. Also, Kluck Nursery, T11N/R3E/S2, 09/10/01, under leaf litter along a drainage ditch by an open, grassy field. Also, Oakwood Cemetery, T12N/R4E/S30, 09/24/01, in and under a small pile of trash located under juniper shrubs in a landscape bed in the cemetery. **Sanilac Co.**, T13N/R12E/S18, 08/18/01, inside bark on a dam log. **Tuscola Co.**, near Vanderbilt Park, T14N/R7E/S28, 08/08/01, edge of drainage ditch along an agricultural field. Also, T11N/R7E/S28, 09/25/01, in a pile of large woody debris on the banks of the Cass River. **Washtenaw Co.**, Ann Arbor, 08/05/01, under and in logs and other smaller woody debris in leaf humus in a shaded garden. **Wayne Co.**, near Belleville, T35/R8E/S21, 11/22/01, in woody debris and leaf litter in a wooded area with mixed deciduous and coniferous trees (overstory composed largely of Scotch pines and red pines). **Wexford Co.**, T23N/R12W/S11, 08/12/01, grass and sedge litter in very wet, organic soil near banks of Manistee River.

**Trichoniscus pusillus** Brandt. (Fig. 1c). MICHIGAN collection records: **Antrim Co.**, Jordan River Campground area, T30N/R6W/S10, 07/14/01, in white pine and hemlock litter on a muddy creek bank, also musk soil in the Jordan River floodplain. Also, Cascade Road, T30N/R6W/S21, 07/14/01, in rotten logs and damp soil; along creek bank; in mucky soil in floodplain. **Bay Co.**, Maple Leaf Golf Course, T16N/R4E/S33, 09/11/01, edge of drainage ditch. **Benzie Co.**, T27N/R14W/S29, 08/11/01, near Platte River. **Charlevoix Co.**, T33N/R4W/S34, 07/15/01, in damp leaf litter near the bottom of a ravine in an oak site with a red maple component. **Cheboygan Co.**, University of Michigan Biological Station, Grapevine Point Nature Trail, T37N/R3W/S28, 07/12/01, in and under rotting wood. **Crawford Co.**, T28N/R4W/S35, 08/08/01, in very wet soil under grass and wood litter near the Au Sable River. **Emmet Co.**, T37N/R4W/S29, 07/29/01, in rotten wood and wet leaf litter in the floodplain of the west branch of the Maple River. **Kalkaska Co.**, near Wood Road, T28N/R7W/S2, 08/08/01, in very wet northern white cedar litter in the flats along the Rapid River. **Lake Co.**, T19N/R13W/S11, 08/12/01, in litter on the banks of the Little Manistee River. **Leelanau Co.**, T28N/R11W/S28, 08/11/01, in damp leaf litter along an unnamed creek in a small woodlot. **Manistee Co.**, T21N/R4W/S8, 08/11/01, very wet soil near Pine Creek. **Mason Co.**, Ludington State Park, T19N/R18W/S17, 08/12/01, in litter in a swampy area by Lost Lake. **Midland Co.**, Dow Gardens, Midland, 07/21/97 - 07/30/97, taken in pitfall traps in several ecosystem types: seasonally flooded lowland deciduous woodlot areas in the Snake Creek floodplain; upland deciduous woodlot areas; areas of non-irrigated, low maintenance turf; beds of ostrich ferns; beds of spreading junipers; beds of dense, creeping or trailing ground cover of various species commonly used in landscaping; large beds of needle mulch under groups of many pine trees; smaller oblongs of needle mulch surrounded by turf under pairs of trees; and shady beds with complex vegetation structure dominated by coniferous overstory trees and including ericaceous and other shrubs with a weedy ground cover layer. **Montmorency Co.**, T29N/R2E/S9, 07/25/01, muck soil along Avery Creek. **Oceana Co.**, T16N/R17W/S10, 08/12/01, damp organic material on flats along the north branch of the Pentwater River. **Osceola Co.**, T18N/R7W/S1, 08/06/01, muddy banks of sloughs by Muskegon River. **Presque Isle Co.**, T35N/R3E/S22, 07/28/01, northern white cedar needle litter and wood pieces near banks of Ocqueoc River. **Saginaw Co.**, Oakwood Cemetery, T12N/R4E/S30, 09/24/01, in a large pile of coarse woody debris mixed with maple leaves and other deciduous leaf litter in a woodlot area. **Wexford Co.**, T23N/R12W/S11, 08/12/01, grass and sedge litter in very wet, organic soil near banks of Manistee River.
Section Crinocheta

Superfamily Oniscoidea

Family Oniscidae

*Oniscus asellus* Linnaeus. (Fig. 2). MICHIGAN collection records: 

**Alpena Co.**, Ella S. White Elementary School Nature Area, Alpena, 07/27/01, under wood and rocks; also in leaf litter under shrubs. **Benzie Co.**, T26N/R14W/S8, 08/11/01, in grassy litter on the banks of the Platte River. **Huron Co.**, T15N/R9E/S8, 08/18/01, in and under wood and leaf litter in soils that varied from sandy to heavy clay along the Sebewaing River. **Jackson Co.**, T2S/R2E/S10, 11/04/01, oak leaf litter and oak wood by seasonal pond. **Kent Co.**, Rockford, 10/19/01, small patch of trees including walnut and small box elders in an urban area next to a factory parking lot, with a small drainage ditch down a steep slope of 4-5 m; isopods were inside walnut shells, woody debris, leaf litter, under cinder blocks, and in miscellaneous trash items left at the site; one large, mature, intermolt, individual caught had a very unusual color pattern for this species, featuring a checkering of dark patches on a snowy white background. **Leelanau Co.**, T28N/R11W/S28, 08/11/01, in damp leaf litter along an unnamed creek in a small woodlot. **Midland Co.**, Dow Gardens, Midland, 07/25/97, taken in pitfall traps in seasonally flooded lowland deciduous woodlot areas in the Snake Creek floodplain. **Presque Isle Co.**, T35N/R2E/S2, 07/28/01, grassy litter on banks of Rainy River. **Saginaw Co.**, Oakwood Cemetery, T12N/R4E/S30, 09/24/01, in a large pile of coarse woody debris mixed with maple leaves and other deciduous leaf litter in a woodlot area; there was a very high density of this species here, especially on and in the woody debris. Also, Oakwood Cemetery, T12N/R4E/S30, 09/24/01, in and under a small pile of trash located under juniper shrubs in a landscape bed in the cemetery. **Tuscola Co.**, T11N/R7E/S28, 09/25/01, in a pile of large woody debris on the banks of the Cass River. **Wayne Co.**, near Belleville, T8S/R8E/S21, 08/05/01, in a wood pile; in a compost heap; inside walnut shells; very large populations were present in all of these microsites, with this species being much more abundant than the co-occurring *Porcellio scaber* Latreille.

Superfamily Porcellionoidea

Family Armadillidiidae

*Armadillidium nasatum* Budde-Lund. (Fig. 3a). MICHIGAN collection records: 

**Genesee Co.**, Captain's Club Golf Course, T6N/R7E/S36, 09/27/01, under rocks piled near the maintenance building in a very dry area at the edge of non-irrigated turf. **Midland Co.**, Dow Gardens, Midland, 07/22/97 – 07/29/97, taken in pitfall traps in several ecosystem types: areas of irrigated, high maintenance turf; beds of ostrich ferns; beds of spreading junipers; beds of annual flowers; and shady beds with complex vegetation structure dominated by deciduous overstory trees and including shrub and weedy ground cover layers. There was an extremely dense population of this species in one large bed of spreading junipers at the side of a pond. Also collected in a greenhouse, where it was present in large numbers.

*Armadillidium vulgare* (Latreille). (Fig. 3b). MICHIGAN collection records: 

**Alpena Co.**, Ella S. White Elementary School Nature Area, Alpena, 07/27/01, under wood and rocks; also in leaf litter under shrubs. Also, T31N/R5E/S23, 07/27/01, in litter in cattail swamps along the lower south branch of Thunder Bay River. Also, T30N/R5E/S17, 07/27/01, in dead wood on the shore of Fletcher Pond. **Antrim Co.**, T31N/R5W/S8, 08/09/01, in grassy litter in a damp ditch bordering farm fields. **Benzie Co.**, T26N/R14W/S8, 08/11/01, in grassy litter on the banks of the Platte River. **Charlevoix Co.**, T32N/R5W/S16, 08/09/01, on the grassy banks of a river near Boyne Mountain. **Crawford Co.**, T28N/R4W/S35, 08/08/01, in very wet soil under grass and wood litter near the Au Sable River. **Grand Traverse Co.**, T26N/R11W/S5, 08/10/01, in
small rocks mulching a dry landscape bed of junipers surrounded by concrete at a
gas station. Also, T27N/R10W/S30, 08/11/01, along banks of Mitchell Creek, in
area of cattails. **Hillsdale Co.**, T7S/R2W/S15, 11/04/01, in stones of an old build-
ing foundation; dry area. **Huron Co.**, Sebewaing, T15N/R9E/S8, 08/18/01, in
very dry area of landscaping rocks around grave stones in city cemetery. **Isabella
Co.**, Central Michigan University Dow Science Building, Ottawa Road, Mount
Pleasant, 07/24/01, under and around rocks in a dry landscape bed. Also, Cen-
tral Michigan University Botany Greenhouse, Mount Pleasant, 07/24/01, in leaf
litter in dry landscape beds outside the greenhouse building. Also, Preston and
Washington Streets, Mount Pleasant, 07/24/01, in damp leaf litter and rotten
logs in a small woodland. **Jackson Co.**, T2S/R2E/S11, 11/04/01, woody litter and
leaf litter by the side of a drainage ditch. **Kalkaska Co.**, near Wood Road, T28N/
R7W/S21, 08/08/01, in very wet northern white cedar litter in the flats along the
Rapid River. **Kent Co.**, Rockford, 10/19/01, small patch of trees including wal-
nut and small box elders in an urban area next to a factory parking lot, with a
small drainage ditch down a steep slope of 4-5 m; isopods were inside walnut
shells, woody debris, leaf litter, under cinder blocks, and in miscellaneous trash
items left at the site. **Lake Co.**, T19N/R13W/S11, 08/12/01, in litter on the banks
of the Little Manistee River. **Leelanau Co.**, Lincoln Road near Co. 633 or Cherry
Bend Road, T28N/R11W/S29, 08/11/01, under stones in a very dry landscape bed
with junipers. Also, T28N/R11W/S28, 08/11/01, in damp litter along an unnamed
creek in a woodlot. **Manistee Co.**, T22N/R14W/S33, 08/11/01, under logs in
floodplain of Manistee River. **Mason Co.**, Ludington, 08/12/01, under shrubs in
a dry landscape bed surrounded by cement at a gas station. **Midland Co.**, Dow
Gardens, Midland, 07/21/97 – 07/30/97, taken in pitfall traps in several ecosys-
tem types: seasonally flooded lowland deciduous woodlot areas in the Snake

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**Figure 2.** Michigan distribution of isopod species in the family Oniscidae: *Oniscus
asellus* Linnaeus.
Figure 3. Michigan distribution of isopod species in the family Armadillidiidae: a) *Armadillidium nasatum* Budde-Lund and b) *Armadillidium vulgare* (Latreille).

Creek floodplain; upland deciduous woodlot areas; areas of irrigated, high maintenance turf; areas of non-irrigated, low maintenance turf; beds of ostrich ferns; beds of spreading junipers; beds of annual flowers; beds of dense, creeping or trailing ground cover of various species commonly used in landscaping; large beds of needle mulch under groups of many pine trees; smaller oblongs of needle mulch surrounded by turf under pairs of trees; small circles of needle mulch surrounded by turf under individual pine trees; shady beds with complex vegetation structure dominated by deciduous overstory trees and including shrub and weedy ground cover layers; and shady beds with complex vegetation structure dominated by coniferous overstory trees and including ericaceous and other shrubs with a weedy ground cover layer. This species was especially common under junipers and in various-sized beds of pine needle mulch, being encountered most times these types of habitats were examined. Very high density populations, on the other hand, were located in a particular bed of landscaping groundcover and in a bed of ferns. Also collected inside a greenhouse. **Otsego Co.**, Department of Natural Resources, Region 5 Headquarters, Gaylord, 08/08/01, under shrubs in dry landscape beds. **Presque Isle Co.**, T35N/R2E/S2, 07/28/01, grassy litter on banks of Rainy River. **Saginaw Co.**, Saginaw Country Club, T12N/R4E/S28, 08/27/01, in a flight trap (approx. 1 m tall) set for Japanese beetle adults baited with floral attractants and a pheromone lure. Also, T11N/R6E/S27, 09/10/01, under stones and logs and in leaf litter on the banks of the Cass River. **Tuscola Co.**, near Vanderbilt Park, T14N/R7E/S28, 08/08/01, edge of drainage ditch along an agricultural field. Also, T11N/R7E/S28, 09/25/01, in a pile of large woody debris on the banks of the Cass River. **Wexford Co.**, T23N/R12W/S11, 08/12/01, grass and sedge litter in very wet, organic soil near banks of Manistee River.
Family Cylisticidae

*Cylisticus convexus* (DeGeer). (Fig. 4). **MICHIGAN** collection records: **Crawford Co.,** T28N/R4W/S35, 08/08/01, in very wet soil under grass and wood litter near the Au Sable River. **Hillsdale Co.,** T7S/R2W/S15, 11/04/01, in stones of an old building foundation; dry area. **Isabella Co.,** Preston and Washington Streets, Mount Pleasant, 07/24/01, in damp leaf litter and rotten logs in a small woodlot; very large numbers of this species were present at high density in the rotting logs. **Kent Co.,** Rockford, 10/19/01, small patch of trees including walnut and small box elders in an urban area next to a factory parking lot, with a small drainage ditch down a steep slope of 4-5 m; isopods were inside walnut shells, woody debris, leaf litter, under cinder blocks, and in miscellaneous trash items left at the site. **Midland Co.,** Dow Gardens, Midland, 07/21/97 - 07/30/97, taken in pitfall traps in several ecosystem types: seasonally flooded lowland deciduous woodlot areas in the Snake Creek floodplain; upland deciduous woodlot areas; beds of ostrich ferns; beds of spreading junipers; beds of annual flowers; beds of dense, creeping or trailing ground cover of various species commonly used in landscaping; large beds of needle mulch under groups of many pine trees; small circles of needle mulch surrounded by turf under individual pine trees; and shady beds with complex vegetation structure dominated by deciduous overstory trees and including shrub and weedy ground cover layers. They were particularly abundant in juniper beds.

Figure 4. Michigan distribution of isopod species in the family Cylisticidae: *Cylisticus convexus* (DeGeer).
Family Porcellionidae

Porcellio scaber Latreille. (Fig. 5a). MICHIGAN collection records: Kent Co., Rockford, 10/19/01, small patch of trees including walnut and small box elders in an urban area next to a factory parking lot, with a small drainage ditch down a steep slope of 4-5 m; isopods were inside walnut shells, woody debris, leaf litter, under cinder blocks, and in miscellaneous trash items left at the site. Mason Co., Ludington, 08/12/01, under shrubs in a dry landscape bed surrounded by cement at a gas station. Midland Co., Dow Gardens, Midland, 07/21/97 – 07/28/97, taken in pitfall traps in large beds of needle mulch under groups of pine trees and in small circles of needle mulch surrounded by turf under individual pine trees. Wayne Co., near Belleville, T3S/R8E/S21, 08/05/01, in a wood pile; in a compost heap; inside walnut shells.

Porcellio spinicornis Say. (Fig. 5b). MICHIGAN collection records: Alpena Co., Ella S. White Elementary School Nature Area, Alpena, 07/27/01, under wood and rocks; also in leaf litter under shrubs. Huron Co., Sebewaing, T15N/R9E/S8, 08/18/01, in dry landscaping rocks around grave stones in city cemetery; very dry area; there was a very large population present at this site. Isabella Co., Central Michigan University Botany Greenhouse, Mount Pleasant, 07/24/01, in leaf litter in dry landscape beds outside the greenhouse building. Also, Preston and Washington Streets, Mount Pleasant, 07/24/01, in damp leaf litter and rotten logs in a small woodlot. Midland Co., Eastman Avenue, Midland, 07/20/01, in deep, damp leaf litter; in rotting hole filled with organic material in a tree trunk; and on brick walls in a very shady urban garden. Tuscola Co., T11N/R7E/S28, 09/25/01, in a pile of large woody debris on the banks of the Cass River. Wayne Co., near Belleville, T3S/R8E/S21, 11/22/01, in leaf litter under bricks.

No new county records have been found to date in this survey for Porcellionides pruinosus (Brandt) (also in family Porcellionidae) (Fig. 5c), Trachelipus rathkei (Brandt) (section Crinocheta, superfamily Porcellionoidea, family Trachelipidae) (Fig. 6), or Ligidium elrodii Packard (section Diplocheta, family Ligiidae) (Fig. 7).

DISCUSSION

Distribution and dispersal of isopods. The terrestrial isopod fauna is quite rich throughout much of the world. In their 1993 publication, Oliver and Meechan reported that there were approximately 900 species of terrestrial isopods known worldwide. More recently, number of terrestrial isopod species known worldwide has been placed at 4,000–5,000 (Kensley et al. 2002, Brusca 1997). It is thought that a large number of isopod species in the world are yet to be described. Greece alone, for example, hosts close to 200 known terrestrial species and is expected to yield numerous additional new species upon further exploration (Sfenthourakis and Giokas 1998).

By comparison, the North American fauna is rather depauperate in terms of known species. In Michigan, only 11 terrestrial isopod species were known as of 1990 (Snider 1991). Eleven additional species not previously reported from Michigan have been identified in the surrounding areas of Ohio, Indiana, Illinois, Wisconsin, or southern Ontario (Jass and Klausmeier 2001, 1996, 1990; Belaoussoff et al. 1998, Keeney 1990, Hobbs and Flynn 1981, Schultz 1976, Judd 1965, Vandel 1965, Muchmore 1964, Eberly 1953, Hatch 1947, Van Name 1940, 1936; Thompson 1932, Walker 1927, Richardson 1905). One of these species that was previously unknown in Michigan, Haplothalamus danicus, was discovered in this survey to exist here as well, bringing the current state tally to 12 terrestrial isopod species.

Except for Ligidium elrodii, all of the terrestrial isopod species identified in Michigan to date are exotic organisms of European origin which have become
naturalized in North America (Jass and Klausmeier 2001, 2000; Muchmore 1990). Many of these species are reported to be rather synanthropic in their native locations (Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972), and it is hypothesized that they were introduced to various places in North America and around the world with plants and other material moved by humans or in ballast soil that was off-loaded from ships (Sutton 1972). In North America, these isopods are still frequently found in synanthropic situations, but they have in many cases also spread very successfully into areas quite some distance from their probable places of introduction. Others have suggested that such spread may have been possible due to the availability of previously unfilled niches or to efficient resource use that aided the isopods in outcompeting native organisms with possibly similar ecology, such as some of the millipedes (Sutton 1972, Van Name 1936).

In the present study, isopods were frequently encountered in synanthropic locations such as near buildings and parking lots, in landscape beds and urban

Figure 5. Michigan distribution of isopod species in the family Porcellionidae: a) *Porcellio scaber* Latreille, b) *Porcellio spinicornis* Say, and c) *Porcellionides pruinosus* (Brandt).
garden, and in cemeteries, golf courses, nurseries, and parks. However, many other specimens were taken in areas with less obvious human influence—areas along waterways or in rural forests that had not been modified by human earth-moving, planting of landscape materials, or dumping. In more remote areas, as well as near settlement, isopods seemed to be found especially commonly on the banks or in the floodplains of waterways.

Bodies of water, whether flowing or still, are likely important as refuges for maintenance of populations during dry periods. Many small isopod species, in particular, desiccate very rapidly and perhaps can only persist in areas that regularly have rather high moisture content, such as in litter on beaches or banks (Jass and Klausmeier 1996, Oliver and Meechan 1993, Sutton 1972, Tack and Edgar 1966). In some locations, conditions are appropriate for populations of these isopods to spread out away from the waterside and live in forest litter or similar situations in surrounding areas. However, it is possible that the populations in woodland litter or other places may be strongly affected or even potentially die out if serious drought conditions occur for extended periods, as can happen during Michigan summers. Areas near bodies of water may then potentially serve as a source of re-colonizers when moister conditions return. For other species that can more easily move further afield, perpetually damp areas at watersides could serve as important places for nearby individuals to move toward during periods of extended drought.
Figure 7. Michigan distribution of isopod species in the family Ligiidae: *Ligidium elrodii* Packard.

**Collecting methods used.** This study made use of both pitfall trapping and hand sorting of litter to collect isopods in Michigan ecosystems. Pitfall trapping was used in the finer-scale, more intensive investigation that took place in Midland County, MI, while hand sorting was the method employed in the broader-scale investigation made throughout numerous Michigan counties. Pitfall traps have the advantage of operating constantly, often collecting large numbers of specimens with relatively little effort and allowing collection of species that are active at night but that may not be as easily hand-collected during the day. Hand sorting has some benefits over pitfall trapping, however, because pitfall traps measure the activity-density of organisms rather than simply species presence. That is, species that are very mobile are taken more readily in traps. Species that are less mobile or that carry out their activity and movement in cryptic areas such as inside of large, downed woody items or under the soil surface instead of moving across the forest floor will be taken only infrequently or not at all in the traps. Differences in agility among the species can also affect the usefulness of pitfall traps in their capture. For mobile isopod species, traps may collect large numbers of individuals, impacting the population in the area around the trap to a greater extent than is necessary for the goals of the study. Very small or highly agile species may be more able to avoid falling into traps when they are encountered because the trap lip represents a wide area for these small organisms, and they may have great ability to turn quickly from their path. An additional advantage of hand-sorting over pitfall trapping is that when isopods are collected live by hand, one can easily examine the pseudotracheae on the organisms, the presence and number of which are important characters for delineating certain groups. Presence or absence of white patches on the
exopodites of pleopods, indicating pseudotracheae, cannot be readily determined after an isopod has been killed or preserved, however. Although each of these collecting methods has advantages and disadvantages, employing the different techniques in combination in this study allowed me to fit my methods to the goals set in the different study areas.

Species accounts. Since terrestrial isopods are very common organisms in many ecosystems, it is surprising that relatively little detailed information is available on habitat/microhabitat associations and ecology of the various species. A great deal of the information that is known comes from Europe, where these organisms have been more extensively studied. The findings of this Michigan survey support much of the information reported in other literature but also reveal some differences as compared to previously published findings.

Haplophthalmus danicus. H. danicus, previously unknown in Michigan, has been found in seven counties in the central and northern portions of the Lower Peninsula during the first portion of this survey. It was previously reported to be locally common in eastern North America north to Newfoundland in moist litter and decaying wood (Muchmore 1990). European sources indicate that this species is strongly associated with deciduous woodlands that have very humus-rich, free-draining soil, where H. danicus is found deep in the litter, in the upper layers of the soil, or under the bark of fallen trees (Oliver and Meechan 1993, Harding and Sutton 1985). It has also been reported in some synanthropic situations where there is damp, humus-rich soil (Harding and Sutton 1985). This Michigan survey likewise tended to find H. danicus in association with decaying woody litter in very damp soils, particularly near waterways. In some situations, the soils were quite wet and not particularly free-draining. H. danicus was never observed on or near the surface of the litter, but was generally on top or in the first few centimeters of the soil underneath a considerable covering of litter. By far the majority of the situations where H. danicus was found involved litter of deciduous trees. One exception was its presence in landscape beds in Midland County that were planted with spreading junipers. However, despite the fact that a great deal of juniper needle litter was present in these beds, there was also a fair amount of deciduous leaf litter because the shrubs’ architecture caused them to catch and hold masses of fallen leaves as they blew about in autumn. In general, beds of landscape junipers often hosted a high diversity and high density of many types of terrestrial isopods. H. danicus, however, although present under junipers, was not found at high densities in these settings, but rather as occasional specimens.

Hyloniscus riparius. This is another species that for some time was thought not to be present in Michigan. H. riparius remained unknown in the state until 1990, when one adult and two juveniles were collected in Ingham County (Snider 1991). The present survey has now located this species in 14 additional counties scattered throughout the Lower Peninsula, and I expect to find it in many more counties as this survey extends its reach throughout the state in the future. H. riparius was previously reported in several of the eastern states in the U. S. and has been found north to Newfoundland in moist litter and refuse (Muchmore 1990). Also reported from Wisconsin, this species is said to be associated with leaf litter near wooded streams and river bottoms (Jass and Klausmeier 1996). While many of the locations where H. riparius was taken in this survey are in excellent agreement with this, I also located this species in some places that seem less typical. In the intensive Midland County work, H. riparius was found in large beds of pine needle mulch under groups of pine trees and in smaller circles and oblongs of pine needle mulch around individual landscape conifers or pairs of conifers set into turf areas. It was also found in Midland County in beds with complex vegetation structure dominated by coniferous overstory trees and ericaceous shrubs and in a small wooded area in Wayne County with a conifer-dominated overstory and much needle litter. It is likely that the litter layer and at least the upper soil layer are somewhat acidic in areas where thick
beds of pine needle mulch have been maintained under conifer trees for many years. *H. riparius* was also found in Midland County in a few open, sunny areas of non-irrigated, low-maintenance turf, which seems to dry out severely and where the grasses go dormant in mid and late summer. In one case, it was taken in a sunny, dry bed of annual flowers that had no mulch of any type on the soil surface. Outside the boundary of the flower bed was turf. The flowers were grown from seed in sterile media in an on-site greenhouse prior to planting out, and it was highly unlikely that the isopod was introduced to the bed with this plant material. Less severe locations, but still places that seem somewhat atypical for the species based on previously published information, were the occurrences in upland deciduous woodlots located well above area waterways and numerous collections made in beds of juniper shrubs in two counties. Locating *H. riparius* in many of these settings was surprising because this species desiccates rather rapidly when removed from its habitation to the open; yet some of the locations where it was collected were environments that did not seem possible to describe as regularly moist. However, these collections are not likely a fluke, since *H. riparius* was taken in multiple patches of each of these ecosystem types, with the exception of the single capture in one annual flower bed. Possibly this species is transient in these areas, being present only during times when moisture conditions are suitable for it.

**Trichoniscus pusillus.** Another small, moisture-sensitive species reported to be widespread from eastern North America to Newfoundland is *T. pusillus* (Muchmore 1990). Previously known from only two counties in Michigan, this survey has located it in an additional 19 counties. So far, with the exception of a prior researcher’s record of this species in Washtenaw County, its distribution appears to be more central and northern in the Lower Peninsula, in contrast to *H. riparius*, for which all but two locality records have occurred in southern and central counties of the Lower Peninsula. This seeming distribution difference may simply be an artifact of the survey being incomplete at this point. However, collections made in 13 counties in the northern half of the Lower Peninsula revealed the presence of *T. pusillus* but not *H. riparius*, while collections in five southern counties yielded *H. riparius* but no *T. pusillus*. In the central portion of the Lower Peninsula, both species were present in the collections of three counties, only *T. pusillus* was found in one county, and only *H. riparius* was found in four counties. Additional up-coming survey work will further examine this issue.

In the literature, *T. pusillus* has, on one hand, been reported to prefer wet areas, even waterlogged habitats, in deciduous woods (Muchmore 1990, Sutton 1972, Hatchett 1947). On the other hand, it has also been reported to have a very wide range of habitats, occurring in most situations including grassland, acid moorland, and synanthropic situations (Oliver and Meechan 1993, Muchmore 1990, Harding and Sutton 1985, Sutton 1972). Most of the locations where this species has been collected so far in the Michigan survey were quite wet, many times waterlogged, and usually along waterways occurring in deciduous woodland areas. This accords well with what has been reported for this species by workers in nearby Wisconsin (Jass and Klausmeier 1996). However, on several occasions it also has been found in wet coniferous litter along waterways, including litter from white pine, hemlock, and northern white cedar. It has additionally been found in conifer-dominated habitat patches that are considerably drier, including beds of landscape junipers, beds of pine needle mulch under large groups of pines or around pairs of landscape conifers, and beds with complex vegetation structure dominated by coniferous overstory trees and including ericaceous shrubs. *T. pusillus* also was collected in upland deciduous woodlots and once in an area of non-irrigated, low-maintenance turf that goes dormant in mid and late summer due to lack of moisture. These other collections indicate that *T. pusillus* may have a somewhat wider habitat range than was previously thought for Michigan (Hatchett 1947).
Oniscus asellus. *O. asellus* is another species whose Michigan distribution records have been expanded considerably during this survey. Previously known from only three counties in the state, it has been located in 11 additional counties scattered throughout the Lower Peninsula. Reported to be widely distributed in the northern United States and southern Canada (Muchmore 1990), *O. asellus* is frequently abundant around human habitations, both in Europe and North America (Muchmore 1990, Harding and Sutton 1985, Sutton 1972, Hatchett 1947). This species favors moist areas with rotting wood, occurring in almost any natural or synanthropic habitat where these two features are found, even in acidic conditions (Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972). Jass and Klausmeier (1996) associated it especially with microhabitats under loose tree bark on dead wood. Catches of *O. asellus* in the present study were in locations that were in good agreement with the comments published by other workers. The most surprising factor for this species was that in the more intensive survey area in Midland County, *O. asellus* was taken only in areas of seasonally flooded lowland deciduous woodlot. Given that several other ecosystem types surveyed also would have contained moist, rotting wood, and given the fact that often catches of other species in the intensive survey area included more habitat breadth than was expected for them, it is surprising that *O. asellus* was so limited in its occurrence here.

Armadillidium nasatum. *A. nasatum* is a species that is reported to be locally common in North America (Muchmore 1990). Although it has been observed outdoors in relatively dry, sunny habitats in Wisconsin (Jass and Klausmeier 1996), no populations of this organism have previously been found established outdoors in Michigan (R. J. Snider, Dept. of Zoology, Michigan State University, East Lansing, MI, pers. comm. 2001; Hatchett 1947). Rather, all records of *A. nasatum* in this state are from glasshouses, a habitat where it is also frequently reported to exist in other localities (Oliver and Meechan 1993, Muchmore 1990, Harding and Sutton 1985). However, during the course of this study, I located clearly established populations of *A. nasatum* living outdoors in two counties near the central part of the Lower Peninsula. In Genesee County, this species was common under rocks at the edge of non-irrigated turf in a quite open, sunny, dry location near a golf course maintenance building. This habitat is in excellent agreement with information in the literature, which states that *A. nasatum* prefers rather dry areas and is frequently associated with stones or old quarries, particularly in calcareous conditions, as well as being found in disturbed, exposed grasslands and near human habitations (Jass and Klausmeier 1996, Oliver and Meechan 1993, Muchmore 1990, Harding and Sutton 1985, Sutton 1972). In Midland County, low numbers of this species were found in three different areas of irrigated, high-maintenance turf, in two locations in beds of dense ostrich ferns, in two beds of annual flowers with bare soil and no mulch, and in one instance in a shady bed with complex vegetation structure dominated by deciduous overstory trees. In addition to these several scattered occurrences of low population levels, a very high density *A. nasatum* population was found in a bed of landscape junipers at the side of a pond.

Armadillidium vulgare. Another Armadillidiid, *A. vulgare*, was frequently encountered during this study and is notable for the habitat breadth it displays in comparison to most other isopods. This species is reported by Muchmore (1990) to be more widespread than *A. nasatum* and found in a wide variety of habitats, but like *A. nasatum* it is often located in very dry areas and may be numerous in glasshouses. When Hatchett published his 1947 paper, *A. vulgare* was unknown anywhere north of Bay City, MI, in the central part of the Lower Peninsula, except for one collection in Cheboygan County. Hatchett felt that this Cheboygan County observation was an aberrant result due to the isopods likely being imported with landscaping materials that were brought into the site just shortly before he made his collection. Between 1947 and the present study, no additional county records were secured for *A. vulgare* in the
northern part of the Lower Peninsula. However, the present survey has established new locality records for *A. vulgare* in 14 counties in the northern half of the Lower Peninsula, in addition to adding five counties to the known distribution records for this species in the central portion of the Lower Peninsula and three more counties in the southern portion.

In the literature, *A. vulgare* is reported occurring in habitats that range from very dry to moist and was said rarely to be far from humans (Jass and Klausmeier 1996, Hatchett 1947). Ecosystems cited for it include coastal locations, sand dunes, grassland, stony areas, and areas with calcareous soil (Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972). In Michigan, I likewise commonly found this species in sites at both ends of the moisture spectrum, as well as at many points between. It was very common to find *A. vulgare* in quite moist litter on banks and beaches, near watercourses in seasonally flooded lowland deciduous woodlots, and even in cattail swamps along rivers. However, I also encountered it numerous times in very dry ecosystems such as in between stones in an old building foundation located on a dry site, in very dry landscape beds of junipers surrounded by concrete in cities, in very dry areas of rocks around gravestones, and in areas of non-irrigated turf. In the intensive study carried out in Midland County, this species was especially common under junipers and in various-sized beds of pine needle mulch, being encountered most times these types of habitats were examined. However, the highest density populations were located in a particular bed of dense landscaping groundcover and in a bed of ferns.

**Cylisticus convexus.** *C. convexus* is another species that was found in a wide variety of conditions, although perhaps not quite as wide as *A. vulgare*. While some workers have stressed that this species has a greater preference for moisture (Jass and Klausmeier 1996, Hatchett 1947), others have noted that it may also be found in dry sites, sunny positions, disturbed areas, rocky areas, exposed sites with little vegetation, quarries, and old walls (Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972). Most sources have additionally noted the strong association of this species with humans in synanthropic habitats. Although I did not as commonly encounter this isopod as some of the other species, I did find *C. convexus* in both wet and dry habitats. I was somewhat surprised that I did not locate this species more frequently. Muchmore (1990) noted that it is widespread in the northern half of the United States and southern Canada; Hatchett (1947) stressed that it is broadly distributed in Michigan with a spread second only to *T. rathkei*; Snider (1991) compiled existing records for this species in 30 of Michigan’s 83 counties; and Jass and Klausmeier (1996) reported it as one of only three species known to be found in every county in Wisconsin. To date, this survey has added only five new counties to the distribution records for *C. convexus*. Perhaps future survey work will amend the lack of new records for this species in Michigan, and it will yet be proven to be in most counties of the state, as one might expect based upon the experience with this species in Wisconsin.

**Porcellio scaber.** *P. scaber* is another species reported to be widespread and very common in the United States and Canada (Muchmore 1990) but little encountered in new locations at this point in the Michigan survey. It is cited in others’ work from diverse habitats, with some authors stressing a hygrophilous nature for the species (Hatchett 1947, Blake 1931), while others remark upon its adaptation to drier habitats, even sites that are compacted, detritus-poor, sandy, or acidic (Belaoussoff et al. 1998, Muchmore 1990, Sutton 1972). While common in both grasslands and woodlands, it is also said to be often found in synanthropic situations like many other isopod species (Jass and Klausmeier 1996, Oliver and Meechan 1993, Muchmore 1990, Harding and Sutton 1985). Hatchett (1947), however, disagreed with a strictly synanthropic nature for the species, stating that he had also located it in Michigan in forest areas with no habitations and at some distance from human activity. It appears to be somewhat unusual
in that, in addition to its typical ground-dwelling habit, it has been noted to frequent bark of living trees, being found to carry out its activity somewhat up the trunk above the ground (Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972). In the current study, *P. scaber* was found only in urban settings or suburban garden settings. In the intensive investigation in Midland County, *P. scaber* was taken only in variously sized beds of pine needle mulch. It seems surprising that it was not encountered in any of the several other ecosystem types examined.

**Porcellio spinicornis.** *P. scaber*’s congener, *P. spinicornis*, is noted in the literature for strong association with crevices in calcareous rocky areas such as limestone, sandstone, and mortared walls, as well as a preference for dry sites and a synanthropic nature (Jass and Klausmeier 1996, Oliver and Meechan 1993, Harding and Sutton 1985, Sutton 1972, Hatchett 1947, Stoller 1902). Muchmore (1990) states that this species is widespread and common in the United States and Canada. Hatchett (1947) remarks that the Upper Peninsula of Michigan is nearly at the northern boundary of the species’ range and that in most of the widely scattered Michigan counties where it had been located only a few specimens were found, these being from very limited areas in each county. Jass and Klausmeier (1996), however, report this species to be present in every county in Wisconsin. Previously known from nine counties scattered throughout Michigan, this survey has been able so far to add only six more counties to *P. spinicornis*’ known distribution in the state. While some of these collections were from the expected types of locations, this species was also taken in damp leaf litter, inside rotting logs and woody debris, and in one case in a rotting hole in a tree trunk that was filled with organic matter. Only relatively few individuals were observed in these other settings, however. The single large aggregation seen of this species was in dry rocks around grave stones. On balance, *P. spinicornis* does seem at this point to perhaps not be as common as several of the other species in the state.

**Ligidium elrodii, Porcellionides pruinopus, and Trachelipus rathkei.** I found no new county records for three isopod species that are known to be present in Michigan. These species include *T. rathkei*, which at this point has the widest known distribution of any terrestrial isopod species in the state. This species is unknown only from most of the western two-thirds of the Upper Peninsula. The lack of new county records for *T. rathkei* in this study is due to the fact that the Upper Peninsula was not investigated during the first two years of work; rather, it is slated to be surveyed in the upcoming field seasons. *T. rathkei* was frequently observed in counties where it has already been recorded, however. Like *A. vulgare*, this species seems to occur over quite a wide range of conditions and habitats in Michigan. It was the most frequently encountered isopod during this survey work. The other two species for which no new locality records were determined are *L. elrodii* and *P. pruinopus*. Both of these species have been very seldom recorded in Michigan, with *L. elrodii* known only from a single county and *P. pruinopus* collected in only five counties of the state. In each case, the collections have occurred in counties in the southern quarter of the Lower Peninsula, an area not yet extensively explored by the present survey. Collections have likely not been extensive enough at this point to pick up these perhaps more rare and perhaps more southerly-distributed species.

**Conclusion.** Jass and Klausmeier (1996) described particular species associations, or groups of isopod species that may commonly be found together in Wisconsin. Such groups were less easy to delineate in this study. For instance, I found both *T. rathkei* and *A. vulgare* co-occurring at some time or another with each of the other species encountered in this study. Presence or absence of a species at a particular location is likely controlled by the general site characteristics and by the microsites available nested within that. Certain sites investigated supported several species. For instance, three sites each had
six different species present, while numerous other sites each had five species present. Species that are habitat-restricted in some way or that occupy habitats with more extreme conditions tend to be most limited in terms of their co-occurrence with other species since they are only associated with others who can handle the same types of habitat conditions. Unfortunately, much of the habitat information available at this time seems somewhat general and often repetitious across species. This is due either to many species being truly somewhat general in their habitat preferences, or to lack of adequately specific, detailed information for the various species. Further study is needed on associations of isopod species with particular microhabitat characteristics to allow us to better understand fine divisions in the way various species partition available habitats and to provide insight into their ecological interactions in these locations.

ACKNOWLEDGMENTS

Richard Snider (Dept. of Zoology, Michigan State University, East Lansing, MI) kindly consulted with me on numerous questions and provided species verifications on a number of my early samples including the first specimen taken of the state record species reported here; equally importantly, he enthusiastically encouraged me to pursue further work on isopods in this region. Joan Jass (Zoology Section, Milwaukee Public Museum, Milwaukee, WI) supplied a useful description for separating some of the "little guy" isopod species. Mark Obrien (Museum of Zoology, University of Michigan, Ann Arbor, MI) shared information on museum holdings with me. John Witter (School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI) willingly stopped numerous times at likely-looking sites when we were out doing field work for other projects. My assistant, Rebecca Dyer, patiently and carefully sorted much material from pitfall trap samples and waded through many bags of "schmuck" brought back from field collections. Numerous individuals involved in isopod research from around the world generously sent me copies of various keys, species lists, and journal reprints. Laboratory space and other background support for this project were supplied by the Dow Gardens, Midland, MI. Many useful comments for improving this manuscript were provided by Joan Jass, Barbara Klausmeier, John Witter, William Muchmore, and an anonymous reviewer.

LITERATURE CITED


FIRST CANADIAN RECORD OF HEXACOLA NEOSCATELLAE (HYMENOPTERA: FIGITIDAE: EUCOILINAE), A PARASITOID OF THE SHORE FLY, SCATELLA STAGNALIS

Joshua C. Diamond\textsuperscript{1}, Vanessa A. Carney\textsuperscript{2}, Graeme D. Murphy\textsuperscript{2}, and Wayne R. Allen\textsuperscript{2}

ABSTRACT

This paper documents the first occurrence of Hexacola neoscatellae, a shore fly parasitoid, in Canada. The discovery of \textit{H. neoscatellae} is significant because currently there are no suitable biological control agents available for shore fly control to the floriculture industry.

\textit{Scatella stagnalis} Fallen (Diptera: Ephydridae) is a worldwide cosmopolitan species (Zack and Foote 1978). This species of shore fly is commonly found in greenhouses where it breeds on algae growing on the potting mix, pots, benches and floors. Shore flies have been traditionally identified as a nuisance pest to greenhouse workers and consumers of potted crops (Vanninen and Koskula 1998). Recently, \textit{S. stagnalis} has been implicated as a vector of plant pathogens, increasing the incidence of root disease. Goldberg and Stanghellini (1990) documented the acquisition and aerial transmission of \textit{Pythium aphanidermatum} (Edson) by shore flies from infected to healthy plants in greenhouses. Adult shore flies also cause indirect damage to ornamentals by leaving fecal spots on the foliage, thus reducing the aesthetic value of the plant (Lindquist et al. 1994).

The use of chemicals has been the cornerstone for insect control in greenhouses. However, the floriculture industry has experienced a reduction in both the number and classes of traditional pesticides available because fewer products are being registered and many older products are not being registered again. There are also growing health and environmental concerns influencing this reduction. The trend toward an increased use of biological controls for management of other crop pests is another incentive to move away from the application of chemicals to control shore flies. As yet, there are few effective shore fly control alternatives available (Vanninen and Koskula 1998).

In our greenhouses where shore flies exist, yellow sticky-card monitoring revealed a resident population of a \textit{Hexacola} sp. \textit{Hexacola neoscatellae} Beardsley is known to be a parasitoid of Ephydridae (Beardsley 1989). These specimens (Fig. 1) from our greenhouses were identified as \textit{Hexacola neoscatellae} Beardsley by Matthew Buffington (Texas A. & M. University) and John W. Beardsley (University of Hawaii). We report here that specimens from our greenhouse were observed parasitizing shore fly larvae and pupa (Figs.2-3). Previously, \textit{H. neoscatellae} has only been identified from greenhouses at University of California Riverside, and occurs naturally throughout Hawaii (Beardsley 1989). It is likely \textit{H. neoscatellae} arrived in our greenhouses by being carried on nursery stock.

Another species, \textit{Hexacola hexatoma} (Hartig), has been reported to parasitize shore flies (Gill and Sanderson 1998). However, according to Göran Nordlander (pers. comm.), this association is likely due to a misidentification of \textit{H. neoscatellae} as \textit{H. hexatoma}, a well-known parasitoid of frit flies (Diptera:

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FIG. 1. *Hexacola neoscatellae*: 1, Adult.

FIGS. 2-3. *Hexacola neoscatellae*: 2, shore fly pupal case containing the developing wasp (white) and the remnants of the dead shore fly pupa (black); 3, parasite dissected from the shore fly pupa.
Chloropidae). Beardsley's (1989) comparison of \textit{H. neoscatellae} to \textit{H. hexatoma} indicates that these species differ in a number of morphological characteristics, such as: the antennae are not pale basally and do not have a clearly defined six-segmented club with rhinaria on all six segments; the back of the head is not discernibly striate and the basal hair ring of the gaster is not dense. Therefore, we find it possible that \textit{H. neoscatellae} has either been misidentified as \textit{H. hexatoma} or these two distinct species have an overlapping host range. In either case, and with regards to our findings, specimens of \textit{H. hexatoma} that have been confirmed as a parasitoid of shore flies should be viewed as suspicious and specimens should be reevaluated to determined its correct identification to resolve this issue.

This population of \textit{H. neoscatellae} found in Vineland Station, Ontario (43°11'NN; 79°24'NW), is the first to be documented within Canada. This discovery provides a potential new biological control agent that once introduced, could sustain itself and maintain \textit{S. stagnalis} below nuisance levels at little or no cost to greenhouses operators. Optimal parameters for rearing (e.g., temperature, light, relative humidity, host rearing) and the testing of the biological control potential of this parasitoid is being determined. Voucher specimens of this species are now housed at Canadian National Insect Collection, ECORC-AAFC, Ottawa.

**ACKNOWLEDGMENTS**

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**LITERATURE CITED**


HAWKMOTHS (LEPIDOPTERA: SPHINGIDAE) COLLECTED IN GRAND TRAVERSE AND ADJACENT COUNTIES, MICHIGAN

Andrew W. Douglass¹, Christopher B. Douglass¹, and John F. Douglass²

ABSTRACT

Thirty-two (32) species of hawkmoths (Sphingidae) are reported from Grand Traverse and adjacent counties, Michigan, based on collecting carried out in 1979-1997 and an inventory of museum records.

The Grand Traverse Region is in an especially interesting position biologically in that it is part of a zone of transition in Michigan in which Carolinian floral and faunal elements intergrade with species typical of the Canadian zone (biotic provinces of Dice 1938; Douglass 1977, 1983, 1985, 1992).

To date, 48 species of hawkmoths have been recorded from Michigan (Nielsen 1997); two additional species are of possible occurrence in the state. We have been motivated by the work of Nielsen (1997 and pers. comm. 1980 to present) to begin a survey of the hawkmoths of Grand Traverse County, in northwestern Lower Michigan.

MATERIALS AND METHODS

Specimens were obtained almost exclusively by searching areas brightly illuminated with artificial lights at night. The majority of records cited in this paper were obtained by Andrew W. Douglass (AWD) and Christopher B. Douglass (CBD) during numerous nighttime collecting trips made to such localities during the period 9 July 1994-14 October 1997. In addition, John F. Douglass (JFD) collected specimens and made scattered observations in the area between June 1979 and September 1985.

Principal collecting localities were as follow, in descending order of our frequency of collecting visits to them:

- Site NCR - Lights just SE of jct. U.S. 31 & M-137 (T26N R12W, NE 1/4 Sec. 16);
- Site CNR - Lights just SW of jct. U.S. 31 & M-137 (T26N R12W, NW 1/4 Sec. 16);
- Site HBS - Lights just NW of jct. U.S. 31 & Co. 633 (T26N R11W, NW 1/4 Sec. 7), village of Grawn;
- Site YRD - Douglass property overlooking Green Lake, 1 mi. SW of village of Interlochen (T26N R12W, SW 1/4 Sec. 21);
- Site MCC - Monroe Center Cemetery (flowering shrubs), just E of Co. 633 (T26N R11W, NW 1/4 Sec. 31).

Small series of each species observed were collected: JFD’s specimens have been donated to Michigan State University, East Lansing; those of AWD and CBD remain in their private collections.

In order that we might cite museum specimen records which put our Grand Traverse Co. findings in broader context, one of us (JFD) visited five public collections in Lower Michigan during 1999-2000, at each of which all hawkmoth specimens of special zoozographic interest related to this report were examined: Michigan State

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RESULTS AND DISCUSSION

I. SPECIES ACCOUNTS

S 7771 Agrius cingulata (Fabricius), Pink-spotted Hawkmoth, Sweetpotato hornworm. Grand Traverse Co., outskirts of Traverse City, T27N R11W, NW 1/4 Sec. 22, 14 Oct. 1997, 1 ♀ (very fresh condition), A. W. Douglass. This primarily southern species is occasionally encountered in Michigan as a stray (Moore 1955, Hodges 1971, Covell 1984). Our single GT Co. specimen was found perched on the wall of a building; it appears to represent the northernmost known occurrence of cingulata in the state. Other NLP records: Isabella Co., 3 Sept. 1970, 1 specimen (very worn) [CMU]; Mason and Newaygo counties (NMap).

S 7775 Manduca sexta (Linnaeus), Carolina Sphinx, Tobacco hornworm. Grand Traverse Co., Sites NCR & HBS, 1 ♂, 2 ♀, 14 July 1995, 14 July 1996, 21 July 1997 (1 ♀, slight wear). Uncommon in GT Co. The northernmost previously reported Michigan locality for sexta is Eaton Co. in the SLP (Opler 1995). Our three specimens and one from Emmet Co. (below) appear to represent the northernmost known occurrences of sexta in the state.
Other NLP records: **Emmet Co.**, 31 Aug. 1945, 1 specimen [MSU]; **Grand Traverse Co.**? (no locality labels), 4 specimens [NwMC]; **Isabella Co.**, 2 Nov. 1997, 1 specimen (good condition) [CMU]; **Oceana Co.**, yrs. 1964-1975, 4 specimens [MSU].

S 7776 *Manduca quinquemaculata* (Haworth), Five-spotted Hawkmoth, Tomato hornworm. **Grand Traverse Co.**, 21 & 26 July 1965, 2 specimens (one is in excellent condition) [NwMC]; GT Co., 9 July 1985, 2 specimens [Dill collection]. Records of *quinquemaculata* exist from nine additional counties in the NLP (NMap, DSun).


S 7796 *Sphixx eremitus* (Hübner), Hermit Sphinx. **Antrim Co.**, 4 July 1960, 1 specimen [MSU]; this appears to represent the northernmost known Michigan locality for this species to date. Other NLP records: **Clare Co.**, MSU; **Isabella Co.**, NMap, CMU; **Lake Co.**, MSU; **Midland Co.**, MSU.


S 7807 *Sphinx canadensis* Boisduval, Canadian Sphinx. **Grand Traverse Co.**, Site CNR, 13 July 1985 (1 fresh ♂, 1 ♀), 1 Sept. 1985 (1♂), J. F. Douglass. Uncommon in GT Co. Museum and literature records of *canadensis* exist from scattered counties in the SLP, NLP, and UP.

S 7809 *Sphinx kalmiae* J. E. Smith, Laurel Sphinx. **Grand Traverse Co.**, Sites NCR & HBS, 2 July 1994, 9 June-12 July 1995, 7♂♂, 1 ♀. Fairly common in GT Co. All eight of our specimens show moderate wear; two fresh individuals were seen 20 June 2000.

S 7810.1 *Sphinx poecila* Stephens, Northern Apple Sphinx. **Grand Traverse Co.**, Sites CNR & NCR, 6 specimens (2♂♂, 4♀♀), all det. M. C. Nielsen; 16 June 1982 (1♀, fresh), 10 August 1985 (1♂, very worn), 26 May 1986, 16 June 1995. An additional individual was seen 20 June 2000. Fairly common in GT Co. Caution must be used in distinguishing this taxon from the closely similar *S. gordius* and from worn ♀♀ of *S. luscitiosa* (M. C. Nielsen pers. comm.). Riotte’s (1980) distribution map indicates that *poecila* occurs throughout Upper and Lower Michigan. M. C. Nielsen (pers. comm.) reports having found a nearly full-grown larva of *poecila* (reported as *gordius* in Voss 1969) on sweet gale (*Myrica gale L.*) in Cheboygan Co.

S 7811 *Sphinx luscitiosa* Clemens, Clemens’ Sphinx. **Grand Traverse Co.**, Sites CNR & NCR, 26 May 1985, 11 August 1985, 22 June 1995, 3♀♀ (all show slight wear). Uncommon in GT Co. Worn ♀♀ of this species are easily confused with members of the *S. poecila-S. gordius* complex.

common in GT Co. Our freshest specimen is a ♀ collected 26 June 1995; a ♀
collected 21 July 1994 shows much wear.

7817 *Lapara bombycoides* Walker, Northern Pine Sphinx. *Grand
Traverse* Co., Sites CNR, NCR, & YRD, 5♂♂: 16 June 1982 (our freshest
specimen), 2 June 1985 (1♂, much wear), 2 July 1994, 26 June 1996 (2♂♂♂, much
wear). A fresh individual was seen 25 May 1998. Fairly common in GT Co.

7821 *Smerinthus jamaicensis* (Drury), Twin-spotted Sphinx. *Grand
Traverse* Co., Sites CNR & NCR, 3♂♂: 11 August 1985 (1♂, fresh), 16-25 June
1995 (2♂♂, worn). Fairly common in GT Co.

7822 *Smerinthus cerisyi* W.F.Kirby, One-eyed Sphinx. *Grand
Traverse* Co., Site NCR, 16-20 June 1995, 3♂♂, 1♀ (all four specimens show

7824 *Paonias excaecatus* (J. E. Smith), Blinded Sphinx. *Grand
Traverse* Co., Sites CNR, NCR, YRD, & Traverse City, 10 August 1985, 14
June-12 July 1995, 7 July 1996, 4♂♂, 3♀♀. Fairly common in GT Co. Our only
fresh specimens are a ♀ collected 10 August 1985 and a ♀ collected 12 July
1995; an additional fresh individual was seen 2 July 2000.

7825 *Paonias myops* (J. E. Smith), Small-eyed Sphinx. *Grand Traverse*
Co., Sites YRD, CNR, & NCR, 14 July 1985, 11 June-12 July 1995, 26 June-3 July
other ♀♀ from mid-June to mid-July show considerable wear.

S 7827 *Laothoe juglandis* (J. E. Smith), Walnut Sphinx. *Grand
Traverse* Co., Site NCR, late June 1995, 1♀ (moderately worn), A. W. Douglass;
GT Co., 16 May 1970, 1 specimen [NWMC]; GT Co., 12 July 1985, 4 specimens
[Dill collection]. Uncommon in GT Co. Records of *juglandis* exist from seven
additional counties in the NLP (NMap, DSum).

7828 *Pachysphinx modesta* (Harris), Big Poplar Sphinx. *Grand
Traverse* Co., Sites CNR & NCR, 2 June-14 July 1985, 9 July 1994, 16 June-
12 July 1995, 5♂♂, 6♀♀. Common to abundant in GT Co. Our freshest speci-
mens are from 2 June 1985 (1♂), 14 July 1985 (1♀), and 12 July 1995 (1♀).

7833 *Hemaris thysbe* (Fabricius), Hummingbird Clearwing. Humming-
bird Moth. *Grand Traverse* Co., Site MCC, 4 & 6 June 1979, 1♂, 1♀, J. F.
Douglass. Apparently common in GT Co. Both individuals collected were seen
avidly visiting flowers of lilac (*Syringa vulgaris* L.) during daylight (1400-1500
h EDT). In addition, two *thysbe* adults were watched avidly visiting flowers of
spotted knapweed (*Centaurea maculosa* Lam.) on a sunny afternoon (1400 h
EDT), 7 August 2002.

7854 *Hemaris gracilis* (Grote & Robinson), Slender Clearwing. Spe-
cies *gracilis* almost certainly occurs in GT Co. (M. C. Nielsen pers. comm.);
records exist from as close to the Grand Traverse Region as Mason,
Roscommon, Crawford, and Otsego counties (Moore 1955, LSSS 1967[1968],
UMMZ).

7855 *Hemaris diffinis* (Boisdruval), Snowberry Clearwing, Bumblebee
Moth. *Grand Traverse* Co., Site MCC & at a leatherleaf depression in T26N
R12W, 4 & 5 June 1979, 3♂♂ (all show slight to moderate wear). J. F. Douglass.
Apparently common in GT Co. Each of the ♀♀ collected was seen avidly visiting
flowers: two were visiting lilac (*Syringa vulgaris* L.); the third and an addi-
tional individual were visiting chokeberry (*Aronia prunifolia* (Marsh.) Rehder)
at the leatherleaf site. Additional observations of flower visitation by *diffinis*
in GT Co.: one individual was seen avidly visiting flowers of lilac, 23 May 1980;
one was avidly visiting flowers of lilac and honeysuckle (*Lonicera* sp.), 26 May
1980. Each of the preceding observations of flower visitation (involving six
individual *diffinis*) occurred during daylight (1200-1400 h EDT).
S 7861 Eumorpha achemon (Drury), Achemon Sphinx. Voss’s (1969) record of achemon from Cheboygan Co. [UMBS collection] was overlooked in an earlier report (Douglass 1992) in which a Benzie Co. 2 (5 July 1984) was cited as Michigan’s northernmost record to date. One of the Benzie Co. specimen’s tarsi has a milkweed pollinarium (Asclepias sp.) attached. Other NLP records: Bay Co., MSU; Mason Co., MSU; Midland Co., UMMZ; Oceana Co., LSSS 1990[1991], LSSS 1997[1998], UMMZ.

S 7870 Sphecodina abbottii (Swainson), Abbot’s Sphinx. Grand Traverse Co., Site YRD, 21 May 1988, 1♀ (Douglass 1992); Site NCR (3 specimens, A. W. Douglass), 22 June 1995 (slight wear), 21 June 1997 (fresh/slight wear), 28 June 1997 (moderate wear); GT Co., T27N R11W, 1 June 1970, 1 specimen [NwMC]. Uncommon to locally common in GT Co. The above records represent Michigan’s northernmost known localities for this species. The only previously reported NLP locality for abbottii is Bay Co. (Opler 1995, NMap); the CMU collection contains one specimen from Kent Co. in the SLP (14 June 1983). The capture of rather fresh individuals at the same microlocality in GT Co. in successive years suggests that abbottii may be reproducing in the vicinity.


S 7873 Amphion floridensis B. P. Clark, Nessus Sphinx. Grand Traverse Co., T26N R12W, SE 1/4 Sec. 34, 6 June 1982, 1♀ (much-worn), J. F. Douglass; GT Co., years 1963-1987, 4 specimens [NwMC]. Uncommon in GT Co. Our single specimen was collected during daylight (6 June 1982) as it alit near a stream crossing. Additional observations of floridensis made in GT Co.: one individual was seen hovering around oozing willow trunks, 8 June 1979; one alit in sun, 13 June 1979; one was seen hovering around fluid-stained (oozing) willow trunks, 16 June 1979 (several butterflies, i.e., Vanessa atalanta, Polygonia comma, and P. interrogationis, were seen visiting these trunks at the time, alighting and actively probing with their proboscises). Each of the three preceding observations was made during daylight (1400-1500 h EDT) at a willow thicket at the microlocality of capture of the 6 June 1982 specimen; Virginia creeper (Parthenocissus sp.), one of the reported foodplants of floridensis (Mitchell and Zim 1977), is common in and around this thicket.

S 7884 Darapsa versicolor (Harris), Hydrangea Sphinx. Grand Traverse Co., Site NCR, 4 July 1996 (1 adult ♀, fresh), 23 June 1997 (1 adult ♀, moderate wear), A. W. Douglass. Uncommon in GT Co. These and the larval records reported below appear to represent the northernmost known occurrences of versicolor in the state. One mature (pre-pupal) versicolor larva was collected as it fed actively on leaves of Decodon verticillatus (L.) Ell. along the Little Betsie River (T26N R12W, SE 1/4 Sec. 20) on 12 August 2000. At the same microlocality on 20 August 2000, a smaller larva of the same species, with numerous braconid wasp cocoons attached, was collected as it rested on a sprig of D. verticillatus. D. verticillatus is abundant along streams in GT Co., and it appears that versicolor may be maintaining itself in the area. Other NLP records: Bay Co., NMap; Clare Co., 14 July 1969, 1 specimen [MSU]; NMap. The northernmost records of versicolor in the SLP are from Gratiot and Montcalm counties (NMap).


S 7893 *Hyles gallii* (Rottemburg), Galium Sphinx. **Grand Traverse** Co., Site HBS (i.e., village of Grawn), 7 July 1996, 1♀ (fresh condition), A. W. Douglass. Apparently rare in GT Co. In Michigan, *gallii* is known from the SLP (7 counties), NLP (6 counties), and UP (11 counties) (NMap, DSum).

7894 *Hyles lineata* (Fabricius), White-lined Sphinx. **Grand Traverse** Co., Sites CNR, NCR, & HBS, 3♂ 1♀, 11 August 1985 (found dead, dry), 24 August 1994 (1♂, moderate wear), 14 June 1995 (1♀, fresh), 26 June 1996 (1♂, fresh). Fairly common in GT Co. Voss (1969) reported this species to be very rare in the extreme NLP of Michigan (Emmet and Cheboygan counties).

II. SPECIES OF POSSIBLE OCCURRENCE

A number of additional hawkmoth species may be found to occur in the Grand Traverse Region of Michigan in the future. Most sphingids are strong fliers, and some species may occur infrequently in Michigan under unusual conditions of weather. It seems, too, that the present warming trend in climate will increase the likelihood that particular southern species will be recorded in the area as strays or colonists.

The following species are included here based on published reports (Moore 1955, Hodges 1971, Covell 1984, others cited in DSum), maps (Opler 1995, NMap), Nielsen’s (1997) checklist, and discussions with M. C. Nielsen (pers. comm. 2000). Two species not appearing in Nielsen (1997) are added here, bringing the total number of species treated in this report (i.e., those collected (above) plus those of possible occurrence (below)) to 50. Although 7877 *Proserpinus flavofasciata* (Walker), the Yellow-banded Day Sphinx, is occasionally encountered in the UP (uncommon resident), its possible occurrence in the Grand Traverse Region is doubtful (M. C. Nielsen pers. comm.).

Species of possible occurrence as strays or colonists in the NW Lower Peninsula (details are in DSum):

1) Species known as residents in the SLP
   P 7789 *Ceratomia catalpae* (Boisduval), Catalpa Sphinx.
   P 7790 *Ceratomia hageni* Grote, Hagen’s Sphinx.
   P 7793 *Paratrea plebeja* (Fabricius), Plebeian Sphinx.
   P 7810 *Sphinx gordius* Cramer, Apple Sphinx.
   P 7859 *Eumorpha pandorus* (Hübner), Pandorus Sphinx.

2) Primarily southern or tropical species, known in Michigan as strays
   P 7774 *Neococytius cluentius* (Cramer), Cluentius Sphinx.
   P 7834 *Erinnyis ello* (Linnaeus), Ello Sphinx.
   P 7837 *Erinnyis obscura* (Fabricius), Obscure Sphinx.
   P 7847 *Aellopos tantalus* (Linnaeus), Tantalus Sphinx.
   P 7849 *Aellopos titan* (Cramer), Titan Sphinx.
   P 7851 *Enyo lugubris* (Linnaeus), Mournful Sphinx.
   P 7864 *Eumorpha vitis* (Linnaeus), Vine Sphinx.
   P 7865 *Eumorpha fasciata* (Sulzer), Banded Sphinx.
   P 7866 *Eumorpha labruscae* (Linnaeus), Gaudy Sphinx.
   P 7890 *Xylophanes tersa* (Linnaeus), Tersa Sphinx.
3) Species not yet recorded from Michigan

P 7803 *Sphinx vashti* Strecker, Vashti Sphinx. Expected as a stray from the west.

P 7892 *Hyles euphorbiae* (Linnaeus), Spurge Hawkmoth. Expected as a stray or colonist from the east.

**ACKNOWLEDGMENTS**

We are greatly appreciative of help we have received from Mogens C. Nielsen of Lansing, who has been a wonderful source of encouragement and has provided determinations of specimens and distributional information on hawkmoth species in Michigan. For their promotion of our shared interest and their tireless provision of logistical support, we sincerely thank Katharine C. Douglass and Dr. Bruce G. Douglass of Traverse City, parents of AWD and CBD, without whose help this study would never have been possible. Thomas W. Carr of Whitehouse, Ohio, provided invaluable help in verifying sex and species determinations.

For facilitating access to collections for examination of specimens in their care, we sincerely thank the following persons: Mogens C. Nielsen, Department of Entomology, MSU; Mark F. O’Brien, Insect Division, UMMZ; Dr. Roger G. Bland, CMU; Kirk Waterstripe, Dr. William C. Scharf, and Dr. Keith E. Overbaugh, NWMC; Dr. Brian G. Scholtens and Robert J. Vande Kopple, UMBS; the Dill family (Traverse City).

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In addition, we are appreciative of the efforts of the many collectors who over the years have generously deposited specimens in public collections (incl. M. C. Nielsen, E. A. Herig Jr., F. W. Stehr, E. H. Metzler, W. P. Westrate Jr., R. W. Hodges, many others).

Finally, we thank Charlotte N. Douglass and Dr. Bruce E. Douglass (parents of JFD, Rochester, MN) and the Jesuit Community of St. John’s (Toledo, OH) for their steadfast support.

**LITERATURE CITED**


SECOND LOCATION FOR TWO RARE ODONATA IN OHIO, NANNOTHEMIS BELLA AND LADONA JULIA, (ODONATA: LIBELLULIDAE) DISCOVERED AT SINGER LAKE BOG, SUMMIT COUNTY, OHIO.

Robert C. Glotzhober1 and Eric Chapman2

Abstract

Previously the dragonflies (Odonata, Libellulidae) Ladona julia and Nannothemis bella were known in Ohio from only one extant population each: L. julia from extreme northwest Ohio in Williams County and N. bella from west-central Ohio in Champaign County. During the summer of 2000 populations of each of these species were found in close proximity to each other at Singer Lake, a wetlands complex in southern Summit County in northeastern Ohio. This new location is also home to a population of another rare Ohio dragonfly, Dorocordulia libera (Odonata, Corduliidae) that was discovered during 1999. The Singer Lake wetlands are proving to be a very significant habitat for Ohio Odonata.

Ladona julia (Uhler) (Odonata, Libellulidae) (synonym Libellula julia) has a widespread, northern distribution, with populations reported in a relatively narrow band coast to coast through southern Canada and the northern United States (Bick & Mauffray, 2001; Dunkle, 2000). In Michigan, it is widespread and often abundant at many sites (Mark O'Brien, personal communication). Indiana has records from 1917 in three northern counties, but there is only one small extant population currently known (Curry, 2001).

Ohio has three very old records of L. julia from 1898 and 1900, all from Stewart’s Lake, Portage County, Franklin Township, Kent, Ohio. James S. Hine collected one male on 23 June 1898 (specimens at University of Michigan, Museum of Zoology). R. C. Osburn collected two other males, one on 21 June 1898 and one on 22 June 1900 (specimens at The Ohio State University, Museum of Biological Diversity). This species has not been collected at this location during the 100 plus years following. Stewart’s Lake is approximately 32 kilometers north, north east of the Singer Lake site discussed in this paper. More recently a large and continuous population was discovered by Homer Price at Mud Lake in extreme northwestern Williams County on 30 May 1940 (Price 1950). Visits to Mud Lake during the last decade by the authors and several other workers have confirmed the continued existence of this population. Until the summer of 2000, no extant populations of this species were known from other locations in Ohio. The Ohio Odonata Society has recently recommended L. julia for addition to the Ohio endangered species list.

The Elfin Skimmer, N. bella (Uhler) (Odonata, Libellulidae) is the smallest dragonfly in North America, measuring only 18 to 21 mm in total length. Its distribution includes a swath through southeastern Canada and the northern United States from Minnesota to New England extending south to northeastern Illinois, east through Pennsylvania and New York, south along Atlantic coast to Virginia, inland through the hill region and south to northern Florida, Alabama and Louisiana (Bick and Mauffray 2001, Dunkle 2000). Within this range, populations are considered “local” in distribution, inhabiting only small

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25251 Verner Road, Kent. Ohio 44240
pockets within larger habitats that may be suitable for species with less stringent habitat requirements (Dunkle 2000). Walker and Corbet (1975) consider it widespread but "almost exclusively an inhabitant of floating sphagnum bogs, where it is sometimes quite abundant." Kielb (1997) noted that while it is rare in collections, it may be underrepresented in those collections from Michigan. He suggested that its restriction to sphagnum bogs, its low flight habit, and its small size may lead to it being overlooked (Kielb 1997). Curry (2001) reports that in Indiana $N. bella$ is "rare" and found in bogs and fens in five counties at the northern edge of the state.

Donald Borror (1930) first collected $N. bella$ in Ohio at Cedar Bog Nature Preserve in Champaign County, Ohio. Three females were collected in 1933 at a marl fen near Kennard, Champaign County, Ohio by Edward S. Thomas and Charles F. Walker and reside in the collections of the Ohio Historical Society (Glotzhober 1997). The area around Kennard was searched during 1995 with no trace of remaining peatlands surviving (Glotzhober 1997). In 1959 Alrutz collected ten males and five females from Silver Lake in eastern Miami County (Alrutz 1961). Alrutz revisited this site in 1992 (Alrutz 1993) and the senior author has made subsequent visits. Alrutz (1993) concludes that the habitat has changed significantly. No remnant of the Silver Lake population appears to survive. For many years $N. bella$ has been represented in Ohio by a single known population at Cedar Bog (Glotzhober 1997). In 1997 the Ohio Department of Natural Resources, Division of Wildlife listed $N. bella$ as a State Endangered species.

RESULTS AND DISCUSSION

On 1 June 2000 Jim Bissell of the Cleveland Museum of Natural History and John Pogacnik of Lake Metro Parks were exploring the Singer Lake area in Summit County, Green Township. This site is just north of the Stark County line, its center being approximately 40° 55'N and 81° 29'W. That same day they e-mailed the senior author with a report of finding 25 to 30 individuals of $N. bella$ and 8 to 10 of $L. julia$ on or near a floating sphagnum bog on the property. A single voucher of each of these two species was collected by Pogacnik and ultimately deposited at the Cleveland Museum of Natural History. On 3 June Pogacnik sent digital images of specimens of each to the senior author for tentative confirmation. On 7 June the junior author confirmed their report on site, followed up by a visit by both authors and Pogacnik on 9 June 2000. Additional specimens of each were collected and deposited in the natural history collections of the Ohio Historical Society. On this later visit we were accompanied by Renee Schrift and Katie Lublin from the Cleveland Museum of Natural History and Larry Rosche and Lou Gardella members of the Ohio Odonata Society. In the intervening week, additional individuals of $N. bella$ had emerged and we observed tenerals, adults, and adults in copula. The adult population visible that day on the floating sphagnum mat was conservatively estimated at between 50 to 100 individuals. In the nearby woods/bog edge we also observed a smaller number of $L. julia$, noting from one to two dozen individuals.

Singer Lake is a glacial relict wetland complex with a shallow boggy pond dominated by spatterdock ($Nuphar$ sp.), plus several bogs and kettle ponds separated by sandy hills. One of the leatherleaf ($Chamaedaphne calyculata$) bogs covers 10.5 hectares (26 acres) and is the largest leatherleaf bog in Ohio (Jim Bissell, pers. comm.). Depending on what areas are included, the total wetland area is somewhere between 61 and 142 ha. Portions of the area recently have been purchased as a nature preserve by the Cleveland Museum of Natural History. The Singer Lake area was outlined by Bissell (2001) in which he summarized the area’s rich botanical diversity, highlighting many of the basin’s rare and endangered plants.
The bog where *N. bella* was found is a large (circa 0.8 ha), old age floating sphagnum mat. It is bordered to the north and west by forest, from which it is separated by a moat of water from 10 to 30 m wide and about 1-2 m deep. The mat fades to more open swamp to the east and south. Jim Bissell (personal communication) provided the following botanical description. Compared to the other sphagnum mats in the Singer complex that are dominated by leatherleaf (*C. calyculata*), this mat is much more open. The edge of the floating mat has a discontinuous outer ring of poison sumac (*Rhus vernix*), and contains scattered clumps of leatherleaf and high bush blueberry (*Vaccinium corymbosum*). Spike rush (*Eleocharis erythropoda*) grows throughout the mat, and the southernmost portion has a sedge meadow of *Carex utriculata*. There are small open pools throughout the mat that contain spatterdock (*Nuphar* sp.) and swamp loosestrife (*Decodon verticillatus*) both of which also grow around the edge.

The Singer Lake wetlands are proving to be highly significant for Odonata in Ohio. In addition to the two rare species reported in this paper, Chapman (1999) reported the discovery of a large apparent breeding population of the *Dorocordulia libera* from Singer Lake – the first find of this species in Ohio in 75 years. Table 1 gives a current Odonata list from the site. The authors believe other interesting finds may yet be made among the many different wetland habitats within this wetland basin.

Table 1. Odonata of Singer Lake Wetlands

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus, species, Author</th>
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<tbody>
<tr>
<td>Lestidae</td>
<td><em>Lestes dryas</em> Kirby</td>
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<tr>
<td></td>
<td><em>Lestes eurinus</em> Say</td>
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<tr>
<td>Coenagrionidae</td>
<td><em>Enallagma hageni</em> (Walsh)</td>
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<td></td>
<td><em>Enallagma aspersum</em> (Hagen)</td>
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<td></td>
<td><em>Ischnura posita</em> (Hagen)</td>
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<tr>
<td></td>
<td><em>Ischnura verticalis</em> (Say)</td>
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<tr>
<td>Gomphidae</td>
<td><em>Gomphus exilis</em> Selys</td>
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<tr>
<td></td>
<td><em>Arigomphus villosipes</em> Selys</td>
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<tr>
<td>Aeshnidae</td>
<td><em>Aeshna mutata</em> Hagen</td>
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<td></td>
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<tr>
<td></td>
<td><em>Anax junius</em> (Drury)</td>
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<td>Corduliidae</td>
<td><em>Dorocordulia libera</em> (Selys)</td>
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<td></td>
<td><em>Epitheca cynosura</em> (Say)</td>
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<td></td>
<td><em>Epitheca princeps</em> Hagen</td>
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<tr>
<td>Libellulidae</td>
<td><em>Erythemis simplicicollis</em> Say</td>
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<td></td>
<td><em>Ladona julia</em> (Uhler)</td>
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<td><em>Libellula luctuosa</em> Burmeister</td>
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<td><em>Libellula cyanea</em> Fabricius</td>
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<td><em>Nannothemis bella</em> (Uhler)</td>
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<td><em>Pachydiplax longipennis</em> (Burmeister)</td>
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<td><em>Perithemis tenera</em> (Say)</td>
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<td><em>Plathemis (Libellula) lydia</em> Drury</td>
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<td><em>Sympetrum obtusum</em> (Hagen)</td>
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<td><em>Sympetrum rubicundulum</em> (Say)</td>
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<tr>
<td></td>
<td><em>Tramea lacerata</em> Hagen</td>
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</tbody>
</table>
ACKNOWLEDGMENTS

The authors thank Jim Bissell and other staff from the Cleveland Museum of Natural History for inviting us to explore this area over the last few years, and John Pogacnik for alerting us to these finds. The participation of Renee Schrift, Katie Lubin, Larry Rosche, and Lou Gardella to our field trip aided in orientation to the site and improved observations. Our thanks to Mark O'Brien for sharing information about distribution of the species in Michigan. This work is an outgrowth of the Ohio Odonata Survey, a project funded in part by the “Do Something Wild” income tax checkoff program from the Ohio Department of Natural Resources, Division of Wildlife.

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Bissell, J. K. 1998. A case for protection of Singer Lake Basins, City of Green, Summit County, Ohio. Natural Areas Division, Cleveland Museum of Natural History. 6 March 1998. 5p, 2 maps, 38 p. appendix with plant records.


TIPHIA VERNALIS (HYMENOPTERA: TIPHIIDAE) PARASITIZING ORIENTAL BEETLE, ANOMALA ORIENTALIS (COLEOPTERA: SCARABAEIDAE) IN A NURSERY

Michael E. Reding and Michael G. Klein

Tiphia vernalis Rohwer is native to China, Japan, and Korea where it is an external parasite of Popillia spp. (King 1931). It was released into the United States from China and Korea during the mid-1920s through early 30s (Fleming 1968). After it became established in the United States, releases were made from domestic sources beginning in 1931 (King et al. 1951). Tiphia vernalis was released into Ohio sporadically during 1936-1953 (King et al. 1951). Tiphia vernalis has been reported parasitizing Popillia spp. (P. quadriguttata (Fabricius) in Korea; P. chinensis (Frivaldsky) and P. formosana (Arrow) in China; and P. japonica Newman in Japan) exclusively in the field (Balock 1934, Fleming 1968). It accepted Anomala (=Exomala) orientalis Waterhouse (oriental beetle) as a host in the laboratory and cocoons were obtained (King et al. 1927, Balock 1934), but there are no previously published reports of T. vernalis parasitizing A. orientalis in the field.

In the spring of 2001 we found numerous A. orientalis grubs parasitized by T. vernalis at a commercial nursery in Lake County, OH. This nursery has only field planted trees and shrubs with no containerized material. Established blocks (> 1 year old) have trees and shrubs planted in weed-free strips with primarily grass between the rows. We found parasitized A. orientalis at two locations in this nursery about 300 m apart. One site (site-1) bordered a newly planted (2001) block of trees. The sample site contained a mixture of alfalfa, various grasses, wild flowers, and weeds. The second site (site-2) was within a block of maple trees that were planted in 1998. Samples were collected from the grass areas between the rows. Each site was sampled twice (site-1, sampled 5 and 7 June; site-2, sampled 7 and 12 June).

The Tiphia at this nursery in the spring were previously identified as T. vernalis. Moreover, the location on the grubs where the parasites attached, which is considered characteristic in Tiphia spp., was consistent with T. vernalis (Clausen et al. 1927). Eggs of T. vernalis are placed in the suture between the third thoracic segment and the first abdominal segment (Clausen et al. 1927). The most common white grubs in this nursery were in descending order A. orientalis, Maladera castanea Arrow (Asiatic garden beetle), Rhizotrogus majalis Razoumowsky (European chafer), and Popillia japonica Newman (Japanese beetle). The numbers of P. japonica grubs were relatively low compared to the other grub species. Therefore, we were surprised to see large numbers of male T. vernalis casting (wide zigzag flight) back and forth over the ground searching for females. In addition, we regularly found male and female T. vernalis in nearby maple and crabapple trees. Because the large population of T. vernalis was apparently inconsistent with the small population of P. japonica, we began examining all grub species for the presence of T. vernalis eggs/larvae. Parasitized A. orientalis grubs were first detected in the 5 June sample at site-1, but rate data was not recorded. Parasitization rate for the 7 June sample at this site was 6.4%. At site-2 parasitization rates were 23.1 and 9.1% for the 7 and 12 June samples, respectively, with a combined rate of 14.3%. Five P. japonica grubs were found versus 134 A. orientalis grubs (all samples combined), with one P. japonica parasitized. None of the M. castanea or R. majalis were parasitized.

The rate of parasitization suggests that T. vernalis may be a significant mortality factor of A. orientalis in this nursery. This discovery should encourage

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surveys in other locations where both *T. vernalis* and *A. orientalis* occur. In addition, redistribution of *T. vernalis* from sites where they are found to parasitize *A. orientalis* to locations where *A. orientalis* occur, but *T. vernalis* is absent, may be useful for managing *A. orientalis*.

**ACKNOWLEDGMENTS**

We thank our technician Jim Moyseenko for his technical assistance and hard work on this project.

**LITERATURE CITED**


Clausen, C. P., J. L. King and C. Teranishi. 1927. The parasites of *Popillia japonica* in Japan and Chosen (Korea), and their introduction into the United States. United States Department of Agriculture Bulletin No. 1429.


ABSTRACT

More than 2,100 adult, drifting giant water bugs (Lethocerus americanus) were collected from the upstream face of the uppermost raceway screens at a run-of-river trout hatchery on a Wisconsin tributary to Lake Superior during December 1991-May 1997. This drift was greatest from mid-October through March at water temperatures lower than 4° C, and was rare during summer. Individuals that were collected from the screens, marked, and released above the hatchery were rarely recovered, hence the location of the source population and drift distances are speculative. The sex ratio overall was close to 1:1, with males dominating numerically in 1994 and 1997, and females in 1993 and 1996. Females averaged 56.5 mm in total length (range 51-63 mm), and males 50.7 mm (range 47-56 mm). There was significant interannual variation in the mean lengths of males, but not of females. No differences in mean lengths or sex ratios between early- and late-winter collections were evident for any year. We suggest that the drift of these insects is best explained as a dispersal mechanism following the final molt and that winter is selected for dispersal to minimize predation risks.

Giant water bugs (Lethocerus americanus [Leidy]) are large, predatory insects belonging to the belostomatid subfamily Lethocerinae. Although drifting is a common feature of the ecology of many aquatic macroinvertebrate taxa, aquatic Heteroptera and particularly the Belostomatidae, are not commonly known to exhibit this tendency. Because they are large in size and have low benthic densities relative to other macroinvertebrate taxa, belostomatids are only rarely encountered in the small drift nets commonly used by ecologists to sample aquatic insects (DuBois and Stoll 1995). To our knowledge, drifting has been documented among the Lethocerinae only for L. americanus. DuBois and Rackouski (1992) reported an unusual, cold-weather drift pattern for this species in Wisconsin's Bois Brule River, but they were not able to sample throughout the winter. Although relatively few studies have examined macroinvertebrate drift throughout the year, drift densities of all other taxa were invariably lowest during winter in northerly regions of the temperate zone (Waters 1969, Stoneburner and Smock 1979).

Life history information for L. americanus is sketchy and no information is available on sex ratios or sexual dimorphism. Hoffman (1924), Hungerford (1919, 1925), and Rankin (1935) described various aspects of their biology and life history, and Hilsenhoff (1984) reported that in Wisconsin, L. americanus overwinter in deep lentic habitats or fly from summer breeding ponds to overwinter in streams. Our study extends current knowledge about this insect by describing sex ratios and sexual dimorphism of adults in a coldwater stream, and by providing additional information about their pattern of cold-weather drift.
MATERIALS AND METHODS

The Little Brule River (46°30'N, 91°35'W) in eastern Douglas County, WI (USA), is a stable, spring-fed tributary to the Bois Brule River. The Little Brule River features an unnamed spring pond near its source (Figure 1), drains a watershed of 21.3 km², and is 4.5 km in length. The mean flow is 0.36 m³/sec., mean width is 5.2 m, and mean depth is 24 cm. The water is clear with a pH of 7.3 and methyl purple alkalinity of 66 ppm. The stream bottom is mostly sand with scattered patches of gravel and little instream vegetation. The Little Brule watershed was described in greater detail by DuBois and Schram (1993) and detailed physical descriptions of the entire Bois Brule River watershed are also available (DuBois 1993, DuBois and Pratt 1994).

The Little Brule River serves as the water source for a state-owned trout rearing station (hereafter referred to as the hatchery) located about 2.5 km downstream from the spring pond (Figure 1). Most of the river flow is directed through the hatchery which comprises 29 raceways and ponds. Some flow can be shunted through a bypass channel during peak-flow events to moderate high flows within the hatchery. Although discharge was not measured, notes on flow fluctuations made by hatchery personnel were sufficient to establish that discharge varied little in this stable-flow stream during the study period, especially during winter when most of the drift occurred. Water temperatures were recorded three times each day with a hand-held thermometer (1991-95) or continuously with a Hobo Data Logger, model H8 (1996-97). Weather conditions, including formation of ice cover, were also recorded daily.

Figure 1. Map of the study area.
Adult *L. americanus* were collected from the upstream-facing sides of the upper six raceway screens at the upstream end of the hatchery complex (Figure 1) as hatchery personnel made their daily rounds to clean the screens. Both 6.35-mm and 12.7-mm square-mesh hardware cloth was used for raceway screening; both sizes were small enough to retain adult male and female *L. americanus*. Collections were made continuously from December 1991 through May 1997. Most *L. americanus* were counted and returned to the water below the raceway screen from which they had been collected. Numbers counted per year underestimate, but are likely close to, the total numbers drifting in the Little Brule River. Small numbers may have circumvented the hatchery through the small bypass channel (Figure 1) or climbed over the raceway screens during mild weather. Broodstock trout were sometimes present in the upper-most raceway ahead of the first series of screens and they could have preyed upon some. Also hatchery personnel may have missed some individuals when examining the screens.

Specimens were periodically preserved in 70% isopropanol for measurement of total length (not including the air straps) and sex determination. Other groups were marked live and released at various locations both above and below the site of capture to study movement patterns and rates. The marking procedure involved drying the pronotum and applying dots of fingernail polish or liquid paper (correction fluid) of various colors which were then covered with a layer of cyanoacrylate (superglue) and allowed to dry. This method produced a mark that was readily recognizable up to 10 weeks later.

All statistical tests were performed using the SigmaStat statistical software (SPSS Inc. 1997) with alpha set at 0.05. Statistical assumptions were tested using the Kolmogorov-Smirnov test for normality and the Levene Median test for equal variance. Mean lengths of *L. americanus* in samples collected within and among years were examined for differences using *t*-tests, analysis of variance (ANOVA), and pairwise multiple comparison procedures (Tukey test). When assumptions of normality were not met, nonparametric ANOVAs on ranks (Kruskal-Wallis test) and nonparametric pairwise multiple comparisons (Dunn's method) were used.

**RESULTS AND DISCUSSION**

**Sex Ratios and Sexual Dimorphism.** The sex ratio was nearly 1:1 overall, but was skewed toward males in 1994 and 1997 and toward females in 1993 and 1996 (Table 1). Females averaged 56.5 mm in total length, with a range from 51-63 mm, and males were smaller (*P < 0.001*) having a mean length

<table>
<thead>
<tr>
<th>Year</th>
<th>Total number drifting</th>
<th>Number sampled for lengths and sex ratios</th>
<th>Sex ratio (M : F)</th>
<th>Mean lengths (mm)</th>
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<tr>
<td></td>
<td></td>
<td>Total</td>
<td></td>
<td>Males</td>
</tr>
<tr>
<td>1991</td>
<td>30</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>1992</td>
<td>214</td>
<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>1993</td>
<td>262</td>
<td>89</td>
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<tr>
<td>1994</td>
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<tr>
<td>1995</td>
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<td>597</td>
<td>31</td>
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</tr>
<tr>
<td>1997</td>
<td>358</td>
<td>63</td>
<td>1.2 : 1</td>
<td>51.0</td>
</tr>
<tr>
<td>Total</td>
<td>2,132</td>
<td>311</td>
<td>1 : 1.1</td>
<td>50.7</td>
</tr>
</tbody>
</table>

*Collections made only in December.*

*Collections made only during January-May.*
of 50.7 mm, and a range from 47.56 mm (Table 1). Thus, female *L. americanus* averaged about 11% longer than males. This degree of sexual dimorphism is similar to that observed for *L. colossicus* (R. Macias-Ordonez, pers. comm.) and *L. medius* (R. Smith, pers. comm.), but substantially less than that reported for *L. deyerlei* (Ichikawa 1991). Mean lengths did not differ significantly between early winter and late winter collections for either sex in any year. Mean lengths of females did not differ among years, but males were significantly smaller in 1996 than in 1997 (*P* = 0.039).

**Timing and Magnitude of the Drift.** More than 2,100 adult *L. americanus* were collected during the study from the raceway screens at the upstream end of the hatchery. These specimens provided clear evidence of drift because no *L. americanus* were observed flying in the vicinity of the hatchery at any season and none could have flown to the collection site at the low temperatures that occurred when most movement was documented.

Drift of substantial numbers of *L. americanus* typically began in October, increased through November and December, peaked in January and February, declined through March and essentially ended in April (Figure 2). This pattern of drift was consistent with that reported during April through November in 1989 and 1990 from a salmonid smolt trap operated in the lower Bois Brule River about 38 km farther downstream (DuBois and Rackowski 1992).

Numbers of drifting *L. americanus* varied annually from about 200 to nearly 600 (Table 1). Because drift rates were low, it was difficult to correlate drift with abiotic variables. However, more than 85% of the drift occurred at water temperatures lower than 4°C and it was most intense during short periods of slight warming that occurred periodically each winter. Most drift occurred during winter base-flow conditions and was virtually absent during spring run-off or summer spates.

**Drift Distances.** We sought to determine drift distances by mark and recapture experiments. A sand- and gravel-bottomed trout stream over most of its length, the Little Brule River upstream of the hatchery provides little of the slow-flowing, vegetated habitat suitable for *L. americanus*. *L. americanus* was

![Figure 2. Mean numbers by month (1992-97) of drifting *Lethocerus americanus* (bars) and water temperature (line) at the Brule Trout Rearing Station on the Little Brule River.](image-url)
never seen in the Little Brule River between the hatchery and the spring pond when it was electrofished annually for salmonids, even though the species was readily collected with this gear from other streams in the area (RBD, pers. obs.). Thus, we tentatively assumed that the headwater spring pond held the source population of these insects and that drift distances of 2.5 km were commonly negotiated. Marked *L. americanus* were released in a small impoundment of the river just above the hatchery and at the State Highway 27 (SH 27) road crossing 2.5 km farther upstream (just below the spring pond - Figure 1). Rates of recovery of marked specimens were low. Only 1 of 48 marked individuals released at SH 27 was recovered at the hatchery; that individual was at large for 77 days. Of 60 marked individuals that were released immediately above the hatchery in the small impoundment, only 6 (10%) were recovered on the hatchery screens; these individuals were at large from 3 days to 2 months. The marking process may have altered the behavior of these insects or affected their survival even though they appeared robust at the time of release. We repeatedly noticed that *L. americanus* collected during winter had difficulty adjusting to changes in water temperature. When we brought them indoors in pails of water they often became lethargic and many died as the water warmed, even when we warmed them slowly. The recovery of a marked specimen from the upper-most release point 2.5 km upstream after 11 weeks demonstrated that drift of 2.5 km was possible for these insects. Drift distances of benthic invertebrates are typically short, from a few centimeters to tens of meters, but distances up to several hundred meters have occasionally been reported (reviewed by Brittain and Eikeland 1988). Further, Hemsworth and Brooker (1979) showed that some invertebrate taxa could be displaced about 10 km downstream during a generation. From a lack of suitable habitat immediately upstream of their collection site in the same watershed, DuBois and Rackouski (1992) also concluded that drifting *L. americanus* must have been coming from considerable distances, perhaps many kilometers.

**Ecosystem Significance of the Drift.** In an early paper, Muller (1954) concluded that drift serves to regulate populations by preventing over abundance of progeny in upstream areas. Studies since then have shown that seasonal fluctuations in macroinvertebrate drift are usually related to prepupation and emergence activities (Waters 1969; Reisen and Prins 1972), breeding activity (Muller 1974), or periods of maximum growth (Elliott 1967; Kohler 1983). None of these factors were linked in any obvious way with drift of *L. americanus* in the Little Brule River because mid-winter is not a time of pupation, emergence, breeding activity, or maximum growth. A density dependent aspect of macroinvertebrate drift has often been noted with seasonal declines in drift density paralleling seasonal declines in the benthos (Walton 1980; Allan 1987). Because many *L. americanus* were observed swimming above the raceway screens and crawling on the screens, this drift evidently had an active component.

The question of why these insects drift most abundantly in mid winter is perplexing. Aquatic insect larvae are known to be active during winter in temperate regions, but drift rates are generally low at this time (McLay 1968; Stoneburner and Smock 1979). We are aware of no similar case of peak drift in winter for any other taxon. However, comparing the behavior of *L. americanus* with that of other aquatic insects may be inappropriate because they differ from the norm in their large body size, unique reproduction involving exclusive postzygotic paternal care of the young (Smith 1997), the apparently long distances that they drift, their method of respiration, their strategy of overwintering as adults, and in their requirement of vertebrate prey.

We suggest that this phenomenon of mid-winter drift is explained most consistently with the evidence as an active form of distributional drift, that is, as a mechanism for regulating crowding. Cullen (1969) suggested that in at least some species of Lethocerinae, young adults disperse only once, after their final molt, and then remain for the rest of their reproductive life at one site. This is
consistent with our observations that these were relatively young individuals because they exhibited little body wear (missing leg segments, torn wings, or dirt or algae on the wings). The fact that the sex ratio was close to 1:1 further supports the idea that these insects were young-of-the-year because a population with a mix of young and older adults is likely to contain more females (R. Smith, pers. comm.). Although other species of *Lethocerus* are known to disperse by flight, *L. americanus* may in addition have adapted the dispersal mechanism of drifting in rivers until suitable habitat is encountered. We further suggest that dispersal occurs during winter to reduce predation risks. Many aquatic insects, including larger instars of *Baetis*, are thought to avoid drifting during the day to avoid predators (Skinner 1985). Because dispersal of *L. americanus* could require lengthy drift distances in rivers, they may have evolved to disperse during winter when predation risks from vertebrate predators are reduced.

Clearly, other plausible explanations exist for the mid-winter drifting of these insects. For example, increased swimming activity in the spring pond could have predisposed *L. americanus* to enter the drift (behavioral drift) when they were near the outlet of the pond. Several factors could have contributed to increased swimming activity in this area. Shortages of food are known to stimulate increased activity of aquatic invertebrates which can lead to increased drift (Brittain and Eikeland 1988). Also, increased swimming activity of insects can occur when regulation of oxygen consumption via positioning changes are insufficient to meet respiratory needs (Wiley and Kohler 1980). It is possible that restricted access to oxygen as the spring pond freezes over could have forced them toward the outlet and eventually out into the main channel of the stream. In either case, once caught in the current they may continue downstream for considerable distances because suitable habitat is not readily found. We invite further research on the dispersal behavior of these interesting insects to test these ideas.

**ACKNOWLEDGMENTS**

We thank D. Thompson, S. Plaster, and W. Nelson for assistance with collection of specimens. We are especially grateful to R. Macias-Ordonez who visited our site on several occasions and provided us with a wealth of perceptive insights. We further benefited from discussions with R. Smith, D. Lytle, and L. Corkum about the relevance of the findings. We thank T. Edsall, J. Pleski, and an anonymous reviewer for helpful comments on this manuscript. This research was supported in part by funds from the Wisconsin Department of Natural Resources.

**LITERATURE CITED**


**Arcynopteryx compacta (McLachlan)** is included in a small group of stoneflies that can be described as circumpolar. This species is broadly distrib­­uted throughout the northern Holarctic region in a circular manner mainly south of the Arctic Circle. The other members of this group are *Diura bicaudata* (Linnaeus), *Nemoura arctica* Ebsen-Peterson, *Plumiperla diversa* (Frison), and *Podmosta weberi* (Ricker) (Stewart and Ricker 1997). Aside from North America, *A. compacta* is locally distributed across Siberia and the Russia Far-Eastern region (Levanidova and Zhiltzova 1979), Scandinavia (Lillehammer 1985), and high-altitude habitats in the French Pyrenees (Lavendier 1979). *Arcynopteryx compacta* inhabits streams and can be a dominant predator along the rocky shorelines of lakes (Stewart and Stark 1988).

In North America, *A. compacta* is found along a wide latitudinal band at higher latitudes and altitudes (Ricker 1944, 1964; Hynes 1988). *Arcynopteryx compacta* is distributed in Alaska (Stewart et al. 1990), Yukon (Stewart and Ricker 1997), Saskatchewan (Stewart and Stark 1988), lakes of the Canadian Rockies (Donald and Anderson 1980) south to isolated patches in Montana, Colorado and Wyoming (Baumann et al. 1977), and east to highly-localized populations in Maine, New Hampshire, and possibly New York (Hanson 1942, Mingo 1983). Ricker (1964) provided a distribution map for this species in North America and noted that *A. compacta* exuviae were collected from boulders along the Lake Superior shoreline of the Keweenaw Peninsula in the Upper Peninsula of Michigan. This nominal collection provided the basis for inclusion of Lake Superior as a distribution point in Ricker’s (1952) treatment of Perlodinae.

During recent collecting trips to Michigan’s Upper Peninsula, the senior author collected fresh material of *A. compacta* from habitats similar to that described by Ricker (1964). Collecting trips were made to this region in May 1995, June 1996, and June 2001. Nymphs were hand-picked from boulders along a wave-swept shoreline and adults were located by searching among drift­wood and associated rubble. Additional stonefly species collected with *A. compacta* included *Capnia vernalis* (Newport), *Paracapnia angulata* Hanson, *Isogenoides frontalis* (Newman), *Isoperla bilineata* (Say), *I. cotta* Ricker, and immature chloroperlid nymphs.

To date, there has not been a published comprehensive treatment of Michigan’s stonefly fauna. Only 39 species were listed by Stark et al. (1986),

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**ABSTRACT**

*Arcynopteryx compacta*, a northern Holarctic species, is confirmed from Lake Superior along the Keweenaw Peninsula of Michigan’s Upper Peninsula. A checklist of stoneflies of Michigan is provided, reporting 58 species plus a list of an additional 19 species that are likely to occur in the state.
followed by 42 (Stewart and Stark 1988), and 40 (Stark 2001) species, respec­tively (Table 1). This paper reports 16 “new” state records, which are listed below. Six novel records are noted based on material obtained by the senior author (detailed records limited to two occurrences where males, if obtained, were collected), three records solely from literature (only one record listed), including electronic resources (i.e., Illinois Natural History Survey (INHS 2001)), and an additional seven records based on a combination of the authors’ collections, literature, and/or museum holdings.

Family Nemouridae
Geneus Ostrocerca
O. albidipennis (Walker): Chippewa Co., spring into Taqhuamenon River, near Lower Falls, Taqhuamenon Falls State Park, 05/24/95, SAG, 1 ♂. This record indicates a western range extension. O. albidipennis is mainly an Appa­lachian-distributed species that flanks slightly east into the upper Piedmont and Ontario to the west.

Family Taeniopterygidae
Geneus Oemopteryx
O. glacialis (Newport): Delta Co., Escanaba River, 04/08/49, S. Lievense, 3 ♀ ♂ (UMMZ).

Genus Strophopteryx
S. fasciata (Burmeister): Berrien Co., Dowagiac Creek, Niles, 04/15/95, SAG, 1 ♀; Calhoun Co., South Branch Kalamazoo River, 5.5 km SSW Albion, 03/03/1992, Ethan Bright (EB), 1 larva; Delta Co., Sturgeon River, Nahma Junction, 05/12/41, T. H. Frison (THF), 1 ♂ (INHS 2001).

Genus Taeniopteryx
T. burksi Ricker & Ross: Berrien Co., St. Joseph River, Niles, 04/07/96, SAG, 2 ♂♂, 2 ♀ ♀; Dowagiac Creek, U.S. 31, Niles, 04/07/96, SAG, 2 ♂♂. In their revision of North American Taeniopteryx, Ricker and Ross (1968) listed this species from Clinton and Ingham Counties.


Family Capniidae
Geneus Capnia
C. vernalis (Newport): Keweenaw Co., Lake Superior, Keweenaw Pen­insula, 8 km E Eagle Harbor, 05/27/95, SAG, 3 ♀♀; Isle Royale Co., Isle Royale, 07/14/05, H. A. Gleason (Needham and Claassen 1925).

Genus Paracapnia
P. opis (Newman): Keweenaw Co., Montreal River, 8 km SE Eagle Harbor, 06/04/01, SAG and Dana E. King-Grubbs (DEG), 5 ♂♂, 29 ♀♀.

Family Leuctridae
Geneus Leuctra
L. ferruginea (Walker): Alger Co., Valley Spur Creek, 3 km SW Munising, 06/05/95, SAG, 4 ♂♂, 1 ♀; Keweenaw Co., Silver River, 06/03/49, J. W. Leonard and F. A. Leonard, 3 ♂♂, 3 ♀♀ (UMMZ).

Family Pteronarcyidae
Geneus Pteronarcys
P. dorsata (Say): Berrien Co., Dowagiac Creek, Niles, 04/15/95, SAG, 2 ♂♂, 2 ♂♂; Lake Co., Little Manistee River, near Peacock, 05/10/40, THF, 1 ♂ (INHS 2001).
Table 1. Comparison of previous compilations of stoneflies listed from Michigan.

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<td>X(^2)</td>
<td>X(^2)</td>
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<tr>
<td></td>
<td><em>Paragnetina media</em></td>
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<tr>
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<td><em>Perlinella drymo</em></td>
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\(^1\) listed as *Cultus decisus*, but Stark et al. (1988) split this species into three taxonomic units, *C. d. decisus*, *C. d. isolatus*, and *C. verticalis*.
\(^2\) listed as *A. evoluta*, but Stark & Brown (1991) described *A. frisoni*, replacing *A. evoluta*, which replaced *A. meia*. 

Family Perlodidae

Genus Arcynopteryx

A. compacta (McLachlan): Keweenaw Co., Lake Superior, Keweenaw Peninsula, 8 km E Eagle Harbor, 06/27/95, SAG, 1 ♂, 10 nymphs; 06/09/96, SAG, 3 ♂♀, 2 ♀♂.

Genus Isoperla

I. frisoni Illies: Crawford Co., North Branch AuSable River, 06/16/35, JWL, 2 ♂♂, 3 ♀♀ (INHS 2001); Luce Co., Two Hearted River, 36 km E Grand Marais, Lake Superior State Forest, 06/02/01, SAG and DEG, 5 ♂♂, 1 ♀; Wexford Co., Manistee River, 9 km N Manton, 06/01/01, SAG and DEG, 1 ♂.

I. nana (Walsh): Mason Co., Big South Branch Pere Marquette River, 9 km S Walhalla, Manistee National Forest, 05/26/98, SAG, 2 ♂♂, 1 ♀.

Family Chloroperlidae

Genus Haploperla

H. orpha (Frison): Oscoda Co., Mio, 05/29/37, THF, 1 ♂, 1 ♀, (INHS 2001). Frison determined these specimens in 1942. Both abdomens are clipped and cleared, but do not appear to bear a central abdominal stripe. In addition, both specimens are discolored such that pronotal pigmentation was indistinguishable. The quadrate epiproct tip is apparent and very similar to fresh material obtained during the course of this study that clearly lack both abdominal and pronotal coloration. All Haploperla specimens obtained during this study, regardless of variation in epiproctal shape, have been conservatively assigned to H. brevis (Banks).

Family Perlidae

Genus Perlesta

P. shubuta Stark: Berrien Co., Dowagiac Creek, Niles, 06/30/94, SAG, 5 ♂♂, 4 ♀♀; 06/07/01, SAG and DEG, 4♂♂, 2 ♀♀.

Genus Perlinella

P. ephyre (Newman): Berrien Co., St. Joseph River, Niles, 06/08/01, SAG, 3 ♂♂, 8 ♀♀; Dowagiac Creek, Niles, 05/25/98, SAG, 1 ♀.

Overall, 58 species have been confirmed from Michigan (Table 2). Yanoviak and McCafferty (1996) included records for Leuctra tenella Provancher and Isoperla richardsoni Frison from the Huron Mountain region of the Upper Peninsula. We have omitted these records as new because both determinations were based on nymphs, although both species may occur in Michigan. Nymphs of Leuctra are difficult to identify to species (Stewart and Stark 1988), despite the taxonomic treatment by Harper and Hynes (1971), and examination of the nymphs identified as L. tenella proved inconclusive. Nymphal material of I. richardsoni was not available for study. Adult material determined as L. tenella by J. W. Leonard in the University of Michigan Museum of Zoology was available for study, but all adults were misidentifications of either Leuctra tenuis or L. ferruginea.

Stout and Rondinelli (1995) reported the occurrence of Suwallia, Paranemoura, and Oemopteryx glacialis from the Ford River, also in the Upper Peninsula. Identical to Yanoviak and McCafferty (1996), however, these determinations were based from nymphs and material was not available for study. Suwallia (as S. marginata (Banks)) is expected to occur in Michigan, especially in the Upper Peninsula or the northern tier of the Lower Peninsula. Although the presence of Paranemoura is unlikely, the occurrence of Ostrocerca albipennis (Walker) in the eastern portion of the Upper Peninsula raises the
Table 2. Revised checklist of stoneflies reported from Michigan. **“new” state records, + potential additions based on known occurrences from adjacent state(s) or Ontario.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>New or potential state Record</th>
<th>Known locations</th>
<th>Biogeographic distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nemouridae</td>
<td><em>Amphinemura delosa</em> (Ricker)</td>
<td></td>
<td></td>
<td>EB</td>
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<tr>
<td></td>
<td><em>A. linda</em> (Ricker)</td>
<td></td>
<td></td>
<td>EB</td>
</tr>
<tr>
<td></td>
<td><em>Nemura trispinosa</em> Claassen</td>
<td></td>
<td></td>
<td>WB</td>
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<tr>
<td></td>
<td><em>Ostrocerca albidipennis</em> (Walker)</td>
<td>**</td>
<td></td>
<td>AP</td>
</tr>
<tr>
<td></td>
<td><em>Prostoia complea</em> (Walker)</td>
<td></td>
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<td>EB</td>
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<td></td>
<td><em>P. similis</em> (Hagen)</td>
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<td>EB</td>
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<tr>
<td></td>
<td><em>Shipsa rotunda</em> (Claassen)</td>
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<td>WB</td>
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<tr>
<td></td>
<td><em>Soyedina vallieularia</em> (Wu)</td>
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<td>EB</td>
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<tr>
<td>Taeniopterygidae</td>
<td><em>Oemopleryx glacialis</em> (Newport)</td>
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<tr>
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<td><em>Strophopteryx fasciata</em> (Burmeister)</td>
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<tr>
<td></td>
<td><em>Taeniopteryx burksi</em> Ricker and Ross</td>
<td>**</td>
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<td><em>T. mauro</em> (Picket)</td>
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<tr>
<td></td>
<td><em>T. parvula</em> Banks</td>
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<td>WB</td>
</tr>
<tr>
<td>Capniidae</td>
<td><em>Allocapnia frisoni</em> Ricker and Ross</td>
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<td>EB</td>
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<td><em>A. granulata</em> (Claassen)</td>
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<td><em>Capnia vernalis</em> (Newport)</td>
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<td><em>P. pictetti</em> Hagen</td>
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<th>Known locations</th>
<th>Biogeographic distribution</th>
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<td>A. banksi Frison</td>
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<td>A. frisoni Stark and Brown</td>
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<td>A. internata (Walker)</td>
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<td>N. stewarti Stark and Baumann</td>
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<td>N. mainensis Banks</td>
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<td>P. decipiens (Walsh)</td>
<td>+</td>
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<td>P. shubuta Stark</td>
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<td>Perlinella drymo (Newman)</td>
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<td></td>
<td>P. ephyre (Newman)</td>
<td>**</td>
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possibility of a Michigan record of Paranemoura, as the latter species shares a similar distribution in the northern Appalachians with P. claasseni Baumann and P. perfecta (Walker).

The presence of Neoperla has been confirmed based a nymphal record from the Huron River in Washtenaw County, in the southern part of the Lower Peninsula. Three species are likely to occur in southern Michigan (see table 2). Nymphs are very difficult to identify with confidence, and we prefer to await the collection of adult material before attempting specific-level diagnoses.

The stonefly fauna of Michigan can be conveniently split into five overlapping distributional units (Table 2): (1) widespread boreal (WB), defined as species which occupy portions of both the eastern and western regions of North America, using the Mississippi River and James Bay as approximate dividing lines; (2) eastern boreal (EB), defined as species that range mainly throughout eastern North America; (3) northern boreal (NB), defined as species that only occupy northern regions in eastern North America; (4) northern Holarctic (NH), defined as species distributed as circumpolar; and (5) Appalachian (AP), defined as species that are found primarily in the Appalachian Mountain range. In order of decreasing predominance, the EB group is most common to Michigan (32 species), followed by WB (12 species), NB (12 species), and NH and AP (1 species each).

The landscape of Michigan can be simply divided into two obvious geographic units, the Lower Peninsula and the Upper Peninsula. This dichotomy, however, does not reflect natural boundaries according to climatic, geologic, physiographic, or vegetation units. A basic classification system may follow Bailey and Cushwa (1981), which separates the Upper Peninsula and northern and central portion of the Lower Peninsula from the southern unit of the Lower Peninsula according to mixed coniferous-deciduous ('northern') and deciduous ('southern') geographic units. However, because a systematic collecting effort throughout both peninsulas has not been attempted, a potential grouping of like assemblages of species into the ecosystem classification scheme created by Albert (1995), ecoregions (Omernik 1987, Bailey et al. 1995) and/or U.S.G.S. hydrologic unit codes is not yet possible.
ACKNOWLEDGMENTS

We thank Arwin Provonsha (Purdue University), Colin Favret (Illinois Natural History Survey), and Mark O’Brien (University of Michigan Museum of Zoology) for making material available for study. Boris Kondratieff (Colorado State University), Stan Szczytko (University of Wisconsin Stevens-Point), and Richard Merritt (Michigan State University) improved the quality of this manuscript through pre-publication reviews.

LITERATURE CITED


DISCRIMINATIONS OF COLOR AND PATTERN ON ARTIFICIAL FLOWERS BY MALE AND FEMALE BUMBLE BEES, BOMBUS IMPATIENS (HYMENOPTERA: APIDAE)

Dana Church¹, Catherine Plowright¹, and Diana Loyer¹

ABSTRACT

This study examined the performance of male bumble bees (Bombus impatiens) in color and pattern discriminations and compared it to that of female bees. Bees were trained to forage from rewarding (S+) and unrewarding (S-) artificial flowers which differed in color (blue vs yellow) or pattern (e.g., concentric vs radial). Learning of the discrimination by the bees was then assessed by examining choice proportions of different flower types while none of the flowers offered reward. Color discriminations were made with 98% accuracy by the males, and the choice proportion was no different for females. Pattern discriminations were very poor or nonexistent for males but significantly better for females, especially in one of three pattern discriminations (radial vs concentric patterns).

In colonies of honey bees and bumble bees males and females do not share equally in the labor. It is the females, the "workers," that gather nectar and pollen from flowers, bring it back to the colony, and feed it to the larvae. The males perform none of these duties. Once mature, they leave the colony, seek out conspecific queens, and mate. In the species used in the present study, Bombus impatiens Cresson, mating occurs away from colonies, though in other species males may fly to other colonies and mate near the entrance. During that time, they need only collect enough nectar to satisfy their own energetic needs (for a general review of the workings within a colony, see Alford 1975, Free and Butler 1959). Not surprisingly, the study of foraging behavior in social bees has been the study of female bees. Male bees have been studied, but for other reasons. Research topics on males have included mating behavior (e.g., Baer and Schmid-Hempel 1999, Bergman and Bergstrom 1997, Duchateau and Velthuis 1988, Free 1971), territoriality and competition (Alcock and Alcock 1983, O'Neill et al. 1991, Van der Blom 1986), analysis of paternity (Collins and Donoghue 1999, Haberl and Tautz 1998), sex ratios in colonies (Beekman and Van Stratum 1998), flight paths (Jennersten et al. 1991), energy expenditure (Bertsch 1984), spectral sensitivities (Menzel et al. 1988) and neurophysiology (Fahrbach et al. 1997).

An extensive literature on foraging mechanisms in bees details how workers succeed in the task of finding and returning to rewarding flowers. For example, workers learn discriminations between patterns of various colors and complexities (Brown et al. 1998, Couvillon and Bitterman 1980, Dukas and Real 1993, Gould 1986, Horridge 1997, Horridge and Zhang 1995, Lehrer et al. 1995, Srinivasan 1994). The abilities of males in color and pattern discriminations are little known, and the primary objective of this paper was to investigate them.

A natural extension of this project was to compare the performance of male bees to that of females under comparable conditions. A priori, given that males are not the providers in the colony, there should be a lesser incentive for them to collect food, and we speculated that they might be less adept at learning floral discriminations.

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One impediment to studying male foraging behavior is that they rarely if ever return to the colony once they have left. In a laboratory flight cage, however, they station themselves on the walls and occasionally "swoop down" onto artificial flowers and collect sugar solution. In the following study rewarding (S+) and unrewarding (S-) artificial flowers, differing either in color or in pattern, were arranged in the flight cage. The colors and patterns were chosen on the basis of previous literature: blue vs yellow is commonly used in studies of floral discriminations (e.g. Free 1970, Dukas and Real 1993). Female honey bees also show preferences for radial patterns over concentric patterns and they choose low spatial frequencies over high frequency patterns (Lehrer et al. 1995). Following training, the bees were tested on empty flowers and their choices examined. To ensure that choice of one stimulus over the other could be traced to learning of the discrimination during training rather than some unlearned preference, the S+ and S- were interchanged. The first few choices were examined and the choice proportions for the S+ by the males were compared both to chance levels and to the choice proportions recorded for females.

**MATERIALS AND METHODS**

**Subjects.** Two colonies of bumble bees, *Bombus impatiens* (Cresson), were obtained from Koppert Biological Systems, Inc. (Ann Arbor, Michigan). One colony was used for testing males and the other colony was used later for testing females. Male and female bees were labelled using numbered plastic discs glued to their thorax.

**Flight Cage and Housing.** The bees were trained and tested in a wooden framed, screened flight cage (183 by 188 by 190.5 cm). Males were removed from the first colony, labelled and placed in a small wooden box (20 by 10 by 15 cm) covered with a removable glass plate. A small hole allowed the bees access to the flight cage.

The colony used for testing workers was housed in a wooden container (30 cm by 15 cm by 15 cm) which was connected to a wooden corridor (30 cm long) covered with removable glass plates. The corridor was connected to the flight cage. A vertical plastic gate allowed the experimenter to control which bees entered and exited the colony. Inside the flight cage, radiating black stripes marked the entrance to the corridor to aid workers returning to the colony.

The average temperature in the room was 20°C (range: 18°C-22°C). Illumination on a 12 L: 12 D light: dark cycle was provided by fluorescent lights on the ceiling of the testing room and above the ceiling of the flight cage. We have obtained over 80% success in some subtle pattern discriminations using the same species, the same flight cage, and the same fluorescent lights (Korneluk and Plowright 1995, Plowright 1997, Plowright et al. 2001), notwithstanding the possibility that the flicker in the fluorescent lights is perceived by the insects.

**Artificial Flowers.** Each flower consisted of a wooden rectangular box (12.5 cm long by 8 cm large) supported by a rod (60 cm high). A disc made of construction paper (15 cm diameter) covered in clear plastic vinyl was placed on top of each box. For the first set of visual stimuli, "Yellow/Blue," three discs were blue and three discs were yellow (Figure 1). In the three following sets, each flower contained both blue and yellow: (1) "Quarters/Sixths," where all flowers had a radial pattern of alternating blue and yellow, but three of the flowers had alternating sixths and the other three had alternating quarters (Figure 2); (2) "Sixths/Concentric," where three of the flowers had alternating sixths and three had four alternating blue and yellow concentric circles (Figure 3); (3) "Quarters/Concentric," where three of the flowers had the "Quarters" pattern and three had the "Concentric" pattern (Figure 4). For each colony, each condition (i.e. each set of visual stimuli) was run once with one pattern as the S+ and the other as the S-, and then once again with the S+ and S- reversed.
Figure 1. Pie graphs displaying the proportions of S+ choices and S- choices for the Blue vs Yellow condition. The total number of observations for each is also given.

Figure 2. Pie graphs displaying the proportions of S+ choices and S- choices for the Sixths vs Quarters condition. The total number of observations for each is also given.
Figure 3. Pie graphs displaying the proportions of S+ choices and S- choices for the Concentric vs Sixths condition. The total number of observations for each is also given.

Figure 4. Pie graphs displaying the proportions of S+ choices and S- choices for the Concentric vs Quarters condition. The total number of observations for each is also given.
with different bees (so 4 sets of visual stimuli X 2 S+/S- assignments X 2 sexes = 16 combinations).

In the center of each disc was a small plastic vial cap (2.5 cm diameter, approximately 5 ml). During training, caps on rewarding flowers (S+) contained honey solution (2 parts honey to 1 part water by volume), and caps on unrewarding flowers (S-) contained water colored yellow with food coloring. During testing, both types of flowers were unrewarding and contained only colored water. New discs and caps were used after training for the testing conditions.

**Training (Males).** Bees were given unrestricted access to the flight cage. Upon entering the flight cage, bees would usually fly for a short period of time, land on the sides or ceiling of the flight cage, and feed from the artificial flowers several times per day. Training for each pattern condition lasted for two days, during which time the experimenter would replenish the honey solution in the S+ flowers when these became empty, rinse and wipe clean each cap, and put new water in the S- flowers. The positions of the S+ and S- flowers were changed at the beginning of each day and each time the flowers were refilled. A bee was used in testing only if it had been observed foraging from at least one S+ flower at least once during training. The honey solution was nearly depleted each time the positions of the S+ flowers were changed, indicating that the bees foraged from the S+ flowers.

**Testing (Males).** After two days of training and each bee was observed foraging at least once, testing began. Six new discs and new caps were placed on the flowers in an arrangement that was different from that in training. (For instance, if the flower had a blue disc (S+) during training, the flower would have a yellow disc (S-) during testing.) All flower caps were filled with water colored to look like honey, thus no reward and no scent was available during testing. A choice of a flower was recorded if a bee either hovered over the cap for two or more seconds, landed on the flower, and/or grasped the cap. As soon as a bee made a response, the experimenter recorded the color or pattern of the flower the bee chose for as long as the bee continued to visit flowers. Only the first six choices were analyzed because as the testing session with empty flowers progressed, there would be more opportunity for unlearning any discrimination.

Testing sessions lasted approximately one hour; after one hour bees no longer approached the flowers but remained stationary on the sides or ceiling of the flight cage. At the end of the testing session all discs and caps were removed from the flowers. The training discs and their caps were then placed on the flowers in the same arrangement as in testing. Bees were then allowed to train again until they were tested the following day. Testing followed by training continued in this fashion until a minimum of 100 responses was recorded for that condition (though only the first six choices by each bee were used). Testing lasted two to seven days.

**Training (Females).** Training methods for the female bees were the same as for the males except for the following. During the training sessions the experimenter, using the gate in the corridor, would allow labelled bees to enter the flight cage. The experimenter would record the number of times each bee foraged from the S+ (rewarding) flowers, and allow the bees to return to the colony after they had foraged. Training sessions lasted 2-3 hours each. Worker bees were given a much shorter training period than the males because they visit many more flowers in a shorter period of time. Positions of the S+ and S- flowers were changed 2-3 times during a training session.

**Testing (Females).** Testing methods for the female bees were the same as for the males except for the following. Bees were allowed to enter the flight cage one at a time. Bees were allowed to visit flowers for as long as possible but again, only the first six choices were analyzed. Once the bee began flying around the cage and ceased to approach the flowers, she was captured and returned to the colony. Testing sessions lasted approximately 2-3 hours.
Statistical Analysis. Because the data were counts with replication within individual bees, a replicated goodness-of-fit test with the G-statistic was used (Sokal and Rohlf 1981). In tests of significance, the G test-statistic is compared to a chi-square value. Two G-values were obtained: G_w which tests for heterogeneity or individual differences, and G_p, which tests whether the pooled data (i.e., the group data) deviate from the expected proportion, which is a chance level of 50:50.

The analysis above could only detect deviations of group proportions from a theoretical value. A further analysis compared the four choice proportions in each of Figures 1-4. A logistic model which specifies a binomial error term was fit to the individual choice proportions using GLIM (Francis et al. 1993). We tested for the effect of sex, of stimulus assignment (for example whether yellow was the S+ and blue the S- or vice-versa), and their interaction.

RESULTS

A summary table of the analyses comparing each choice proportion to chance is given in Table 1.

Blue vs Yellow. For male and female bees the choice proportions and total number of observations for this condition are shown in Figure 1. Both the males and the females could discriminate between blue and yellow flowers significantly better than chance, both when the blue flowers were the S+ and the yellow flowers were the S- and vice-versa. All the G values were significant for this discrimination. No significant individual differences were found (nonsignificant G_w; see Table 1).

The logistic analysis revealed no sex difference ($\chi^2 = 1.8; df = 1$, NS). The discrimination was better when the blue flowers were the S+ ($\chi^2 = 3.9; df = 1$, $p < .05$) though this effect was due to the poorer performance of the females when the yellow flowers were positive—the males performed at 98% accuracy in both stimulus assignments. The interaction between sex and stimulus assignment was not significant ($\chi^2 = 3.5; df = 1$, NS). No change between the first three and second three choices was detected ($\chi^2 = 0.1; df = 1$, NS) so the bees did not react to the absence of reward.

Two Radial Patterns (Sixths vs Quarters). Figure 2 displays the choice proportions and total number of observations. For the male bees, when the sixths pattern was the S+ and the quarters pattern was the S-, the choice proportions did not deviate significantly from chance (G was nonsignificant; see Table 1). When the S+ and the S- were reversed, however, the S- (sixths pattern) was chosen significantly more often. There were no significant individual differences (nonsignificant G_w; see Table 1) and so this result can not be attributed to aberrant behavior on the part of a few bees compared to the rest of the group. For the females neither of the choice proportions differed significantly from chance nor were individual differences significant (Table 1).

The logistic analysis yielded no effect of sex ($\chi^2 = 3.22; df = 1$, NS), no effect of stimulus assignment ($\chi^2 = 2.10; df = 1$, NS), and no interaction ($\chi^2 = 2.11; df = 1$, NS). No change between the first three and second three choices was detected ($\chi^2 = .02; df = 1$, NS).

Concentric vs Sixths. The choice proportions and total number of observations for this condition are shown in Figure 3. Neither the males nor the females showed choice proportions which differed significantly from chance. For the females, however, both choice proportions were approximately equal to 60%, whereas for the males they were closer to 50%. Pooling the data across stimulus assignment revealed that the discrimination was significant for the females ($\chi^2 = 4.07; df = 1$, $p < .05$) but not for the males ($\chi^2 = .76; df = 1$). Individual differences were not significant (Table 1).
Table 1. Summary of G-Statistic Results for Each Testing Condition

<table>
<thead>
<tr>
<th>Condition</th>
<th>Sex</th>
<th>df</th>
<th>Gd</th>
<th>df</th>
<th>Gp</th>
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<tr>
<td>Blue vs. Yellow</td>
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<tr>
<td>B (S+) vs. Y (S-)</td>
<td>M</td>
<td>9</td>
<td>4.27</td>
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<td></td>
<td>F</td>
<td>7</td>
<td>4.31</td>
<td>1</td>
<td>56.82*</td>
</tr>
<tr>
<td>Y (S+) vs. B (S-)</td>
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<td>4.80</td>
<td>1</td>
<td>74.36*</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>7</td>
<td>5.00</td>
<td>1</td>
<td>32.14*</td>
</tr>
<tr>
<td>Sixths vs. Quarters</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>S (S+) vs. Q (S-)</td>
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<td>8</td>
<td>7.70</td>
<td>1</td>
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</tr>
<tr>
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<td>F</td>
<td>4</td>
<td>2.38</td>
<td>1</td>
<td>0.36</td>
</tr>
<tr>
<td>Q (S+) vs. S (S-)</td>
<td>M</td>
<td>8</td>
<td>5.36</td>
<td>1</td>
<td>5.95+</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>5</td>
<td>3.95</td>
<td>1</td>
<td>1.00</td>
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<td>Concentric vs. Sixths</td>
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<td></td>
<td></td>
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<tr>
<td>C (S+) vs. S (S-)</td>
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<td>4.68</td>
<td>1</td>
<td>0.47</td>
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<td>F</td>
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<td>3.67</td>
<td>1</td>
<td>2.50X</td>
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<tr>
<td>Quarters vs. Concentric</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Q (S+) vs. C (S-)</td>
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<td>4.37</td>
<td>1</td>
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<tr>
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<td>3.93</td>
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<tr>
<td></td>
<td>F</td>
<td>4</td>
<td>3.47</td>
<td>1</td>
<td>2.16</td>
</tr>
</tbody>
</table>

Choices of S+:
* Above chance, p < .01
+ Below chance, p < .05
X When results from the two groups marked with an X were pooled, pooled results were above chance, p < .05

The logistic analysis showed that the sex difference in favor of females was significant (χ² = 4.16; df = 1, p < .05). The effect of stimulus assignment was not significant (χ² = 0; df = 1) and its interaction with sex was not significant either (χ² = .04; df = 1, NS). No change was detected between the first three choices and the second three choices (χ² = .06; df = 1).

**Concentric vs Quarters.** Figure 4 displays the choice proportions and total number of observations for this condition. For males, when the quarters pattern was the S+ and the concentric pattern was the S-, the choice proportion did not differ from chance (Table 1). When the contingencies were reversed, however, a significant preference for the S- (the quarters) was found. Individual differences were not significant. For the females, the choice proportions did not differ from chance regardless of which pattern was the S+ and which pattern was the S-.

The logistic analysis did not reveal any sex difference (χ² = 2.75; df = 1) though an effect of stimulus assignment was detected (χ² = 4.85, df = 1, p < .05); choice proportions were higher when the quarters pattern was positive. The interaction between sex and stimulus assignment was not significant (χ² = 1.45; df = 1). No change between the first and second three choices was found (χ² = .77; df = 1).

In the pattern discriminations the G-tests and the logistic analyses might seem to yield conflicting results. In the first and third comparisons no sex difference was found even when one of the G-statistics was significant. The conflict, however, is only apparent. Notwithstanding the fact that the two kinds of analyses make different sorts of comparisons, whenever there was a significant effect, it always pointed to the same conclusion of superior performance by
the female bees. Indeed, pooling the data across the whole experiment, a significant sex difference was found ($\chi^2 = 7.6; \text{df} = 1, p < .01$) with a 10% advantage for the females (choice of the S+ was, overall, 59% for males and 69% for females).

**DISCUSSION**

Male bees are uncooperative subjects in foraging studies: in our study they were much more “reluctant” to work than female bees. Nonetheless, the results on color discrimination validate the method: males could learn either that the blue flowers were rewarding or that the yellow flowers were rewarding. Indeed, the choice proportions could hardly have been higher: 98% in both cases. Of course, discrimination might have been less well achieved if colors other than blue and yellow had been used: blue and yellow artificial flowers elicit the shortest search times from bumble bees, at least for large flowers such as ours (Spaethe et al. 2001). Nonetheless, with respect to the primary objective of this paper, we can conclude that male bumble bees can attend to, learn and remember colors to discriminate between rewarding and unrewarding flowers. Moreover, their performance is comparable to that of workers. The same cannot be said, however, for the pattern discriminations.

Three pairs of patterns were examined: (1) Radial Sixths vs Radial Quarters, (2) Concentric vs Radial Sixths, and (3) Radial Quarters vs Concentric. In the second pair, a significant sex difference was found: females showed choice proportions of about 60% regardless of which pattern was the S+, and males did worse (Figure 3). For the other two comparisons, the patterns were not discriminated, and no sex difference was found. The discrimination failures might be attributable to insufficient statistical power and future research would benefit from larger samples (the results for the females in Figure 3 suggest twenty bees as a target figure for detecting a 60:40 discrimination). Pattern discriminations are indeed more difficult than color discriminations (Srinivasan 1994), especially if the flowers are presented horizontally rather than vertically. Males showed two choice proportions which were significantly below chance (Figures 2 and 4), and these remain a puzzle. If the bees could not learn a discrimination, choice proportions of chance would have been expected. If the bees had pronounced unlearned preferences, then a significant preference for a particular pattern should have been obtained not only when it was the S- but also when it was the S+.

Overall the females outperformed males in pattern discriminations. From a functional point of view, this result confirmed our prediction that males would be less adept at floral discriminations because the cost of failure is only paid by the individual male and not by the brood which depend on females for nourishment. Although the data are suggestive and encourage further research, they most certainly do not justify any conclusions regarding possible sex differences in cognition such as attention, pattern recognition, associative learning and/or memory. Further research might show, for example, that the relatively poor performance of the males was due to a self-inflicted impoverishment of the learning conditions. The males were trained for longer periods of time because they were generally less active, and so in terms of opportunity for learning, our procedure was biased in favor of the males, but the numbers of exposures to the S+ and to the S- were not equated between the sexes. Even if they could be, the longer intervals in between flower visits for the males would provide more opportunity for forgetting. Finding a means of equating the learning conditions would be one of many steps in undertaking further male-female comparisons for which the present study has set the stage. One common practice which might be used in future research is to train the bees to asymptotic performance. This method, however, does not necessarily equate learning for males and females for two reasons: (1) such learning would likely take longer time and more floral encounters for the males (2) asymptotic performance is by definition a ceiling
effect and comparisons under those conditions are usually inadvisable. Future research should also include replication between colonies. In this study males came from one colony and workers from another. Although our previous research (Simonds and Plowright, unpublished data) found no colony differences in unlearned color and pattern preferences, we cannot rule out the possibility of colony differences in color and pattern learning ability.

One possible objection to this study is in the use of honey solution rather than odorless sugar solution during training. During training, bees had the opportunity to learn either scent, or pattern/color, or both odor and visual characteristics to discriminate the rewarding from the unrewarding flowers. During testing, however, water instead of honey solution was used and so only pattern/color was available to make discriminations, but not scent. The strong discrimination for the Blue vs. Yellow condition (Figure 1) shows that color was learned in training, regardless of whether scent may also have been used during training. The same can be said for the weak but significant discrimination by the workers in the Concentric vs Radial Sixths condition: the bees must have learned the association between reward and visual pattern. Indeed, our previous work (Korneluk and Plowright 1995, Plowright 1997, Plowright et al. 2001) which used honey solution in training [bumble bees are reticent to land on artificial flowers in the absence of scent (Lunau, Wacht and Chittka 1996)] and water in testing has also shown successful pattern learning and recognition by bumble bees, so the use of honey solution per se is not a concern when pattern discriminations are obtained. More problematic, however, are the conditions where no pattern discrimination was obtained: it is possible that patterns were not learned in training but instead scent may have been used by the bees to discriminate between the rewarding and unrewarding flowers. Perhaps when bees are presented with some complex visual discriminations in training, they then resort to using the cue of scent when foraging and mostly ignore the patterns on the flowers. This interpretation does not undermine the conclusion that some pattern discriminations are particularly difficult, and perhaps especially difficult for males. It does however suggest a possible way of forcing bees to make a discrimination which they otherwise would not make.

Labor division in insect societies is anything but equal, and our results highlight a behavioral correlate of the general rule that female bees work and males don’t: females showed better performance in floral pattern discriminations, though further research is needed to delineate the conditions under which this might occur. Males are quite capable, however, of learning color discriminations between rewarding and unrewarding flowers. The sociobiology of male idleness has been well worked out (Hamilton 1964) but its psychology remains to be elucidated.

ACKNOWLEDGMENTS

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LITERATURE CITED


A TEN-YEAR STUDY TO MONITOR POPULATIONS
OF THE REGAL FRITILLARY, SPEYERIA IDALIA,
(LEPIDOPTERA: NYMPHALIDAE) IN WISCONSIN, U.S.A.

Ann B. Swengel* and Scott R. Swengel

ABSTRACT

We present analyses of our transect survey data from consecutive years at 11 sites in Wisconsin during 1990-99 for the regal fritillary (Speyeria idalia), which is listed under state law as endangered, and the closely related but more widespread and abundant Aphrodite fritillary (Speyeria aphrodite). Within year, the date of peak survey numbers at each site ranged over a period of several weeks or more for each fritillary. Within year and site, the Aphrodite fritillary peak was typically a few days to a week prior to the regal fritillary's peak. Both fritillaries exhibited large annual fluctuations which were significantly correlated between the two species. Relatively larger regal fritillary densities were consistently associated with active non-fire managements (grazing, cutting), relatively lower densities with burning, and widely varying densities with non-management. More unfavorable outcomes from burning occurred at sites where the entire habitat patch was fire-managed. Similar but less sensitive was the Aphrodite fritillary, which did not respond as strongly or clearly to burning, although higher densities were associated with unintensive non-fire managements. In Wisconsin and adjoining areas, the Aphrodite fritillary appears useful as a substitute in tests of techniques for habitat restoration or reintroduction for the regal fritillary. Since the Aphrodite fritillary may be less sensitive than the regal fritillary, success with the former certainly doesn't prove suitability for the latter. But unless and until the method works for the Aphrodite fritillary, it is almost certainly unsuitable for the regal fritillary.


In this paper, we present results from our ten-year study to monitor populations of the regal fritillary in Wisconsin, where it is listed under state law as endangered (Bureau of Endangered Resources 1999). For comparison, we also report results for the Aphrodite fritillary [Speyeria aphrodite (Fabricius 1787)], which is closely related and overlaps in range and habitat with the regal fritillary, but is more widespread and abundant in Wisconsin (Ebner 1970, Opler and Krizek 1984, Scott 1986). Our goal was to monitor individual populations

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in consecutive annual surveys, on a scale sufficient that it might be possible to
distinguish population trends from annual fluctuations. We also explore man­
agement factors associated with differences in relative population size and trend.
These results should be useful for developing effective conservation strategies
for this species.

METHODS

Study sites and surveys. During 1988-99, we conducted transect butter­
fly surveys at 49 grassland study sites in Wisconsin (Swengel 1996, 1997a,
1998; Swengel and Swengel 1997), selected either because they had recent re­
gal fritillary records or potential habitat for this species.

We visited many recent historic sites (records from 1970-89). We also
visited each distinct area or cluster of sites where regal fritillary record(s) oc­
curred in the 1990s, although we did not attempt to visit all known sites, much
less all potential habitat patches, within a cluster. We maintained a core group
of sites surveyed each year once added to the study. At other sites, we surveyed
for a few years, until it appeared unlikely that additional surveys would con­
tribute more information on prairie-restricted butterflies. Most sites were con­
served lands in private or government ownership. In 1988-89, we conducted
informal visits to familiarize ourselves with potential study sites and prelimi­
nary field work to practice the survey method. During 1990-99, we recorded
2746 regal fritillaries and 6766 Aphrodite fritillaries in 624.5 km and 305.3 hr
of formal survey effort.

The butterfly surveys occurred in the same route corridor on each visit to
a site (except for increased length at Pine Island; see Table 1 and results). We
counted all adult butterflies observed ahead and to the sides, to the limit of
species identification (possibly with binoculars after detection) and our ability
to track individuals. We walked at a slow pace (1.5-2 km/hr) on parallel routes
5-10 m apart, or down the middle of this route corridor if surveying alone. We
tried to field both of us together on surveys as much as possible for method­
ological consistency. Surveys by one person were conducted to fill data gaps
caused by scheduling constraints and poor weather on days when both survey­
ors could be fielded. All surveys in this study were conducted by one or both
of the authors, which may afford more methodological consistency than if all sur­
veys were conducted by two people, but with changeover in personnel.

A new sampling unit was designated whenever the habitat along the route
corridor changed markedly in vegetation type, degree of degradation, or man­
agement. Routes crossed rather than followed ecotones and management bound­
aries to reduce edge effects, and were designed to maximize sampling per unit
but minimize number of unit changes during the site survey, while sampling
representative areas of the site. For each unit survey, temperature and time
spent surveying were recorded, and wind speed, percent time the sun was shin­
ing, percent cloud cover, and route distance were estimated. Surveys occurred
during a wide range of times of day and weather, occasionally in intermittent
light drizzle if butterfly activity was apparent, but not in continuous rain. Data
were kept separate by unit survey. A unit's management was classified based
on treatments observed or evident during the study, including combinations
(e.g., burning+mowing) as appropriate, following information available from
the agencies that owned and/or managed the sites. Management age class
(years since last treatment) was coded as 0 years (<1 year) since last treat­
ment, 1 (>1 but <2 years ago), 2, etc. For units managed with more than one
type, management age class was tracked separately for each management type.

We selected 11 sites for consistent regal fritillary surveying in consecu­
tive years (Table 1, Fig. 1). Both regal and Aphrodite fritillaries were recorded
during this study at all these sites, which include all sites known in 1990-92 to
have regal fritillary records during that period, as well as some of the regal
fritillary sites discovered subsequently. Including all sites with regal fritillary records during the 1990s would be beyond our scope. A single site (in terms of contiguous ownership) was subdivided into multiple study sites if >200 m of wetland, woodland, and/or tilled land intervened among our sampling areas. But we kept Thousand's II and Thomson 2 separate because of their different survey histories (1990-99 at the former, 1992-99 at the latter); likewise for Buena 3A and 3B (1997-99 at the former, 1998-99 at the latter). Based on survey results, we selected "primary" monitoring sites where surveys occurred for >2 years and the species was recorded in most or all years: 7 sites for regal fritillary, 8 for Aphrodite fritillary for comparison with this more widespread and abundant but similarly timed congenor (Klots 1951, Ebner 1970). We surveyed the 11 sites more than once per year except in one year each for two sites, neither of which were primary monitoring sites.

Sites managed with fire were burned primarily in fall or spring (usually the latter), typically in a rotation of units burned in different years, possibly with some mowing or hand-cutting of brush also. Sites with no active management conducted or otherwise evident during the study were categorized as non-managed. Through most of the study, Hogback was a non-conserved site with continuous moderate dairy grazing at about 3-6 AUM/ha/yr (animal use month=500 kg of cattle for 1 month) but grazing did not occur after 1997, following conservation acquisition. Non-broadcast managements (e.g., hand-cutting of brush at Thomson 2) were counted as a treatment only in years when substantial alteration of canopy occurred.

Table 1. Summary information on surveys at monitoring sites: first year of consecutive-year surveys during regal fritillary flight period, survey route length (km), and percent years regal and Aphrodite fritillaries were recorded on these surveys during 1990-99. Monitoring areas at Buena Vista sites are only portions of surveyed areas in these sites. The sites are conserved land owned by the state except as footnoted.

<table>
<thead>
<tr>
<th>Site</th>
<th>Patch size (ha)</th>
<th>First Route</th>
<th>Route length (km)</th>
<th>% years recorded</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>prairie grassland</td>
<td>year</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Buena Vista Wildlife Area 1</td>
<td>-</td>
<td>1352</td>
<td>1997</td>
<td>1.6</td>
</tr>
<tr>
<td>*Buena Vista Wildlife Area 3A</td>
<td>-</td>
<td>550</td>
<td>1997</td>
<td>0.8</td>
</tr>
<tr>
<td>Buena Vista Wildlife Area 3B</td>
<td>-</td>
<td>550</td>
<td>1998</td>
<td>0.8</td>
</tr>
<tr>
<td>*Hogback</td>
<td>16</td>
<td>16</td>
<td>1992</td>
<td>2.0</td>
</tr>
<tr>
<td>*Muralt Bluff</td>
<td>15</td>
<td>15</td>
<td>1990</td>
<td>2.9</td>
</tr>
<tr>
<td>Oliver</td>
<td>2</td>
<td>2</td>
<td>1990</td>
<td>0.4</td>
</tr>
<tr>
<td>*Pine Island Wildlife Area 1</td>
<td>20</td>
<td>121</td>
<td>1993</td>
<td>0.6&lt;sup&gt;1&lt;/sup&gt;, 1.5&lt;sup&gt;2&lt;/sup&gt;, 1.9&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
<tr>
<td>Pine Island Wildlife Area 2</td>
<td>12</td>
<td>12</td>
<td>1993</td>
<td>0.4&lt;sup&gt;1&lt;/sup&gt;, 0.7&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>*Thomson 1</td>
<td>5</td>
<td>121</td>
<td>1990</td>
<td>1.5</td>
</tr>
<tr>
<td>*Thomson 2</td>
<td>32</td>
<td>121</td>
<td>1992</td>
<td>1.8</td>
</tr>
<tr>
<td>Thousand's II</td>
<td>2</td>
<td>121</td>
<td>1990</td>
<td>0.8</td>
</tr>
</tbody>
</table>

*primary regal fritillary monitoring sites (7 sites); the eighth primary monitoring site for Aphrodite fritillary was Pine Island 2
<sup>1</sup>1993-94
<sup>2</sup>1995-96
<sup>3</sup>1997-99
*owned by county
<sup>c</sup>owned by The Nature Conservancy (a private non-profit conservation organization)
<sup>u</sup>owned by the University of Wisconsin
During June-September, we surveyed the 11 monitoring sites on average 3.1 times per year (range 1-9) and for 4.0 years (range 2-10) counting only years when a site was visited at all. We recorded 2369 regal fritillaries (2063 males, 177 females, 129 unsexed) and 4717 Aphrodite fritillaries in 341.0 km and 170.1 hr of surveying at these sites.

**Data analysis.** For each fritillary, we identified the “regional peak” as the date each year with the highest observation rate of each fritillary (based on total individuals recorded per effort spent surveying per date, at all sites in Wisconsin where we had ever recorded the species during 1990-99). We measured effort as both time and distance surveyed, and these measures covaried strongly ($r = +0.869$, $N=1529$ unit surveys, $P<0.0001$, Spearman rank correlation). Thus, standardizing observations to rates based on time or distance should yield similar results.

Since distance was constant within site among surveys, we used raw survey totals to identify the peak count (sum of totals for each unit surveyed within that site) for each year at each monitoring site. For ties, we selected the date of the highest observation rate (individuals per survey time). If all surveys at a site were 0 in a year, we needed to select which of these survey dates to use as the peak count. We used the survey nearest in date to the peak count at a nearby site that had survey total(s) >0. If no nearby site had survey totals >0 that year, or if
nearby sites varied substantially in peak date, then we used the survey on the date nearest to the regional peak. For the Aphrodite fritillary, if a tie still existed, we used the same date as the regal fritillary peak in that site. We followed the same procedure to identify the second highest count per site. Because of the intervals between our surveys, these peak dates represent a crude approximation, not exact peak dates. Only weekly, or even biweekly counts, could identify peak with any degree of precision, but this was beyond our scope. We tried as much as possible to visit all the monitoring sites at around the same dates each year, to ensure the main flight period was covered similarly at all sites, but unfavorable weather could confound these efforts.

Weather conditions on the surveys at the 11 monitoring sites nearest in date to the regional peak were either >20°C with >0% sunshine (in >90% of cases with <20% sunshine, the temperature was >24°C) or >20% sunshine with >15°C. On the actual peak surveys at these sites, which did not always occur on the survey nearest in date to the regional peak, weather conditions were likewise, except for the regal fritillary at Thomson 1 (also a primary monitoring site) in 1992 (>18°C, 0% sunshine). In comparison to the British Butterfly Monitoring Scheme (Pollard and Yates 1993), our minimum survey temperature was higher (13 vs. 15°C, respectively), while the standard for sunshine was variable but relatively similar: ours was lower for 15-17°C (20% vs. 60%) but higher for 17-20°C (20% vs. 0%).

It was not valid to make one- and two-surveyor counts comparable by multiplying one-surveyor counts by two. On two-surveyor counts, we surveyed together in one party - as construed in the Christmas Bird Count and Fourth of July Butterfly Count (Swengel 1990) - and had one recorder to eliminate double-counting when both surveyors observed the same butterfly. Two surveyors would not necessarily record twice as many butterflies as one surveyor. It was also undesirable to limit analyses only to two-surveyor peak counts, as some of these were lower than one-surveyor counts at some sites in some years. It is not possible to know how many butterflies would have been recorded if both of us had been present for those few one-surveyor counts. However, we tested for significant differences in peak counts between one- and two-surveyor surveys at the same sites using the Mann-Whitney U test.

We used the peak count (sum of totals for each unit surveyed in the site) per year as a population index for each fritillary species at each monitoring site. With the Spearman rank correlation, we tested the degree of covariance between this peak count and sum of the two highest counts per site per year for each species, and the degree of covariance of peak counts, and of the sum of the two highest counts, between fritillary species. These tests would indicate how similarly these different indices would rank sites (population sizes) and years (annual fluctuations) within species, and how similarly the population sizes and annual fluctuations ranked between regal and Aphrodite fritillaries. Data were inadequate to calculate population indices from three or more counts per site per year.

We averaged the peak counts per year at the primary monitoring sites to serve as a regional population abundance index. Similarity in changes of the annual population indices between the regal and Aphrodite fritillaries were tested with the Spearman rank correlation.

For primary monitoring sites surveyed for >3 years, we tested for population trend with Spearman rank correlations of population indices with year, using two types of population indices: the peak count (sum of totals for each unit surveyed in the site) per year, and the difference between peak count and regional population index (to account for annual fluctuation, by using an index that measured how much the peak count differed each year from the regional population index). Since the test for trend was non-parametric (by ranking), log-transformation of population indices was irrelevant. We used arithmetic
and not logarithmic scaling of population indices in the figures to facilitate visualization of how many butterflies were recorded at the sites.

To compare relative abundance among primary monitoring sites with respect to habitat management, we calculated rates of observation as total individuals per total survey time at each site, using all peak surveys for the years 1993-99 for sites with data from each of these years. We present these management results both by each year since last treatment (i.e., unit surveys pooled by management year classes), and combining all unit surveys for all management year classes.

All statistics were calculated using ABstat 7.20 (1994, Anderson-Bell, Parker, Colorado, USA), with statistical significance set at two-tailed $P < 0.05$. Since significant results occurred at a frequency well above that expected due to spurious Type I statistical error, the critical $P$ value was not lowered further, as more Type II errors (biologically meaningful patterns lacking statistical significance) would be created than Type I errors eliminated.

RESULTS

Flight period. During 1992-99, we obtained 70 population indices each for regal and Aphrodite fritillaries at the 11 monitoring sites. For the regal fritillary, in 66 of these instances (94%), a survey in appropriate weather (defined in Methods) occurred at the site within seven days of the regional peak date (although the actual peak count may not have occurred at a site then). In the remaining 4 instances, such a survey occurred between 11 days before to 15 days after the regional peak (Hogback and Pine Island 1 and 2 in 1994; Hogback in 1996). For the Aphrodite fritillary, in 60 instances (86%), a survey occurred in appropriate weather within seven days of the regional peak, and within the period from 8 days before to 9 days after in 66 instances (94%). In 2 instances (Thomson 2 and Thousand's II in 1996), the nearest survey was 13 days before, and in 2 instances (Hogback and Thomson 2 in 1992), 22 to 27 days after.

We conducted formal surveys in only three different (but non-consecutive) weeks in 1990, but in a mean of 5.1 different weeks (range 4-7) during 1991-98, and in 9 in 1999. For the years when we surveyed adequately for the regal fritillary both early and late in the flight period (1992-94, 1996-97, 1999), the flight span we observed was a mean of 55 days (range 41-63 days). In all study years except 1991, we surveyed broadly in the Aphrodite fritillary flight period, with a mean span of 67 days (range 43-81). First and peak dates regionally tended to be slightly earlier for the Aphrodite than regal fritillary in most years.

Peak surveys. All surveys during 1990-91 were by two surveyors. During 1992-99, of the 70 instances where we obtained population indices, 52 (74%) had a count at the site by two surveyors in appropriate weather (defined in Methods) within seven days of the regional peak for regal fritillary, and 62 (89%) within 12 days. For the Aphrodite fritillary, in 55 instances (79%), a two-surveyor count occurred within seven days of the regional peak, and in 61 (87%), within 13 days. During 1993-94, all surveys at Pine Island were by one person. Once we refound the regal fritillary there (mid-season in 1995), we surveyed there together as much as possible. In all other cases where the peak count for either fritillary occurred on a one-person survey, we conducted at least one two-person survey the same year at the site during the species' main flight period, except for Oliver in 1996. For the primary monitoring sites, peak surveys with >0 individuals conducted by one person occurred five times for the regal fritillary - Pine Island 1 (1995, 1997), Thomson 1 (1996), Thomson 2 (1996), and Muralt (1996) - and eight times for the Aphrodite fritillary - Pine Island 1 and 2 (1993-95), Muralt (1994), and Thomson 2 (1996).

Single-surveyor peak counts were lower on average than two-surveyor peaks at the same sites, but these differences were rarely significant (Table 2). Nonetheless, it appears likely that single-surveyor peak totals were lower than they
would have been if both of us had been able to survey that day. However, the peak totals would have been lower yet if we had restricted our analyses only to counts from two-person surveys.

Within each year, the variation in peak date among primary sites encompassed spans of 20-49 days for Aphrodite fritillary and 1-49 days (10-49 excluding 1990-91) for regal fritillary (counting only positive peak surveys). Within site, the peak date (including peak surveys of 0) for Aphrodite fritillary preceded that for regal fritillary by a mean of 4.5 days (11 monitoring sites) and 4.4 days (7 primary sites), with a range of 42 days earlier to 21 days later for both groups of sites. Because sites were not surveyed weekly and weather conditions varied among visits, these are crude analyses indicating only very general patterns.

The peak count and sum of peak two counts per site per year covaried very strongly for both fritillaries (Spearman rank correlations, \( P < 0.001 \)). When ranking these indices with all primary sites pooled, \( r = +0.988 \) for regal fritillary (\( N = 48 \) pairs of indices from 7 sites) and \( +0.992 \) for Aphrodite fritillary (\( N = 55 \) pairs of indices from 8 sites). For indices ranked separately for each site, \( r = +0.990 \) and \( +0.950 \), respectively. These results indicate that, in our study, these two types of abundance indices ranked similarly among years, both within and among sites.

The peak counts for and Aphrodite fritillaries per year at the primary regal fritillary sites covaried strongly (Spearman rank correlation, \( P < 0.01 \)). When ranking these indices with all sites pooled, \( r = +0.673 \) for peak counts and \( +0.726 \) for sums of peak two counts (\( N = 49 \) and 48 pairs of indices respectively, as a second count was missing for Hogback in 1992). For indices ranked separately for each site, \( r = +0.420 \) and \( +0.440 \), respectively. These results indicate that annual relative abundance (i.e., relative population sizes and/or annual fluctuations) ranked similarly for both fritillaries, both within and among sites.

Table 2. Means of peak survey total per site per year, by number of surveyors (one or two) conducting survey along similar routes within each site. Sites are included in this analysis only if it had peak survey totals by both one and two surveyors (all other sites had peak surveys only by two surveyors). Out of all monitoring sites (11 sites), this analysis includes 6 sites for Aphrodite (with 11 one-surveyor and 41 two-surveyor peak surveys) and 7 for regal (13 and 49 surveys, respectively). Out of the primary monitoring sites (8 sites for Aphrodite, 7 for regal), this analysis includes 4 sites for each fritillary (8 one-surveyor and 24 two-surveyor peak surveys for Aphrodite, 7 and 28 respectively for regal).

<table>
<thead>
<tr>
<th></th>
<th>Aphrodite fritillary</th>
<th>Regal fritillary</th>
</tr>
</thead>
<tbody>
<tr>
<td>All monitoring sites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>one surveyor</td>
<td>10.6(^1)</td>
<td>3.1(^2)</td>
</tr>
<tr>
<td>two surveyors</td>
<td>19.3</td>
<td>10.2</td>
</tr>
<tr>
<td>Primary monitoring sites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>one surveyor</td>
<td>11.3(^*)</td>
<td>5.0(^4)</td>
</tr>
<tr>
<td>two surveyors</td>
<td>31.9(^*)</td>
<td>16.5</td>
</tr>
</tbody>
</table>

\(^*\) significantly different (Mann-Whitney U test, two-tailed \( P < 0.05 \))

\(^1^4\) If counting only surveys with two surveyors, the sample of sites drops (Pine 1 1993-95 and Pine 2 1993-94 had only one-surveyor counts) and the means would be:

\(^1^7.7\)

\(^2^2.5\)

\(^3^12.3\)

\(^4^5.0\)
Fluctuations and trends. The peak survey counts per site for both Aphrodite and regal fritillaries varied greatly not just among sites, but also among years within site (Figs. 2-3). The mean of peak counts from the two sites with the longest consecutive years of survey data deviated the most from the general pattern found for the means of larger pools of sites surveyed for fewer consecutive years, likely due to sampling error (Fig. 4). This difference was more pronounced for the regal fritillary (divergences in direction in 1997-99) than for the Aphrodite fritillary (divergences in degree but not direction in 1997-99, and in direction but with only slight differences in values in 1995). The means from all the larger pools of sites (i.e., excluding the two-site pool) had very similar lines in both direction and degree of change, with the highest mean in 1998 and lowest in 1994 for both species. While larger samples of sites are desirable, four sites appeared sufficient, at least compared to 7-8 sites, for analysis of annual fluctuation, even though individual sites would have other confounding trends such as due to habitat management or changing landscape context. Of these
larger pools (>2 sites), the means from four sites (chosen because it had the most years) covaried strongly between regal and Aphrodite fritillaries ($r=+0.929$, $N=8$ years, Spearman rank correlation $P<0.01$), indicating similar annual fluctuations between the two species.

At the primary monitoring sites surveyed for >3 years, only at Muralt did regal fritillaries decline significantly in peak counts during this study (Table 3). The peak regal fritillary counts at Thomson 2 increased significantly, but when these were adjusted by comparison to annual fluctuations (i.e., compared to the mean of peak survey totals during 1992-99 in Fig. 4), this significance disappeared. For the Aphrodite fritillary, three sites had significant increases in peak counts during this study, but when these were adjusted for annual fluctuation, a significant increase persisted only for Hogback. Two sites had positive correlations (whether significant or not) for their peak Aphrodite fritillary counts, but these became significantly negative when adjusted for annual fluctuation (i.e., the increasing peak surveys lagged behind the regional increase due to annual fluctuation). Aphrodite fritillary had no significant trend at Muralt.

Management. Three management types occurred at only one site, and data for each year class >0 came from only one year: grazing (Hogback, with year classes 1-2 in 1998-99, respectively), mowing (Thomson 1, with year classes 1-4 from 1996-99; these areas were burned during this study before but not after mowing), and hand cutting of brush (Thomson 2, with year classes 1-2 from 1998-99; some of these areas were burned before but not after cutting). Thus, in these instances, it is not possible to separate influences of annual fluctuation from years since management.

For two management types (fire, non-management), the samples came from multiple sites (Fig. 5). Since burned sites had fires (usually in only part of the site) in different years, and surveys from unmanaged sites occurred in all years during 1993-99, management year class was desynchronized from annual fluctuation. Because the results for each year class after fire are averaged from unit surveys in multiple years, they are useful for portraying relative fritillary distribution within sites with respect to management age class. But they do not indicate whether a population increased or decreased over time (for that, see population indices in Figs. 2-3), or whether such a trend is attributable to management.

Figure 3. Peak Aphrodite fritillary survey total per year at the eight primary monitoring sites (Table 1).
The mean abundance for each year class after burning (Fig. 5) suggests that neither fritillary has a simple linear or bimodal response to time since fire. The postfire plots were similar in shape between both fritillaries except in year 2, when the Aphrodite but not regal fritillary declined, and in year 8+, when the increase was greater for Aphrodite than regal fritillary. However, results for year 8+ should be interpreted with caution, as they come from only

Figure 4. Mean of peak survey totals (as shown in Figs. 2-3) at the primary monitoring sites (Table 1), in pools of sites surveyed for the same number of consecutive years, for (a) regal and (b) Aphrodite fritillaries.
one site (Muralt) and only during 1997-99, when the regal fritillary population there was much lower than earlier in the study (Fig. 2) but Aphrodite fritillaries there and regionally experienced a higher fluctuation (Figs. 3-4). If a very long time after fire (at the least, a year class >8 years) approaches comparability to non-management, then our data suggest that after this transition from the influence of burning to the influence of non-management, the regal fritillary will be relatively more abundant than in all fire age classes, while the Aphrodite fritillary will decline. However, the latter will still be much more abundant than in the first year (year 0) after fire, and slightly more abundant (index = 31.7) than the mean of the first five years after fire (mean of years 0-4 = 28.4).

For differences in relative abundance among management types within site (Fig. 6), the comparison of fire and non-management was more robust at Thomson 2, where both occurred throughout the study, than at Pine Island 1 and 2, where fire in surveyed areas only occurred in later years (1996-99), which had a large increase in annual fluctuation compared to the earlier survey years there (1993-95). For comparisons among sites, Hogback and Muralt were most comparable to each other vegetatively (upland prairie of substantially native flora), and Pine Island 1 and 2 and Thomson 2 to each other (substantially degraded grassland, with a small component of native prairie flora), while Thomson 1 had about equal areas of high-quality and degraded flora, but see Table 1 for differences in patch sizes at all these sites.

In comparisons of relative abundance (individuals/time on peak surveys) by management type at primary sites surveyed each year during 1993-99 (Fig. 6), the Aphrodite fritillary was more abundant than the regal fritillary except for fire+mow at Thomson 1 and non-management at Thomson 2. Both species were more abundant in grazing (Hogback) and cutting (Thomson 2). The regal fritillary was also more abundant in non-management at Thomson 2 but less abundant with fire, fire+mow, fire+cut, and non-management at Pine Island 1.

Table 3. Population trends (i.e., Spearman rank correlations with year) at the primary monitoring sites surveyed at least seven consecutive years (Table 1), calculated two ways: using peak survey totals per site per year (Figs. 2-3; N=7-10 years), and using the differences between peak survey totals at individual sites from the mean for these totals at all sites for that year (mean calculated for 1992-99 as in Fig. 4; N=7-8 years per site; positive coefficients indicate trends greater than the mean, negative coefficients were less than the mean).

<table>
<thead>
<tr>
<th>Site</th>
<th>Regal fritillary peak survey</th>
<th>difference from regional mean</th>
<th>Aphrodite fritillary peak survey</th>
<th>difference from regional mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hogback</td>
<td>+0.548</td>
<td>+0.571</td>
<td>+0.857 **</td>
<td>+0.857 **</td>
</tr>
<tr>
<td>Muralt</td>
<td>-0.891 **</td>
<td>-0.714 *</td>
<td>+0.442</td>
<td>-0.690</td>
</tr>
<tr>
<td>Pine1</td>
<td>+0.450</td>
<td>-0.571</td>
<td>+0.955 **</td>
<td>-0.286</td>
</tr>
<tr>
<td>Pine2</td>
<td>-</td>
<td>-</td>
<td>+0.429</td>
<td>-0.643</td>
</tr>
<tr>
<td>Thom1</td>
<td>+0.714 *</td>
<td>+0.619</td>
<td>+0.491</td>
<td>-0.762 *</td>
</tr>
<tr>
<td>Thom2</td>
<td>+0.438</td>
<td>-0.405</td>
<td>+0.676 *</td>
<td>-0.786 *</td>
</tr>
</tbody>
</table>

* P < 0.05
** P < 0.01
In the relatively large regal fritillary population at Thomson 2 (Fig. 2), abundances were similarly high in cutting and non-management, and similarly low in fire and fire+cut. For the relatively small regal fritillary population at Pine Island 1, abundances were similarly low in fire and non-management. By contrast, Aphrodite fritillary abundance was much more variable relative to burning (alone or in combination) and non-management. Numbers were higher at Thomson 2 in non-management than fire+cut, which in turn were higher than fire; numbers were similar between fire and non-management at Pine Island 2, but lower in non-management than fire at Pine Island 1.

The most unfavorable regal fritillary results at burned sites occurred at Muralt, Oliver, and Pine Island 2. Regal fritillaries significantly declined at Muralt (Table 3, Fig. 2), where the entire habitat patch was managed with rotational fire during the study period, with 10-40% burned per year except for no fires in 1990, 1993, and 1998. The two highest peak counts at Muralt were in 1990 and 1993, while very low numbers occurred in 1997-99. Numerous times during 1992-99, we communicated with the state agency overseeing management at Muralt via unpublished data analyses, meetings, and reprints about the risk of burning and dwindling numbers here. At Oliver, Borth (1992) reported multiple individuals per visit formerly observed regularly, but we found 1-4 individuals on five dates in 1991, 1993, and 1994, and none since (Fig. 2). This small patch (Table 1) of excellent prairie flora was entirely burned in 1989, 1992, and 1997. At Pine Island 1 and 2, we noted no burning for the ten years before 1995. We recorded no regal fritillaries on surveys here in 1993-94, but found multiple individuals per visit at both sites in 1995-96, including parts of the survey route in 1993-94. While we assume the regal fritillary was most likely present but undetected in 1993-94, our data are inadequate for concluding whether the species was present all along, or absent and then (re-)established, during our
study. The senior author communicated with the Pine Island manager in 1995-96 about the presence of this species and its sensitivity to fire via unpublished data analyses, reprints, and a site visit. Pine Island 2 was entirely burned in spring 1997 and again in 1998; we found no regal fritillaries there in 1997-99.

By contrast, all of the much larger patch at Pine Island 1 has recently been burned through partial fires in 1995 (in an area not included in our transect), 1997 (when we expanded our route to the remaining unburned part), and 1999. The peak counts were higher in 1995-96 than the next year, when we surveyed more area but the first fire occurred along our route (Fig. 2). At Thomson 2, half the site was burned in spring 1992, with steadily decreasing areas burned in 1995 and 1997, and the smallest fire in 1996. While the 1995 fire reduced the never burned area to about 30% of the patch, this area has not decreased further since, and this is the area where we record more regal fritillaries (Fig. 6: cut and unmanaged parts of Thomson 2), both in relative and absolute numbers. We cannot know how many regal fritillaries we would have observed at both sites had no fires occurred during the 1990s. But we did record multiple regal fritillaries at Pine Island 1 each year during 1995-99 (Fig. 2), and at Thomson 2, numbers have steadily increased during the study period, even in comparison to the regional mean (although not significantly: Table 3). At Thomson 1, the entire site has been managed with fire, with large portions burned in 1990, 1992, and 1993. Our peak survey was 0 or 1 during 1990-93, but >1 in 1994-99 except for 0 in 1998. Since 1992, we made similar communications about this species with the managing agency of Thomson 1-2.

At Buena Vista, the widespread distribution of regal fritillaries (multiple locations in an area of about 13 x 16 km: Swengel 1997b, Swengel and Swengel 1999), and localized areas of abundance (Fig. 2), are consistent with the management patterns observed for the species at longer surveyed sites (Fig. 6). Since 1992, only about 5% of this site was burned per year, usually in 16, 32, and 48 ha patches (out of >4500 ha in conservation management) while about 7% per year was cattle grazed on similar patch scales, with lesser amounts subject to haying and brush control by mowing or spot-herbiciding (J. Keir, personal communication; pers. obs.).

![Figure 6. Relative abundance (individuals/time on peak surveys during 1993-99) of regal and Aphrodite fritillaries at primary monitoring sites surveyed each year during 1993-99 (Table 1), by management type at each site.](image-url)
DISCUSSION

**Flight period.** Since we could not survey all sites each week throughout the flight period, we did not presume that our peak counts could all come from a narrow period right at peak time. Instead, we aimed to survey each site during the main flight period, a relatively broad period because of the study species' long flights. But we obtained surveys nearer our observed peak more often than expected. During 1992-99, of the 70 population indices obtained for each species, 94% had surveys at the site within 10 days of our regional peak date. While this date only approximates true peak (since we did not survey weekly), the study sites were treated similarly with respect to this date, making comparisons of relative abundance among sites more robust. Furthermore, we surveyed most sites multiple times in most years, and the peak counts at some sites did not occur during the ten-day period around the regional peak date. Thomas (1983) had a similar method with comparable precision regarding survey timing relative to peak flight at individual sites. His research team obtained population indices for most sites based on a single site visit in a "period of about 20 days spanning the peak day" for the study species.

**Peak surveys.** Despite our wide range of survey conditions and our inability to field surveys weekly or always with two observers, our dataset produced generally consistent patterns in annual fluctuations and management responses for the two fritillaries. Thus, data obtained in less than ideal conditions would appear useful, if handled with appropriate care. Furthermore, our results were similar between population indices using the peak count and the sum of the highest two counts. This suggests that, given our limited resources for conducting butterfly surveys, it would have been less useful to insist on a stricter protocol (e.g., all surveys by two surveyors, sites resurveyed more frequently) at the expense of getting fewer sites surveyed at all. This resonates with Thomas's (1983) observation that his team's population indices (obtained from single site surveys during a 20-day period) could have been even cruder, yet still would have been adequate to assess relative abundance among sites because of the vast variation in population sizes. Likewise, in the British Butterfly Monitoring Scheme (Pollard and Yates 1993), "recorder effect" (i.e., who did the survey) had negligible statistical influences, as also usually did weather and time of day within the range of conditions set in the survey methodology.

Nonetheless, our results should be interpreted with the caution that these population indices are relatively crude. Their meaning derives not from the anecdotes of individual surveys but from the overall patterns in large samples from multiple sites and years.

**Fluctuations and trends.** Both fritillaries exhibited large annual fluctuations (Fig. 4). These may sometimes be relatively synchronized not just on the scale of a state but even on larger scales. In 1998 (a very high year for both species in Wisconsin), the first records for regal fritillary were reported in Saskatchewan and eight counties in Colorado (The Lepidopterists' Society 1999), which are on the northern and western edges of the species' range. This likely does not correspond simply to increased surveying and reporting, since these and other reporters provided similar coverage in prior years, especially in Colorado (The Lepidopterists' Society 1990-98). How much this increase is attributable to climatic variation or habitat change is unclear. But on both state and rangewide scales, it is important yet difficult not to conflate annual fluctuations with trend, or decadal trends attributable to climate with those attributable to site management or landscape change.

**Management.** Relatively larger regal fritillary densities were consistently associated with unintensive non-fire managements (grazing, cutting), relatively lower densities with burning, and widely varying densities with non-management. Similar but less sensitive was the Aphrodite fritillary, which did not respond as strongly or clearly to burning, although higher densities were
associated with unintensive non-fire managements. A net benefit from fire for the regal fritillary is difficult to identify - any habitat benefits seem not to outweigh costs to the regal fritillary itself, even compared to doing nothing (non-management). Little change seemed to occur year to year in the unmanaged sites, compared to rather dramatic changes in vegetation and regal fritillary densities possible with burning. Over a period longer than this study, an unknown number of sites may have lost regal fritillaries, as well as a prairie (or even grassland) vegetative cover, due to long-term non-management. But in the short term, for the current year in an occupied site, non-management appears more (or as) favorable for regal fritillaries than burning.

However, both non-management and burning appear less favorable as the primary long-term management for the regal fritillary than other feasible managements (light grazing, localized cutting, rotational mowing) (Fig. 6). As Williams (1997) noted, a grazing history is often associated with regal fritillary populations in Wisconsin. Farm grazing occurred within the decade prior to conservation acquisition and/or management at Hogback, Muralt, Pine Island 1, and Thomson 2 (pers. obs. and personal communication from site managers), and Buena Vista is grazed as part of its conservation management. Haying/mowing is not known to figure prominently in the history of Wisconsin's regal fritillary populations. This does not mean such management is unfavorable, but rather that it may not have been a major agricultural practice in regal fritillary habitat here. Unintensive grazing and haying/mowing are associated with regal fritillary populations and/or relatively higher regal fritillary densities elsewhere (Swengel 1996, 1998; Swengel and Swengel 1997; Wagner et al. 1997, Schlicht and Orwig 1998).

Regal fritillary populations may persist in sites with relatively long histories of burning. In regions with more and larger populations, numerous regal fritillaries may occur in some burned sites, although at lower densities than in comparable sites with more favorable management (Swengel 1996, 1998; Swengel and Swengel 1997). However, some regal fritillary populations (defined as multiple individuals seen on visits to the site on multiple dates in multiple years) have disappeared after conservation management (i.e., burning) began in their habitat. Examples from adjacent northern Illinois include Ginzburg-Markham (last individual seen in the 1980s, with extensive surveys since; R. Panzer, personal communication), Harlem Hills (last seen in 1987, A. Branhagan, personal communication; we observed none on six dates in 1993-97 when we found the species at another site in the region), and possibly Byron (species known from one specimen dated 1991 in the nature center there, thus inadequate data to corroborate a population; we saw none on five dates in the species' flight period in 1993-94). Examples in Wisconsin include Oliver (Borth 1992 vs. our survey results), Pine Island 2 (this study), and Spring Green (Kirk 1994). Consistent with this is the strong decline at Muralt (from the 1980s to the early 1990s described by Borth 1992, and the continued decline during the 1990s in this study: Table 3).

For many regal fritillary populations extant on fire-managed sites, data are inadequate or unavailable to assess long-term trend. However, no data available to us suggest that a regal fritillary population anywhere has "recovered" (significantly increased in density or patch occupancy) after conversion to management primarily by burning. The more frequent and large the burns and more fragile the regal fritillary population, the more unfavorable the outcome appears relative to fire. While a population may disappear suddenly after one fire (e.g., Pine Island 2), it is likely that declines associated with fire management would usually transpire over many years, since only a portion of a site is usually burned each year, at least in the sites we study.

As an overall pattern, fritillary density tended to increase with more years since fire (Fig. 5). Very low numbers in the first year postburn are easily attributed to fire mortality, as the burns are typically timed broadly in the cool season (fall to spring; pers. obs.) when the fritillaries are immatures. All available data
locate regal fritillary and Speyeria immatures above ground in the herb layer (fuel), based on oviposition behavior and larval location (Kopper 1997, pers. obs.), and chrysalis attachment to herbaceous flora (Klots 1951, Allen 1997).

However, the increase in fritillary density through the years postfire was not continuously progressive (Fig. 5). This non-linearity could be attributed to stochastic variation, but it persisted in averages from multiple sites with fires desynchronized by year. While the flush of some flowers in the first growing season (year 0) postfire (Henderson 1982, Glenn-Lewin et al. 1990, Swengel 1996, pers. obs.) may attract some individuals, fritillaries were more numerous in years 1-3, when flowers tend to be fewer. This suggests that other factor(s) affect the distribution of fritillaries, which appear able, with their powerful and wide-ranging flight, to choose their location on the scale of the entire site. Multiyear patterns of litter accumulation postfire can also be non-linear: high vegetative productivity of dominant grasses postfire rebuilds litter to prefire levels within several years, but subsequent decreases in productivity longer postfire can lead to a reduction in litter, if breakdown increases relative to accumulation (Kucera and Ehrenreich 1962, Henderson 1982, Gibson 1988). Cool-season fires can be of immediate disadvantage to cool-season growers (Daubenmire 1968; Glenn-Lewin et al. 1990; Howe 1994, 1995), such as violets, depending on fire timing relative to violet phenology. But then periods of lower rather than higher litter may be more favorable for violets, in turn perhaps attractive to fritillaries.

If butterfly numbers become similar within a few weeks or years between burned and unburned units within a site, or peak and then decline within the time scale of a fire rotation, these patterns may be interpreted as indicating "recovery" or overall population stability relative to that management long-term (e.g., Huebschman and Bragg 2000). However, this study cautions that such assumptions should not be made. Distribution of regal fritillaries might seem to rebuild within a few years postfire (Fig. 5), but the overall population can still significantly decline over the year, as at Muralt (Fig. 2, Table 3).

**Applications to butterfly conservation.** To obtain more meaningful results than anecdotal suggestion, it was essential for our study to be long-term. For example, data from Muralt in any set of only a few consecutive years out of the last decade would not indicate the significant long-term decline there. But it was difficult to find reliable sources of sufficient funding for work compatible with our long-term goals (e.g., not just visiting "new" places, but also resurveying the same known sites year after year). This underscores the potential value of (very dedicated) volunteers, who may not be able to invest intense effort in a given field season but might conduct lesser amounts of field work spread over many years.

Studying widespread congenor(s), such as the Aphrodite fritillary, with close affinity to the rare species can also be valuable for increasing the sample and testing conclusions by comparison. More common congenors can also be useful surrogates in experiments needed to develop conservation strategies for rare species. In Wisconsin and adjoining areas, the Aphrodite fritillary appears useful as a substitute in tests of techniques for habitat restoration or reintroduction for the regal fritillary. Since the Aphrodite fritillary may be less sensitive than the regal fritillary, success with the former certainly doesn't prove suitability for the latter. But unless and until the method works for the Aphrodite fritillary, it is almost certainly unsuitable for the regal fritillary.

Obtaining more conclusive knowledge about a rare species is useful to its conservation only to the degree that this information is applied in a timely and appropriate manner. But it has been much more difficult than expected to get our data on this butterfly, even with its popularity and state-level legal protection, appropriately and adequately applied to the theory and practice of ecosystem management in regal fritillary habitat. Thus, a long-term commitment is useful not just for field research but also for trying to get the results applied sufficiently soon and enough.
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