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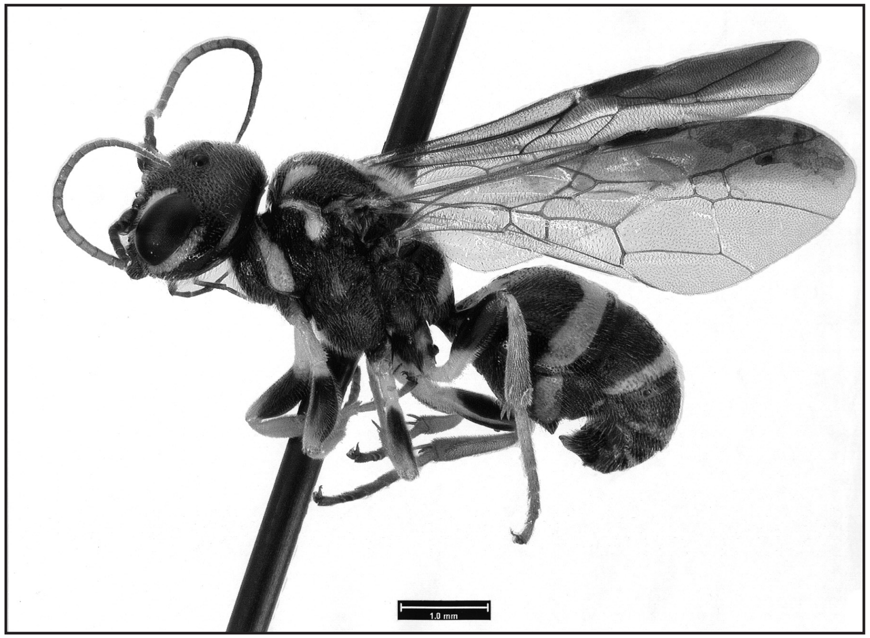

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OVIPOSITION AND DEVELOPMENT OF EMERALD ASH BORER (*AGRILUS PLANIPENNIS*) (COLEOPTERA: BUPRESTIDAE) ON HOSTS AND POTENTIAL HOSTS IN NO-CHOICE BIOASSAYS

Andrea C. Anulewicz[1], Deborah G. McCullough[1,2], and Deborah L. Miller[3]

ABSTRACT

Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) is an invasive phloem-feeding pest native to Asia. It was first identified in North America in 2002 and has killed millions of ash (*Fraxinus* spp.) trees in southeast Michigan and Essex County, Ontario. Since then, additional populations have been discovered across Michigan and in areas of Ohio, Indiana, Illinois, Maryland, Pennsylvania and West Virginia. In Asia, *A. planipennis* reportedly colonizes other genera, including species of *Juglans*, *Pterocarya* and *Ulmus*. In North America, attacks on non-ash species have not been observed but there is concern about host switching as ash mortality progresses. From 2003 to 2005, we evaluated *A. planipennis* oviposition and larval development on 4 North American ash species: green ash (*F. pennsylvanica* Marshall), white ash (*F. americana* L.), black ash (*F. nigra* Marshall), blue ash (*F. quadrangulata* Michaux), and 6 potential alternate hosts including privet (*Ligustrum* and *Forestiera* spp.), Japanese tree lilac (*Syringa reticulate* (Blumb) Hara), American elm (*Ulmus americana* L.), black walnut (*Juglans nigra* L.), hickory (*Carya ovata* (Miller) K. Koch) and hackberry (*Celtis occidentalis* L.). In no-choice tests using cut branches in cages, female *A. planipennis* oviposited on all species tested. Larvae on green ash, white ash, black ash, blue ash and privet developed to the second instar before branches desiccated. Larvae attempted to feed on some black walnut, Japanese tree lilac, American elm and hackberry branches but died as first instars. There were no feeding attempts on hickory branches. We also conducted no-choice tests by placing adult *A. planipennis* in cages that encircled the lower 1 m of the trunk of live green ash, white ash, black walnut and Japanese tree lilac nursery trees. High densities of larvae developed on green ash and white ash nursery trees but there was no evidence of any larval survival, feeding, or development on the Japanese tree lilac or black walnut nursery trees.

INTRODUCTION

Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae) has become one of the most important invasive forest pests in North America. This phloem-feeding insect is native to northeastern China, Japan, Korea, Mongolia, the Russian Far East and Taiwan (Yu 1992, Jendek 1994). *A. planipennis* was recently synonymized with *A. marcopoli* Obenberger (in China), *A. feretrius* Obenberger (in Taiwan) and *A. marcopoli ulmi* Kurosawa (in Korea and Japan) by Jendek (1994). *A. planipennis* was likely introduced into North America in solid wood packing material by the early 1990s but was first identified in 2002 as the cause of widespread ash (*Fraxinus* spp.[Oleaceae]) mortality in southeast Michigan and Essex County, Ontario (Cappaert et al. 2005b, Poland and McCullough 2006, Siegert et al. 2007b). Since then, additional populations

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have been found across lower Michigan and in areas of Ohio, Indiana, Illinois, Pennsylvania and Maryland (EAB Info 2007).

The life cycle of *A. planipennis* in North America is generally completed in 1 yr, although some individuals may require 2 yr to complete development (Cappaert 2005a, Siegert and McCullough 2005, Petrice and Haack 2006, Siegert et al. 2007a). Studies in southeast Michigan have shown emergence of *A. planipennis* adults generally begins in mid- to late May (Brown-Rytlewski and Wilson 2005, Cappaert et al. 2005b). Adult beetles live for 3-6 wk (Cappaert et al. 2005b). Beetles feed on ash foliage for 5-7 d before mating and females feed for at least another 5-7 d before oviposition begins (Bauer et al. 2004). Females generally lay 30-60 eggs (Chinese Academy of Science 1986, Yu 1992), although individuals have produced up to 258 eggs in laboratory conditions (Lyons et al. 2004). Eggs are laid individually on or just under the bark surface and inside bark cracks and crevices (Chinese Academy of Science 1986, Yu 1992, Bauer et al. 2004). Eggs are initially creamy white, gradually changing to reddish brown after a few days and hatch in 2-3 wk. Larvae feed under the bark in the cambium and phloem from July to October in distinctive serpentine galleries that eventually score the outer sapwood. Larval galleries disrupt vascular tissue, effectively girdling and killing branches or the entire tree. Larvae pass through four instars (Cappaert et al. 2005b) and most overwinter as prepupal larvae in the outer sapwood or in the thick bark of large trees (Cappaert et al. 2005a).

Although *A. planipennis* is not considered a major pest in Asia (Akiyama and Ohmomo 2000), this invader is aggressively attacking healthy, as well as stressed ash trees in North America. More than 20 million green ash (*F. pennsylvanica* Marsh.), white ash (*F. americana* L.), black ash (*F. nigra* Marsh.) and blue ash (*F. quadrangulata* Michx.) had been killed in southeast Michigan alone as of early 2007 (EAB Info 2007). In China, the host range of *A. planipennis* is reportedly limited to *Fraxinus* sp., including *F. chinensis* Roxb., *F. mandshurica* Rupr., *F. pennsylvanica*, *F. rhynchophylla* Hance and *F. velutina* Torr. (Chinese Academy of Science 1986, Yu 1992, Liu et al. 2003). In Japan, however, *A. planipennis* has been recorded from *F. mandshurica* var. *japonica* Maxim., *Juglans mandshurica* Maxim var. *sieboldiana* Makino and var. *sachalinensis* (Miyabe et Kudo) Kitamura, *Pterocarya rhoifolia* Sied. et Zucc. (Juglandaceae) and *Ulmus davidiana* var. *japonica* (Rehd.) Nakai (Ulmaceae) (Akiyama and Ohmomo 1997 cited in Haack et al. 2002, Sugiura 1999). North American members of these genera or families, including American elm (*U. americana* L.) (Ulmaceae), black walnut (*J. nigra* L.) (Juglandaceae), and hickory (*Carya* sp.) (Juglandaceae), are common in landscapes and wooded areas in North America, including areas with high density *A. planipennis* populations. Other members of the ash family (Oleaceae), such as privet (*Ligustrum* spp.) and Japanese tree lilac (*Syringa reticulata* (Blumb) Hara), are also commonly used in landscape settings throughout much of the eastern and central U.S (Boris and Kielbaso 1999, MacFarlane and Meyer 2005, Poland and McCullough 2006).

To date, attacks on non-*Fraxinus* genera have not been observed in North America but there is concern about the potential for additional hosts to be affected by *A. planipennis*, especially as population densities increase and ash trees die. A related species, the twolined chestnut borer, *A. bilineatus* (Weber), became an important pest of oaks (*Quercus* sp; Fagaceae.) after the introduction of chestnut blight caused the demise of American chestnut [*Castanea dentata* (Marsh.) Borkh; Fagaceae] (Haack and Acciavatti 1992). If *A. planipennis* can attack additional species, environmental and economic impacts in North America will increase dramatically. Given the extensive damage already caused by *A. planipennis*, there is an urgent need to evaluate the susceptibility of other common landscape and forest trees that may serve as alternate hosts for *A. planipennis*. We conducted no-choice studies using cut branches and live trees to assess *A. planipennis* oviposition and larval development on North American ash species and potential alternate host species.

MATERIALS AND METHODS

Cut branch bioassays

2003 bioassay. Branches of green ash, white ash, American elm, black walnut, shagbark hickory [*Carya ovata* (Miller) K. Koch.] and hackberry (*Celtis occidentalis* L.*)*, a relative of elm in the Ulmaceae family, were harvested from healthy trees at Michigan State University's W.K. Kellogg Forest, Kalamazoo Co., MI on 16 June 2003. Black ash was collected from Kensington Metropark, Oakland Co., MI on 28 May 2003. Swamp privet (*Forestiera acuminata* (Michx.) Poir.), Chinese privet (*Ligustrum sinense* Lour.) and glossy privet (*L. lucidum* Ait.) (hereafter collectively referred to as 'privet') branches were collected in Stoneville, Mississippi from the Delta Experimental Forest on 4 June 2003 and sent by overnight mail to Michigan. Branches were harvested from multiple trees of each species. The ends of the freshly cut bolts were waxed after cutting to reduce desiccation. Bolts remained in cold storage at 1-2° C with RH ≥ 80% until the bioassay began. On 2 July, 7 branches of green and white ash and 5 branches of the remaining species, each approximately 6.5 to 10 cm diam., were cut to approx. 17 cm in length (44 sections total) (Table 1). Each section was then cut in half vertically down the center. All cut surfaces were again waxed with paraffin to slow desiccation.

Each branch section was placed in a clear, plastic box (14 × 20 × 10 cm) ventilated with small holes in the sides and lid. One green ash leaf, with the petiole submerged in a vial of water to slow desiccation, was included in each box. Green ash leaves were collected from an untreated, infested tree in Washtenaw County.

Adult beetles were collected on 1 July 2003 from wild populations at Bicentennial Park in Livonia, Wayne Co., MI. Although age and mating status of the beetles were unknown, they exhibited behaviors consistent with mated adults and oviposition activity. Adult beetles were caged in a screened box overnight and provided with green ash leaves for feeding. The following day, beetles were sexed and one male/female pair was placed in each plastic box (44 pairs total). There were seven replicates (consisting of one branch section) of the ash species and five replicates of the non-ash species. Boxes were kept in a growth chamber at 24°C, 70% RH, and 16:8 light:dark photoperiod. Condensation and frass in boxes were removed at 2-3 day intervals. Growth chamber humidity was eventually reduced to 40% to prevent mold.

Boxes were checked and ash foliage was replaced twice a week until the female beetle in the box died. Number of eggs laid on the inner surface of each box was recorded. Those eggs were removed each time foliage was replaced. Upon death of the female beetle, the branch section was removed from the growth chamber then stored on a lab bench at 24°C. The first branch section was removed from its box on 9 July and the last section was removed on 11 August 2003. Branch sections were left undisturbed for 34 to 52 days after removal, allowing time for egg hatch and early instar development.

To evaluate branch sections, we first inspected the outer bark for eggs with a magnifying lens. Eggs were removed with forceps to prevent them from being recounted. Forceps or a small knife were used to chip off bark flakes to reveal eggs hidden in bark layers. After 15 min of searching, total number of eggs on the branch section was recorded.

Larval feeding was assessed by carefully peeling bark down to the wood using a knife or chisel. Number and stage of larvae on each branch section were recorded. Surface area was calculated using the vertical length and horizontal width of the sapwood surface on each branch section (Table 1). Gallery density was standardized by 100 cm^2 of surface area.

2004 bioassay. We repeated this bioassay three times in 2004 with the same eight species used in 2003, plus the addition of blue ash and Japanese

Table 1. Summary results (mean ± SE) of the 2003 no-choice cut branch bioassay for *Agrilus planipennis* early instar larval development on three North American ash species and five potential alternate host species.

	Green ash	**White ash**	**Black ash**	**Privet**[1]	**American elm**	**Black walnut**	**Hickory**	**Hackberry**
No. branch sections	7	7	4	5	5	4	5	5
Diameter (cm)	8.3 ± 0.2	8.4 ± 0.1	6.6 ± 0.3	4.8 ± 0.4	7.8 ± 0.1	8.0 ± 0.1	9.2 ± 0.1	8.9 ± 0.2
Length (cm)	16.7 ± 0.3	17.3 ± 0.3	17.3 ± 0.5	17.0 ± 0.3	17.2 ± 0.4	17.0 ± 0.1	15.2 ± 0.6	16.4 ± 0.6
Surface area (cm^2)	257 ± 12	247 ± 17	232 ± 13	176 ± 14	243 ± 2	1251 ± 22	251 ± 12	259 ± 6
Total galleries	44	72	37	22	0	0	0	0
No. branch sections	3	4	3	4	0	0	0	0
Mean no. galleries/ 100cm^2	2.3 ± 1.11 **ab**	4.2 ± 1.70 **a**	4.1 ± 1.38 **a**	2.7 ± 1.35 **a**	0 **b**	0 **b**	0 **b**	0 **b**
Total unsuccessful larval feeding attempts	0	0	0	0	3	11	0	5
No. branch sections w/ unsuccessful larval feeding attempts	0	0	0	0	1	2	0	1

Within rows, letters following the mean values indicate statistically significant differences among species (Kruskal-Wallis test and nonparametric multiple comparison procedure; $P < 0.05$).

[1] Includes *F. acuminate*, *L. sinense*, and *L. lucidum*.

tree lilac. Branches from several trees of each species for the bioassays were collected from the same sites used in 2003 on 24 May and again on 12 July 2004. Blue ash was harvested from a private woodlot in Superior Township, Washtenaw Co., MI on the same dates. Branches of Japanese tree lilac were collected from trees on the campus of Michigan State University, Ingham Co., MI on 20 May 2004. A different species of privet, *Ligustrum amurense* Carr., was collected from Wooster, Wayne Co., OH on 25 May 2004 and sent by overnight mail to Michigan. All branches were maintained in cold storage at 1-2ºC with a minimum of 80% RH until needed for bioassays. Eight branches of each species were cut to approx. 17 cm in length (Table 2) at the beginning of each bioassay; however, the branches were not cut vertically as they were in 2003. Cut ends were waxed with paraffin. Boxes were set up using the same methods as in 2003, except that 20 ml vials of water with cotton wicks were included in each box to provide water for the beetles. Additional holes were added to the sides and lids of the boxes to increase ventilation.

Adult beetles used in the 2004 bioassays were reared from bolts of infested ash trees collected in heavily infested sites in southeast MI. After emergence, similarly-aged groups of beetles (approx. 200) were placed in screen cages (60 × 60 × 60 cm) to feed on green ash foliage collected from an untreated, infested green ash tree. Cages were kept in growth chambers at 24ºC, 60% RH and 16:8 light:dark photoperiod. Beetles were allowed to feed and mate for 2 wk before bioassays began.

On each day that bioassays were initiated, beetles were sexed and 1 male/female pair was placed in each box (80 pairs total). The first bioassay, conducted from 18 June to 5 August, included 2 replicates of each species (20 branch sections total). The second and third bioassays were comprised of 3 replicates of each species and were conducted from 14 July to 14 August and 20 August to 14 September, respectively. Boxes were kept in growth chambers at 24ºC, 60% RH and 16:8 light:dark photoperiod. If a female beetle died during the first 3 d of the bioassay, she was replaced with a similarly-aged beetle. Thereafter, upon death of the female beetle, the branch was removed and stored on a lab bench at 24ºC. The total number of eggs laid on the inside of each box was recorded at this time.

The entire surface of each branch was inspected for eggs and bark was peeled to assess larval feeding 42-45 d after the branch was removed from its box. Diameter of each branch was measured and total bark surface area was calculated (Table 2). Branches were inspected, peeled, and larval density assessed using the same methods as in 2003.

Caged stem bioassay

2004 bioassay. On 12 May 2004, green ash, white ash, Japanese tree lilac, and black walnut balled-and-burlapped trees were delivered from Poplar Farms Nursery, Waterman, IL and planted at Matthaei Botanical Gardens, Washtenaw Co., MI. Trees were planted in an open field, 3 m apart, in 5 rows of 8 trees using a randomized complete block design (40 trees total). The partially exposed root balls were covered with composted wood mulch and drip line irrigation was installed for frequent watering. Trees had an overall mean (± SE) diameter at breast height (DBH) of 5.8 (± 0.1) cm (Table 3) and height of 4.0 (± 0.2) m.

Screen cages, approx. 90 cm tall and 30 cm in diameter, were constructed to confine live beetles around the lower 1 m of the stem of each tree. Two 120 cm long pieces of contractor's lathe driven into the root ball provided support for the cage. A green plastic disc (25 cm diam.) was cut to fit the stem and served as the top of the cage. A small piece of carpet (8 cm diam.) was wrapped around the stem under the plastic disc to close any gaps and ensure beetles could not escape. The plastic disc was stapled to the lathe and 18 ×16 aluminum mesh

Table 2. Summary results (mean ± SE) of the 2004 no-choice cut branch bioassay for *Agrilus planipennis* early instar larval development on three North American ash species and five potential alternate host species.

	Green ash	**White ash**	**Black ash**	**Blue ash**	**Privet**	**Japanese tree lilac**	**American elm**	**Black walnut**	**Hickory**	**Hackberry**
No. branch sections	8	8	8	8	8	8	8	8	8	8
Diameter (cm)	9.0 ± 0.6	8.8 ± 0.5	7.7 ± 0.2	7.2 ± 0.3	6.4 ± 0.3	4.6 ± 0.3	9.3 ± 0.2	9.5 ± 0.1	9.7 ± 0.1	9.3 ± 0.2
Length (cm)	16.8 ± 0.3	16.8 ± 0.3	16.6 ± 0.5	16.5 ± 0.3	16.9 ± 0.2	16.9 ± 0.2	15.4 ± 1.1	15.7 ± 0.6	17.0 ± 0.3	16.6 ± 0.3
Surface area (cm^2)	409 ± 25	409 ± 17	352 ± 9	317 ± 21	319 ± 15	225 ± 16	408 ± 31	393 ± 23	458 ± 8	406 ± 23
Total galleries	110	105	83	95	77	0	0	0	0	0
No. branch sections w/ galleries	6	5	7	6	6	0	0	0	0	0
Mean no. galleries/ 100 cm^2	3.6 **a** ± 1.08	3.1 **a** ± 1.43	2.9 **a** ± 0.89	3.3 **a** ± 1.43	3.1 **a** ± 1.08	0 **b**	0 **b**	0 **b**	0 **b**	0 **b**
Mean % area w/ galleries	49.2 ± 11.65	4.8 ± 2.32	12.0 ± 7.19	23.7 ± 14.65	8.2 ± 2.20	N/A	N/A	N/A	N/A	N/A
Total unsuccessful larval feeding attempts	0	0	0	0	0	30	8	26	0	1
No. branch sections w/ unsuccessful larval feeding attempts	0	0	0	0	0	4	1	3	0	1

Within rows, letters following the mean values indicate statistically significant differences among species (Kruskal-Wallis test and nonparametric multiple comparison procedure; $P < 0.05$).

Table 3. Mean (± SE) tree diameter at breast height (DBH), surface area and number of *Agrilus planipennis* galleries per m^2 for four species of trees used in no-choice caged stem bioassays in 2004 and 2005.

	Green ash	**White ash**	**Tree lilac**	**Black walnut**
2004				
DBH (cm)	6.0 ± 0.2	6.3 ± 0.2	4.6 ± 0.	16.4 ± 0.2
Surface area (m^2)	0.13 ± 0.00	0.14 ± 0.01	0.09 ± 0.00	0.13 ± 0.00
Total no. of galleries	49	1	0	0
Mean no. galleries/m^2	34.8 ± 24.9 **a**	0.8 ± 0.8 **ab**	0 **b**	0 **b**
2005				
DBH (cm)	6.8 ± 0.2	6.6 ± 0.1	5.4 ± 0.2	7.0 ± 0.2
Surface area (m^2)	0.17 ± 0.01	0.17 ± 0.01	0.11 ± 0.00	0.18 ± 0.01
Total no. of galleries	136	98	0	0
Mean no. galleries/m^2	78.2 ± 27.0 **a**	60.0 ± 38.4 **a**	0 **b**	0 **b**

Within rows, letters following the mean values indicate statistically significant differences among species (Kruskal-Wallis test and nonparametric multiple comparison procedure; $P < 0.05$).

screen was wrapped around the circumference of the cage, stapled to the plastic disc, and sealed with caulk. Excess screen above the disc was wrapped tightly around the stem of the tree and secured with a plastic cable tie. Excess screen at the bottom of the cage overlapped the root ball and was covered with mulch to seal the bottom. The lower 25 cm of the cage, above the root ball, was covered with plastic wrap. The top of the root ball was covered with approx. 20 cm of sand to prevent beetles from reaching the mulch. A small flap (approx. 15 cm × 20 cm) was cut into the screen 50 cm above the base of the cage and secured with Velcro® to provide access into the cage. A 5 cm long piece of garden hose was attached vertically to one piece of lathe inside the cage to hold shoots of green ash foliage collected from untreated, infested green ash trees. Stems of ash foliage were placed in plastic floral water pics to slow desiccation and foliage was changed every 2-3 d as needed.

Beetles used for this study were reared from infested logs following methods described in the 2004 bioassays. After 2 wk of feeding, beetles were sexed and 3 male/female pairs were placed in each tree cage (six beetles per cage). Cages were checked and foliage misted with water daily. Beetles that died were replaced with similarly-aged beetles of the same gender 2-3 times between 10 June and 13 September 2004 (586 beetles total). Number of live female beetles in each cage was tallied daily to determine total number of adult female days. For example, if 3 female beetles were alive in a cage for 5 d, the number of beetle days for that cage was 15 d.

Four of the 10 blocks of trees, selected randomly, were harvested on 1 and 2 November and returned to the laboratory. The portion of the stem that had been caged was dissected between 1 and 7 November 2004. In the lab, bark was inspected for eggs then carefully peeled down to the sapwood using a drawknife. Number and stage of larvae were recorded and gallery density was standardized by m^2 of surface area. Remaining trees were felled and dissected in March 2005.

For all trees, relative roughness of the bark on the caged portion of the stem was qualitatively estimated as low (very few to no cracks or crevices in the bark), medium (moderate abundance of cracks and crevices for oviposition) or high (abundant cracks and crevices).

2005 bioassay. The study was repeated in 2005 using the same four species supplied by the same Illinois nursery. Root balls left from the 2004 trees were removed and new trees were planted in the existing holes on 13 May 2005. Exposed root balls were again covered with mulch and irrigation was re-installed. Trees had an average DBH of 7.1 (± 0.2 SE) cm (Table 3).

Cages were constructed using methods from 2004. In addition, the stems of each tree were partially wrapped with thin strips of white, plastic Easy Gardener® Tree Wrap 513 (Easy Gardener Products, Inc., Waco TX) to provide beetles with additional crevices for egg laying. The wrap was cut into 2.5 cm wide strips and wrapped around the stems leaving 3-4 cm of exposed bark between each strip of tree wrap. Small, potted green ash trees (approx. 50 cm tall) were placed in each cage to provide foliage for feeding.

Beetles were reared and caged using methods from 2004. Beetles were replaced as they died, typically 1-2 times between 31 May and 19 August 2005 (408 beetles total). The caged portion of the ash stems were cut and dissected on 9 August 2006, after adult emergence was complete. Walnut and tree lilac stems were cut and dissected on 15 November 2006. Stems were peeled using methods from 2004.

Statistical analysis. Data were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots. Variables were not normal and could not be normalized with transformations. Therefore, the nonparametric Kruskal-Wallis test was used to determine significant differences among species (Kruskal and Wallis 1952) using SAS statistical software (PROC NPAR1WAY, SAS Institute, Inc. 2003). When the Kruskal-Wallis test was significant, nonparametric multiple comparisons tests ($P < 0.05$) were used to identify differences among species (Conover 1971, Zar 1984).

RESULTS

Cut branch bioassays

2003 bioassay. Adult *A. planipennis* lived from 8 to 43 d in the boxes and eggs were laid on branch sections from all tree species included in the test. We found a total of 525 eggs, including 323 eggs on 29 of the 42 branch sections we examined (1 black ash and 1 black walnut branch section with abundant mold were removed from the growth chamber and destroyed). Number of eggs found in 15 min of searching per branch section was highly variable, ranging from 0 to 65 with a mean of 12.5 (± 2.5) eggs per branch section. There were 202 eggs laid on the lid, sides, and bottom of 20 of the 44 plastic boxes. Number of eggs on the plastic boxes (not on the branch sections) ranged from 0 to 93 per box with an average of 4.8 (± 2.2).

White ash, black ash, and privet branches had significantly higher densities of larval galleries (number of galleries per 100 cm^2) than elm, walnut, hickory, and hackberry, while densities on green ash were intermediate (χ^2 = 17.53, df = 7, 34, P = 0.0143) (Table 1). Fifty-three percent of the larvae found on ash were first instars, 33% were second instars and 14% were third instars. All larvae were either dead or dying when the branches were peeled because of the relatively rapid desiccation of the small branch sections. A total of 22 galleries were excavated on four of the five privet sections (Table 1). Four galleries contained second instar larvae, while the others had first instar larvae. When only branch sections with galleries (ash and privet) were analyzed, gallery density did not differ significantly (χ^2 = 1.19, df = 3, 19, P = 0.75).

Although there were no actual galleries on elm, walnut, or hackberry sections, first instar larvae did occasionally attempt to feed on these species. Unsuccessful feeding attempts were observed on 1 elm, 2 walnut and 1 hackberry sections (Table 1). These feeding attempts consisted of galleries less than 1 mm wide and 5 mm to 10 cm long on the sapwood surface. All larvae that attempted to feed on these species, however, died without any development or growth. No evidence of any feeding attempts were found on hickory sections. Density of unsuccessful feeding attempts among elm, walnut, hickory, and hackberry did not differ significantly ($\chi^2 = 3.53$, df = 3, 15, $P = 0.09$).

2004 bioassay. Adult *A. planipennis* lived from 8 to 63 d in the boxes. Females laid eggs on all 10 of the species tested in 2004. We found a total of 577 eggs on 48 of the 80 branches. Number of eggs found per branch section in 15 min of searching ranged from 0 to 73, with an average of 7.2 (± 1.3). A total of 79 eggs were laid on the insides of 8 of the 80 boxes. Number of eggs laid on the boxes (not on branches) ranged from 0 to 47 with an average of 1.0 (± 0.6).

We found galleries on 24 of the 32 ash branches and on 6 of the 8 privet branches (Table 2). As in 2003, all larvae that were recovered were either dead or dying because of branch desiccation. Overall, there was a total of 393 galleries on 24 ash branches and gallery density averaged across all four ash species was 12.3 (± 2.3) galleries per branch. The four ash species and privet had significantly higher gallery densities than tree lilac, elm, walnut, hickory and hackberry ($\chi^2 = 38.11$, df = 9, 70, $P < 0.0001$) (Table 2). Sixty-two percent of the larvae on ash were first instars, 24% were second, 12% were third and 2% were fourth instars at the time of branch dissection. A total of 77 galleries were excavated on 6 privet branches (Table 2). There were 51 first instars, 7 second instars and 14 third instar larvae.

Four tree lilac, 1 elm, 3 walnut and 1 hackberry branches had unsuccessful *A. planipennis* feeding attempts made by first stage larvae (Table 2). No galleries or feeding attempts were found on hickory branches. As in the 2003 bioassay, when larvae attempted to feed on species other than ash and privet, galleries were abnormally small and resulted in larval death. Similarly, the density of unsuccessful feeding attempts did not differ significantly among these species ($\chi^2 = 8.05$, df = 5, 35, $P = 0.08$).

Caged stem bioassays

2004 bioassay. Overall, the mean number of female beetle days per cage was 40 (± 2) d. Individual female beetles lived from 1 to 34 d in cages. A total of 49 galleries were excavated on 4 green ash stems and a single gallery was excavated on 1 white ash stem. No galleries or feeding attempts were found on the other 6 green ash or 9 white ash stems, nor on any of the walnut or tree lilac stems (Table 3). Green ash stems had significantly greater mean gallery densities than black walnut and tree lilac stems, but did not differ significantly from white ash stems ($\chi^2 = 10.08$, df = 3, 36, $P = 0.0179$) (Table 3).

Bark roughness was ranked as high on all of the black walnut stems, while all of the Japanese tree lilac stems had medium bark roughness. Four of the 10 green ash stems had high bark roughness. All of the white ash stems and the remaining 6 green ash stems had low bark roughness. Three of the 4 green ash stems that had eggs and galleries had rough, flaky bark; the other infested green ash stem had smooth bark.

2005 bioassay. Overall, the mean number of beetle days per cage was 17 (± 2). Individual female beetles lived from 1 to 29 d in cages. We found a total of 136 galleries on 8 green ash stems and 98 galleries on 8 white ash stems (Table 3). Thirty-two small unsuccessful feeding attempts were found on 6 of the tree lilac stems. These feeding attempts were similar to those observed on cut branch sections. Unsuccessful feeding attempts were no more than 1 mm wide and 3 cm long and consistently resulted in death of first instar larvae. No galleries or feeding attempts were found on walnut stems (Table 3). Green and white ash stems had significantly higher gallery densities than black walnut and tree lilac stems ($\chi^2 = 26.17$, df = 3, 36, $P < 0.0001$) (Table 3).

As in 2004, all of the black walnut stems had high bark roughness, while all Japanese tree lilac stems had medium bark roughness. All white ash stems had low bark roughness. Bark roughness was ranked as high on 5 of the 10 green ash stems and as low on the other 5 green ash. The 2 green ash stems without galleries and all of the white ash stems had smooth bark.

DISCUSSION

Our first goal was to determine if *A. planipennis* would oviposit on non-ash species in a no-choice situation. We found eggs on all species used in the bioassays with cut branch sections, indicating that female beetles will lay eggs on species other than ash. Our results were at least partly attributable, however, to the no-choice setting presented to the beetles, given that eggs were also laid on the plastic boxes. In related studies conducted in field settings, *A. planipennis* females occasionally oviposited on cut logs or live trees of non-ash species, but at densities considerably lower than on ash species (Anulewicz 2006, Anulewicz et al. 2007).

Our ability to find eggs varied among species and branch sections and was particularly affected by bark texture. For example, privet, tree lilac and hackberry branch sections had relatively smooth bark with few crevices for females to hide eggs; eggs were easily detected with little manipulation of the bark. In contrast, the ash, elm, walnut and hickory sections often had rough bark and finding eggs in crevices and under bark layers was difficult.

When beetles were caged on live trees in 2004, they spent a substantial amount of time on the tops and sides of the cages, which likely reduced oviposition activity. Other studies have also reported poor oviposition when buprestids were reared in cages (Nash et al. 1951, Barter 1957, Akers and Nielson 1990). In 2004, most of the eggs that were laid on the stems of the live trees were on the green ash trees that had rough, flaky bark. We typically found eggs hidden in cracks and under bark flakes on these trees. We found only 2 eggs on smooth-barked white ash trees and only 1 yielded a viable larva. That egg was positioned at the site of an old, healed-over branch junction where the bark was creased and roughened. Barter (1957) reported that *A. anxius* Gory also favored rough bark for oviposition and Loerch and Cameron (1984) found that almost 70% of *A. anxius* eggs were laid in rough crevices in the dark triangular patch at branch origins.

When we repeated the study with live trees in 2005, we wrapped the stems of the trees with tree wrap. This provided additional crevices for egg laying and more oviposition occurred. Additional research needs to be done to further examine the influence of bark texture or tactile stimuli on *A. planipennis* oviposition behavior.

Our second goal was to determine whether early instar *A. planipennis* larvae would develop on non-ash species. In the cut-branch bioassays, all larvae were dead or dying when we dissected the branch sections simply because the small sections had dried out. Eighty-six percent of larvae on ash sections were first or second instars when branches were peeled. More larvae reached later instars on black ash and blue ash sections than on green or white ash sections, probably because the black and blue ash retained higher levels of moisture over time.

Unlike any of the other non-ash species studied, approx. 25% of the larvae on the privet branch sections developed to the second or third instar. In a previous study, male beetles survived 20 d on privet (*Ligustrum* sp.) and 13 d on swamp privet (*Forestiera* sp.) when caged with small discs of foliage. Male beetles survived 17 to 21 d on discs from green ash, black ash, evergreen ash (*F. uhdei* (Winzig) Lingelsh.) and velvet ash (*F. velutina* Torr.) leaves (Haack et al. 2004). Female longevity in this study was not reported. In two-choice and multiple-choice tests with small discs of foliage in confined conditions in the laboratory, *A. planipennis* fed readily on privet foliage (*Ligustrum* and *Forestiera* spp.) in the presence of ash foliage (Haack and Petrice 2005). In a replicated study with intact leaves on shoots, mortality rates of male and female adult *A. planipennis* did not differ significantly between green ash or privet foliage over a 9 d bioassay, although beetles consumed significantly more green ash foliage than privet foliage (unpublished data). From 2003 to 2006, however, we intensively examined live privet shrubs growing in areas with high densities of *A. planipennis*. We have not observed any evidence of *A. planipennis* feeding on privet leaves or colonizing privet phloem, even in locations where ash trees growing near or adjacent to privet shrubs were killed by *A. planipennis*. Moreover, results of current research indicate *A. planipennis* larvae are unable to complete development on live privet (unpublished data). Further monitoring of privet in field settings and additional evaluation of live and cut privet would be useful, however, to identify secondary compounds or nutritional variables that may inhibit or support successful development of *A. planipennis* larvae.

Some first instar larvae attempted to feed on black walnut, American elm and hackberry but invariably failed to develop or survive and there was no evidence of any feeding on hickory. These North American species appear to be unsuitable hosts for *A. planipennis*.

In China, the host range of *A. planipennis* is apparently limited to *Fraxinus* spp. (Chinese Academy of Science 1986, Yu 1992, Liu et al. 2003) but attacks on *Juglans*, *Pterocarya* and *Ulmus* reportedly occur in Japan or Korea (Sugiura 1999, Akiyama and Ohmomo 2000). The apparent variation in host range within Asia may reflect difficulties in distinguishing the systematic relationships of *A. planipennis* and closely related species. Several previously described Asian beetles including *A. marcopoli* Obenberger, *A. molco-poli* [sic!]: Miwa and Chujo, *A. feretrius* Obengerger and *A. marcopoli* var. *ulmi* Kurosawa were synonymized as *A. planipennis* by Jendek (1994). Host range for *A. planipennis* subsp. *ulmi*, however, included *Juglans* sp. and *Ulmus* sp., as well as ash, in China, Japan, Korea and Mongolia (Akiyama and Ohmomo 2000). In Japan, *Ulmus propinqua* Koidz was reported to be a host for *A. molco-poli* Miwa (Kurosawa 1956). To-date, *A. planipennis* attacks in North America have only been observed on *Fraxinus* species, which may reflect a founder effect associated with an accidental introduction of relatively few colonists from one origin. An increased understanding of relationships among the geographically distinct *A. planipennis* populations in Asia would be useful in assessing the potential ability of *A. planipennis* populations in North America to shift or expand their host range in areas where virtually all ash trees have succumbed. Additional studies to evaluate development of North American *A. planipennis* beetles on the Asian tree species reported as hosts for *A. planipennis* in the literature would also be valuable.

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DIVERSITY OF CICADELLIDAE AND CERCOPIDAE (HEMIPTERA) ON SAND PRAIRIES OF NEWAYGO COUNTY, MICHIGAN

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ABSTRACT

Sand prairies in the Great Lakes region occur as small sites dispersed throughout a heavily disturbed landscape. These unique natural areas are dominated by dry prairie grasses and are inhabited by a diversity of insects of which Cicadellidae and Cercopidae are among the most diverse groups. Their species compositions have been implicated as being potential indicators of ecological quality that could be used to rank the quality of prairie vegetation. In Newaygo Co., Michigan, 12 sand prairies were surveyed for Cicadellidae and Cercopidae and these data were then used to estimate species diversity for each site by the Simpson's Dominance and the Brillouin Diversity indices. A ranking of ecological quality of each site was also done by using an inferential analysis. Results from these indices indicated that the Big Finger prairie and the Michigan Nature Association's North prairie ranked the highest in diversity. Other highly ranked sites were the Cottonwood Street prairie and the Newaygo Prairie Study Area. The Locust Street prairie, although ranking low in diversity as determined by the Brillouin index, was dominated by *Philaenarcys bilineata* (Say) (Hemiptera: Cercopidae) a "Threatened" species, and *Flexamia delongi* Ross and Cooley (Hemiptera: Cicadellidae) a species of "Special Concern", indicating the importance of preserving this site even though its species richness and biodiversity rankings were low. Seven species of Cercopidae were collected including *Lepyronia gibbosa* Ball a state "Threatened" species, and *P. bilineata* and *Prosapia ignipecta* (Fitch), state species of "Special Concern".

Twenty species of Cicadellidae were identified of which *F. delongi*, a species of "Special Concern", was collected from all sites. Several prairie obligate species from both families were collected from each site. Eight Michigan state "Special Concern" or "Threatened" species, four new state records, and two new county records were collected. These results indicate the biological uniqueness of these sand prairies with evidence that all of these sites warrant conservation oriented management.

Cicadellidae and Cercopidae (Hemiptera) are diverse taxa in grassland ecosystems and their community composition allows their use as an index of the ecological quality of prairie vegetation. Nymphs and adults of these insects are herbivorous. Many species have close associations with their food plants and are easily sampled and determined (Hamilton 1995, 2005). Key species and community composition of these insects may help delimit the pre-settlement distribution of the sand prairie that now occurs as small patches in a mosaic of human development, abandoned agricultural fields, conifer plantations, oak openings and pine-barrens (Hauser 1953, Chapman and Crispin 1984, Hamilton 2005).

There are 208 species of Cicadellidae (Taboada 1964) and 19 species of Cercopidae in Michigan (Hanna and Moore 1966, Hanna 1970). Several species are designated by the state as "Special Concern" or "Threatened" in Michigan's sand prairies and pine-barrens including *Lepyronia gibbosa* Ball (Cercopidae) (Dunn et al. 2002). Although species lists for these two families exist for Michigan (Taboada 1964, Hanna and Moore 1966, Hanna 1970) there have been no recent or comprehensive surveys of the species on Michigan sand prairies.

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Sand prairies were once common in Muskegon, Newaygo, and Oceana Counties of west Michigan on old lake plains that are characterized by Sparta sandy loam (Hauser 1953, Chapman and Crispin 1984, Dunn et al. 2002). During the 19th century, the prairies were damaged first by agriculture, which failed due to dry and infertile soils, and later planted to conifers to reduce erosion. A survey of the region concluded that most of the remaining patches of prairie vegetation have been disturbed; few, if any, escaped cultivation (Chapman and Crispin 1984).

Sand prairies typically have low plant canopy coverage with spots of bare soil and abundant clumps of encrusted lichens (*Cladonia* spp.; Cladoniaceae). The dominant native grass is *Schizachyrium scoparium* (Michaux) Nash (Poaceae) with scattered patches of *Andropogon gerardi* Vitman (Poaceae) growing along more mesic edges. Other grasses or sedges include *Danthonia spicata* (L.) R. & S. (Poaceae), *Panicum* spp. (Poaceae), and often dense stands of *Carex pensylvanica* Lam. (Cyperaceae), the dominance of which has greatly increased in recent years (Winn and Kapp 1987, Dunn et al. 2002). These sites are also home to diverse native forbs including *Liatris* spp. (Asteraceae), *Asclepias* spp. (Asclepiadaceae), *Euphorbia corollata* L. (Euphorbiaceae), and *Viola pedata* L. (Violaceae) (see Winn and Kapp 1987). Several state "Threatened" plant species also occur on some of these sites including *Geum triflorum* Pursh. (Rosaceae), *Aster sericeus* Vent. (Asteraceae), and *Bouteloua curtipendula* (Michaux) Torrex. (Poaceae). Rare insects known to be on these sites include the state "Threatened" species, *L. gibbosa,* (Winn and Kapp 1987, Dunn et al. 2002), *Hesperia ottoe* W. H. Edwards (Hesperiidae) and *Speyeria idalia* (Drury) (Nymphalidae) (Nielsen 1999).

Knowledge of the species that inhabit a habitat may be important in ecosystem management. Several important ecological functions are related to species richness (Tilman and Downing 1994, Kinzig et al. 2001). Our objectives were to survey the sand prairies of Newaygo Co. for Cicadellidae and Cercopidae and to add to the known species for the area. It was not our intent to do a complete inventory of species, but to rank the quality of the remaining sites by comparing species richness and ecological indices and to add to a growing species list. Species composition of Cicadellidae and Cercopidae can also be used in determining which sites should be preserved, restored, or be assigned management priority (Hamilton 2005).

MATERIALS AND METHODS

We conducted a one sweep survey for Cicadellidae and Cercopidae on each of 12 sand prairies in Newaygo Co., MI, that were first described by Chapman and Crispin (1984) (Table 1). Each site still had a dominant cover of *S. scoparium* and a cover of diverse native forbs. Sampling occurred on 19, 20 or 24 July 2000. All days were warm and sunny. Collections were done between 1000-1500 hours. Diversity of these taxa is generally highest here in July when both early and late season species are present (Taboada 1964, Hanna 1970, Hamilton 1995). Importantly, most species are adults by mid-July which facilitates their determination. Insects were collected by sweeping (38 cm diam. net) through the plant canopy along meandering transects that were walked throughout the entire site for 15 minutes. Sweeping distances were recorded by a pace-calibrated pedometer and counts expressed per 500 m of linear vegetation. Heights of plants in these ecosystems are typically less than 40 cm.

Cercopidae were determined to species using the keys of Hanna and Moore (1966) and Hamilton (1975, 1982). Cicadellidae were identified first to genera by the regional key of Hamilton (unpublished), then to species by the keys of Beirne (1956), Ross and Hamilton (1972), Oman (1985), Whitcomb and Hicks (1988), Hamilton (1994, 1995, 1998, 1999) and Sinada and Blocker (1994). Voucher

Table 1. Sand prairies of Newaygo Co., MI, surveyed for Cicadellidae and Cercopidae in July 2000.

Site letter code, name of preserve, managing agency, township, and USGS coordinates	
A	Ore-Ida Preserve, Brooks Twp. (T12 N, R12 W, Sec 4, S1/2 of SE ¼).
B	40th at Locust St. prairie, Manistee National Forest, Croton Twp. (T13N R11W Sec 30 N1/2 of SE ¼).
C	Cottonwood Road - Stearns prairie relict, Manistee National Forest, Croton Twp. (T12N R11 W Sec 10 E ½).
D	Big Finger prairie - Little Scherrar prairie relict, Manistee National Forest, Brooks Twp. (T12N R12W Sec 35 SW ¼).
E	Research Natural Area at Oak and 48th - Merengo relict, Manistee National Forest, Brooks Twp. (T12NR12W Sec 2).
F	Oak and Poplar - Merengo prairie relict, Manistee National Forest, Brooks Twp. (T12NR12W Sec 2 W ½).
G	Newaygo Prairie Preserve, Popular Rd, Michigan Nature Association, Brooks Twp. (T12N R12W Sec 2 SW ¼).
H	Pine St. powerline - Big prairie relict, Consumers Power, Big Prairie Twp. (T13N R11W Sec 19 W ½).
I	Newaygo bowl prairie - Michigan Nature Association, Brooks Twp. (T12N R12W Sec11 SW1/4).
J	Newaygo Prairie Study Area - Little Scherrar relict, Manistee National Forest, Brooks Twp. (T12N R12W Sec35 NE ¼).
K	Oak St. powerline - Little Scherrar prairie relict, Consumers Power, Brooks Twp. (T12NR12WSec26 SE ¼).
L	Rollways prairie, Manistee National Forest, Brooks Twp. (T12NR12W Sec 27 S1/2).

specimens were deposited in the biological collections of Grand Valley State University. Plant nomenclature follows Gleason and Cronquist (1991).

Standard ecological diversity indices as described in Magurran (1988) and Krebs (1989) including the Simpson's Dominance Index (I) and the Brillouin Diversity Index (HB) were analyzed by EcoStat Software (Trinity Software Inc.) and results compared among all sites. Simpson's Dominance Index is best used to identify the ecological importance of a common species which occurs within a community that has a large number of rarer species (Margurran 1988, Krebs 1989), with higher calculated values indicating single species dominance. The Brillouin Diversity Index is best used when samples are drawn from a community in which few species are known (Pielou 1966) which was the case in this study. Higher values indicate higher species diversity. Individual prairies were ranked by species richness and abundance using the formula from Bomar (2001)

$$\sum 1/\,(p/\,N)$$

where p represents the total number of prairies inhabited by a given species and N is the total number of prairies ($N = 12$). This formula minimizes the importance of common species and favors those species that were less common. By summing the species present at a given site, a score was generated (Table 2). The highest score represents the highest quality for species diversity and inferentially the highest quality prairie. Bomar (2001) used this analysis with Acrididae to assess prairie quality in Wisconsin.

Relationships between prairie area and species richness (Table 2) were analyzed by Pearson correlations and then by Spearman rank order correlation test (Lehmann 1975) by comparing the four largest prairies (> 3 ha) to the eight smallest prairies (<3 ha) using Statistix (Analytical Software 2003).

Table 2. Species diversity rank, score and richness of Cicadellidae and Cercopidae from 12 sand prairies of Newaygo Co., MI, July 2000.

Prairie	Site code	Rank	Score	No. of species	Area (ha)
Big Finger	D	1	50.2	15	3.2
MNA – north	G	2	48.3	14	4.6
Rollways	L	3	36.1	13	.2
Cottonwood	C	4	27.0	17	3.6
MNA – south bowl	I	5	25.4	12	34.0
Pine St. power line	H	6	25.2	10	1.2
Newaygo Prairie Study Area	J	7	20.8	12	32.0
Ore-Ida	A	8	17.5	10	5.3
Oak St. power line	K	9	14.4	9	1.2
Oak and Poplar	F	10	14.1	9	1.7
Research Natural Area	E	11	13.3	9	8.2
Locust St.	B	12	10.9	7	4.2

RESULTS AND DISCUSSION

Seven species of Cercopidae (Table 3) were collected including a Michigan "Threatened" species, *L. gibbosa,* which was collected at nine sites. Two Cercopidae species of "Special Concern" in Michigan were collected including *Philaenarcys bilineata* (Say) at all sites and *Prosapia ignipectus* (Fitch) at two sites (Table 3). Two of the seven species are considered to be prairie specialists including *L. gibbosa* (Hamilton 1995, Panzer et al. 1995, Dunn et al. 2002) and *P. ignipectus*, considered a moderate prairie remnant dependant species (Panzer et al. 1995). The remaining four species are highly polyphagous upon prairie plants and also feed upon several species of woody plants and, so, are not prairie obligates (Hanna and Moore 1966; Hamilton 1982, 1995; Reed 1996). *P. ignipectus* is a new record for Newaygo Co. (Taboada 1964, Hamilton 1995).

Twenty species of Cicadellidae were collected (Table 3) with the dominant species being *Flexamia delongi* (Ross and Cooley)*,* a prairie specialist (Panzer et al. 1995, Reed 1996) and a Michigan species of "Special Concern". It was collected from all sites, with the highest counts of 66 individuals per 500 meter of swept vegetation on the bowl-prairie preserved by the Michigan Nature Association.

Other suspected prairie specialists as designated by Hamilton (1995) and Panzer et al. (1995) included *Laevicephalus unicoloratus* (Gillette and Baker) (Cicadellidae), which was collected from all sites and, *Auridius helvus* (Delong) (Cicadellidae), a new Michigan record that is listed as a species of "Greatest Need of Conservation" in Illinois suggesting that this species should be considered for listing in Michigan. Other new Michigan cicadellid records include *Athysanella longicauda* Beirne*, Acinopterus viridus* Ball*, and Limotettix osborni* (Ball). A new record for Newaygo Co., was *Diplocolenus configuratus* (Uhler) (Cicadellidae) (Hamilton 1995). Invasive species of leafhoppers were collected, including *Athysantus argentarius* Metcalf (Cicadellidae) at three sites and *Doratura stylata* (Boheman) (Cicadellidae) at four sites, especially at the Michigan Nature Association (MNA) bowl prairie (Table 3).

Species richness of Cercopidae and Cicadellidae among the sites ranged from 17 species at the Cottonwood Road prairie to just six species at the Locust St. prairie (Table 2). Other prairies with high species richness were the Big Finger prairie with 15 species and the MNA - North prairie preserve with 14 species. Counts per 500 m also varied among sites and ranged from 189 at the

Table 3. Number of each species per 500 meters of native vegetation as collected by sweep net sampling from 12 remnant dry sand prairies in Newaygo County, Michigan, July, 2000. Site letter codes: A = Ore-Ida Preserve, B = Locust St. prairie, C = Cottonwood Rd., D = Big Finger prairie, E = Research Natural Area at Oak and 48th , F = Oak and Poplar, G = Newaygo Prairie Preserve - Michigan Nature Association, H = Pine St. powerline - Big prairie relict, I = Newaygo bowl prairie - Michigan Nature Association, J = Newaygo Prairie Study Area, K = Oak St. powerline - Little Scherrar prairie relict, L = Rollways prairie.

	Prairies[a]											
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
a. Cicadellidae												
Flexamia delongi (Ross & Cooley) *+	11	8	20	1	12	16	66	9	13	18	15	28
Laevicephalus unicoloratus (Gillette & Baker) *+	6	5	9	21	31	15	10	4	2	20	14	2
Latalus sayi (Fitch)	3	0	10	3	5	2	16	0	3	6	9	4
Chlorotettix unicolor (Fitch)	11	1	5	8	1	1	10	4	2	20	14	2
Athysanus argentatus Metcalf	11	0	1	0	1	0	0	0	0	0	0	0
Diplocolenus configuratus (Uhler)	11	0	6	3	3	0	7	0	0	2	1	1
Aceratagallia sanguinolenta (Provancher)	0	1	0	6	0	0	10	2	18	4	2	2
Empoasca fabae (Harris)	0	0	2	13	0	1	4	24	0	0	0	0
Doratura stylata (Boheman)	0	0	1	1	0	0	0	0	44	1	0	0
Macrosteles fascifrons (Stal)	0	0	1	2	0	1	0	0	1	1	0	0
Scaphytopius frontalis (Van Duzee)	0	0	1	1	0	0	1	1	0	0	0	0
Athysanella longicauda Beir. #	1	0	0	0	0	0	3	0	3	0	0	0
Draeculacepha antica (Walker)	0	0	0	1	0	0	1	0	0	0	0	1
Polyamia apicata (Osborn)	0	0	0	0	0	0	1	0	0	0	0	0
Auridius helvus (Delong) #	0	0	0	0	0	0	1	1	1	0	0	0
Acinopterus viridus Ball #	0	0	0	0	0	0	0	1	0	0	0	1
Vestocephellus sp.	0	0	1	0	0	0	0	0	0	0	0	0
Tinobregmus sp.	0	0	1	0	0	0	0	0	0	0	0	0
Scleroracus osborni (Ball) #	0	0	0	1	0	0	0	0	0	0	0	0
Laevicephalus sylvestris (Osborn and Ball)	0	0	0	0	0	0	0	0	0	1	0	0

Table 3. Continued.

	Prairies[a]											
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
b. Cercopidae												
Lepyronia gibbosa Ball ** +	8	0	60	22	0	0	2	2	15	5	4	8
Philaenarcys bilineata Say *	11	20	59	53	32	9	12	19	24	14	4	6
Philaenus spumarius L.	5	0	9	19	0	6	0	0	0	4	1	5
Philaenus lineatus L.	0	1	2	0	4	1	0	0	0	0	0	1
Prosapia ignipectus (Fitch) * +	0	0	1	0	0	0	0	0	2	0	0	0
Aphophora parallela (Say)	0	0	0	0	0	0	0	0	0	0	0	7
Clastoptera obtuse (Say)	0	0	0	0	1	0	0	0	0	0	0	0

* Michigan species of “Special Concern”

** Michigan “Threatened” species

\+ prairie specialist (Hamilton 1995, Panzer et al. 1995)

\# New Michigan state record

Cottonwood prairie to 36 at the 40th and Locust St. prairie. Other prairies with high abundances of these taxa included the Big Finger prairie with 158 individuals and the MNA North prairie with 144 individuals collected.

Species dominance varied among sites with the highest Simpson's Dominance Index (I) values at the Locust St. prairie (B) with a value of 0.36, dominated by *P. bilineat*a, Michigan "Threatened" species and, *F. delongi,* a Michigan species of "Special Concern" (Fig. 1). The dominance by these two species at this site may indicate its ecological importance even though its overall species diversity was the lowest (Table 2). The lowest dominance value of 0.14 was measured at the 42 ha. Newaygo Prairie Study Area (J) which had an even distribution of 12 species within the second largest site (Fig. 1 A).

Analysis of species diversity by the Brillouin index indicated that diversity of these taxa was highest at Big Finger (D), Newaygo Prairie Preserve (J) and the Cottonwood Rd. (C) (Fig. 1 B). The Big Finger and the Newaygo Prairie Preserve area are currently managed as prairie but the Cottonwood Rd. site is currently a general management unit of the Manistee National Forest. Our data indicate the importance for this site to be managed as prairie.

Inferential analysis of prairie quality using a species richness index (Bomar 2001) indicated that the two highest quality prairies were the Big Finger (D) with a score of 50.2 and the MNA - North prairie (G) with a score of 48.3. Both of these sites had the second and third highest number of species at 15 and 14, respectively. The Cottonwood Rd. prairie had the greatest number of species with 19 but ranked fourth in quality with a score of 27 (Table 2). Another prairie of high quality according to this index was the Rollways prairie (L). The lowest scoring prairies were the Research Natural Area (E) with a score of 13.3 and the Locust St. prairie with a score of 10.9 which indicated both low species richness and abundance.

The sites varied in area from 1.2 ha to 34 ha (Table 2). There was a positive correlation between area and number of species by Pearson correlation ($P = 0.053$) and the Spearman rank order correlation test for sites larger than 3 ha (n = 4) when compared to those less than 3 ha (n = 8) ($P < 0.001$). The three sites with the most species were seventh, fifth, and eighth in size, respectively (Table 2) The biodiversity-inferential score of the two largest sites (32 and 34 ha) ranked fifth and seventh among the 12 sites sampled (Table 2).

These results indicate the biological uniqueness of these sand prairies of Newaygo Co., as a total of nine sites with the state "Threatened" species and three species of "Special Concern", four sites with new state records, and two sites with new county records, were collected. An immediate concern is that the ecological quality of these sites is in decline due to woody plant encroachment, itself due to the elimination of natural fire, and in some cases by off-road vehicle use. The invasion of exotic species such as *Centaurea maculosa* Lam. (Asteraceae) and *Hypericum perforatum* L. (Clusiaceae) and the native species *C. pensylvanica*, which is more typical of the forest understory, are competing with prairie plants (Dunn et al. 2002). These 12 sites in Newaygo Co. are some of the last remaining habitats for these rare species in Michigan, and if not soon preserved and more suitably managed, could be extirpated from Michigan. Similar sites have occurred in surrounding counties but most have been developed, indicating the overall importance of saving the Newaygo area prairies.

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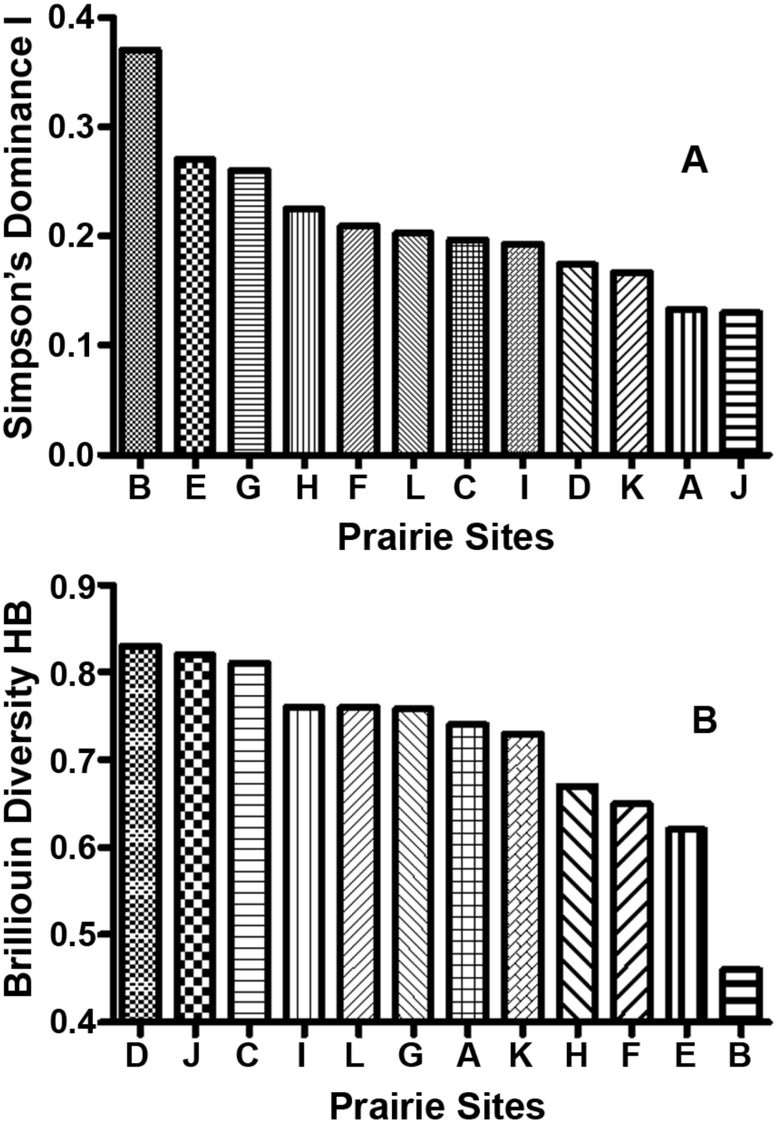

Figure 1. A comparison of Cicadellidae and Cercopidae species dominance and richness among 12 sand prairies in Newaygo Co., MI., July 2000 by A. the Simpson's Dominance Index (I) and B. the Brilliouin (HB) Index. Site letter codes: A = Ore-Ida Preserve, B = Locust St. prairie, C = Cottonwood Rd. prairie, D = Big Finger prairie, E = Research Natural Area, F = Oak and Poplar, G = Newaygo Prairie Preserve - Michigan Nature Association, H = Pine St. powerline - Big Prairie relict, I = Newaygo south bowl prairie - Michigan Nature Association, J = Newaygo Prairie Study Area- Forest Service, K = Oak St. powerline - Little Scherrar prairie relict, L = Rollways prairie.

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PRELIMINARY INVENTORY OF LEPIDOPTERA FROM COOK COUNTY, MINNESOTA: HESPERIOIDEA, PAPILIONOIDEA, DREPANOIDEA, GEOMETROIDEA, BOMBYCOIDEA, SPHINGOIDEA AND NOCTUOIDEA

David B. MacLean[1]

ABSTRACT

Four hundred and sixty five species of butterflies, skippers and moths, collected from 1988 through the summer of 2007, are reported from Cook County, MN. Included are data for three butterfly species of special concern: *Lycaeides idas nabokovi* Masters, *Erebia discoidalis* (Kirby) and *Oeneis jutta* (Hübner). Numbers of species recorded for the following families were: Hesperiidae (14), Papilionidae (2), Pieridae (7), Lycaenidae (14), Nymphalidae (24), Satyridae (6), Danaidae (1), Thyatiridae (4), Drepanidae (3), Geometridae (99), Lasiocampidae (2), Saturniidae (4), Sphingidae (16), Notodontidae (20), Arctiidae (19), Lymantriidae (5) and Noctuidae (225). *Euphydryas phaeton* (Drury) (Nymphalidae) is reported for the first time from Cook County, MN and *Pontia protodice* (Boisduval & LeConte) (Pieridae) and *Hyalophora columbia* (Smith) (Saturniidae) for the first time from northeastern Minnesota.

The purpose of this paper is to report species of butterflies, skippers and moths collected in Cook County, Minnesota (MN), from 1988 through August 2007. The author is unaware of a published list of Lepidoptera from Cook County; however, an estimate of the number of species present can be gleaned from published reports from nearby states and provinces. Ronald L. Huber (Bloomington, MN, pers. comm.) records 169 species of butterflies from Minnesota, including 89 species of butterflies from Wadena County, which is the only published county inventory of Minnesota butterflies to date (Oehlenschlager and Huber 2002). Ferge and Balogh (2000) recorded 1,209 species of moths in 13 families from Wisconsin. Rockburne and Lafontaine (1976) recorded 603 species of Noctuidae from Ontario and Quebec. Voss (1981, 1983 and 1991) reported 531 species from two northern counties of the Lower Peninsula of Michigan in the following families: Noctuidae (311 species), Thyatiridae (3), Drepanidae (4), Lasiocampidae (4), Notodontidae (38), Lymantriidae (6) and Geometridae (165). For all of Michigan, Nielsen provided preliminary lists of the state's butterflies and skippers (159 species; Nielsen 1998a), the macrolepidopteran moths (1,304 species; Nielsen 1997), and the microlepidopteran moths (1,217 species; Nielsen 1998b). Cook County, MN, lies entirely within the northern coniferous forest (Marschner 1974). Three landscape ecosystems that lie within Cook County (North Shore Highlands, Border Lakes, and Nashwauk Uplands; Albert 1994) provide varied habitats for larval host plants of butterflies and moths. The North Shore Highlands extend inland along the Lake Superior shoreline for approximately 15 km. The growing season ranges from approximately 121 to 135 days, being about 10 days longer along the Lake Superior shoreline than further inland (Albert 1994). Following logging in the late 19th and early 20th centuries, the extensive white pine (*Pinus strobus* L.) and red pine (*Pinus resinosa* Aiton) forests of the North Shore Highlands were replaced by trembling aspen (*Populus tremuloides*

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Michaux) and paper birch (*Betula papyrifera* Marshall). Northern hardwood forest, upland northern white cedar (*Thuja occidentalis* L.) forest and forested bog communities occur throughout the North Shore Highland landscape. Sugar maple (*Acer saccharum* Marshall) and white ash (*Fraxinus americana* L.) occur on ridges within 13-16 km of the Lake Superior shoreline (Albert 1994).

The Border Lakes landscape ecosystem within Cook County extends inland to the Canadian border and includes the eastern portion of the Boundary Waters Canoe Area Wilderness (BWCAW). This region has a cool continental climate with short warm summers and long winters (Heinselman 1973). The growing season ranges from approximately 108 to 123 days. The vegetation of the Border Lakes consists primarily of jack pine (*Pinus banksiana* Lambert) forest, white pine-red pine forest and hardwood-conifer forest dominated by balsam fir [*Abies balsamea* (L.) Miller], white spruce [*Picea glauca* (Moench) A. Voss], paper birch and trembling aspen. Heinselman (1973) considered the vegetation to be transitional between the Great Lakes-St. Lawrence and boreal forest regions.

The easternmost portion of the Nashwauk Uplands enters the southwestern part of Cook County (Albert 1994). The vegetation consists primarily of conifer-aspen-birch forest and the growing season ranges from approximately 106 to 121 days.

METHODS

Most of the data for this preliminary inventory of Cook County Lepidoptera were based on records in the author's personal collection dating back to 1988. Relatively few collections were made throughout the 1990s; however, more intensive collecting efforts began in 2000 and continued through the summer of 2007. Additional records of Cook County moths were based on light trap surveys conducted in 2000 and 2001 of the Grand Portage National Monument (MacLean 2002a) and the Grand Portage Indian Reservation (MacLean 2000b, 2001b, 2002b, 2003). Moths were collected by means of netting, picking specimens from a sheet illuminated by a 15-watt black light placed at the author's residence and operated on 2 nights in 2001, 24 in 2002, 56 in 2003, 51 in 2004, 59 in 2005, 61 in 2006, and 14 in 2007. Depending on the year and weather conditions, collections were made from mid April to late October or early November. In addition, one or more 22-watt portable blacklight traps were operated at 36 locations throughout Cook County. Fourteen blacklight trap collections were made in 2000, 6 in 2001, 1 in 2002 and 2003, 16 in 2004, 8 in 2005, 13 in 2006 and 8 in 2007. In 2000 and 2001 the author conducted a survey of butterflies of special concern of the Superior National Forest for the United States Forest Service (MacLean 2000a, 2001a).

The following references were used to identify butterflies and skippers: Brock and Kaufman (2003), Layberry et al. (1998), Nielsen (1999), and Scott (1986). The following references were used to identify moths: Bolte (1990), Covell (2005), Ferguson (1972, 1978), Forbes (1948, 1954), Franclemont (1973), Hodges (1971), Lafontaine (1987, 1998, 2004), Lafontaine and Poole (1991), Poole (1995), Rockburne and Lafontaine (1976), and Wagner et al. (2001). Identification of *Euxoa messoria* (Harris) and *Euxoa comosa altera* McDunnough was based on genitalia preparations. Specimens of some species were sent to Leslie A. Ferge (Madison, WI) for identification.

I categorized the relative abundance of each species based on the number of specimens that I collected from 1988 to 2007 within Cook County. The five categories I used were: rare (represented by a single specimen), uncommon (2-5 specimens), common (6-10 specimens), very common (11-20), and abundant (> 20 specimens). I recognize that these categories no doubt underestimate the true population size of many species.

RESULTS AND DISCUSSION

This report lists 465 species of butterflies, skippers and moths from Cook County, MN, for the following families: Hesperiidae (14), Papilionidae (2), Pieridae (7), Lycaenidae (14), Nymphalidae (24), Satyridae (6), Danaidae (1), Thyatiridae (4), Drepanidae (3), Geometridae (99), Lasiocampidae (2), Saturniidae (4), Sphingidae (16), Notodontidae (20), Arctiidae (19), Lymantriidae (5) and Noctuidae (225). The majority of butterflies, skippers and moths recorded from Cook County are widespread and common across the northern United States and southern Canada. Uncommon species of butterflies with localized distributions in extreme northeastern Minnesota included *Pontia protodice* (Boisduval & LeConte), *Euchloe ausonides* (Lucas), *Lycaena dorcas* Kirby, *Lycaena epixanthe* (Boisduval & LeConte), *Chlosyne harrisii* (Scudder), and *Euphydryas phaeton* (Drury). The list also includes three species of special concern (MN DNR 2007), *Lycaeides idas nabokovi* Masters, *Erebia discoidalis* (Kirby) and *Oeneis jutta* (Hübner). *Euphydryas phaeton* (Drury) (Nymphalidae) is reported for the first time from Cook County, MN.

Butterflies and skippers recorded from Cook County, MN (Opler et al. 2006) but not recorded in this inventory were: *Atalopedes campestris* (Boisduval), *Amblyscirtes hegon* (Scudder) (Hesperiidae); *Nathalis iole* Boisduval (Pieridae); *Satyrium edwardsii* (Grote & Robinson), *Incisalia polia* Cook & Watson, *Hemiargus isola* (Reakirt) (Lycaenidae); *Polygonia interrogationis* (Fabricius), *Euptoieta claudia* (Cramer) and *Boloria eunomia* (Esper) (Nymphalidae).

Overall, 28% of moth species were represented by a single specimen and were judged to be rare. Similarly, 38% were categorized as uncommon, 29% common, 4% very common, and 1% abundant.

Table 1 lists the number of species recorded for all years (1998-2007) by month from April to October for the five most abundant moth families. The total number of species recorded for each month increased dramatically from 20 in April, to a peak of 171 in July, and then declining to 14 in October (Table 1). The number of species of Noctuidae collected each month far surpassed the number collected for the other most common moth families (Table 1). While most species of Geometridae, Sphingidae, Notodontidae, and Arctiidae were recorded in early to mid summer, species richness of the Noctuidae remained high into late summer and early fall.

Species of *Abagrotis, Agrotis, Amphipoea, Apamea, Autographa, Euxoa, Papaipema, Syngrapha*, *Xestia* and others were most abundant in late summer and fall. Some species were more common than indicated by their ranking here as not all individuals attracted to the blacklight sheet were collected. Thus, the results no doubt underestimate the relative abundance of species such as *Enargia decolor* (Walker), *Helicoverpa zea* (Boddie), *Nephelodes minians* Guenée, and *Pseudaletia unipuncta* (Haworth), which were very common in late summer and

Table 1. Number of Geometridae, Sphingidae, Notodontidae, Arctiidae and Noctuidae species collected in Cook County, MN, during 1988-2007 by month.

	April	**May**	**June**	**July**	**Aug.**	**Sept.**	**Oct.**
Geometridae	5	23	48	40	28	7	5
Sphingidae	0	1	13	10	4	1	0
Notodontidae	1	8	14	14	5	0	0
Arctiidae	0	0	9	14	9	2	0
Noctuidae	14	22	64	93	90	68	9
Totals	20	54	148	171	136	78	14

early fall. Also, *Malacosoma disstria* Hübner was extremely abundant during a population outbreak in the early 2000s.

The majority of moths recorded from Cook County are generalists that are widespread across the eastern United States and southern Canada. Most species were collected at a variety of sites; however *Caripeta divisata* Walker, *C. angustiorata* Walker, and *Panthea pallescens* McDunnough occurred only at sites dominated by conifers. *Sthenopis argenteomaculatus* (Harris), *Ematurga amitaria* (Guenée), *Bellura gortynoides* Walker, *Bellura obliqua* (Walker), *Phlogophora iris* Guenée, *Phlogophora periculosa* Guenée, *Epiglaea decliva* (Grote), *Epiglaea apiata* (Grote), *Polia nimbosa* (Guenée), *Polia imbrifera* (Guenée) and *Euxoa velleripennis* (Grote) occurred at wetlands or near lakeshores with alder (*Alnus*). *Hypoprepia miniata* (Kirby), *Apamea impulsa* (Guenée), *Athetis mendosa* McDunnough, *Leucania commoides* Guenée, *Leucania pseudargyria* Guenée and *Pseudohermonassa tenuicula* (Morrison) were collected along the Lake Superior shoreline with cutworms that were common in late summer and early fall. Adults of *Megalographa biloba* (Stephens) were obtained from larvae reared on a *Delphinium* species cultivar.

Ferge (1983) recorded *Hyalophora columbia* (Smith), a tamarack specialist, from 12 Wisconsin counties, however *H. columbia* has rarely been reported from Minnesota. Specimens have been recorded from Beltrami, Lake of the Woods (Tuskes et al. 1996) and Clearwater (Itasca State Park) counties in northwestern Minnesota and Aitkin County in northcentral Minnesota (Ronald L. Huber, pers. comm.). The specimen collected from Cook County represents the first published record of *H. columbia* from northeastern Minnesota.

In Table 2, I have listed the 465 species of Lepidoptera collected in Cook County, MN, by family and provided for each its Hodges number (Hodges et al. 1983), and comments on relative abundance and seasonal distribution.. A more detailed list of species with collection dates, numbers collected or observed, and the collection methods is available from the author upon request. While no specimens of either *Papilio polyxenes* Fabricius or *Hyalophora cecropia* (Linnaeus) were collected or observed by the author, these two species were reported from Cook County based on reliable observations of the former and photographs of the latter. A third species reported from Cook County, *Lymantria dispar* (Linnaeus), for which no specimens were taken, has been well documented by pheromone traps operated by the Minnesota DNR. (Cremers 2006).

Table 2. Annotated checklist of Lepidoptera collected from Cook County, MN, during 1988-2007, including the Hodges species number (Hodges et al. 1983) and notes on relative abundance and seasonal distribution. Except where noted, all species are in the author's personal collection. Scientific names of moths follow that of Ferge and Balogh (2000), those of butterflies follow Nielsen (1999).

Family
Hodges number, species, relative abundance, and seasonal distribution

HESPERIDAE - duskywings and skippers
  3910 *Thorybes pylades* (Scudder): common, June.
  3945 *Erynnis icelus* (Scudder & Burgess): common most years, late May, June and early July.
  3982 *Carterocephalus palaemon* (Pallas): common, mid - late June.
  4012 *Thymelicus lineola* (Ochsenheimer): widespread invader colonizing northeastern Minnesota, extremely abundant during late 1990s, numbers declined in early 2000s, June - July.
  4020 *Hesperia comma* (Linnaeus): common, August.
  4033 *Hesperia sassacus* Harris: common, June.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

4036 *Polites peckius* (Kirby): common, July - August.
4041 *Polites themistocles* (Latreille): common most years, late June - July.
4043 *Polites mystic* (Edwards): uncommon, local, late June - July.
4047 *Wallengrenia egeremet* (Scudder): uncommon, July - August.
4058 *Poanes massasoit* (Scudder): uncommon, August.
4059 *Poanes hobomok* (Harris): common most years, June - mid July.
4078 *Euphyes vestris* (Boisduval): common, late June - July.
4105 *Amblyscirtes vialis* (Edwards): common, June - mid July.

PAPILIONIDAE - swallowtails
4159 *Papilio polyxenes* Fabricius: not seen but reliable sight records from extreme southwestern Cook County.
4176a *Papilio canadensis* Rothschild & Jordan: abundant most years, however numbers declined in early 2000s, late May - early July.

PIERIDAE - whites and sulphurs
4193 *Pontia protodice* (Boisduval & LeConte): stray, first northeastern Minnesota record (Ronald L. Huber pers. comm.) 08 Aug 2006.
4195 *Pieris napi oleracea* (Harris): common, late May - August.
4197 *Pieris rapae* (Linnaeus): common most years, abundant in 2006, June - late August.
4200 *Euchloe ausonides* (Lucas): very local, occurs only in extreme northern Cook County where its host plant *Arabis glabra* (Linnaus): grows, mid - late May.
4209 *Colias philodice* Godart: common most years, uncommon in 2006, May - late September.
4210 *Colias eurytheme* Boisduval: uncommon most years, not seen in 2006, often not seen until late summer or early fall, June - September.
4220 *Colias interior* Scudder: common to abundant, late June - early August.

LYCAENIDAE - harvesters, coppers, hairstreaks and blues
4260 *Lycaena epixanthe* (Boisduval & LeConte): local, rare, early July.
4261 *Lycaena dorcas* (W. Kirby): local, rare, July.
4285 *Satyrium liparops* (LeConte): uncommon, July.
4322 *Incisalia augustinus* (W. Kirby): common most years, rare in 2005, 2006 and 2007, late May - mid June.
4328 *Incisalia niphon* (Hübner): local, uncommon, mid May - early June.
4329 *Incisalia eryphon* (Boisduval): local, uncommon, mid May - early June.
4336 *Strymon melinus* Hübner: rare, late July.
4361 *Everes comyntas* (Godart): uncommon, August.
4362 *Everes amyntula* (Boisduval): uncommon, June.
4363 *Celastrina ladon* (Cramer): common most years, uncommon in 2006, May - June.
4363.1 *Celastrina neglecta* (W. H. Edwards): uncommon but may be overlooked, June and August.
4372 *Glaucopsyche lygdamus* (Doubleday): common most years, June - early July.
4374 *Lycaeides idas nabokovi* Masters: a Minnesota DNR species of special concern, very local, occurs only where its host plant *Vaccinium cespitosum* Michx. grows, mid June - mid July.
4376 *Plebejus saepiolus* (Boisduval): common - most years, abundant in 2005 & 2006, June - mid July.

Table 2. Continued.

Family	**Hodges number, species, relative abundance, and seasonal distribution**
NYMPHALIDAE - brush-footed butterflies	
4421	*Polygonia comma* (Harris): common most years, May - mid July.
4423	*Polygonia faunus* (W. H. Edwards): common some years, June and August.
4427	*Polygonia gracilis* (Grote & Robinson): local, uncommon, early June & August.
4429	*Polygonia progne* (Cramer): local, uncommon, July.
4430	*Nymphalis vau-album* (Denis & Schiffermüller): common most years, uncommon - rare in 2004 - 2007, late April - May, August, September - October.
4432	*Nymphalis antiopa* (Linnaeus): common most years, abundant in 2001, scarce 2002 - 2004, common 2007, May - September.
4433	*Nymphalis milberti* (Godart): common most years, May, July - August.
4434	*Vanessa virginiensis* (Drury): common some years, absent others, abundant in 2005, May - July.
4435	*Vanessa cardui* (Linnaeus): migrant, common - abundant some years, absent in others, June - September.
4437	*Vanessa atalanta* (Linnaeus): migrant, scarce or absent most years, common in 2001, 2007, May - June.
4440	*Junonia coenia* Hübner: migrant, absent - uncommon most years, common 2007, June - July.
4450	*Speyeria cybele* (Fabricius): more common in the southwestern part of Cook County along the Lake Superior shoreline, July.
4451	*Speyeria aphrodite* (Fabricius): common most years, July.
4459	*Speyeria atlantis* (W. H. Edwards): common - abundant most years, late June July.
4464	*Boloria selene* (Denis & Schiffermüller): local, common most years, June - August.
4465	*Boloria bellona* (Fabricius): common most years, June - August.
4471	*Boloria freija* Thunberg: locally common, May - early June.
4475	*Boloria chariclea* (Schneider): very local, uncommon, August.
4481	*Phyciodes selenis* (W. Kirby): common - abundant, June - mid July.
4482	*Phyciodes batesii* (Reakirt): common, June - early August.
4490	*Chlosyne nycteis* (Doubleday & Hewitson): common - abundant most years, June - mid July.
4491	*Chlosyne harrisii* (Scudder): very local, uncommon, June.
4516	*Euphydryas phaeton* (Drury): new Cook Co. MN record, very local, known from one location in Cook County where its primary host plant *Chelone glabra* L. grows, larvae in May, adults in mid - late June.
4522	*Limenitis arthemis* (Drury): common - abundant most years, June – August.
SATYRIDAE - Satyrs, wood nymphs, alpines and arctics	
4568.1	*Enodia anthedon* A. H. Clark: common most years, June - mid June.
4583	*Coenonympha tullia inornata* W. H. Edwards: uncommon most years, late June - mid July.
4587	*Cercyonis pegala* (Fabricius): uncommon, July - August.
4596	*Erebia discoidalis* (W. Kirby): a Minnesota DNR species of special concern, very local near bog edges and grassy wetlands, locally uncommon - common, late May - early June.
4605	*Oeneis macounii* (W. H. Edwards): local, uncommon, only observed in even numbered years, mid June - mid July.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

4611 *Oeneis jutta* (Hübner): a Minnesota DNR species of special concern, very local, black spruce bogs with *Eriophorum* spp., the larval host plant, uncommon, June.

DANAIDAE - Milkweed butterflies
4614 *Danaus plexippus* (Linnaeus): numbers fluctuate widely, common to abundant in 2001, 2005, 2006 and 2007, scarce other years, noncultivated patches, the larval host plant *Asclepias syriaca* L. is very rare and local in Cook County, late May - September.
FAMILY THYATIRIDAE - false owlet moths
6235 *Habrosyne scripta* (Gosse): common, June - August.
6236 *Habrosyne gloriosa* (Guenée): rare, early July.
6237 *Pseudothyatira cymatophoroides* (Guenée): uncommon, late June- July.
6240 *Euthyatira pudens* (Guenée): uncommon, late May - June.

FAMILY DREPANIDAE - hooktip moths
6251 *Drepana arcuata* Walker: common, May - July.
6252 *Drepana bilineata* (Packard): common, May - June.
6255 *Oreta rosea* (Walker): rare, early July.

FAMILY GEOMETRIDAE - Geometer moths
6256 *Archiearis infans* (Möschler): rare, April.
6290 *Macaria loricaria julia* (Hulst): uncommon July.
6303 *Macaria subcessaria* (Walker): uncommon, July - August.
6330 *Macaria ulsterata* (Pearsall): uncommon, June - July.
6342 *Macaria bisignata* Walker: rare, August.
6344a *Macaria signaria dispuncta* Walker: uncommon, June - July.
6347 *Macaria pinistrobata* Ferguson: local, June, July.
6436 *Ematurga amitaria* (Guenée): uncommon, late May - June.
6570 *Aethalura intertexta* (Walker): fairly common, mid May - June, August.
6583 *Iridopsis ephyraria* (Walker): common, late July - August.
6588 *Iridopsis larvaria* (Guenée): fairly common, July - mid August.
6590 *Anavitrinella pampinaria* (Guenée): uncommon, mid June.
6597.1 *Hypagyrtis unipunctata* (Haworth): common, mid July - August.
6598 *Protoboarmia porcelaria indicataria* (Walker): common, mid June, August.
6621 *Melanolophia signataria* (Walker): rare, May.
6639 *Eufidonia discospilata* (Walker): rare, June.
6640a *Biston betularia cognataria* (Guenée): common, June - July.
6658 *Phigalia titea* (Cramer): rare, April.
6665 *Erannis tiliaria* (Harris): common, October.
6666 *Lomographa semiclarata* (Walker): common, mid-late May.
6668 *Lomographa glomeraria* (Grote): uncommon, mid May.
6677 *Cabera erythemaria* Guenée: uncommon, July.
6678 *Cabera variolaria* (Guenée): uncommon, July - August.
6726 *Euchlaena obtusaria* (Hübner): uncommon, June - July.
6729 *Euchlaena johnsonaria* (Fitch): common, July.
6734 *Euchlaena marginaria* (Minot): uncommon, June.
6737 *Euchlaena tigrinaria* (Guenée): uncommon, mid July.
6740 *Xanthotype urticaria* Swett: uncommon, late June - July.
6743 *Xanthotype sospeta* (Drury): common, July.

Table 2. Continued.

Family

Hodges number, species, relative abundance, and seasonal distribution

6754	*Pero ancetaria* (Hübner): common, mid June - July.
6763	*Phaeoura quernaria* (J. E. Smith): uncommon, June.
6796	*Campaea perlata* (Guenée): common, June - August.
6797	*Ennomos magnaria* Guenée: common, August - September.
6804	*Petrophora subaequaria* (Walker): common, late May - June.
6807	*Tacparia detersata* (Guenée): common, late May - June.
6812	*Homochlodes fritillaria* (Guenée): uncommon, June, August.
6818	*Selenia kentaria* (Grote & Robinson): common, late May - June.
6819	*Metanema inatomaria* Guenée: uncommon, May - June.
6820	*Metanema determinata* Walker: uncommon, June - July.
6822	*Metarranthis duaria* (Guenée): uncommon, June.
6826	*Metarranthis hypochraria* (Herrich-Schäffer): rare, late June.
6837	*Probole alienaria* Herrich-Schäffer: uncommon, May, July.
6838	*Probole amicaria* Herrich-Schäffer[1]: rare, July.
6841	*Plagodis kuetzingi* (Grote): uncommon, May - June.
6842	*Plagodis phlogosaria* (Guenée): uncommon, May - June, August.
6844	*Plagodis alcoolaria* (Guenée): rare, late June.
6863	*Caripeta divisata* Walker: local, common, June - July.
6867	*Caripeta angustiorata* Walker: local, uncommon, early July.
6884	*Besma endropiaria* (Grote & Robinson)[1]: uncommon, late June.
6885	*Besma quercivoraria* (Guenée): rare, July.
6888	*Lambdina fiscellaria* (Guenée): common, August.
6906	*Nepytia canosaria* (Walker): common, August - September.
6912	*Sicya macularia* (Harris): common, July - September.
6963	*Tetracis crocallata* Guenée: common, June.
6964	*Tetracis cachexiata* Guenée: common, June.
6966	*Eutrapela clemataria* (J. E. Smith): common, June, August.
6982	*Prochoerodes transversata* (Drury): common, August - September.
7009	*Nematocampa resistaria* (Herrich-Schäffer): common, June - August.
7048	*Nemoria mimosaria* (Guenée): rare, June.
7139	*Cyclophora pendulinaria* (Guenée): uncommon, June, August.
7159	*Scopula limboundata* (Haworth): uncommon, July.
7182	*Dysstroma citrata* (Linnaeus): very common, June - August.
7189	*Dysstroma hersiliata* (Guenée): uncommon, late June - July.
7201	*Eulithis testata* (Linnaeus): uncommon, August.
7206	*Eulithis explanata* (Walker): very common, July - August.
7216	*Plemyria georgii* Hulst: uncommon, August.
7235	*Hydriomena divisaria* (Walker): uncommon, May - June, August.
7236	*Hydriomena renunciata* (Walker): common, June - August.
7257	*Hydriomena furcata* Thunberg: rare, August.
7290	*Coryphista meadii* (Packard): common, April - June, September - October.
7291	*Rheumaptera undulata* (Linnaeus): uncommon July.
7293a	*Rheumaptera hastata gothicata* (Guenée): diurnal, common most years uncommon in 2006, June.
7294	*Rheumaptera subhastata* (Nolcken): uncommon, June.
7307	*Mesoleuca ruficillata* (Guenée): rare, mid-June.
7312	*Spargania magnoliata* Guenée: uncommon, July - August.
7316	*Perizoma basaliata* (Walker): uncommon, July - August.
7329	*Anticlea vasiliata* Guenée: rare, mid May[1]
7368	*Xanthorhoe labradorensis* (Packard): uncommon, July.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

7388 *Xanthorhoe ferrugata* (Clerck): uncommon, June - July.
7390 *Xanthorhoe lacustrata* (Guenée): common, June - August.
7394 *Epirrhoe alternata* (Müller): uncommon, June, August.
7399a *Euphyia intermediata* (Guenée): uncommon, early July.
7414 *Orthonama obstipata* (Fabricius): uncommon, October.
7416 *Costaconvexa centrostrigaria* (Wollaston): uncommon, October.
7425 *Venusia cambrica* Curtis: rare, July.
7428 *Venusia comptaria* (Walker): uncommon, May.
7433a *Epirrita autumnata henshawi* (Swett): common, September.
7437a *Operophtera bruceata* (Hulst): uncommon most years, October.
7445 *Horisme intestinata* (Guenée): uncommon, early July.
7449 *Eupithecia palpata* Packard: uncommon, May.
7474 *Eupithecia miserulata* Grote: uncommon, September.
7492 *Eupithecia casloata* (Dyar): uncommon, June.
7520c *Eupithecia* near *satyrata dodata* Taylor: rare, June.
7543 *Eupithecia annulata* (Hulst): uncommon, May.
7605 *Eupithecia ravocostaliata* Packard: uncommon, May.
7635 *Acasis viridata* (Packard): rare, May.
7637 *Cladara limitaria* (Walker): common, April - June.
7639 *Cladara atroliturata* (Walker): common, April - May.
7640 *Lobophora nivigerata* Walker: common, May - early July.

FAMILY LASIOCAMPIDAE - tent caterpillar & lappet moths
7687 *Phyllodesma americana* (Harris): abundant, May - July.
7698 *Malacosoma disstria* Hübner: population outbreaks every 10-12 years with massive defoliation mainly of *Populus* spp., huge population in 2000-2003, late June - August.

FAMILY SATURNIIDAE - giant silkworm moths
7757 *Antheraea polyphemus* (Cramer): common - very common most years, mid June - early July.
7758 *Actias luna* (Lunnaeus): common - very common most years, late May - mid July.
7767 *Hyalophora cecropia* (Linnaeus): uncommon and apparently local, not collected but verifiable photos seen from May 2000.
7768 *Hyalophora columbia* (Smith): very local (black spruce bogs) and rare, early June; first published record from northeastern Minnesota.

FAMILY SPHINGIDAE - sphinx moths
7787 *Ceratomia undulosa* (Walker): common, June - mid July.
7809 *Sphinx kalmiae* J. E. Smith: common some years, June - early August.
7810 *Sphinx gordius* Cramer: very common, late May - early August.
7811 *Sphinx luscitiosa* Clemens: rare, early June.
7812 *Sphinx drupiferarum* J. E. Smith: rare, July.
7821 *Smerinthus jamaicensis* (Drury): very common, June, August.
7822 *Smerinthus cerisyi* Kirby: common - very common, late May - mid July.
7824 *Paonias excaecatus* (J. E. Smith): very common, mid June - early July.
7825 *Paonias myops* (J. E. Smith): uncommon, July.
7827 *Laothoe juglandis* (J. E. Smith): rare, early June.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

7828 *Pachysphinx modesta* (Harris): common - very common most years, late June - July.
7853 *Hemaris thysbe* (F.): uncommon, June.
7855 *Hemaris diffinis* (Boisduval): common most years, not observed in 2004 & 2005, June - July.
7873 *Amphion floridensis* B. P. Clark: uncommon, June.
7886 *Darapsa pholus* (Cramer): rare, August.
7894 *Hyles lineata* (Fabricius): common some years, late summer and early fall, August - September.

FAMILY NOTODONTIDAE - prominents
7895 *Clostera albosigma* Fitch: common, May - August.
7901 *Clostera apicalis* (Walker): rare, May.
7902 *Datana ministra* (Drury): uncommon, late July.
7915 *Nadata gibbosa* (J. E. Smith): very common, Late May - July.
7919 *Peridea basitriens* (Walker): rare, June.
7921 *Peridea ferruginea* (Packard): common, June - August.
7922 *Pheosia rimosa* Packard: common, June - August.
7924 *Odontosia elegans* (Strecker): uncommon, June - July.
7928 *Notodonta simplaria* Graef: common, May - August.
7929 *Nerice bidentata* Walker: uncommon early July.
7931 *Gluphisia septentrionis* Walker: common, May - mid July.
7933 *Gluphisia avimacula* Hudson: uncommon, late May.
7934 *Gluphisia lintneri* (Grote): rare, late April.
7939 *Furcula occidentalis* Lintner: uncommon, late May - mid June.
7941 *Furcula modesta* (Hudson): uncommon, late May - July.
7990 *Heterocampa umbrata* Walker: uncommon, late June - July.
7994 *Heterocampa guttivitta* (Walker): uncommon, June - July.
7995 *Heterocampa biundata* Walker: uncommon, late June - July.
8005 *Schizura ipomoeae* Doubleday: rare, July.
8011 *Schizura leptinoides* (Grote): common, late June - early August.

FAMILY ARCTIIDAE - tiger, lichen & wasp moths
8043 *Eilema bicolor* (Grote): rare, August.
8089 *Hypoprepia miniata* (Kirby): rare, July.
8090 *Hypoprepia fucosa* Hübner: uncommon, August - September.
8098 *Clemensia albata* Packard: local, uncommon, July-August.
8112 *Haploa confusa* (Lyman): common, June - July.
8114 *Holomelina laeta* (Guérin & Méneville): rare, July.
8121 *Holomelina aurantiaca* (Hübner): common, June, August.
8129 *Pyrrharctia isabella* (J. E. Smith): rare, June.
8134 *Spilosoma congrua* Walker: uncommon, late June - July.
8137 *Spilosoma virginica* (Fabricius): common, June - August.
8140 *Hyphantria cunea* (Drury): uncommon, adults June, larvae late July.
8158 *Phragmatobia assimilans* Walker: uncommon, June.
8162 *Platarctia parthenos* (Harris): common, late June, July.
8166a *Arctia caja americana* Harris: common some years, late summer and early fall.
8186 *Grammia williamsii* (Dodge): uncommon, mid July - August.
8196 *Grammia parthenice* (Kirby): common, July - early August.
8197 *Grammia virgo* (Linnaeus): common, mid July - August.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

8214 *Lophocampa maculata* Harris: very common, June - July.
8262 *Ctenucha virginica* (Esper): common, late June - mid July.

FAMILY LYMANTRIIDAE - tussock moths
8293 *Dasychira dorsipennata* (Barnes & McDunnough): uncommon, early August.
8305 *Dasychira pinicola* (Dyar): local, July.
8308a *Orgyia antiqua nova* Fitch: uncommon, September.
8316 *Orgyia leucostigma intermedia* Fitch: common, mid August - September.
8318 *Lymantria dispar* (Linnaeus): abundant based on MN DNR 2000 - 2005 annual pheromone trap records, but as of 2006 it occurred only locally on the Grand Portage Reservation in extreme northeastern Cook County.

FAMILY NOCTUIDAE - noctuids
8322 *Idia americalis* (Guenée): common, July - mid September.
8323 *Idia aemula* Hübner: rare, mid August.
8334 *Idia lubricalis* (Geyer): uncommon, August.
8338 *Phalaenophana pyramusalis* (Walker)[1]: rare, late June.
8341 *Zanclognatha theralis* (Walker): rare, July.
8351 *Zanclognatha cruralis* (Guenée): rare, June.
8352 *Zanclognatha jacchusalis* (Walker): uncommon, August.
8353 *Zanclognatha ochreipennis* (Grote): rare, July.
8356 *Chytolita petrealis* Grote: rare, July.
8357 *Macrochilo absorptalis* Walker: rare, July.
8365 *Phalaenostola hanhami* (J. B. Smith): rare, mid August.
8442 *Bomolocha baltimoralis* (Guenée): rare, late May.
8443 *Bomolocha bijugalis* (Walker): uncommon, June, August.
8452 *Bomolocha edictalis* (Walker): rare, early August.
8455 *Lomanaltes eductalis* (Walker): uncommon, June - July.
8461 *Hypena humuli* Harris: rare, mid May.
8465 *Plathypena scabra* (Fabricius): rare, September.
8479 *Spargaloma sexpunctata* Grote: uncommon, June - July.
8536 *Calyptra canadensis* (Bethune): uncommon, July - August.
8555 *Scoliopteryx libatrix* (Linnaeus): uncommon, June - July, September.
8689 *Zale lunata* (Drury): uncommon, late May - mid June.
8697 *Zale minerea* (Guenée): very common, late May - mid July.
8702 *Zale submediana* Strand: rare, mid June.
8727 *Parallelia bistriaris* Hübner: rare, mid July.
8738 *Caenurgina crassiuscula* (Haworth): uncommon, late July - August.
8739 *Caenurgina erechtea* (Cramer): uncommon, late August - September.
8803 *Catocala relicta* Walker: common some years, mid August - late September.
8805 *Catocala unijuga* Walker: common, late July - mid September.
8817 *Catocala briseis* Edwards: absent most years, common in 2005, adults fly later in the season than other *Catocala*, late September - October.
8821 *Catocala semirelicta* Grote: generally uncommon, late August - September.
8833 *Catocala concumbens* Walker: common most years, late August - September.
8857 *Catocala ultronia* (Hübner): common most years, mid August - mid September.
8867 *Catocala blandula* Hulst: uncommon, late July - mid September.
8887 *Trichoplusia ni* (Hübner): uncommon, mid September - early October.
8890 *Pseudoplusia includens* (Walker): uncommon, September.
8895 *Rachiplusia ou* (Guenée): rare, October.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

8896 *Diachrysia aereoides* (Grote): uncommon, mid July - August.
8897 *Diachrysia balluca* Geyer: uncommon, late July - August.
8907 *Megalographa biloba* (Stephens): uncommon, June-July.
8908 *Autographa precationis* (Guenée): uncommon, late August - September.
8911 *Autographa bimaculata* (Stephens): uncommon, late July - August.
8923 *Autographa ampla* (Walker): uncommon, June, August.
8924 *Anagrapha falcifera* (Kirby): uncommon, late May, July, August.
8926 *Syngrapha octoscripta* (Grote): uncommon, late July - August.
8928 *Syngrapha selecta* (Walker): uncommon, July - August.
8929 *Syngrapha viridisigma* Grote: uncommon, August.
8942 *Syngrapha rectangula* (Kirby): uncommon, July, September.
8950 *Plusia putnami* Grote[2]: rare, late June.
8952 *Plusia contexta* Grote: uncommon, July.
8969 *Baileya doubledayi* (Guenée): rare, July.
8971 *Baileya dormitans* (Guenée): rare, June.
8975 *Nycteola frigidana* (Walker): rare, September.
8977 *Nycteola cinereana* Neumoegen & Dyar: rare, August.
9047 *Lithacodia muscosula* (Guenée): rare, July.
9048 *Lithacodia albidula* (Guenée): uncommon, June - July.
9050 *Lithacodia concinnimacula* (Guenée)[1]: rare, late June.
9177 *Panthea acronyctoides* (Walker): uncommon, late May - mid July.
9183 *Panthea pallescens* McDunnough: rare, early July.
9184 *Colocasia flavicornis* (J. B. Smith): uncommon, late May - June.
9189 *Charadra deridens* (Guenée): common, mid June - July.
9193 *Raphia frater* Grote: very common, late May - early August.
9200 *Acronicta americana* (Harris): very common, Mid June - July.
9203 *Acronicta dactylina* Grote: uncommon, late June, August, October.
9205 *Acronicta lepusculina* Guenée: rare, June.
9207 *Acronicta innotata* Guenée: common, mid June - early August.
9209 *Acronicta radcliffei* (Harvey): rare, late July.
9212 *Acronicta grisea* Walker: very common, mid June - July.
9221 *Acronicta funeralis* Grote & Robinson: rare, mid June.
9226 *Acronicta superans* Guenée: common, late May - mid August.
9229 *Acronicta hasta* Guenée: uncommon, late May - mid June.
9237 *Acronicta interrupta* Guenée: rare, late May.
9241 *Acronicta fragilis* (Guenée): common, mid June early July.
9259 *Acronicta noctivaga* Grote: uncommon, June.
9261 *Acronicta impressa* Walker: common, June.
9280 *Simyra henrici* (Grote): uncommon, August.
9286 *Harrisimemna trisignata* (Walker): uncommon, June.
9318 *Alypia langtoni* Couper: rare, late June.
9326 *Apamea verbascoides* (Guenée): uncommon, July - mid August.
9333 *Apamea lignicolora* Guenée: rare, early August.
9348 *Apamea amputatrix* (Fitch): rare, mid August.
9359 *Apamea commoda* (Walker): rare, early July.
9360 *Apamea impulsa* (Guenée): uncommon, July - early August.
9364 *Apamea sordens* (Hufnagel): rare, late June.
9364.1 *Apamea ophiogramma* (Esper): uncommon, July.
9365 *Apamea lateritia* (Hufnagel): rare, June.
9367 *Apamea dubitans* (Walker): common, late July - early September.

Table 2. Continued.

Family **Hodges number, species, relative abundance, and seasonal distribution**	
9367.1	*Apamea cogitata* (J. B. Smith): rare, early July.
9382	*Apamea devastator* (Brace): common, August.
9396	*Eremobina claudens* (Walker): uncommon, September.
9415	*Oligia bridghami* (Grote & Robinson): rare, September.
9420	*Oligia illocata* (Walker): common, mid August - mid September.
9431	*Parastichtis suspecta* (Hübner): rare, late August.
9433	*Xylomoia chagnoni* Barnes & McDunnough: rare, mid July.
9437	*Chortodes inquinata* (Guenée): rare, late July.
9452	*Macronoctua onusta* Grote: rare, early September.
9453	*Celaena reniformis* (Grote): uncommon, August - September.
9454	*Amphipoea velata* (Walker): uncommon, late July - early September.
9456	*Amphipoea interoceanica* (J. B. Smith): uncommon, September.
9457	*Amphipoea americana* (Speyer): uncommon, late July, September.
9478	*Papaipema leucostigma* (Harris): common, September.
9480	*Papaipema pterisii* Bird: common, September.
9483	*Papaipema inquaesita* (Grote & Robinson): common, September.
9501	*Papaipema eupatorii* (Lyman): uncommon, September.
9509	*Papaipema unimoda* (J. B. Smith): common, late August - mid September.
9514	*Hydraecia micacea* (Esper): rare, mid September.
9523	*Bellura gortynoides* Walker: uncommon, June - early July.
9525	*Bellura obliqua* (Walker): common, late June - July.
9545	*Euplexia benesimilis* McDunnough: uncommon, mid June - mid July.
9546	*Phlogophora iris* Guenée: common, mid June - July.
9547	*Phlogophora periculosa* Guenée: common, late July - August.
9549	*Enargia decolor* (Walker): common, mid August - mid September.
9550	*Enargia infumata* (Grote): common, September.
9555	*Ipimorpha pleonectusa* Grote[1]: rare August.
9556	*Chytonix palliatricula* (Guenée): uncommon, mid June - July.
9564	*Andropolia contacta* (Walker): uncommon, August - early September.
9578	*Hyppa xylinoides* (Guenée): common, June, August, September.
9633	*Callopistria cordata* (Ljungh): rare, mid August.
9638	*Amphipyra pyramidoides* Guenée: rare, September.
9649	*Athetis mendosa* (McDunnough): uncommon, July - early August.
9666	*Spodoptera frugiperda* (J. E. Smith): uncommon, early October.
9688	*Galgula partita* Guenée: rare, June.
9696	*Condica vecors* (Guenée): rare, June.
9873	*Xylena nupera* (Lintner): uncommon, late April - May.
9874	*Xylena curvimacula* (Morrison): uncommon, mid April - May.
9876	*Xylena cineritia* (Grote): rare, late April.
9878	*Lithomoia germana* (Morrison): common, late August - mid September.
9881	*Homoglaea hircina* (Morrison): rare, late April.
9884	*Litholomia napaea* (Morrison): common, May, September.
9891	*Lithophane amanda* (J. B. Smith): rare, late September.
9892	*Lithophane disposita* Morrison: rare, early September.
9910	*Lithophane antennata* (Walker): uncommon, late April - May.
9916	*Lithophane unimoda* (Lintner): rare, mid April.
9917	*Lithophane fagina* Morrison: uncommon, late April, September.
9922	*Lithophane pexata* Grote: uncommon, late April, June, September - October.
9928	*Lithophane thaxteri* Grote: rare, late April.
9936	*Eupsilia morrisoni* Grote: uncommon, April.

Table 2. Continued.

Family
Hodges number, species, relative abundance, and seasonal distribution

9946 *Epiglaea decliva* (Grote)[1]: uncommon, August - September.
9947 *Epiglaea apiata* (Grote)[1]: rare, mid September.
9952 *Eucirroedia pampina* (Guenée): rare, early September.
9957 *Sunira bicolorago* (Guenée): uncommon, September.
9962 *Anathix puta* (Grote & Robinson): rare, late August.
9965 *Xanthia* sp. near *togata* (Esper): uncommon, late August - early October.
9967 *Hillia iris* (Zetterstedt): uncommon, early September.
9974 *Fishia enthea* Grote: uncommon, early September.
9989 *Sutyna privata* (Walker): uncommon, mid September.
9992 *Pachypolia atricornis* Grote: common, September.
10005 *Feralia jocosa* (Guenée): rare, mid April.
10008 *Feralia comstocki* (Grote): common some years, May.
10011 *Brachionycha borealis* (J. B. Smith): rare, late April.
10021 *Copivaleria grotei* (Morrison): uncommon, May.
10199 *Cucullia omissa* Dod: rare, mid August.
10223 *Discestra trifolii* (Hufnagel): rare, mid July.
10275 *Polia nimbosa* (Guenée): very common, late June - early August.
10276 *Polia imbifera* (Guenée): very common, late June - early August.
10280 *Polia purpurissata* (Grote): common, early July - early August.
10288 *Polia detracta* (Walker): rare, late June.
10292 *Melanchra adjuncta* (Guenée): uncommon, June - early July.
10295 *Melanchra assimilis* (Morrison) rare, early-mid July.
10300 *Spirameter grandis* (Guenée): common, mid June - July.
10303 *Trichordestra tacoma* (Strecker): uncommon, early June.
10370 *Lacinipolia lustralis* (Grote): uncommon, early July.
10397 *Lacinipolia renigera* (Stephens): common, July - early August.
10405 *Lacinipolia lorea* (Guenée): common, late June - early July.
10406 *Lacinipolia olivacea* (Morrison): common, August - early September.
10436 *Aletia oxygala* (Grote): common, late July - August.
10438 *Pseudaletia unipuncta* (Haworth): very common, mid May, June, August - mid October.
10444 *Leucania phragmatidicola* Guenée: uncommon, late July - August.
10446 *Leucania multilinea* Walker: rare, mid July.
10447 *Leucania commoides* Guenée: rare, late July.
10462 *Leucania pseudargyria* Guenée: uncommon, July - early August.
10471 *Stretchia plusiaeformis* Hy. Edwards: uncommon, April.
10490 *Orthosia revicta* (Morrison): uncommon, May - early June.
10495 *Orthosia hibisci* (Guenée): rare, early May.
10513 *Egira dolosa* (Grote): uncommon, late May.
10521.1 *Morrisonia latex* (Guenée): uncommon, late may - June.
10524 *Nephelodes minians* Guenée: very common most years, August - mid September.
10563 *Protorthodes oviduca* (Guenée): uncommon, June.
10585 *Orthodes crenulata* (Butler): fairly common, mid July - early August.
10587 *Orthodes cynica* Guenée: uncommon, late June - mid August.
10589.1 *Orthodes goodelli* (Grote): uncommon, June - early July.
10641 *Agrotis vetusta* Walker: common, August - early September.
10651 *Agrotis venerabilis* Walker: common, late August - mid September.
10663 *Agrotis ipsilon* (Hufnagel): uncommon, early August - mid September.
10670 *Feltia jaculifera* (Guenée): uncommon, late August.
10674 *Feltia subgothica* (Haworth): common, late July - August.

Table 2. Continued.

Family

Hodges number, species, relative abundance, and seasonal distribution

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10676 *Feltia herilis* (Grote)[2]: rare, late August.
10705 *Euxoa messoria* (Harr.): rare, early September.
10738 *Euxoa mimallonis* (Grote): rare, late August.
10780 *Euxoa comosa altera* McDunnough: rare, mid August.
Euxoa comosa ontario (Smith): rare, late July.
10801 *Euxoa ochrogaster* (Guenée): uncommon, September.
10803 *Euxoa velleripennis* (Grote): rare, early July.
10805 *Euxoa tessellata* (Harris): uncommon, July - early August.
10891 *Ochropleura implecta* Lafontaine: rare, late August.
10915 *Peridroma saucia* (Hübner)[2]: rare, mid July.
10917 *Diarsia rubifera* (Grote): rare, late June.
10921 *Diarsia rosaria* (Grote): uncommon early July.
10926 *Spaelotis clandestina* (Harris): uncommon, September.
10928 *Graphiphora augur* (Fabricius): common, late July - August.
10929 *Eurois occulta* (Linnaeus): rare, late August.
10930 *Eurois astricta* Morrison: common, mid July – August.
10942 *Xestia c-nigrum* (Linnaeus): common, early July- August.
10943 *Xestia normaniana* (Grote): common, August - early September.
10944 *Xestia smithii* (Snellen): very common, mid August - early September.
10947 *Xestia oblata* (Morrison) uncommon, early-mid July[1].
10968 *Xestia badicollis* (Grote): uncommon, late June - July.
10988 *Coenophila opacifrons* (Grote)[1]: local, uncommon, mid August.
10988.5 *Pseudohermonassa bicarnea* (Guenée): uncommon, late July.
10988.6 *Pseudohermonassa tenuicula* (Morrison): rare, early August.
10992 *Paradiarsia littoralis* (Packard): uncommon, late June.
10996 *Cerastis salicarum* (Walker): uncommon, late April - mid May.
10999 *Aplectoides condita* (Guenée): common, mid June, early September.
11000 *Anaplectoides prasina* (Denis & Schiffermüller): uncommon, July - August.
11001 *Anaplectoides pressus* (Grote): common, late June - July.
11004 *Protolampra rufipectus* (Morrison): uncommon, July - early August.
11007 *Eueretagrotis sigmoides* (Guenée): rare, mid July.
11008 *Eueretagrotis perattenta* (Grote): common, mid June - July.
11009 *Eueretagrotis attenta* (Grote): uncommon, July.
11010 *Lycophotia phyllophora* (Grote): rare, early July.
11012 *Cryptocala acadiensis* (Bethune): common, early July - early August.
11012.1 *Noctua pronuba* (Linnaeus): introduced species first collected locally in 2002, common, early August - mid September.
11029 *Abagrotis alternata* (Grote): uncommon, early August - mid September.
11043 *Abagrotis cupida* (Grote): common, mid August - mid September.
11051 *Ufeus satyricus* Grote: common, September - early October.
11064 *Pyrrhia exprimens* (Walker): uncommon, late June - late July.
11068 *Helicoverpa zea* (Boddie): common most years, early September - mid October.

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[1] Specimens are held in the insect collection of the Grand Portage Monument, United States Park Service, Grand Portage MN.

[2] Specimens are held in the invertebrate collection of the Environmental Division, Grand Portage Band, Grand Portage MN.

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VARIATION IN DIEL ACTIVITY OF GROUND BEETLES (COLEOPTERA: CARABIDAE) ASSOCIATED WITH A SOYBEAN FIELD AND COAL MINE REMNANT

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ABSTRACT

Diel activities of carabids (Coleoptera: Carabidae) associated with a coal mine remnant and surrounding soybean field were studied in west-central Illinois from June through October 2002. A total of 1,402 carabids, representing 29 species and 17 genera, were collected using pitfall traps. *Poecilus chalcites* (Say) demonstrated roughly equal diurnal and nocturnal activity in June, but greater diurnal activity thereafter. *Pterostichus permundus* (Say), *Cyclotrachelus seximpressus* (LeConte), *Amara obesa* (Say), and *Scarites quadriceps* Chaudoir showed significant nocturnal activity. Associations between habitat and diel activity were found for three species: *P. chalcites* associated with the remnant and edge habitats showed greater diurnal activity than those associated with the soybean field; *C. seximpressus* was most active diurnally in the remnant, and *Harpalus pensylvanicus* (DeGeer) showed the greatest nocturnal activity in the remnant and edge habitats. We found significant temporal and habitat-related variation in diel activity among carabid species inhabiting agricultural areas in west-central Illinois.

INTRODUCTION

The ground beetles and tiger beetles (Coleoptera: Carabidae) constitute one of the most diverse insect families, with over 40,000 described species (Lövei and Sunderland 1996). Carabids are important predators in many terrestrial ecosystems, and can help suppress pest insect populations in agroecosystems (Cárcamo and Spence 1994, Thomas et al. 1998, Carmona and Landis 1999, Crist and Ahern 1999, Landis et al. 2000, French et al. 2004). Because carabids are often closely associated with factors such as soil type, vegetation cover and microclimate, they can also be useful indicators of habitat conditions (Thiele 1977, Niemelä et al. 1992, Ings and Hartley 1999, Villa-Castillo and Wagner 2002, McCravy and Willand 2005). Microhabitat conditions and diel activity patterns may play a role in interspecific segregation and species richness, at least in tropical tiger beetles (Zerm and Adis 2001). In the Midwestern United States, the landscape is dominated by a mosaic of agricultural lands interspersed with patches of alternative habitats. In west-central Illinois, coal mine remnants (hereafter referred to as "remnants") are one source of alternative habitat. These remnants are the remains of shaft mines that flourished during the late 1800s and early 1900s, but were abandoned and filled by 1960 (Monteith 1976, Hallwas 1984, Murray 1998). Secondary succession produced a diversity of herbaceous and woody vegetation, resulting in habitat "islands" within agricultural fields. These remnants are inhabited by over 40 carabid species that represent an assemblage distinct from that of the surrounding soybean fields (McCravy and Willand 2005). These remnants, therefore, provide an opportunity to study the diel activity of a diverse assemblage of carabids in

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field, edge, and wooded habitats. The objective of this study was to investigate potential habitat-related and temporal variation in diel activity patterns of a carabid assemblage.

METHODS AND MATERIALS

The study was conducted on a remnant and surrounding soybean field near Colchester, Illinois from June through October 2002. The remnant was located at N 40° 25' 21" W 90° 49' 6". Remnant dimensions were as follows: circumference - 237 m, maximum length - 78 m, maximum width - 27 m and maximum canopy height - 17 m. Remnant vegetation was composed primarily of black cherry (*Prunus serotina* Ehrhart), slippery elm (*Ulmus rubra* Muhl.), honeylocust (*Gleditsia triacanthos* L.), bramble (*Rubus* spp.), poison ivy [*Toxicodendron radicans* (L.) Kuntze], and grasses. All plant nomenclature follows that of Gleason and Cronquist (1991). Mean percent ground cover (± SE) in the remnant, as measured by visual estimation in 20 0.5-m^2 plots, was 61.8 ± 6.3%. Mean percent canopy cover (± SE) in the remnant, measured at 20 sample points with a vertical densitometer (Geographic Resource Solutions, Arcada, CA), was 39.0 ± 7.5%. Soybeans (*Glycine max* (L.) Merr.) were planted in the surrounding fields in early June.

Pitfall traps were used to capture carabids. Each trap consisted of two 473 ml plastic cups (Solo®, Urbana, IL) one nested inside the other so that the inner cup could be removed during collections and replaced with a fresh one with minimal disturbance to the trap site. The diameter of the cup opening was 9.3 cm. Traps were placed so the trap rim was flush with the ground, and efforts were made to return surrounding soil and litter to former conditions. Thirty-six traps were used, as follows: 20 in the remnant, 8 in the soybean field, and 8 along the edge of the remnant. The remnant and field traps were deployed in a line through the coal mine remnant and extending 20 m into the soybean field on each end. Traps were placed 4 m apart within the remnant and 5 m apart in the soybean field. The edge traps were placed 30 m apart along the edge of the remnant at the remnant/field interface. Traps were filled with approximately 150 ml of a 50/50 mixture of propylene glycol and water, which acted as a killing agent and preservative. Traps were operated continuously for one 6-day period each month (20-25 June, 14-19 July, 19-24 August, 22-27 September and 13-18 October). Traps were set at dusk of the first day of each trapping period, and were serviced and replaced each day at dawn to collect nocturnally active carabids and at dusk to collect diurnally active carabids. The last collection for each trapping period was at dusk of the last day.

Associations between carabid captures and time of capture (diurnal vs. nocturnal) were analyzed using the single classification chi-square test, with expected frequencies based on the extrinsic hypothesis of a 50:50 ratio of diurnal and nocturnal captures. The more conservative continuity correction was used for species that produced between 25 and 200 total captures. For species with sample sizes between 10 and 25, the exact probabilities of the expected binomial distribution (two-tailed) were used (Sokal and Rohlf 1995). Associations between captures and time of capture were not analyzed for species that produced less than 10 captures. Associations of time of capture (diurnal vs. nocturnal) with month, habitat, and beetle sex were analyzed using two-way contingency tables and the chi-square test. The level of statistical significance was set at $P = 0.05$ for all tests.

RESULTS

A total of 1,402 carabids representing 29 species and 17 genera were collected (Table 1). The three most abundant species [*Poecilus chalcites* (Say), *Pterostichus permundus* (Say), and *Cyclotrachelus seximpressus* (LeConte)] comprised 85.4% of the total. Overall, carabids showed more diurnal activity than expected by chance ($\chi^2 = 53.54$, df = 1, $P < 0.001$), due primarily to the predominantly diurnal activity of *P. chalcites*. When *P. chalcites* was excluded from analysis, the remaining carabids showed more nocturnal activity than expected by chance ($\chi^2 = 49.38$, df = 1, $P < 0.001$). Sample sizes were sufficiently large to allow statistical analyses of associations between sex and time of capture for the five most commonly collected species. Only *P. chalcites* showed a statistically significant association; 79.7% of male vs. 73.4% of female captures were diurnal ($\chi^2 = 4.49$, df = 1, $P = 0.034$).

About 93% of *P. chalcites* were captured in the soybean field (Table 1). This species showed more diurnal activity than expected by chance ($\chi^2 = 229.38$, df = 1, $P < 0.001$). There was a significant association between *P. chalcites* activity patterns and month of collection ($\chi^2 = 151.46$, df = 4, $P < 0.001$). Nocturnal and diurnal activity were roughly equal in June, whereas activity was predominantly diurnal during the remaining months (Fig. 1). There was also a significant association between *P. chalcites* activity and habitat ($\chi^2 = 8.69$, df = 2, $P = 0.013$). In the remnant and edge, 87.5% and 94.3% of *P. chalcites* were captured diurnally, whereas only 74.9% were trapped diurnally in the soybean field (Fig. 2). When *P. chalcites* was excluded from analysis, there was a significant association between time of capture and habitat for all other carabids combined ($\chi^2 = 9.229$, df = 2, $P = 0.010$). Among these carabids, 41.6% of those captured in the remnant were diurnal, whereas 27.0% and 32.7% of those captured in the edge and field, respectively, were diurnal.

Of the remaining species producing greater than ten captures, four species showed significant nocturnal activity (Table 1): *P. permundus* ($\chi^2 = 13.41$, df = 1, $P < 0.001$), *C. seximpressus* ($\chi^2 = 20.31$, df = 1, $P < 0.001$), *Amara obesa* (Say) ($\chi^2 = 15.75$, df = 1, $P < 0.001$), and *Scarites quadriceps* Chaudoir ($P < 0.001$, two-tailed binomial probability). A significant association between time of capture and habitat was found for *C. seximpressus* ($\chi^2 = 18.38$; df = 2; $P < 0.001$), with 51.6% of captures being diurnal in the remnant, but only 21.7% and 17.3% being diurnal in the edge and field habitats, respectively (Fig. 2). No association between time of capture and habitat was found for *P. permundus* ($\chi^2 = 4.06$, df = 2, $P > 0.05$; Fig. 2). Small expected values for contingency table cells precluded statistical testing for *A. obesa* and *S. quadriceps*.

Neither *Harpalus compar* LeConte ($\chi^2 = 1.64$, df = 1, $P > 0.05$), *Harpalus pensylvanicus* (DeGeer) ($\chi^2 = 0.43$, df = 1, $P > 0.05$), *Cyclotrachelus sodalis sodalis* (LeConte) ($P > 0.05$, two-tailed binomial probability), nor *Patrobus longicornis* (Say) ($P > 0.05$, two-tailed binomial probability) showed statistically significant diel activity patterns overall (Table 1). Contingency table cell sample sizes allowed testing for an association between time of capture and habitat for *H. pensylvanicus*, which was significant ($\chi^2 = 12.45$, df = 2, $P = 0.002$). Interior and edge habitats produced only 10.0% and 30.8% diurnal captures, respectively whereas the field produced 78.6% diurnal captures (Fig. 2).

DISCUSSION

Most carabid species showed primarily nocturnal activity in our study (Table 1). These findings are consistent with those of other studies (Luff 1978, Lövei and Sunderland 1996). In the United Kingdom, 60% of species are nocturnal and 20% are diurnal (Luff 1978). In our study, 4 of 5 species showing statistically significant activity patterns were nocturnal, with only *P. chalcites* having significant diurnal activity (Table 1). Larochelle and Larivière (2003) describe *P. chalcites* as mostly nocturnal, and Ellsbury et al. (2005) found *P. chalcites* to be most active around midnight in the northern corn belt of the midwestern United States. However, our results suggest that the behavior of this species includes a strong diurnal component that can vary significantly both seasonally and in relation to habitat (Figs. 1 and 2). Nocturnal activity of

Table 1. Number of carabid beetles captured in pitfall traps in three habitats [coal mine remnant (20 traps), field edge (8 traps), and soybean field (8 traps)] in west-central Illinois during June-October 2002, percent of beetles that were diurnal (captured during dawn to dusk), and for species where more than 10 individuals were captured, the results of chi-square analyses (two-tailed binomial for *C. sodalis sodalis*, *P. longicornis*, and *S. quadriceps*). Analyses were based on the extrinsic hypothesis of a 50:50 ratio diurnal to nocturnal capture rate.

Species	**Remnant**	**Edge**	**Field**	**% Diurnal**	***P*-values**
Poecilus chalcites (Say)	24	35	785	76.1%	< 0.001
Pterostichus permundus (Say)	96	33	65	36.6%	< 0.001
Cyclotrachelus seximpressus (LeConte)	62	46	52	31.9%	< 0.001
Harpalus compar LeConte	14	24	1	38.5%	> 0.05
Harpalus pensylvanicus (DeGeer)	10	13	14	43.2%	> 0.05
Amara obesa (Say)	10	18	0	10.7%	< 0.001
Cyclotrachelus sodalis sodalis (LeConte)	9	4	2	46.7%	> 0.05
Patrobus longicornis (Say)	4	0	8	33.3%	> 0.05
Scarites quadriceps Chaudoir	0	1	10	0.0%	< 0.001
Anisodactylus caenus (Say)	9	0	0	22.2%	
Amphasia sericea (T.W. Harris)	6	0	2	75.0%	
Calathus opaculus LeConte	8	0	0	50.0%	
Anisodactylus ovularis (Casey)	1	2	3	83.3%	
Clivina bipustulata (Fabricius)	3	0	2	20.0%	
Cicindela punctulata Olivier	0	2	3	100.0%	
Anisodactylus carbonarius (Say)	2	1	0	0.0%	
Harpalus caliginosus (Fabricius)	1	2	0	33.3%	
Harpalus protractus Casey	2	1	0	33.3%	
Chlaenius emarginatus Say	1	1	0	0.0%	
Agonum punctiforme (Say)	0	0	1	0.0%	
Amara littoralis Mannerheim	1	0	0	100.0%	
Anisodactylus agricola (Say)	1	0	0	0.0%	
Anisodactylus furvus LeConte	1	0	0	0.0%	
Clivina impressefrons LeConte	0	0	1	100.0%	
Dicaelus elongatus Bonelli	1	0	0	0.0%	
Galerita janus (Fabricius)	1	0	0	100.0%	
Lebia analis Dejean	1	0	0	0.0%	
Poecilus lucublandus (Say)	0	0	1	0.0%	
Pterostichus praetermissus Chaudoir	1	0	0	100.0%	
TOTAL	269	183	950	59.8%	

P. chalcites was greatest in June. This pattern could be related to density of canopy cover. In June the soybeans were recently planted and provided little cover and concealment for the carabids. By July, the soybeans provided denser cover. Honek (1988) and Carmona and Landis (1999) suggested that carabid abundance increased under dense crop cover due to increased humidity and prey availability. Carmona and Landis (1999) also found that cover crops helped to decrease predation upon carabids by providing shelter. Activity peaks of carabids can vary depending on the agroecosystem (Ellsburg et al. 2005). The increase in diurnal activity after June in our study could reflect some combination of more favorable daytime microclimate, increased prey availability, and increased protection from diurnal visual predators such as birds. Catbirds, crows, kingbirds, starlings, thrushes, and woodpeckers are known predators of *P. chalcites* (Larochelle and Larivière 2003). Lower night temperatures in

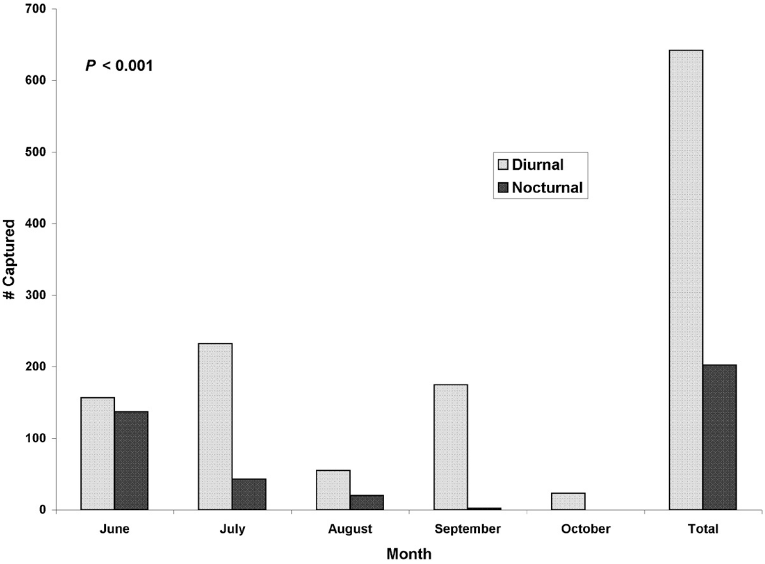

Figure 1. Diel activity of *Poecilus chalcites* (N = 844 individuals) captured in pitfall traps in three habitats [coal mine remnant (20 traps), field edge (8 traps), and soybean field (8 traps)] in west-central Illinois by month in 2002: diurnal = collected during dawn to dusk, nocturnal = collected during dusk to dawn.

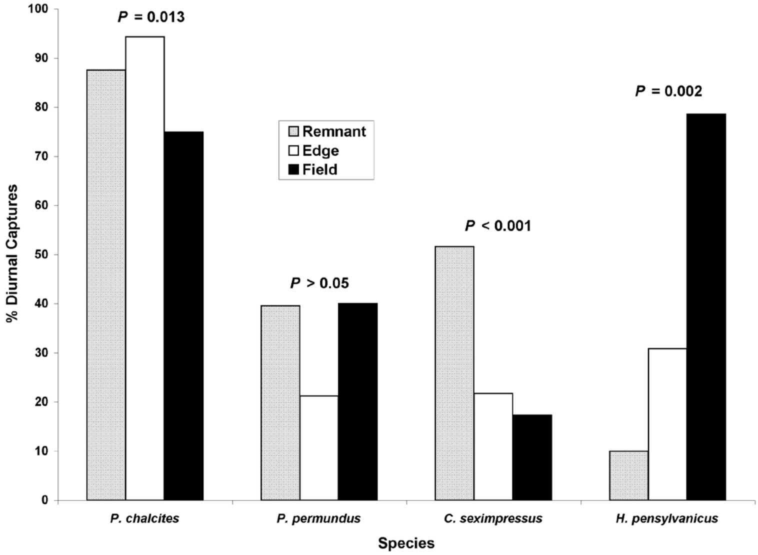

Figure 2. Diurnal activity (i.e., collected during dawn to dusk) of four species of carabid beetles by habitat (coal mine remnant, field edge, and soybean field) in west-central Illinois in 2002 based on captures in pitfall traps: *Poecilus chalcites* (N = 844 individuals), *Pterostichus permundus* (N = 194), *Cyclotrachelus seximpressus* (N = 160), and *Harpalus pensylvanicus* (N = 37).

September and October may have limited nocturnal activity during those collection periods compared with earlier months. Mean minimum daily temperatures (in °C ± SE, based on climatic data obtained from the La Harpe, IL weather station, ca. 25 km NW of the study site) for the trapping periods were 18.8 ± 0.6 in June, 16.8 ± 1.1 in July, 17.4 ± 1.2 in August, 4.4 ± 1.2 in September, and -1.0 ± 0.5 in October. Seasonal changes in diel activity have also been found in *Pterostichus melanarius* (Illiger), which tends to be nocturnal in June and July, but more diurnal in August (Desender et al. 1985).

Poecilus chalcites is a relatively small, dark green, iridescent beetle, and is strongly associated with agricultural fields at our study location (Table 1; McCravy and Willand 2005). Kegel (1990) found that diurnal carabids tend to be small and iridescent, whereas nocturnal species tend to be large and dull black. The four species that showed significant nocturnal activity in our study (*P. permundus*, *C. seximpressus*, *A. obesa*, and *S. quadriceps*) are all larger, dull black carabids. Kegel (1990) and Greenslade (1963) also found that forest carabids are generally nocturnal and field or grassland species diurnal. Excluding *P. chalcites*, carabids in our study tended to be more diurnal in the remnant overall. Of the three species in our study that had statistically significant associations between diel activity and habitat (Fig. 2), only *H. pensylvanicus* showed more nocturnal activity in the remnant than in the field. It may be that the relatively young age and open canopy of the remnant (mean percent canopy cover (± SE) = 39.0 ± 7.5) did not produce environmental conditions conducive to nocturnal activity for most species.

Carabid species of west-central Illinois coal mine remnants can vary substantially in diel activity patterns, and this variation is, to an extent, associated with season and habitat. This variation could result in species-specific responses to habitat and agroecosytem management practices, and these responses may vary temporally. Knowledge of these patterns is important in understanding the ecology and pest management roles of these beetles.

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COMPENSATORY FEEDING AND GROWTH RESPONSES OF *PAPILIO GLAUCUS* (LEPIDOPTERA: PAPILIONIDAE) LARVAE REARED IN DARKNESS.

Jennifer Muehlhaus[1,2] and J. Mark Scriber[1,3]

ABSTRACT

The goal was to determine the potential impact of photoperiod on feeding behavior and larval growth rates. Larvae from six different families of the eastern swallowtail butterfly, *Papilio glaucus* L. (Lepidoptera: Papilionidae) were placed into 3 different photoperiod regimes (long days at 18:6 h, short days at 12:12 h, and total darkness at 0:24 h, all at 27°C) as neonate first instars and reared to pupation. The initial 11 days reflected very slow growth of the larvae in darkness (only half the weight of the long day larvae). No differences in survival at 4 days or 11 days or until pupation were evident between any treatments. Average time to pupation (= total larval duration) was statistically identical between the treatments. However, despite their slow start during the first two instars, the larvae in complete darkness were able to increase their growth rates in the final 3 instars to such magnitude that they grew to the same final pupal size as those in the long day (and bigger than those in the short day) treatments. Such compensatory feeding and growth as a result of photoperiod has not previously been reported. Potential additional causes for such behavioral/physiological compensatory growth rates in caterpillars of other species are discussed.

INTRODUCTION

The importance of getting off to a good start can not be overemphasized with regard to subsequent success for neonate larvae of insects in general, in particular for Lepidoptera (Zalucki et al. 2002). Sometimes this can be facilitated by the butterfly mother producing larger eggs [as in Alaskan *Papilio canadensis* R & J (Lepidoptera: Papilionidae); Ayres and Scriber 1994], and placement of the eggs on the most nutritious of locally-available host plant species (especially where thermal constraints may exist; Scriber and Lederhouse 1992; Scriber 1996, 2002a; Mercader and Scriber 2005), or on young plant parts (Scriber and Slansky 1981; Scriber 1984a).

Sometimes it is also possible for the larvae themselves to "compensate" during later instar feeding for the slow initial growth during early instars. Such compensatory feeding behavior in insect larvae has been described for armyworms, *Spodoptera eridania* Stoll (Lepidoptera: Noctuidae), on hosts of low nutritional value (e.g., low nitrogen; Mattson 1980, Scriber 1984b, Slansky and Scriber 1985, Slansky 1993), low minerals or trace elements (Mattson and Scriber 1987, Fageria and Scriber 2001), or high cellulose/fiber (Peterson et al 1988, Wheeler and Slansky1991). In addition, high allelochemical concentrations as in alfalfa (Scriber 1979, Kingsley et al. 1983), corn (Scriber 1984a, Manuwoto and Scriber 1985) and other plants (Scriber 1978) result in compensatory feeding by the southern armyworm, *S. eridania,* but such feeding compensation is not always seen for butterflies or moths (Scriber and Feeny 1979).

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Another type of stress that resulted in feeding compensation in neonate larvae of *P. canadensis* was described by Tesar and Scriber (2003). Larvae that had been exposed as eggs to cold stress (-8°C) for the longer periods (48 hours, 24 hours, 8 hours) had significantly faster neonate growth rates (0.29, 0.27, 0.24 mg/ mg.d, respectively).

Here we wanted to see the impact of darkness compared to short day 12:12 hour and long day 18:6 hour photoperiods on larval feeding behavior and growth rates of *P. glaucus* at a constant temperature of 27°C. Photoperiod effects on larval growth rates are almost unknown for insects (Slansky and Scriber 1985), and to our knowledge, nothing is known about effects on *Papilio* species. Some evidence exists suggesting that the longer photoperiod favors faster growth rates in hymenopteran sawflies, *Neodiprion swainei* Middleton (Hymenoptera: Tenthredinidae) (Philogéne and Benjamin 1971) and in banded woolly-bear caterpillars [*Pyrrharctia isabella* (J.E. Smith) (Arctiidae); Goettle and Philogéne 1978], and increased duration of *Pieris rapae* L. (Lepidoptera: Pieridae) caterpillars is potentially related to decreased ultraviolet light intensity (Thoms and Philogéne 1979).

Experimentally-restricted consumption rates have been shown to have significant impacts on the consumption and food processing efficiencies of other Lepidoptera larvae, which in turn affected growth rates (Grabstein and Scriber 1982, Tammaru et al. 2004). We therefore evaluated the potential of longer dark phases to constrain feeding behavior and to see whether non-genetic behavioral/physiological plasticity existed for these *Papilio glaucus* L. (Lepidoptera: Papilionidae) larvae.

METHODS

Field-captured females of *P. glaucus* from Nelson Co. Virginia and Clarke Co. Georgia were express-mailed to the laboratory at Michigan State University and set up in oviposition arenas to obtain offspring. Egg counts and removal as well as adult feeding with 15% honey water solution were made daily (see Scriber 1993 for details). Eggs were held at 27°C and newly hatched neonate larvae (within 1-6 hours of eclosion) were transferred using camel hair brushes to host plant leaves [tulip tree, *Liriodendron tulipifera* L. (Magnoliaceae)] and randomly allocated individually into clear plastic rearing dishes 150 mm diameter × 20 mm height. The petioles of tulip tree leaves were supported in a water-filled plastic vial with rubber cap to maintain turgor (Scriber 1977). Equal numbers of larvae (n = 8) from each of six families (= maternal lines) were allocated to Percival Growth Chambers set at 3 photoperiod treatments (18:6, 12:12, or 0:24 = light:dark; all were held at 27°C throughout the rearing period).

Initial larval weights for each family were determined by weighing groups of 4 larvae at a time (since they were so small) on a Mettler Analytical Balance (Model H80). Larvae were reared initially as neonates in groups of 4 per dish but individuals were transferred to separate dishes after a few days to avoid potential competition. Each 2 days, leaves were changed, feces were removed, and filter paper bottom liners were replaced. Weights of individuals were taken at 4 days and again at 11 days (approximately at the time when the second or third instar was completed), and at the pupal stage (3 days after pre-pupal formation). Statistical differences between treatment means (mean of families) were determined using t-tests. We did not test for family effects because the replicates were variable and low (or zero) for some indices.

RESULTS

The survival of neonates through 4 days and through 2 instars or more (at 11 days) appeared similar with the mean survival levels of the 6 families all excellent (79%- 88%) during the 4 day and 11-day period (Table 1). The weight

Table 1. Growth responses of *P. glaucus* larvae to 3 photoperiod treatments (long day18:6h, short day12:12h, and 0:24h = dark). Data are presented as a mean of the 6 family[1] means (± sd).

		SURVIVAL				**WEIGHTS**		
Treatment	**(n)**	**4-day (%)**	**11-day (%)**	**to pupa (%)**	**days to pre-pupa**	**11-day (mg)**	**pupal (mg)**	**GR[2](11-p) mg/day**
Long day (18:6h)								
	8	100.0	100.0	62.5	21.6	508	974	65.7
	8	87.5	87.5	87.5	23.7	245	none	-
	8	100.0	100.0	37.5	21.3	326	1162	95.4
	8	87.5	87.5	25.0	22.5	318	1039	71.4
	8	50.0	50.0	50.0	22.3	440	1283	98.9
	8	100.0	87.5	14.3	22.0	442	1402	78.5
Mean ± sd		**87.5**	**85.4**	**46.1**	**22.2a**	**380a**	**1172a**	**82.0a**
		19.3	18.4	26.6	0.8	99	175	14.6
Short day (12:12h)								
	8	75.0	75.0	25.0	22.0	200	941	62.7
	8	75.0	75.0	12.5	27.0	173	593	27.5
	8	50.0	50.0	37.5	22.0	332	none	-
	8	100.0	87.5	12.5	24.0	307	883	46.1
	8	75.0	75.0	37.5	24.3	409	none	-
	8	110.0	100	25.0	23.0	347	none	-
Mean ± sd		**79.2**	**77.1**	**25.0**	**23.7a**	**295a**	**806 b**	**45.4 b**
		18.8	16.6	11.2	1.9	90	186	17.6
Darkness (0:24h)								
	8	100	100	50.0	22.5	157	852	59.2
	8	87.5	87.5	62.5	23.0	232	921	54.5
	7	71.4	57.1	0	x	147	none	-
	8	75.0	75.0	50.0	22.0	179	940	68.5
	8	100	87.5	62.5	22.2	290	1041	73.1
	8	62.5	62.5	12.5	24.0	144	1065	70.6
Mean ± sd		**82.7**	**78.3**	**39.6**	**22.7a**	**192 b**	**964ab**	**65.2 ab**
		15.6	16.4	26.7	0.8	58	88	7.9

The first (top) 5 families are from Virginia (Nelson Co.), females # 16262, 16268, 16273 (were dark morph), and 16283, 16284 (yellow morphs); the sixth family (# 16287) is from a yellow morph Georgia female (Clarke Co). Some pupae died after prepupal formation and before weighing. Different letters indicate significant differences between photoperiod treatment means of the family means (Tukey *t*-tests; at $P = 0.05$).

[2] Growth rates from day 11 to pupation.

gain at 11 days was least ($P < 0.05$) for the 0:24 (dark) photoperiod treatment (192 mg ± 58 sd). Weight gain under the short day 12:12 photoperiod was 295 mg ± 90 sd, and the long day 18:6 was 380 mg ± 99 sd (but these latter two were not significantly different from each other; Table 1).

While the fast-growing larvae in the 18:6h photoperiod did have the highest mean pupal weights (mean of family means = 1172 mg ± 175 sd), the slow growing early instars at the 0:24 (dark) treatment apparently compensated with increased growth rates in later instars and achieved mean pupal weights that were not statistically different from the long day pupae (964 mg ± 88 sd; $P = 0.056$, *t*-test). The 12:12 photoperiod resulted in the smallest pupae (806 mg ± 186 sd, mean of family means).

The mean number of days to reach the pupal stage (= total larval duration) was virtually identical in all photoperiod treatments (18:6 = 22.2 days ± 0.8 sd, 12:12 = 23.7 days ± 1.9 sd, and the 0:24 = 22.7 days ± 0.8 sd for means of family means; Table 1). The growth rates from day 1 to day 11 were 34.5 mg/day; 26.8 mg/day; and 17.4 mg/day for long day, short day, and darkness, respectively. Growth rates from 11 days to pupation were 82.0 gm/day; 45.4 mg/day; and 65.2 mg/day for long, short, and dark, respectively. It is clear that the growth rates during the second half of the larval development period were about 2-fold faster in long day and 1.5-fold in short day treatments, while the growth rates of larvae in darkness increased 3.4 fold. Compensatory larval growth after day 11 is evident in darkness, with larval growth overtaking that in short days, although not significantly different than in long days (Table 1).

DISCUSSION

The slow start of neonate growth when in total darkness was not unexpected relative to the 12:12 and the 18:6 photoperiod treatments. The 11-day weights (mean of family means) in the dark (191.5 mg) were only about half that seen in the long day treatment (379.9 mg) and means in the short day treatment (12:12h) were intermediate (Table 1). While it was known that *P. glaucus* larvae do feed occasionally at night (Scriber 1975), the total darkness (except at weightings) was an unusual situation that apparently slowed their overall growth rate (neonate through the first 11 days). Although growth was slow in the dark, the survival was as good as seen for larvae in the other photoperiod treatments.

The surprising result was that these slow-growing larvae (during early larval instars) were somehow able to compensate and sufficiently increase their growth rates to achieve pupal sizes similar to those in the long day treatment. This was accomplished in the same amount of time from neonate to pre-pupa (22-23days; Table 1). The highest overall larval mortality from day 11 to day 23 occurred in the 12:12 photoperiod (75%) compared to 54 % in 18:6h and 60% in 0:24h (Table 1). Such mortality in the lab is not atypical during 3-4 week long rearing periods (Scriber, unpublished data). The reasons for the slowest growth and lowest survival in 12:12 photoperiod are not known.

These experimental bioassay results, all at a 27°C thermal regime, suggest that photoperiod alone can differentially affect the survival, growth, and fitness of *P. glaucus*. While these experimental photoperiod treatments were extreme, it has been documented here that sufficient behavioral and physiological flexibility exists to permit compensatory larval growth under such conditions. How quickly a natural field population of *P. glaucus* could adjust with genetically-based responses to photoperiod differences is not certain but rapid evolutionary responses to photoperiods have been shown for mosquitoes (Bradshaw and Holzapfel 2006).

It is known that the polyphagous species, *P. glaucus,* has adult females with extremely flexible oviposition “specificity” to permit local adjustment to differences in abundance and/or availability (or absence) of certain local hosts. Such flexibility persists despite genetically hard-wired “rank-order” oviposition preferences that have been shown to be nearly identical, from Georgia to Michigan and west to Missouri in 7-choice oviposition assays (using plants from 7 different families; Mercader and Scriber 2005; see also Scriber 1993). It has been shown that the primary difference between *P. glaucus* and its polyphagous northern neighbor, *P. canadensis,* to be limited to a shift in host rank hierarchy due to an acceptance of *Populus tremuloides* Michaux (Salicaceae) and reduced specificity for *Liriodendron tulipifera* in *P. canadensis* (Mercader and Scriber 2007). These adult behaviors greatly impact the success of offspring since these butterfly larvae do not change host plants as many moth larvae do (Singer 2001).

Larval “compensatory responses” have also been detected in the northern *P. canadensis* where behavioral and physiological adjustments in feeding of neonates resulted in progressively faster growth in response to longer periods of experimental cold stress (8, 24, and 48 hours) encountered while they were in the egg stage (Tesar and Scriber 2003). In addition to stressful abiotic (cold) conditions and poor host plants (low nutritional value or high allelochemical concentrations; Slansky and Scriber 1985), here we add compensatory feeding by *P. glaucus* in darkness (0: 24h photoperiod).

We do not know whether the increased growth response seen here was possible because of faster consumption rates (RCRs), higher efficiencies (approximate digestibilities =ADs, efficiency of conversion of digested food = ECDs, or efficiency of conversion of ingested food = ECIs; see Scriber and Slansky 1981) or by a combination of these behavioral and physiological adjustments. It is also not clear whether such larval compensatory responses as seen here in “generalist feeders” such as these *P. glaucus* (and *P. canadensis*; Tesar and Scriber 2003; southern armyworms, Scriber 1984a,b; fall armyworms, Wheeler and Slansky 1991; and others reviewed in Slansky 1993) would be expected to occur in host specialists (Scriber 2005). Optimal diet selection does occur in insects (Waldbauer and Friedman 1991) but the physiology and behavioral mechanisms permitting compensatory feeding and growth remain largely unknown (Scriber 2002b). It is also possible that the early instars benefit relatively more from daylight (solar basking; Ayres and Scriber 1994) for growth in the field (and do poorly without it, as seen here), while larger, later instars with smaller surface to volume ratios, might be able to feed very efficiently at night (consuming some water/dew on the leaf surfaces, and also escaping from visual searching predators). In other words, darkness (or perhaps heavy shade in a forest) may not be a natural hindrance for such caterpillars, except for early instars.

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VARIATION IN DETECTING *SCHINIA INDIANA* AND *SCHINIA LUCENS* (LEPIDOPTERA: NOCTUIDAE) IN WISCONSIN

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ABSTRACT

Schinia indiana (Smith) and *Schinia lucens* (Morrison) (Lepidoptera: Noctuidae) are diurnal moths and are well camouflaged when perched on flowers of their larval food plants: *Phlox pilosa* L. (Polemoniaceae) and *Amorpha* (Fabaceae), respectively. We recorded 264 *S. indiana* in diurnal surveys of 28 units of 15 sites in Jackson County, WI, and 25 units of 5 sites in Burnett County, WI, from 23 May (2006) to 15 June (1994). The longest flight periods in single years were 21 days in 1994 and 17 days in 2006. Abundance of individuals was significantly greater when phlox flowering was prepeak and peak, compared to earlier and later in phlox flowering phenology. We recorded 46 *S. lucens* in diurnal surveys of nine sites in six counties in southern Wisconsin and two sites in two counties in northwestern Wisconsin, from 30 June (1998) to 29 July (2002). The longest flight periods in single years statewide were 23 days (2002) and 15 days (2000). One *S. indiana* flushed at 16ºC, but all other flushes occurred when it was > 20ºC, and after 7:41 hr CST. Nonetheless, we detected many *S. indiana* after these flushing thresholds had been reached. *S. indiana* was significantly more likely to move and to flush when it was warmer, sunnier, or later in the day. By contrast, *S. lucens* was not significantly more likely to be active when it was warmer, sunnier or later in the day. Both species showed considerable fluctuation in abundance among years. For detecting *S. indiana*, sunny conditions at any time of day when it is < 16ºC appear ideal, followed by sunny and < 20ºC. When *S. indiana* individuals are active, it is still possible to find them if great caution is taken in approaching phlox flowers, especially by using binoculars to search phlox flowers. Effective diurnal surveys for *S. lucens* may occur in a broad range of weather and time of day.

Schinia indiana (Smith) and *Schinia lucens* (Morrison) (Lepidoptera: Noctuidae) belong to the subfamily Heliothentinae, which includes species active during the day (like the two species studied here), the night, or both (Hardwick 1958, 1996; Covell, Jr. 1984; Matthews 1991). In general, the diurnal species of Heliothentinae usually become active in late morning to fly rapidly among blossoms for feeding and oviposition. While the species vary in degree of protective coloration, the camouflage afforded to individuals perched on flowers of the larval food plant (host) is remarkable in many species. Larvae feed on developing seed capsules or pods of the host, sometimes feeding on the flowers first. The number of generations per year appears determined by the length of the flowering period of the host(s): the moth species is multivoltine if and when the host(s) have a dependably long flowering season but univoltine if the primary period of bloom is relatively short. Univoltine species pass most of the year as pupae. Adults of some *Schinia* species come to ultraviolet light traps.

States with records of *S. indiana* occur primarily in central North America, from Arkansas and Texas to Minnesota, Wisconsin, and Michigan (Hardwick 1958, Balogh 1987). Forbes (1954) also listed North Carolina, but neither Hardwick (1958) nor Balogh (1987) located these specimens. Specimens averaged (± SD) 16.7 ± 1.3 mm in wingspan (N = 43 specimens) (Hardwick 1958). The

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host is downy phlox (*Phlox pilosa* L.) (hereafter called "phlox") (Polemoniaceae) (Hardwick 1958). Both Hardwick (1958) and Balogh (1987) emphasized the relatively inactive behavior of the species, with individuals resting most of the day on or among host blossoms. This species does not come to light traps (Les Ferge, Madison, WI, pers. comm.).

Schinia indiana is legally listed as Endangered in Wisconsin (Wisconsin Department of Natural Resources 2004) and is highly restricted to native sand savanna vegetation (Panzer et al. 1995). This moth is also listed as "Endangered" in Indiana and Michigan, and "Special Concern" in Minnesota, with a common name of phlox moth (Indiana Department of Natural Resources 2002, Michigan Department of Natural Resources 2002, Minnesota Department of Natural Resources 2007b).

The range of *S. lucens* is large, including localized records in Florida, North Carolina, Tennessee, and Michigan, and a wide distribution from central Illinois and southern Wisconsin northwestward to southern Manitoba and southwestward to central Texas (Metzler et al. 2005). Holland (1905) and Hardwick (1996) reported a westward distribution to the Rocky Mountains in Canada, interior Washington state, Arizona, montane southern California, and Baja California Norte, Mexico. Holland (1905) considered the species common in the central Great Plains, while Covell, Jr. (1984) considered it uncommon to rare in eastern North America. Adult wingspan is about 25-28 mm (Covell, Jr. 1984) and they can be found at ultraviolet light traps (The Lepidopterists' Society 1983, 1984). Wyatt (1938) and Hardwick (1996) specify *Amorpha californica* Nuttall and *A. canescens* Pursch (leadplant) (Fabaceae) as host plants. The host for *S. lucens* in the moth's prairie range is restricted to native grassland/ prairie (Metzler et al. 2005).

Although *S. lucens* has no legal status for protection in Wisconsin (Wisconsin Department of Natural Resources 2004), it is highly restricted to native prairie vegetation (Panzer et al. 1995). Most provinces and states, including Wisconsin, have lost more than 99% of their tallgrass prairie in the past two centuries (Samson and Knopf 1994). This moth is legally listed as "Endangered" in Indiana and Michigan and was recently proposed as "Special Concern" in Minnesota, with a common name of leadplant moth or leadplant flower moth (Indiana Department of Natural Resources 2002, Michigan Department of Natural Resources 2002, Minnesota Department of Natural Resources 2007a).

Surveying and monitoring are necessary components of conservation programs, both to identify those species (of the ones effectively sampled) that do and do not require conservation action and to monitor the efficacy of conservation actions (Conrad et al. 2004, Groenendijk and van der Meulen 2004). Transect surveying can be effective in monitoring moth populations, especially of diurnally active species (Groenendijk and van der Meulen 2004, Young and Barbour 2004). However, the small size, high degree of camouflage, and potential activity level of these two *Schinia* species could affect their detectability in surveys.

In this paper, we report on daytime observations of *S. indiana* and *S. lucens* in Wisconsin (which is the northern part of their ranges) during 1994-2006, as well as during 1992 for *S. lucens*. We analyze variation in detection at three temporal scales: daily (weather and time of day variables), seasonal (date, host phenology), and annual (fluctuations in abundance, long-term trends). This information should improve the effectiveness of daytime surveys for these species.

METHODS

We surveyed for *S. indiana* or *S. lucens* during general transect surveys for butterflies (Swengel and Swengel 1999). We conducted transect surveys along like routes within each site (similar to Pollard 1977) as described in Swengel

(1996, 1998). A new survey unit was designated whenever the habitat along the route varied by management or vegetation type. We also surveyed specifically for *S. indiana* by walking from host to host, choosing routes so as to search as many phlox plants as efficiently as possible, and searching especially host flowers and flower buds but also other parts of host plants. We did not follow a set route, but kept our surveying within the bounds of a single unit. For both butterfly and *S. indiana* unit surveys, we recorded time of day, temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Data from each unit were kept separate. Surveys occurred over a wide range of weather conditions and times of day. For nine of these *S. indiana* unit surveys ("informal" samplings in Swengel and Swengel 1999) with nine individuals recorded, we did not record survey distance and/or start/end times, due to time spent during the survey performing non-survey activities (orienteering, mapping, habitat description, etc.). These observations are included in analyses where possible.

Wing wear was evaluated on a categorical scale based on field descriptions and photographs: 1 = fresh, 2 = slightly faded, 3 = faded, 4 = very faded. During 1996-98 and 2001-06, for all unit surveys where we found *S. indiana*, we classified phlox flower phenology into five categories: mostly in bud (very few flowers), prepeak, peak (±0-2 days of peak), postpeak, well past peak (many wilted flowers). In 1997-98 and 2006, we consistently recorded phlox flower phenology in unit surveys throughout the *S. indiana* flight period whether *S. indiana* was recorded or not. The relative abundance of phlox plants (not flowers) for the unit and microsite of the moth's location was recorded using the following categories defined according to relative arithmetic ratios based on orders of magnitude: abundant (10,000), common (1000), uncommon (100), and sparse (10). For intermediate values, we used the average between the two values: e.g., common/abundant (5000), sparse/uncommon (50).

For *S. indiana*, we conducted 659 unit surveys (312 butterfly, 347 *S. indiana*) each year during 1994-2006 at 69 pine-oak barrens/savannas containing its host (264.6 km for all transects, 147.4 hr of total survey time) in central Wisconsin (Jackson, Juneau, Marquette, and northern Sauk Counties) and northwestern Wisconsin (Burnett County). Although the sites in central Wisconsin are at least 220 km from those in northwestern Wisconsin, they have a similar climate in the growing season (Curtis 1959). For *S. lucens*, we conducted 523 unit surveys (152.9 km, 68.8 hr) in 1992 and 1994-2006 at 12 prairies and a prairie garden planting containing its host in the southern half of Wisconsin (Crawford, Dane, Grant, Green, Iowa, and Sauk Counties) and at 3 pine-oak barrens/savannas (Burnett County) and a prairie (St. Croix County) in northwestern Wisconsin. The southern Wisconsin sites for *S. lucens* were a minimum of 240 km away from the northwestern ones.

Schinia indiana was consistently surveyed at four units in Jackson County, Wisconsin, each year during 1994-2006 (one unit was missed in 1994 and another in 1998), and at six units in Burnett County in eight years during 1994-2006 (two units were missed in 2005). We found *S. indiana* in at least three years (maximum 10) at each of these Jackson County units, and in at least one year (maximum six) at each of these Burnett County units. *S. lucens* was surveyed consistently at six sites in southern Wisconsin (Dane, Crawford, Green, Iowa Counties) during 1998-2006 (one site missing in 1998). We recorded *S. lucens* at each site during this period, and in more than one year during this period except at one site. Since we recorded only two *S. lucens* individuals in northwestern Wisconsin, we did not include this region in this analysis. We calculated an annual index of abundance as the mean of the peak observation rate (individuals/hour on a unit survey) at the monitoring units/sites each year. We also calculated an annual index of abundance for other units surveyed for *S. indiana* each year, including only those units where we had ever recorded *S. indiana* (sample of units varied in number and location among years). We did this only for eight years, excluding those years where only 0-2 other units were surveyed during *S. indiana* flight period. We did not perform this analysis for *S. lucens* because we did not survey enough other sites with the species to support analysis.

Survey characteristics (including date, time of day as Central Standard Time [CST], location, weather) and individuals observed were databased both by each unit survey and by individual moth. To make numbers comparable among unit surveys, we standardized them into rates of individuals observed per hour of survey time per unit survey. Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado), with statistical significance set at $P < 0.05$. Since significant results occurred much more frequently than would be expected due to Type I statistical errors (i.e., non-significant results receiving a spuriously significant *P* value), we did not lower the *P* value further, as many more Type II errors (i.e., biologically significant yet statistically non-significant results) would then be created than Type I errors eliminated. Scientific nomenclature for moths follows Hardwick (1996) and for vascular plants follows Kartesz (1994).

For each species, we tested for significant differences in whether individuals were active or not by weather conditions (temperature, percent sunshine, wind speed) and time of day (CST), with the Mann-Whitney U test. For *S. indiana*, we also tested for significant differences in whether individuals flushed or not, and were concealed (obscured by vegetation) or not (readily seen by a person standing near or over host) by the same variables. We did not do this for *S. lucens* because no individuals were concealed and only one individual flushed. Also only for *S. indiana*, we tested for a significant difference in host abundance in unit surveys during *S. indiana* flight period, between those units where we ever recorded *S. indiana* and those where we never did.

We used the Chi Square Goodness of Fit test to check for a significant difference in proportion of observed *S. indiana* individuals in each of the five phenological categories of phlox flowering vs. expected individuals based on survey time in each of these categories in units where we ever recorded *S. indiana* during this study.

All correlations were done with the Spearman rank correlation. We tested for correlation of wing wear rating vs. date (sequentially numbered). We tested for trend (correlation of year vs. annual indices of abundance). We also tested for significant correlation of annual indices of abundance between the long-term units and the other units (*S. indiana* only, by county).

RESULTS

We recorded 264 *S. indiana* in 28 units in 15 sites in Jackson County and 25 units in 5 sites in Burnett County, from 23 May (2006) to 15 June (1994) (Fig. 1) based on 198.7 km of survey transects and 112.7 hr of survey. Both of those dates were from Jackson County. In Burnett County, we recorded them from 25 May (1999) to 13 June (2004). Within year, the longest flight period spans were 21 days in 1994 and 17 days in 2006, both in Jackson County, where we sampled on more dates per year. We found at least one individual in each category of phlox flower phenology, but the abundance of these individuals was significantly skewed to occurring in the prepeak and peak periods (Table 1). Phlox was significantly more abundant in surveys during *S. indiana* flight period in units where *S. indiana* had ever been recorded (mean rating 4213, N = 304 unit surveys) than in units where we never recorded the species (mean rating 2178, N = 101) ($P < 0.001$). Wing wear did not significantly correlate to date ($r = +0.090$, N = 201, $P > 0.10$).

We recorded 46 *S. lucens* in 9 sites in six counties (Crawford, Dane, Grant, Green, Iowa, Sauk) in southern Wisconsin, and 2 sites in two counties (Burnett,

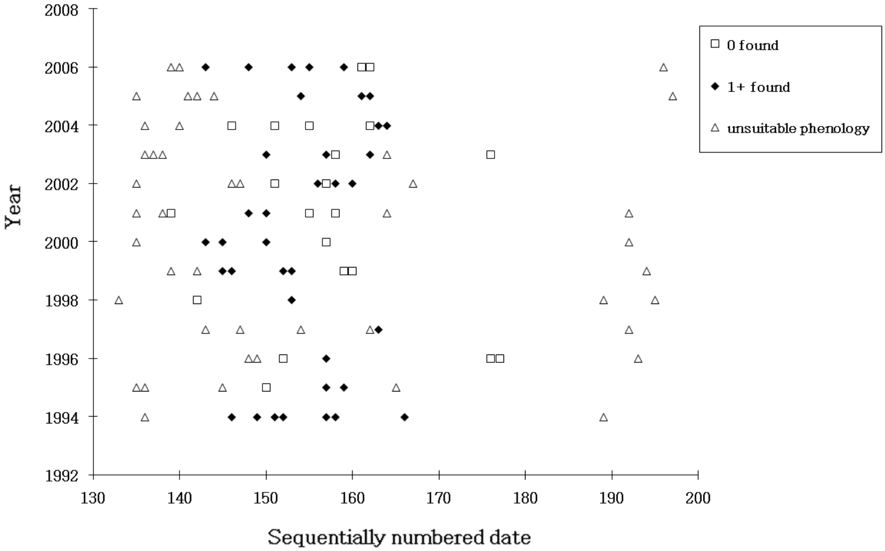

Figure 1. Survey dates in *Schinia indiana* site(s) in Wisconsin by year and phenology: "0 found" means we specifically searched for *S. indiana* and found none, "1+ found" means one or more *S. indiana* were recorded, and "unsuitable phenology" means we did not specifically search for *S. indiana* because it was either too early for phlox flowers or phlox flowering was mostly over. 130 = 10 May; 200 = 19 July. (In 2003, we did not attempt to find any *S. indiana* on 13 June, but we did search on 25 June in a site of slow phenology.) All dates are from Jackson County, WI, except the following are from Burnett County, WI: "0 found" = 142 (1998), 161 (2006), 162 (2006); "1+ found" = 146 (1994), 145 (1999), 146 (1999), 145 (2000), 160 (2002), 157 (2003), 164 (2004), 162 (2005), 148 (2006); and "unsuitable phenology" = 145 (1995), 143 (1997), 146 (2002), 137 (2003), 140 (2006).

Table 1. Distribution of *Schinia indiana* adults on downy phlox plants at five phenological stages of flowering. The number of observed individuals in 1997-98 and 2006 vs. the expected number of individuals based on the proportion of the survey effort in each phenological stage is significantly different (Chi Square = 17.6, $P = 0.0015$).

	All individuals[1]		**Survey time**[2]		**Observed**[3]		**Expected**[3]
Phlox phenology	**N**	**%**	**Hr**	**%**	**N**	**%**	**N**
Mostly in bud	2	1.3	1.98	10.0	1	2.4	4.1
Prepeak	62	41.6	1.66	8.4	6	14.6	3.4
Peak (±0-2 days)	64	43.0	8.35	42.1	28	68.3	17.3
Postpeak	20	13.4	5.43	27.4	5	12.2	11.2
Many wilted flowers	1	0.7	2.41	12.1	1	2.4	5.0

[1] All *S. indiana* individuals were recorded during 1996-1998 and 2001-2006.

[2] Survey time in 1997-98 and 2006 was calculated from all units where we ever recorded *S. indiana* in this study.

[3] Observed individuals were recorded in 1997-98 and 2006; expected individuals were calculated based on proportion of survey time in each phenological category.

St. Croix) in northwestern Wisconsin, from 30 June (1998, Green County) to 29 July (2002, Burnett County) (Fig. 2) in 138.7 km and 62.7 hr of surveys there. Within year, the longest flight period spans statewide were 23 days (2002, starting in southern Wisconsin and ending in northwestern Wisconsin) and 15 days (2000, all in southern Wisconsin). While most visits to Burnett County in northwestern Wisconsin were classified as "casual search", we did routinely watch leadplant flowers for nectaring butterflies, and that is how the one very worn individual there was found. One date (9 July 1999) in northwestern Wisconsin was spent in St. Croix County. Wing wear significantly correlated to date ($r = +0.777$, N = 22, $P < 0.001$).

For both species, when one individual was found, it was useful to look on the same plant for another individual, even if obscured. For *S. indiana*, 80 individuals (30%) occurred in pairs on the same inflorescence/stem (with 18 individuals in mating pairs) and 4 (2%) together on one flower head (none mating). For *S. lucens*, 6 individuals (13%) occurred in pairs on the same flowering stem (none mating). As leadplant is much larger, with multiple branches, we also noted number of individuals per plant: 10 (22%) occurred in pairs on the same plant and in one instance, 3 (7%) occurred on the same plant.

One *S. indiana* flushed at 16ºC, but all other flushes occurred when it was ≥ 20ºC (Fig. 3). We recorded 67 individuals when it was ≤ 16ºC, and 142 individuals when it was ≤ 20ºC. The coldest temperature we recorded when finding *S. indiana* was 7ºC. No *S. indiana* flushed before 7:42 hr CST (Fig. 4); 52 individuals were recorded before this time, 33 at ≥ 16ºC, and 9 at ≥ 20ºC. We

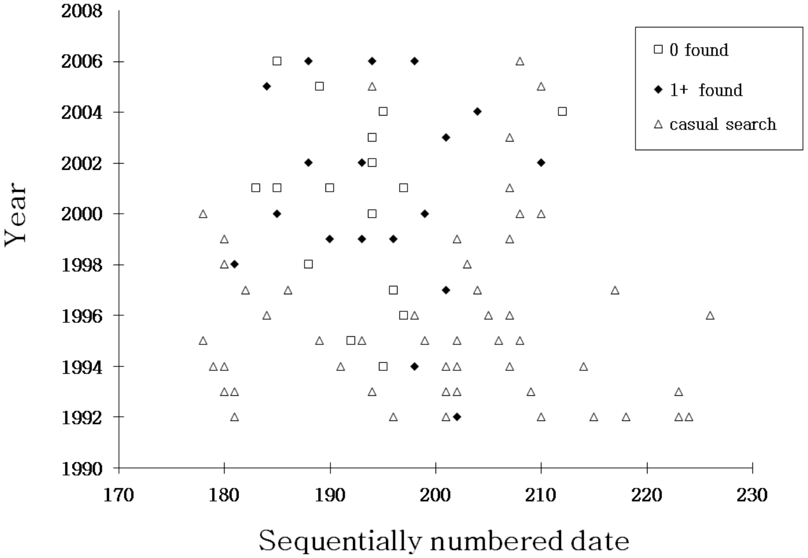

Figure 2. Survey dates in *Schinia lucens* site(s) in Wisconsin by year and phenology: "0 found" means we specifically searched for *S. lucens* and found none, "1+ found" means one or more *S. lucens* were recorded, and "casual search" means we did not specifically search for *S. lucens*, but noted it when we were looking at leadplant for nectaring butterflies (170 = 19 June, and 230 = 18 August). All sampling dates are from southern Wisconsin except the following are from northwestern Wisconsin: "0 found" = 212 (2004); "1+ found" = 190 (1999), 210 (2002); and "casual search" = 210 (1992), 209 (1993), 201 (1994), 202 (1995), 205 (1996), 204 (1997), 203 (1998), 202 (1999), 208 (2000), 207 (2001), 207 (2003), 210 (2005), 208 (2006).

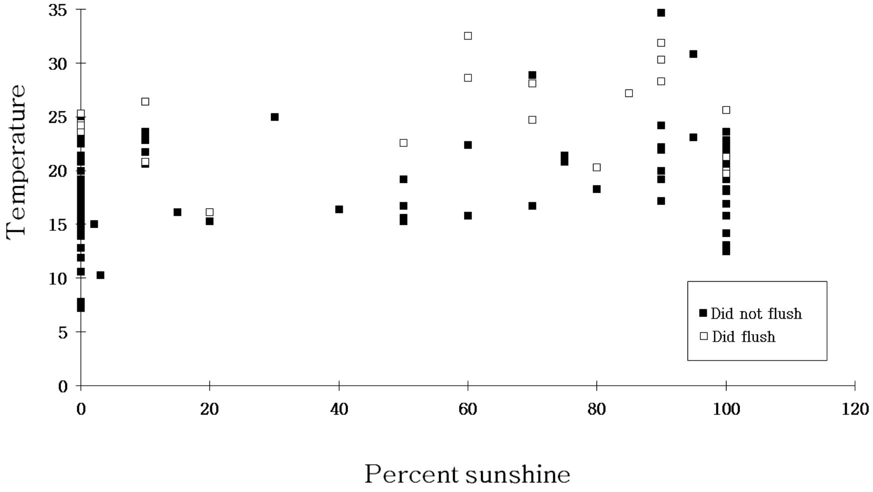

Figure 3. Occurrence of flushing by *Schinia indiana* adults in Wisconsin in relation to air temperature (°C) and percent sunshine.

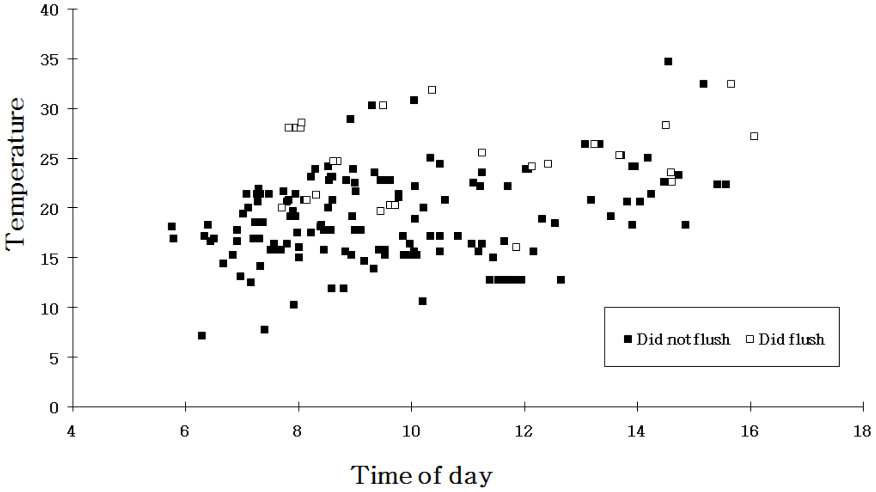

Figure 4. Occurrence of flushing by *Schinia indiana* adults in Wisconsin in relation to air temperature (°C) and time of day (CST, Central Standard Time).

recorded flushing throughout the rest of our survey day; the latest individual recorded was at 16:04 hr, and it flushed. Conversely, we recorded many *S. indiana* after these flushing thresholds had been reached (Figs. 3, 4): 167 did not flush when it was > 16ºC, 94 when it was ≥ 20ºC, 180 when it was later than 7:42 hr, and 85 when it was ≥ 20ºC and later than 7:42 hr.

Schinia indiana was significantly more likely to be active and to flush when it was warmer, sunnier, or later in the day (Table 2). Only 11 inactive individuals occurred when it was > 25ºC, up to 35ºC. They were also significantly more likely to move when it was windier but flushing did not significantly relate to wind (Table 2). Whether *S. indiana* was concealed or unconcealed did not significantly relate to temperature, sunshine, wind, or time of day (Table 2). However, we found only 8 concealed individuals when it was > 23ºC.

Whether *S. lucens* was active or not did not relate significantly to temperature, sunshine, wind, or time of day (Table 2). Active individuals occurred throughout most of the range of temperature (21-29ºC), sunshine (0-100%), and time of day (8:01-14:45 hr CST) as recorded for inactive individuals (19-31ºC, 0-100% sunshine, 7:32-16:20 hr). Only one individual flushed, under relatively warmer, sunnier conditions (28ºC, 85% sunshine) and after noon (12:16 hr). Concealment was not testable for *S. lucens* since they cannot conceal themselves within a leadplant inflorescence.

For *S. indiana*, we compared annual indices of abundance from long-term monitoring units (four in Jackson County, six in Burnett County) (Fig. 5) and other units (varying in number and location per year) in the same county where we had ever recorded the species. While the correlation was positive between long-term and non-long-term indices within county, this was far from significant in either county (r = +0.595 in Jackson County, r = +0.438 in Burnett County, N = 8 and $P > 0.10$ for both). None of these indices had a significant long-term trend (r = -0.049, N = 13 for Jackson County long-term units, -0.190, N = 8 for Jackson County other units, +0.048, N = 8 for Burnett County long-term units, +0.544, N = 9 for Burnett County other units).

At the monitoring sites in southern Wisconsin, *S. lucens* showed great variation in annual indices of abundance (Fig. 6), comparable to the variation in *S. indiana* indices (Fig. 5). *S. lucens* indices showed no trend (r = 0.0, N = 9 years).

DISCUSSION

While we only recorded 26 *S. indiana* individuals that flushed, this was no doubt an undercount, in that other individuals probably flushed before we saw or could identify them. Furthermore, once we had begun to identify the conditions under which activity and flushing became more likely (Swengel and Swengel 1999, which included surveys in other states), we attempted to prevent individuals from being disturbed and flushed (by approaching slowly, crouching over, or scanning flowers with binoculars first). This may explain why we found a few concealed individuals at higher temperatures than previously reported (Swengel and Swengel 1999: no concealed individuals at > 23ºC). Nonetheless, given that we recorded a total of 264 individuals overall, the numbers found after flushing thresholds were reached (Figs. 3, 4: 16ºC strictly, but 20ºC most of the time; 7:42 hr CST) were sufficient motivation for us to continue searching under those conditions. Percent sunshine did not show a threshold pattern (Figs. 3, 4), but in statistical testing, was greater for flushed than non-flushing individuals (Table 2). Temperature, sunshine, and time of day patterns (Table 2) appear directly related to *S. indiana* flushing behavior (as the individual becomes warmer, it becomes more active), but the (weaker) relationship of flushing to wind may be an indirect effect: either wind causes them to readjust position or wind makes it harder for us to search, so that we are more likely to

Table 2. Mean (± SE) time of day and weather variables measured at time of observation of *Schinia indiana* and *Schinia lucens* adults in Wisconsin by species and by whether the moth was active or not, flushed or not, and concealed or not.

	Mean	**SE**	**Mean**	**SE**	***P***
Schinia indiana					
	Not active (N=228)		Active (N=34)		
Temperature (°C)	18.9	0.3	25.3	0.8	<0.001
Percent sunshine	30.8	2.7	62.9	6.3	<0.001
Time of day[1]	9.6	0.2	10.7	0.5	<0.05
Wind (km/hr)	10.1	0.5	14.1	1.6	<0.05
	Not flushed (N=232)		Flushed (N=26)		
Temperature (°C)	19.0	0.3	24.9	0.8	<0.001
Percent sunshine	31.8	2.7	56.7	7.4	<0.01
Time of day[1]	9.6	0.2	10.9	0.5	<0.05
Wind (km/hr)	10.1	0.5	14.0	2.0	<0.1
	Not concealed (N=205)		Concealed (N=46)		
Temperature (°C)	20.0	0.3	19.0	0.9	<0.1
Percent sunshine	37.6	3.0	28.8	6.0	>0.1
Time of day[1]	9.9	0.2	9.4	0.3	>0.1
Wind (km/hr)	10.6	0.5	11.4	1.3	>0.1
Schinia lucens[2]					
	Not active (N=36)		Active (N=9)		
Temperature (°C)	23.8	0.5	25.0	0.9	>0.1
Percent sunshine	60.8	5.6	66.1	10.4	>0.1
Time of day[1]	10.0	0.4	10.9	0.8	>0.1
Wind (km/hr)	10.0	0.9	11.2	1.6	>0.1

[1] CST (Central Standard Time), converted to decimal (e.g., 9:15 hr became 9.25 and 9:30 hr became 9.5)

[2] Flushing and concealment were not analyzed for *S. lucens* because only one individual flushed and none were concealed.

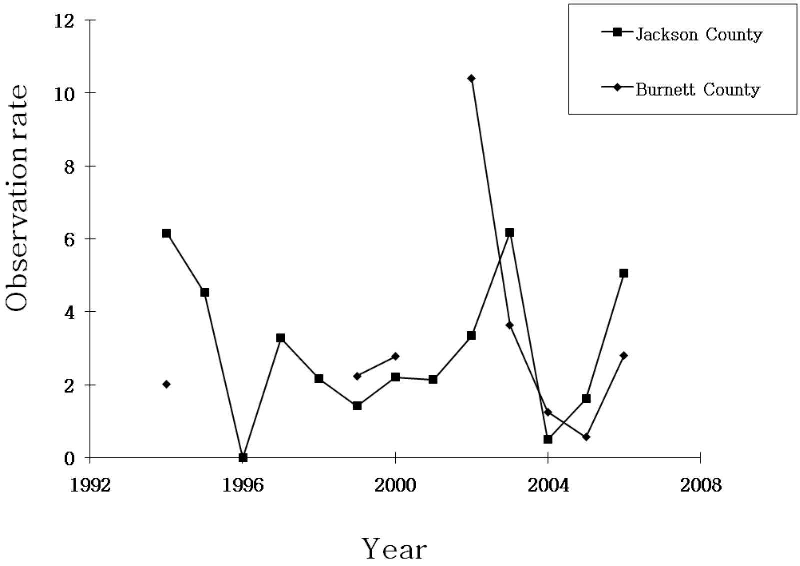

Figure 5. *Schinia indiana* average annual index of abundance (number of individuals observed per hour on the peak survey day for each unit, averaged for all units each year) at long-term monitoring units in Burnett and Jackson Counties, Wisconsin.

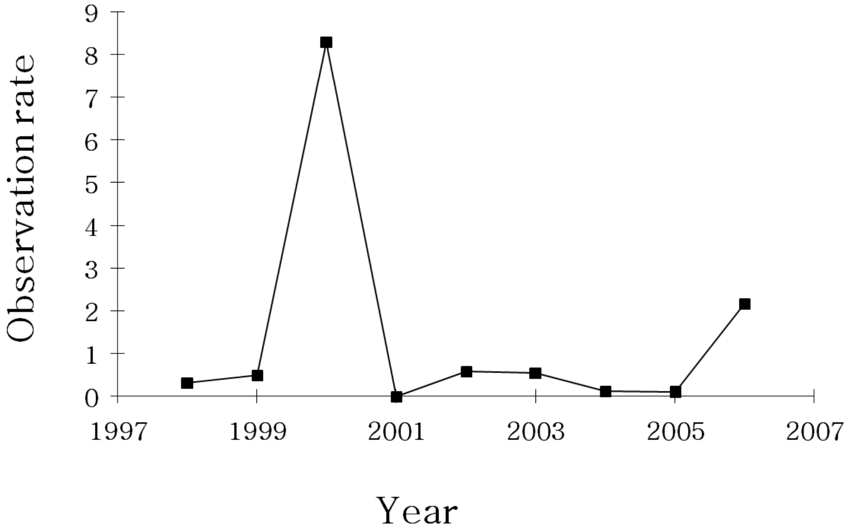

Figure 6. *Schinia lucens* average annual index of abundance (number of individuals observed per hour on the peak survey day for each unit, averaged for all units each year) at long-term monitoring units in southern Wisconsin.

disturb them. The results here slightly modify but remain consistent with our previously reported findings (Swengel and Swengel 1999: *S. indiana* individuals inactive at < 16°C and before 7:30 hr; all individuals active at > 25°C).

By contrast, activity by *S. lucens* showed no significant patterns relative to weather and time of day (Table 2), and we recorded active individuals under similar weather and time of day as inactive ones. In comparison to our previous report, we found a greater range of temperature and time of day for activity (Swengel and Swengel 1999: all *S. lucens* inactive at < 23°C and until 12:00 hr CST). But our previous finding of inactivity at high temperatures (29°C) is consistent with our results here. Furthermore, we detected flushing rarely, so this behavior is not an apparent impediment to detection. Summer conditions throughout a broad range of time of day are so warm that *S. lucens* can be active. They may flush under relatively warmer, sunnier, later conditions (and our relatively small sample may be inadequate to detect such tendencies), but they appear remarkably disinclined to flush. However, *S. lucens* is larger and easier to pick out on its host flowers. While *S. indiana* can hide within the inflorescence, this is not possible for *S. lucens* on leadplant inflorescences, which are also higher up above the ground. Thus, it is possible that our searching is less intrusive and disturbing for *S. lucens* than *S. indiana*.

We conclude that diurnal surveys for *S. lucens* may effectively occur in a broad range of weather and time of day. However, the large and predictable variation in *S. indiana* behavior relative to weather and time of day greatly affects efficacy of surveys for this species. Sunny conditions at any time of day when it is < 16°C are ideal, followed by sunny conditions at ≥ 16°C but < 20°C. In these cases, individuals may be in unconcealed positions so that they may bask, but are unlikely to flush (especially at < 16°C). Searching before 7:42 hr CST is also recommended regardless of sky condition, unless heavy rain occurred since the last time *S. indiana* could have been active. Heavy rain can knock over phlox plants, knock petals off phlox flowers, and, we infer, knock *S. indiana* off the plant (or cause the moth to drop off). If sufficiently warm and sunny conditions have not occurred since then, to allow *S. indiana* to reassume a perch on a phlox flower, then *S. indiana* individuals would be very hard to find in the drenched and knocked down vegetation or leaf litter. However, when rain is not hard enough to knock off petals and knock down plants, it can be a useful time to survey for phlox moths. Furthermore, it can be very effective to survey in cloudy conditions, especially at < 20°C, that follow warm and/or sunny conditions when *S. indiana* could have moved into unconcealed positions. The cloudy conditions would reduce activity by the moth, but it might retain the unconcealed position it adopted when active. When it is > 20°C, regardless of sky condition, *S. indiana* activity hampers detection, which is still possible if great caution is taken in approaching phlox flowers, especially by using binoculars to search phlox flowers. High wind also hampers searching phlox, which is easily moved by the wind.

For our long-term monitoring analyses (Figs. 5, 6), our sample of sites and counties is relatively small. Furthermore, relatively little information is available about the status and trend of these moths in Wisconsin from before our study, so that it is not possible to put our results into a longer-term context. It is inappropriate to use our monitoring results to make general conclusions about the status and trend of these species in Wisconsin. The lack of any significant long-term trends in our study may not be due to the actual lack of any trends for these species in the areas sampled. Rather, we may not have enough years and/or sites to obtain the statistical power necessary to yield significant results. Furthermore, should significant trends in fact be occurring, they may be due to climatic fluctuation rather than management and/or vegetation changes.

Our monitoring analyses (Figs. 5, 6) are most useful for demonstrating the large variability possible in monitoring datasets. This is an additional factor that must be taken into account in monitoring programs, and demonstrates the need to sample multiple sites in multiple years to characterize the occurrence of the species in an area and to learn conditions or techniques that improve survey efficiency.

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ANOPLOPHORA GLABRIPENNIS **WITHIN-TREE DISTRIBUTION, SEASONAL DEVELOPMENT, AND HOST SUITABILITY IN CHINA AND CHICAGO**

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ABSTRACT

Established populations of the Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), were first reported in the United States in New York in 1996, Illinois in 1998, and New Jersey in 2002. A federal quarantine and an eradication program were implemented in 1997, involving tree surveys and removal of infested trees. We recorded the number of *A. glabripennis* life stages found at several locations along the main trunk and major branches of naturally infested trees in China (species of *Populus*, *Salix*, and *Ulmus*) and Chicago, Illinois (species of *Acer*, *Fraxinus*, and *Ulmus*) during 1999 to 2002. Typically, *A. glabripennis* initiated attack near the crown base along both the trunk and main branches. The one exception to this pattern was on *Populus* trees in China that had branches along the entire trunk, in which case *A. glabripennis* initiated attack along the lower trunk. Larvae were the dominant overwintering stage in both countries. A host suitability index for *A. glabripennis* was calculated for each tree with the formula: (number of living life stages + number of exit holes) / number of oviposition pits. The mean host suitability index was higher on *Populus* and *Salix* than *Ulmus* in China, and generally higher on *Acer* and *Ulmus* than *Fraxinus* in Chicago. Eleven genera of trees (N = 1465 trees) were infested by *A. glabripennis* in Chicago; in decreasing order of tree frequency they included *Acer*, *Ulmus*, *Fraxinus*, *Aesculus*, *Betula*, *Salix*, *Celtis*, *Malus*, *Pyrus*, *Sorbus*, and *Tilia*. When the proportion of each genus of infested street trees (N = 958 trees in 7 genera) was compared to its proportion of all Chicago street trees based on a 2003 inventory (N = 539,613 trees in 45 genera), *A. glabripennis* showed a significant preference to infest the genera *Acer* and *Ulmus*. Based on our results, inspectors should focus their efforts on upper trunks and lower branches of *Acer* and *Ulmus* trees.

The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), is one of the most damaging exotic forest insects to become established in the United States in recent years (Haack et al. 1997, Cavey et al. 1998). Established populations were first discovered in the United States in New York in 1996, Illinois in 1998, and New Jersey in 2002 (Poland et al. 1998, Haack 2003a). In addition, breeding populations and associated tree mortality were first reported in Austria in 2001, Japan in 2002, Canada in 2003, France in 2003, Germany in 2004, and Italy in 2007 (Hérard et al. 2005, Takahashi and Ito 2005, Haack 2006, Schroder et al. 2006, Maspero et al. 2007). Solid wood packaging material, such as crating and pallets, used in

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international trade was likely the principal pathway by which *A. glabripennis* was moved among all these countries (Haack 2006).

Anoplophora glabripennis is native to China and the Korean Peninsula where it infests many genera of living hardwood trees (Lingafelter and Hoebeke 2002, Williams et al. 2004). The principal hosts in Asia are species of *Acer* (maple), *Populus* (poplar), *Salix* (willow), and *Ulmus* (elm) (Yan and Qin 1992). To date, the principal hosts in the United States are *Acer*, *Aesculus* (horsechestnut), and *Ulmus* (Haack et al. 1997, Nowak et al. 2001). *Anoplophora glabripennis* is typically univoltine. Adults emerge throughout the summer months by chewing circular exit holes through the bark. Adults feed primarily on the outer bark of twigs and can live for several weeks, during which time they feed, mate, and oviposit. Ovipositing adult females chew a pit in the outer bark into which they deposit a single egg under the bark. Larvae first feed in the inner bark (phloem) and then tunnel deeper into the wood (xylem). Larvae generally keep their galleries clean by regularly expelling frass outside the tree at the point where oviposition occurred. Larvae feed throughout summer and fall, and if not fully developed, they continue to feed the following year. Most *A. glabripennis* pass the winter in the larval stage, with pupation occurring the following spring or summer. Pupation occurs at the distal end of the larval gallery in the wood. After transformation, new *A. glabripennis* adults chew out of the tree and thereby renew the cycle (Yan and Qin 1992, Haack et al. 1997).

Aggressive eradication programs were initiated in North America, Europe, and Japan (Hérard et al. 2005, 2006; Takahashi and Ito 2005; Haack 2006). In each case, eradication efforts entailed surveying individual trees for signs and symptoms of infestation followed by insecticide treatment or cutting and destroying of all infested trees. When conducting surveys, inspectors look for *A. glabripennis* oviposition pits on the bark surface, extruded frass from larval feeding, and exit holes on the bark surface. Knowing where initial *A. glabripennis* oviposition is likely to occur on trees is important when developing surveys, especially when *A. glabripennis* population levels are low. There have been numerous studies on the within-tree distribution of various bark- and wood-infesting beetles (Coleoptera) with the objective of developing survey and sampling techniques (Haack and Benjamin 1982, Wilkinson and Haack 1987, Prenzel et al. 1999, Chung et al. 2003, Fierke et al. 2005, Timms et al. 2006).

While conducting *A. glabripennis* studies in China and the United States (Haack 2003b, Poland et al. 2006), we gathered within-tree and life-stage distribution data from several naturally infested trees. The principal objectives of our studies were to (1) record *A. glabripennis* within-tree distribution by tree species, (2) record the *A. glabripennis* developmental stages recovered by month of sampling, (3) estimate the suitability of each tree species sampled for *A. glabripennis* development, and (4) compare the genera of trees infested by *A. glabripennis* in Chicago to the general composition of all street trees in Chicago.

MATERIALS AND METHODS

We sampled 49 trees infested with *A. glabripennis* near Baiyin, Gansu Province (36.6°N, 104.2°E), and Wuji, Hebei Province (38.2°N, 115.0°E), China, in October 2000, June 2001, and April 2002. These trees consisted of 21 *Populus nigra* var. *thevestina* (Dode) Bean, 11 *Salix matsudana* Koidz, and 17 *Ulmus pumila* L. trees. Most of these trees were relatively small in diameter at breast height (DBH) (Table 1), and had been planted as windbreaks along roads and agricultural fields. We examined the entire trunk of each tree in 1-m-long increments, usually continuing along a major branch. We felled all trees with a chainsaw and then debarked and split them by hand with an ax and a knife. For each tree section, we recorded length and diameter, the number of oviposition pits, and number of exit holes. We also recorded the number of all living life stages encountered. This research was part of a larger study to evaluate the effects of systemic insecticides on *A. glabripennis* (Poland et al. 2006). The data presented here are from the control trees, which received no insecticide treatments.

In Chicago (41.8°N, 87.7°W), we sampled 38 infested trees in 1999, including 3 *Acer negundo* L. (boxelder), 20 *A. platanoides* L. (Norway maple), 13 *A. saccharinum* L. (silver maple), and 2 *Fraxinus pennsylvanica* Marsh. (green ash) trees. Most trees were felled during February to April 1999, with a few more felled in July and September 1999. These trees were relatively large street trees (Table 1) that were felled as part of the eradication program and thus the species sampled represented the trees removed on the days when we were present. For each tree, we cut trunk and branch sections approximately 1-m-long from the base, middle, and upper main trunk; along the trunk near mid-crown; and from the base of one major branch. For each log sampled, we recorded length, diameter, and the number of oviposition pits and exit holes present. We then debarked and split all logs with a log splitter and ax. We recorded the number of all living *A. glabripennis* life stages found.

In Chicago in June 2001, we sampled nine small-diameter infested trees [seven *A. negundo* and two *U. americana* L. (American elm) trees] that were growing along a fence row (Table 1). Because these trees were relatively short compared to the trees cut in Chicago in 1999, we cut trunk sections (ca. 1 to 2 m long) from the lower trunk, upper trunk, and crown positions. These sections were dissected and sampled as described above.

For all trees, the progression of attack was approximated by the distribution and relative proportion of different signs and developmental life stages of *A. glabripennis*. For example, sections with exit holes were assumed to have been infested earlier than sections with only larvae, and sections with late instar larvae were assumed to have been infested earlier than sections with only oviposition pits and eggs.

A host suitability index for *A. glabripennis* was estimated for each tree species. The suitability index value assigned to each tree was calculated on a per-tree basis as follows: number of living *A. glabripennis* life stages plus the number of exit holes divided by the number of oviposition pits. We recognize that an egg is not always laid in each oviposition pit (Zhao et al. 1993, Keena 2002, Smith et al. 2002), but used this approach to approximate initial oviposition.

During the period 1998-2003, 1465 infested trees, representing 11 genera, were removed in Chicago as part of an operational eradication program; 958 trees were classified as street trees and 507 were classified as being on private properties or in parks. No infested trees were found in Chicago from November 2003 to present (December 2007; Christine Markham, USDA Animal and Plant Health Inspection Service, personal communication). We calculated the proportion of all 1465 trees that each genus represented. We also calculated the percentage of all street trees in Chicago by genus based on the 2003 City of Chicago street tree inventory that included 539,613 trees, representing 45 genera (6 conifer and 39 hardwood genera).

The percent of *A. glabripennis* oviposition pits, living life stages, and exit holes within each tree section sampled were calculated on a per-tree basis by dividing the number of each insect parameter in a given section by the total number found for the tree. Similarly, the suitability index was expressed as a percentage value for each tree. Percentage values were transformed (arcsine square-root) to improve normality and analyzed using analysis of variance (ANOVA) (PROC GLM, SAS Institute, 2001). If the ANOVA was significant at the 0.05 level, then a Tukey multiple range test was used to separate the means. For each genus of trees, the proportion of all infested Chicago street trees was compared to the corresponding proportion of all Chicago street trees using the z-test ($\alpha = 0.05$).

Table 1. Number of *Anoplophora glabripennis* (ALB) oviposition pits, living life stages, and exit holes found on sampled trees in China and Chicago by tree species, and the mean (± SE) DBH and suitability index of each tree species that was estimated by dividing the total number of living life stages found plus exit holes by the number of oviposition pits.

Location	**Mean**	**No. ALB signs or live life stages counted**						
Tree species* (No. cut)	**tree DBH (cm)**	**Oviposition pits**	**Eggs**	**Larvae**	**Pupae**	**Callow adults**	**Exit holes**	**Mean host suitability index (%)**
China (2000, 2001 and 2002)								
Elm (17)	10.0 ± 0.8	1217	62	181	17	1	18	26.5 ± 4.8 b*
Poplar (21)	8.4 ± 0.6	1247	14	413	34	46	147	59.8 ± 6.5 a
Willow (11)	9.2 ± 1.2	584	21	197	15	23	55	51.9 ± 8.5 a
P =	0.27							0.0014
F =; d.f.	1.32; 2,46							7.73; 2,46
Chicago (1999)								
Boxelder (3)	20.0 ± 2.0	32	0	16	0	0	5	76.1 ± 12.1 a
Green ash (2)	22.0 ± 0.0	16	0	1	0	0	0	5.6 ± 5.6 b
Norway maple (20)	31.0 ± 2.6	1339	8	390	0	0	42	31.6 ± 3.5 ab
Silver maple (13)	40.3 ± 6.9	611	20	152	0	0	30	43.8 ± 10.2ab
P =	0.246							0.0126
F =; d.f.	1.46; 3,31							4.20; 3,34
Chicago (2001)								
American elm (2)	10.8 ± 2.3	48	0	25	0	0	0	52.1 ± 10.4
Boxelder (7)	11.0 ± 1.1	252	0	73	14	1	30	44.5 ± 13.0
P =	0.91							0.77
F =; d.f.	0.01; 1,7							0.09; 1,7

* Tree species were: American elm = *Ulmus americana*, boxelder = *Acer negundo*, elm = *Ulmus pumila*, green ash = *Fraxinus pennsylvanica*, Norway maple = *Acer platanoides*, poplar = *Populus nigra* var. *thevestina*, silver maple = *Acer saccharinum*, and willow = *Salix matsudana*.

** Means followed by the same letter within columns, for each of the three location-year sections individually, were not significantly different at the 0.05 level, Tukey multiple range test.

RESULTS AND DISCUSSION

Within-tree distribution in China. The trees sampled in China were relatively small in diameter with a mean (± SE) DBH of 9.1 ± 0.5 cm. Mean DBH did not differ significantly among the three species (Table 1). Initial *A. glabripennis* infestation occurred primarily along the main trunk near the first crown branches (2 to 4 m above groundline) in *Salix* and *Ulmus* trees; however, initial infestation in the *Populus* trees tended to start along the lower trunk, based largely on exit hole data (Table 2). These differences in the initial attack pattern were likely influenced by the differences in branching patterns of the three tree species. For example, initial branching in *Salix* and *Ulmus* trees started at 2 to 3 m above groundline, whereas branching in *Populus* trees occurred along the entire trunk beginning at groundline. Given that *A. glabripennis* adults feed on twigs throughout their lifespan and generally walk along branches to reach the trunk to oviposit (Keena 2002, Smith et al. 2002, Morewood et al. 2004, Smith 2006), the presence of branches along the entire trunk of the *Populus* trees would allow adult females to easily feed and oviposit near groundline. On several occasions we found *A. glabripennis* adults feeding and ovipositing at the base of the *Populus* trees that had numerous basal sprouts. In addition, Zhao et al. (1997) stated that *A. glabripennis* prefers to oviposit on the lower trunks of *Populus* trees where tree DBH is less than 15 cm. All *Populus* trees in our study were less than 15 cm DBH.

Within-tree distribution in Chicago. The 38 trees sampled in 1999 were relatively large street trees with a mean DBH of 33.3 ± 2.9 cm; mean DBH did not differ significantly among the four species sampled in 1999 (Table 1). The nine trees sampled in 2001 were relatively small with a mean DBH of 10.9 ± 0.9 cm; mean DBH did not differ significantly between the two tree species sampled in 2001 (Table 1). For all species combined, the trees sampled in Chicago in 1999 were significantly larger than the trees sampled in Chicago in 2001 or in China ($F = 49.2$; df = 2,90; $P < 0.0001$). Overall, for the 1465 infested trees removed in Chicago during the *A. glabripennis* eradication program from 1998 to 2003, mean DBH was 37.2 ± 0.6 cm (Fig. 1).

The *A. glabripennis* colonization patterns were broadly similar among the four tree species sampled in Chicago in 1999 (Table 3). These trees were mostly in their first to third year of infestation based on the presence of various life stages and exit holes. For example, of the 35 trees sampled in Chicago in 1999 that were included in Table 3, we found oviposition pits on all 35 trees, living life stages in 33 trees, but exit holes in only 13 of the trees. We did not try to determine the age of the exit holes, i.e., current year vs. prior year. Typically, infestation occurred first in the upper trunk and major crown branches of these *Acer* and *Fraxinus* trees. The two *Fraxinus* trees sampled in this study were lightly infested, with all living life stages found in the mid-crown trunk section. Similarly, in the lightly infested *A. negundo* trees sampled in our study, *A. glabripennis* exit holes were first found in the mid-crown trunk section, suggesting that this was the first region infested. However, in the *A. platanoides* and *A. saccharinum* trees, initial *A. glabripennis* attack appeared to occur over a larger portion of the upper trunk and crown (Table 3).

Based on the observations in China and Chicago described above, we suggest inspectors focus their surveys on the upper trunk and lower portion of major branches of the principal host trees present in any particular area. Targeting the upper trunk and lower portion of major branches would be recommended for all sizes of trees that have a clear trunk. However, for trees with branching along the entire trunk or with several basal suckers, inspectors should examine the entire trunk, starting from groundline.

Table 2. Mean percent of trunk samples that contained *Anoplophora glabripennis* oviposition pits, living life stages (eggs, larvae, pupae, and callow adults), and exit holes by within-tree location (meters above groundline) and tree species (elm, *Ulmus pumila*; poplar, *Populus nigra* var. *thevestina*; and willow, *Salix matsudana*) for trees sampled in China during October 2000, June 2001, and April 2002.

Height above groundline (m)	**Elm (N = 17)**	**Poplar (N = 21)**		**Willow (N = 11)**		**All (N = 49)**	
Oviposition pits							
6 m	11.6 ± 3.3	1.2 ± 0.7	d	0.0 ± 0.0	d	4.9 ± 1.5	c
5 m	12.3 ± 2.9	4.5 ± 2.0	cd	0.4 ± 0.3	d	6.6 ± 1.5	c
4 m	22.4 ± 4.4	12.0 ± 3.0	bc	13.1 ± 3.8	c	15.9 ± 2.2	b
3 m	20.4 ± 3.2	21.1 ± 3.8	ab	20.7 ± 3.8	bc	20.8 ± 2.1	ab
2 m	16.1 ± 2.9	23.9 ± 3.9	ab	38.6 ± 5.5	a	24.5 ± 2.5	ab
1 m	17.8 ± 5.4	37.7 ± 6.4	a	27.2 ± 3.7	ab	28.4 ± 3.6	a
N (trees) =	17	21		11		49	
$P =$	0.1351	0.0001		0.0001		0.0001	
$F =$; d.f.	1.73; 5,95	16.6; 5,117		25.4; 5,55		21.6; 5,279	
Life stages							
6 m	12.9 ± 5.1	0.5 ± 0.3	d	0.0 ± 0.0	c	4.8 ± 2.0	c
5 m	11.8 ± 4.7	3.8 ± 1.6	cd	0.0 ± 0.0	c	5.9 ± 1.9	c
4 m	21.8 ± 4.6	10.4 ± 2.3	bc	11.0 ± 3.2	bc	14.3 ± 2.1	b
3 m	28.7 ± 6.2	23.9 ± 3.7	ab	31.0 ± 5.4	ab	27.1 ± 2.9	a
2 m	11.5 ± 3.3	28.0 ± 4.3	a	36.7 ± 7.8	a	24.5 ± 3.1	ab
1 m	14.1 ± 6.5	33.6 ± 5.0	a	21.3 ± 4.8	ab	24.3 ± 3.5	ab
N (trees) =	16	21		11		48	
$P =$	0.0651	0.0001		0.0001		0.0001	
$F =$; d.f.	2.16; 5,89	21.02; 5,117		15.21; 5,55		18.2; 5,273	
Exit holes							
6 m	16.7± 16.7	1.5± 1.5	b	0.0 ± 0.0	b	4.4 ± 3.6	c
5 m	0.0± 0.0	11.4 ± 6.6	ab	0.0 ± 0.0	b	6.3 ± 3.8	bc
4 m	27.0± 15.3	17.4 ± 6.7	ab	8.3 ± 6.2	b	17.8 ± 5.3	abc
3 m	39.7± 18.9	18.4 ± 5.3	ab	40.3 ± 10.4	a	27.7 ± 5.8	a

Table 2. Continued.

Height above groundline (m)	**Elm (N = 17)**	**Poplar (N = 21)**		**Willow (N = 11)**		**All (N = 49)**	
2 m	14.3± 14.3	21.0 ± 8.0	ab	43.7 ± 10.5	a	24.0 ± 6.1	ab
1 m	4.8± 4.8	31.0 ± 9.2	a	7.6 ± 4.1	b	20.2 ± 5.8	abc
N (trees) =	7	17		6		30	
P =	0.3493	0.0490		0.0001		0.0029	
F =; d.f.	1.16; 5,35	2.32; 5,94		10.78; 5,30		3.76; 5,171	

* Means followed by the same letter within columns for each parameter were not significantly different at the 0.05 level, Tukey multiple range test.

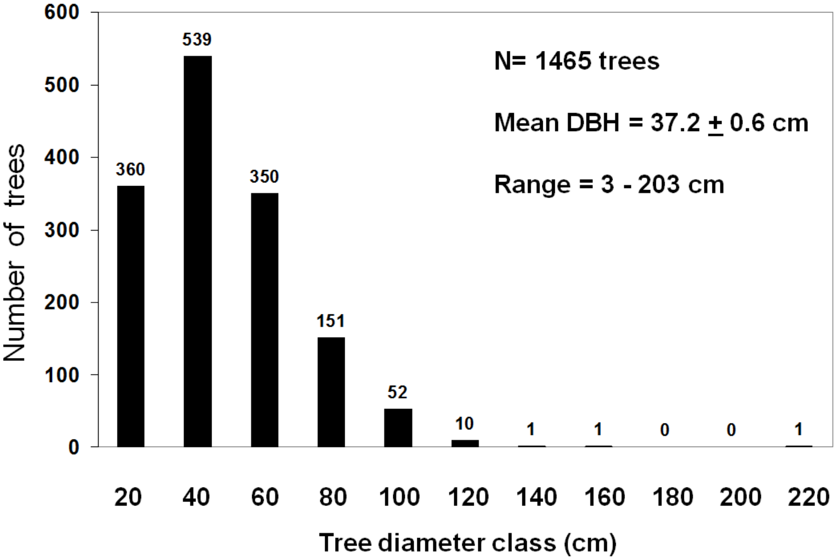

Figure 1. Frequency diagram depicting the number of trees by 20-cm diameter-at-breast-height increments that were apparently infested with *Anoplophora glabripennis* and removed in Chicago during the 1999-2003 eradication program.

Life stages recovered. The proportion of *A. glabripennis* individuals recovered as eggs, larvae, pupae, and callow adults followed similar trends in China and Chicago (Table 4); only trees with living *A. glabripennis* life stages were included in Table 4. During winter and spring, in both China (April) and Chicago (February-April), we recovered mostly larvae and a few apparently viable eggs, indicating that larvae were the principal overwintering stage (Table 4). Although we recovered no pupae or callow adults in our samples from February through April, we did observe one *A. glabripennis* pupa in a Chicago tree that was felled during the eradication program in February 1999 but not included in our study. In June, in both China and Chicago, larvae were still the dominant within-tree life stage. Both pupae and callow adults were also found, but no eggs (Table 4). Apparently, by June, larvae had emerged from all overwintering eggs and no new adult oviposition had yet begun. The two trees sampled in Chicago in July 1999 had only current-year oviposition pits on the bark surface, and only eggs were found in the samples. In fall (October) in China, we found mostly larvae and eggs, but also a few pupae and callow adults (Table 4). This pattern of seasonal development is consistent with earlier reports (Yan and Qin 1992, Haack et al. 1997). The fact that *A. glabripennis* can overwinter in multiple life stages helps explain why adult emergence is staggered over time, which results in adults feeding and ovipositing throughout summer and fall. During the eradication program in Chicago, for example, live *A. glabripennis* adults were observed on trees primarily during July to October, but in one warm year an adult was found ovipositing in early December.

Table 3. Mean percent of trunk samples that contained *Anoplophora glabripennis* oviposition pits, living life stages (eggs, larvae, pupae, and callow adults), and exit holes by within-tree location and tree species (boxelder, *Acer negundo*; Norway maple, *Acer platanoides*; silver maple *Acer saccharinum*; and green ash, *Fraxinus pennsylvanica*) for trees sampled in Chicago in 1999.

Location above groundline*	**Boxelder (N = 2)**	**Norway maple (N = 18)**		**Silver maple (N = 13)**		**Green ash (N = 2)**		**All (N = 35)**	
Oviposition pits									
Section 5	33.3 ± 0.0	23.0 ± 5.1	b**	22.5 ± 4.8	ab	5.6 ± 5.6	b	22.4 ± 3.2	b
Section 4	50.0 ± 16.7	45.6 ± 6.5	a	34.3 ± 7.7	a	80.2 ± 8.7	a	43.6 ± 4.8	a
Section 3	16.7 ± 16.7	30.1 ± 7.6	ab	31.2 ± 7.4	a	14.3 ± 14.3	ab	28.8 ± 4.9	ab
Section 2	0.0 ± 0.0	0.2 ± 0.2	c	2.7 ± 2.2	b	0.0 ± 0.0	b	1.1 ± 0.8	c
Section 1	0.0 ± 0.0	1.1 ± 1.1	c	7.7 ± 7.7	b	0.0 ± 0.0	b	3.4 ± 2.9	c
N (trees) =	2	18		13		2		35	
P =	0.0513	0.0001		0.0003		0.0168		0.0001	
F =; d.f.	5.12; 4,5	18.6; 4,85		6.19; 4,60		8.96; 4,5		29.5; 4,170	
Life stages									
Section 5	66.7 ± 33.3	19.6 ± 4.8	b	30.4 ± 8.1	a	0.0 ± 0.0		26.1 ± 4.7	a
Section 4	16.7 ± 16.7	52.6 ± 7.1	a	31.2 ± 8.2	a	100.0 ± 100.0		43.7 ± 5.5	a
Section 3	16.7 ± 16.7	27.8 ± 7.3	b	27.7 ± 9.3	a	0.0 ± 0.0		26.2 ± 5.3	a
Section 2	0.0 ± 0.0	0.0 ± 0.0	c	7.7 ± 7.7	ab	0.0 ± 0.0		3.0 ± 3.0	b
Section 1	0.0 ± 0.0	0.0 ± 0.0	c	0.0 ± 0.0	b	0.0 ± 0.0		0 ± 0	b
N (trees) =	2	17		13		1		33	
P =	0.1819	0.0001		0.0014		n.a.		0.0001	
F =; d.f.	2.40; 4,5	22.5; 4,80		5.08; 4,60		n.a.		22.2; 4,160	
Exit holes									
Section 5	0.0 ± 0.0	7.1 ± 7.1		23.6 ± 19.4				12.9 ± 8.3	
Section 4	100.0 ± 100.0	44.6 ± 16.8		27.3 ± 19.5				42.2 ± 12.4	
Section 3	0.0 ± 0.0	33.9 ± 17.4		29.1 ± 19.8				29.5 ± 11.8	
Section 2	0.0 ± 0.0	0.0 ± 0.0		20.0 ± 20.0				7.7 ± 7.7	
Section 1	0.0 ± 0.0	14.3 ± 14.3		0.0 ± 0.0				7.7 ± 7.7	

Table 3. Continued.

Location above groundline*	**Boxelder (N = 2)**	**Norway maple (N = 18)**	**Silver maple (N = 13)**	**Green ash (N = 2)**	**All (N = 35)**
N (trees) =	1	7	5	0	13
P =	n.a.	0.1024	0.7565	n.a.	0.0576
F =; d.f.	n.a.	2.12; 4,30	0.47; 4,20	n.a.	2.43; 4,60

* Section 1 = base of trunk, Section 2 = mid-trunk, Section 3 = trunk section near base of crown, Section 4 = Trunk section near mid-crown, and Section 5 = base of a major branch.

** Means followed by the same letter within columns for each parameter were not significantly different at the 0.05 level, Tukey multiple range test.

Table 4. Percentage of living *Anoplophora glabripennis* life stages that were eggs, larvae, pupae, or callow adults at the time of tree dissection in China and Chicago during field studies from 1999 to 2002.

Location	**Percentage found by life stage (%)**				**No. of**	**No. of**
Month and year	**Eggs**	**Larvae**	**Pupae**	**Adults**	**life stages**	**trees**
China						
April 2002	15.5	84.5	0.0	0.0	197	11
June 2001	0	69.2	18.1	12.7	331	19
October 2000	20.7	78.3	0.1	0.9	496	17
Chicago						
February 1999	3.7	96.3	0.0	0.0	451	25
March 1999	0	100.0	0.0	0.0	56	1
April 1999	16.7	83.3	0.0	0.0	62	6
June 2001	0	95.1	4.7	0.2	113	8
July 1999	100	0	0	0	15	2
September 1999	0	100.0	0.0	0.0	5	1

Host suitability index. The mean host suitability index was significantly higher for *Populus* and *Salix* compared with *Ulmus* for the 49 trees sampled in China (Table 1). For the 38 mature trees sampled in Chicago in 1999, the mean host suitability index was highest for *A. negundo*, intermediate for *A. platanoides* and *A. saccharinum*, and lowest for *F. pennsylvanica* (Table 1). For the nine smaller trees sampled in Chicago in 2001, host suitability was similar between *A. negundo* and *U. americana* (Table 1).

The relatively high suitability of *Acer* species for *A. glabripennis* development may help explain the apparent preferential infestation of *Acer* trees by *A. glabripennis* in China (Sun et al. 1990, He and Huang 1993, Gao et al. 1993), Europe (Hérard et al. 2006), New York City (Haack et al. 1997), South Korea (Williams et al. 2004), and Toronto, Canada (Jean J. Turgeon, Canadian Forest Service, personal communication). Similarly, in laboratory tests, various species of *Acer* were generally found to be the most suitable for *A. glabripennis* larval survival and development, whereas *Fraxinus* species were among the least suitable of the tree species tested (Bancroft et al. 2002, Ludwig et al. 2002, Morewood et al. 2003). However, as Keena (2002) noted, adult females reared from lightly infested *Fraxinus* species were larger in average body size and more fecund than females reared from more heavily infested *Acer* species, indicating a trade off between initial egg density, host suitability, and subsequent vigor of the progeny adults.

Infested trees in Chicago. The six most commonly infested tree genera in Chicago, in decreasing order, were *Acer*, *Ulmus*, *Fraxinus*, *Aesculus*, *Betula* and *Salix* (Table 5). The other five infested genera (*Celtis*, *Malus*, *Pyrus*, *Sorbus*, and *Tilia*) were represented by only one or two trees each. It is not certain if *A. glabripennis* would have completed development in all of these latter five genera. At times trees were cut only because *A. glabripennis* oviposition pits were found (*Celtis*, *Malus*, *Pyrus*, and *Tilia*). The one *Sorbus* tree that was removed, however, had both oviposition pits and exit holes. In China, species of *Pyrus* and *Tilia* have been reported as occasional hosts, but not *Celtis* or *Sorbus* (Haack et. al. 1997, Lingafelter and Hoebeke 2002, Smith 2006, Sawyer 2007). Earlier reports of *A. glabripennis* infesting two *Prunus* trees and two *Robinia* trees in Chicago (Nowak et al. 2001) were not substantiated.

When compared to the overall population of street trees in Chicago, the genera *Acer* and *Ulmus* were infested at a rate significantly higher than their actual proportion of the tree population (Table 5). Similarly, *Aesculus*, *Celtis*, *Fraxinus*, *Pyrus*, and *Tilia* were significantly underrepresented among the infested street trees when compared to their overall percentage of the city street-tree population (Table 5). There were no trees identified as either *Malus* or *Salix* in the Chicago street tree inventory. Given the above infestation trends, we recommend that inspectors concentrate their survey efforts on the most common host tree genera in their locality, especially *Acer* and *Ulmus*.

There were 30 genera of hardwood trees ($N = 137{,}601$ trees) that were part of the Chicago street tree inventory that were not recorded as being hosts of *A. glabripennis* in Chicago. In decreasing order of tree frequency, the genera were: *Gleditsia, Quercus, Populus, Platanus, Catalpa, Ginkgo, Alianthus, Prunus, Crateagus, Gymnocladus, Morus, Nyssa, Robinia, Alnus, Magnolia, Zelkova, Juglans, Hibiscus, Cercis, Maclura, Crataegus, Amelanchier, Fagus, Carpinus, Liquidambar, Corylus, Phellodendron, Cornus, Liriodendron,* and *Ostrya.* Of these 30 genera, *Alnus, Carpinus, Fagus, Hibiscus, Morus, Platanus, Populus, Prunus, Quercus* and *Robinia* have been reported as ovipositional hosts on at least one occasion in China, Europe, and New York, although complete development has not been documented in all cases (He and Huang 1993, Haack et al. 1997, Nowak et al. 2001, Hérard et al. 2006). For example, in Europe, *A. glabripennis* exit holes were found on *Fagus*, but the infested *Carpinus*, *Platanus*,

Table 5. The number of trees in Chicago that were found to be infested with *Anoplophora glabripennis* during 1998-2003 and the evidence of infestation recorded; number of infested trees that were on private property or along streets; number of infested street trees expressed on a percentage basis; number and proportion of all street trees in Chicago based on the 2003 inventory; and a *z*-test comparison of the proportions of infested street trees to the overall street tree inventory by tree genus.

	Number of infested trees					All Street trees		Street tree z-test	
Genus	**All**	**Evidence***	**Private**	**Street**	**(%)**	**Number**	**%**	**z**	***P***
Acer	1102	EH, OP	312	790	(82.46)	230,012	42.63	24.9	< 0.001
Aesculus	17	EH, OP	15	2	(0.21)	4762	0.88	2.05	= 0.041
Betula	11	EH, OP	10	1	(0.10)	1469	0.27	0.70	= 0.483
Celtis	1	OP	0	1	(0.10)	8512	1.58	3.54	< 0.001
Fraxinus	64	EH, OP	7	57	(5.95)	91,532	16.96	9.03	< 0.001
Malus	1	OP	1	0		0	n.a.		
Pyrus	1	OP	1	0		8399	1.56	3.77	< 0.001
Salix	9	EH, OP	9	0		0	n.a.		
Sorbus	1	EH	1	0		616	0.11	0.54	= 0.590
Tilia	1	OP	0	1	(0.10)	23,315	4.32	6.34	< 0.001
Ulmus	252	EH, OP	146	106	(11.06)	22,824	4.23	10.4	< 0.001
Unknown	5	EH, OP	5	0		1027	0.19		
Total	1465		507	958		539,613			

* Evidence of *A. glabripennis* infestation was based on the presence of oviposition pits (OP), exit holes (EH), or both.

and *Prunus* trees were destroyed prior to any adult emergence (Franck Hérard, USDA Agricultural Research Service, personal communication.)

The results of our studies indicate that (1) *A. glabripennis* will oviposit throughout the trunk and major branches of host trees, but often starts along the upper trunk and lower portions of major branches; (2) initial infestation can occur along the lower trunk on trees with branches or basal suckers near groundline; (3) larvae are the primary overwintering stage; (4) *Acer* species are highly suitable hosts for *A. glabripennis* development; and (5) *Acer* and *Ulmus* species are preferentially infested in Chicago.

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PATCH-SCALE MOVEMENT DYNAMICS IN THE IOWA GRASSLAND BUTTERFLIES *SPEYERIA CYBELE* AND *MEGISTO CYMELA* (LEPIDOPTERA: NYMPHALIDAE)

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and Keith S. Summerville[1]

ABSTRACT

An understanding of the movement dynamics of invertebrates can be critical to their conservation, especially when managing relatively small, isolated habitats. Most studies of butterfly movement have focused on metapopulation dynamics at relatively large spatial scales, and the results from these studies may not translate well for patchy populations within a single nature preserve. In this work we use individual mark and recapture (IMR) methods to follow the movements of two species of butterfly, *Megisto cymela* (Cramer) and *Speyeria cybele* F. (Lepidoptera: Nymphalidae) within a 240 hectare forest and grassland preserve in central Iowa, USA. Significant redistribution was seen in both species, with 55.7% of *S. cybele* and 31.1% of *M. cymela* undergoing interpatch movement. Median movement rates during the study were 105 m/day for *S. cybele* and 38 m/day for *M. cymela*, with the top decile moving at a rate of over five times these values. This movement did not appear to be random. *S. cybele* exhibited directed movement towards patches with high nectaring potential, although not all such patches were selected. *M. cymela* aggregated in particular prairie patches, especially those with high edge to area ratios, although the reason for aggregation is not clear.

The Iowa landscape has undergone more significant land-use changes than that of perhaps any other state in the United States (Smith 1998). Native tallgrass prairie and savanna ecosystems have been diminished in extent and connectivity, to the point that remnants and newly planted prairie restorations are largely isolated fragments of relatively small size (Rosburg 2001). In such fragmented systems, local extinction rates are likely to be high for insect species if populations are: (i) confined to a spatially limited area; (ii) characterized by small size or; (iii) exposed to localized but potentially frequent disturbances such as prescribed burning (Hammond and McCorkle 1983, Warren 1992, Thomas and Hanski 1997, Thomas 2000). Because connectivity among patches is a critical factor influencing species' distribution among remnant and restored habitat patches, the success with which grassland restorations re-accumulate insect species may in some cases be more a function of landscape context than other commonly used measures of habitat suitability such as habitat area or precise floral assemblage (Packard and Ross 1997, Gutiérrez and Thomas 1999). Some insect species are unwilling to cross hostile matrix, while others are of limited vagility, leading to colonization failure and population aggregation (With and Crist 1995, Schultz and Crone 2001). In highly fragmented landscapes such as the Iowa Tallgrass prairie, interpatch distance often occurs at the scale of 10 km or more, resulting in significant isolation of habitat fragments and potentially exceeding the modal dispersal distance of many grassland insects (Thomas and Hanski 1997). Under these circumstances, within-system dynamics of

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patchy populations (sensu Thomas and Harrison 1992) (on the scale of ½-2 km) becomes the major factor in management and post-disturbance recovery for non-vagile species.

Unfortunately, this type of information is not well-known, especially for butterfly communities in the American Midwest. While there is good large-scale data on some charismatic butterfly species such as *Euphydryas editha bayensis* Sternitzky (Lepidoptera: Nymphalidae) (Harrison 1989) and *Speyeria idalia* Drury (Lepidoptera: Nymphalidae) (Ries and Debinski 2001), pest species (Jones 1977, Root and Kareiva 1984), high altitude species (Matter et al. 2003, Auckland et al. 2004) and European species (Thomas et al. 1992, Thomas and Hanski 1997, Gilbert and Raworth 2005), data that can be used to manage patchy populations in tallgrass prairie regions is lacking (Panzer 2002).

As in many ecosystems, tallgrass floral communities often require burning or other disturbance for their restoration in order to reduce encroachment by native and exotic nonprairie species (Shelford and Winterringer 1959, Leach and Givnish 1996, Wilson and Stubbendieck 1997). Since most remaining prairie habitats are small and fragmented, there is concern that destructive management may have highly deleterious effects upon invertebrate populations (Schlict and Orwig 1998, Swengel 2001). While there is evidence that insect communities may recover after restricted (i.e., partial) burns through local recolonization, even this can be incomplete and populations may suffer depression in the face of repeated disturbance (Panzer 2002, Tooker and Hanks 2004). Because most prairie preserves are managed with fire by splitting them into sub-units and burning at that scale, movement among patches within preserves may be as important as movement among prairies within a landscape (Bestelmeyer et al. 2003).

The goal of this paper is to study the movement patterns of two common butterflies in a tallgrass prairie preserve in central Iowa. In particular, we look at distances traveled and emigration fraction (Hill et al. 1996, Thomas and Kunin 1999) of particular habitat patches. We predicted that the highly vagile *Speyeria cybele* F. (Lepidoptera: Nymphalidae) would move easily between patches, especially as nectaring opportunities shifted throughout the study period (Schneider et al. 2003), thus exhibiting high emigration fraction and large travel distances. On the other hand we predicted that the energetically limited *Megisto cymela (*Cramer) (Lepidoptera: Nymphalidae), whose host plants were common throughout the study site, would exhibit dramatically lower emigration rates and lower travel distances (Auckland et al. 2004). At the same time, because *M. cymela* is an edge associate and may be more tolerant of flying through shady habitat, we expect the matrix to be more permeable to it than to *S. cybele.*

MATERIALS AND METHODS

Study Species. We worked with two species in this study that were chosen for their significant differences in body size, perceived vagility, and predilection for nectaring; both species are relatively common in mesic Tallgrass prairie vegetation in the Midwestern USA (Richard and Heitzman 1996). The first was *S. cybele*, a vagile, non-migratory butterfly, common in Iowa grasslands. In the caterpillar stage, *S. cybele* feeds upon various species of *Viola* (Robinson et al. 2002). As an adult, *S. cybele* actively nectars on a variety of prairie forbs, especially species of *Echinacea* (Asteraceae), *Asclepias* (Ascelepiadaceae), and *Eupatorium* (Asteraceae) (Scott 1986). Adults are ecologically comparable to *S. idalia* (e.g., females aestivate, both species actively nectar on similar species, both are about the same body size), a species of conservation concern in Iowa that is undergoing active reintroduction in other prairies in the state (Shepherd and Debinski 2005).

We also worked with *M. cymela*. Unlike *S. cybele*, *M. cymela* is a fairly weak flyer, whose dispersal ability might be constrained by limited adult feeding.

Adults may feed on some easily accessible food sources (tree sap, fungi, aphid honeydew secretions, and so on), and have occasionally been observed visiting flowers (Scott 1986, Iftner et al 1992), but the majority, if not all, of *M. cymela*'s energy is accumulated in the larval stage (Allen 1997). While *M. cymela* is single-brooded in Iowa, two flight peaks may be occasionally observed due to delayed eclosion of some individuals (Glassberg 1999), or short-term aestivation (Allen 1997). *M. cymela* is an edge associate but not a forest-dwelling butterfly. Iftner et al. (1992) describe the habitat associations of *M. cymela* as "forest margins, brushy meadow, and fields", and Richard and Heitzman (1996) describe it as a species of open woodlands and brushy grasslands. Opler and Krizek (1984) list its host plants as various grasses not found in the forest interior, including *Dactylis glomerata* L. (Poaceae). (Species nomenclature follows Voss 1972, 1985, 1996). Because the canopy cover in the forest was 70-90%, regions between prairie patches were considered interhabitat forest matrix, although forest edge and roadways would be considered habitat.

Site Characteristics. We worked at the Kuehn Conservation Area, a 260 ha tallgrass prairie preserve in southwestern Dallas County, Iowa (41°31'17"N; 94°7'17"W). This region is bordered by the Raccoon River, a private forested area to the east, and a steep woodland ridge system to the west, both serve to contain grassland butterflies largely within the preserve valley (Fig. 1). Kuehn Conservation Area is characterized by six small (0.5-9 ha) prairie openings (Table 1) surrounded by forested ridges dominated by *Quercus alba* L. (Fagaceae),

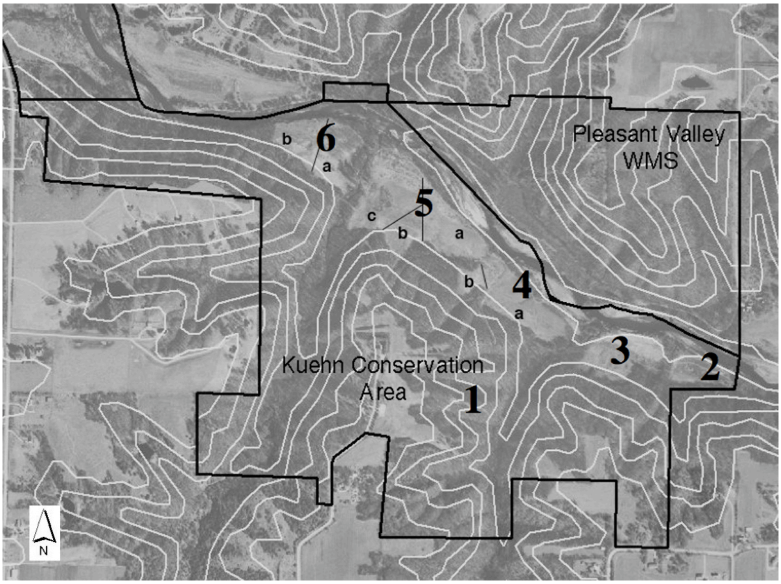

Figure 1: Arial photo of study site with prairies numbered 1-6 (see Methods and Table 1). Contour lines are 10-foot intervals from the United States Geological Survey's 7.5 minute quadrat (distance scale: 2.5 cm ≈ 250 m). All research was conducted within the boundaries of the Kuehn Conservation Area, largely within the valley visible in the center of the figure. The Pleasant Valley WMS is a forested site, dominated by hardwoods (*Quercus* spp. and *Carya* spp.). To the south and west are agricultural lands. Toward the northwest is a wilderness management area consisting of planted forage grasses and *Phragmites australis*.

Table 1. Characteristics of prairie patches. Perimeter to area ratio (P/A Ratio) is the ratio of forest edge to grassland area.

Prairie	**Patch Area (Ha)†**	**P/A Ratio (m/Ha)†**	**Dominant Vegetation‡**
1	0.5	0.071	*Andropogon gerardii, Amorpha canescens, Dalea purpurea., Echinacea pallida*
2	1.1	0.046	*Phalaris arundinacea, Asclepias syrica, Echinacea pallida, Populus deltoides* (saplings)
3	2.91	0.032	*Phalaris arundinacea, Andropogon gerardii, Rubus* spp., *Echinacea pallida*
4	4.14	0.028	*Andropogon gerardii, Sorghastrum nuttans, Ratibida pinnata, Echinacea pallida*
5	8.41	0.018	*Andropogon gerardii, Rubus* spp., *Echinaceae pallida, Phalaris arundinacea*
6	3.96	0.026	*Andropogon gerardii, Helianthus* spp., *Asclepias syrica, Echinaceae pallida*

† Estimates obtained from 2002 digital aerial photos analyzed using ArcView GIS (version 3.2)

‡ From Summerville (unpublished data)

Carya ovata (Miller) K. Koch (Juglandaceae), and *Ulmus* spp. (Ulmaceae). Each of the prairie patches is dominated by grasses (Poaceae), mostly *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, and in more mesic depressions *Phalaris arundinacea* L. Dominant forbs consist of *Echinacea pallida* (Nutt.) Nutt. (Asteraceae*)*, *Ratibida pinnata* (Vent.) Barnhart (*Asteraceae*), *Asclepias syriaca* L. (Asclepidaceae*)*. A variety of other forbs (primarily Asteraceae, Lamiaceae, and Fabaceae) are also frequently encountered throughout the preserve. Prairies 3-6 tended to slope gently downward towards the river, the northeastern regions wetter and generally dominated by *Phragmites australis* (Cav.) Steudel (Poaceae). A region to the west of prairie 1 was actively used for park activities, so was managed as a mix of mown turf grasses and areas of prairie forbs and grasses. Some study species were observed in this area.

This site was optimal for our study because it exhibits natural features of fragmentation and contains the prairie-woodland mosaic typical of Iowa, Missouri, and southern Illinois. This region is deeply bisected by forested habitat (Rosburg 2001), which may affect thermoregulation by individuals attempting to move long distances through a relatively "cooler" habitat type (Daily 1996, Saarinen 2002). The prairie openings at the study site are separated by varying distances through woodlands (70-90% canopy cover in most areas), making this an ideal area to obtain data regarding movement through a heterogeneous landscape, and between habitat patches. The longest measurable distance for travel in our study (a movement from the northwestern edge of Prairie 6 to the southeastern edge of Prairie 2) would have been just over 3 km.

Field Techniques. We used individual mark and recapture (IMR) techniques to obtain data on the large-scale movement of individual butterflies. IMR, where specimens are captured, marked, and then recaptured at some later date to determine characteristics of their movement, provides detailed spatio-temporal information on the individual level which can be directly translated into behaviorally-based models (Odendaal et al 1988, Turchin 1998). GPS was used to determine the location of capture and release and times were recorded for each.

In order to reduce handling stress through multiple recaptures on a given day, and to increase capture efficiency, netted butterflies were immediately transferred to a numbered glassine envelope that was placed within a portable cooler for a period of up to three hours (although periods of 15-60 minutes were more common). Care was taken to avoid damaging wings and legs during transfer. Butterflies were stored with wings in the closed position to reduce stress and unnecessary movement. After capture efficiency decreased markedly at a given site (indicating a high capture fraction), all butterflies were marked and released, and the site was not resampled until a subsequent date. Sites were revisited every 3-5 days depending upon weather conditions. Unique marks were applied with a permanent marker to the underside of the wings according to well-established techniques (Ehrlich and Davidson 1960, Kearns and Inouye 1993, Horner-Devine et al. 2003, Winter 2003). In most cases the marks were easily interpreted upon recapture but occasionally the loss of wing fragments where marks could have been would lead to ambiguous readings. When this occurred, attempts were made to use other information (such as sex, extent of wing damage, and other captures on the same day) to uniquely identify individuals. If this could not be done, the recapture data was not used in subsequent analyses, although the individual was recorded as a recapture.

When capturing, we attempted to walk in a regular pattern throughout the prairie openings. We had one to four researchers working in a patch at a time and when we had more researchers in a patch we also spent time sampling in the forest within about 25 m of the edge. We also sampled along a mown path to the southwest of Prairie 5 and a gravel road to the southwest of Prairie 4. On a few occasions we encountered an individual while outside of the active sampling region. These individuals were also captured and marked.

As shown in Fig. 1, prairie fragments were given a number (1-6), Prairie 1 being a small, isolated prairie in the southern range of the park, 2-6 moving from the southeast to northwest. All prairies were isolated from the others by forest matrix except the two largest prairies: 4 and 5. Although these prairies were connected, the corridor region was relatively small and Prairie 4 sloped uphill away from the corridor, such that the two appeared more distinct at the site than in the photographs. For the less vagile *M. cymela*, the large prairies 4, 5, and 6 were further subdivided according to landscape features (abrupt change in forest edge direction or significant change in slope) also shown in Fig. 1. Prairie 6 is the only prairie where there was no obvious feature to distinguish regions. It was simply split roughly in half.

In order to investigate behavior on a finer scale, we also followed individual butterflies for a period of twenty minutes each, or until the individual was lost, as happened occasionally. We were careful to avoid casting shadows upon the butterflies or otherwise disturbing their behavior. We set marker flags to indicate points of resting between flights, waiting until the individual had risen again to avoid causing premature flight. This process was easier for *M. cymela* than *S. cybela*, because it was very difficult to follow the latter quickly enough to keep it in sight while at the same time not disturbing it. Hence information on these observations will only be reported for *M. cymela*. Occasionally, *M. cymela* would exhibit apparent avoidance behavior where it would spiral rapidly into the forest canopy. As this behavior often appeared to be a response to disturbance from the researchers, we halted tracking at this point. See Schtickzelle and Baguette (2003) for a more complete description of this technique.

Data Analysis. To estimate the total population within the study area, we used the Jolly-Seber method of daily population estimation (Southwood 1978, Blower et al. 1981). This method allowed for the accurate estimation of population size at various times even under conditions of: 1) movement of individuals between habitat patches outside of the study area; 2) emergence and death of new individuals; and 3) unequal sampling effort in any given region on a particular day and similarly unequal time between sampling events.

Given the small populations in individual prairies or prairie fragments, as well as the relatively small number of recaptures within the prairie of initial capture, we did not use the Jolly-Seber method to calculate these population sizes as errors would be large. In this case, we were interested only in relative (rather than absolute) population sizes. Assuming that emergence and death rates were similar throughout the study area, we can determine the fraction of the total population residing in a given patch by calculating a modified Lincoln Index for each patch. There, $P_i = n_i^2 / m_i$, where P_i is the relative population in patch i, n_i is the total number of captures in that patch, and m_i is the number of recaptures of marked individuals in patch i originating from that patch before a given date (Blower et al 1981). We used this estimate to determine the fraction of butterflies in a given prairie patch and then combined this with the Jolly-Seber estimate of the total population to produce population estimates for each patch. Sensitivity values were calculated as the change in the population estimate per patch that would result if one more or one fewer butterflies were recaptured. Most, but not all, of the population estimates were fairly insensitive to small changes in the number of recaptures (the median sensitivity is about 7%). This amount of change led to a difference of about 0.8% when estimating the relative fraction of butterflies within a given patch.

All of our linear regressions and statistical comparisons were made using PC SAS for Windows v 9.1 Service Pack 2 (SAS Institute, 2006). Confidence levels of 95% or greater were considered statistically significant.

RESULTS

We captured 402 individuals of *S. cybele* and 883 individuals of *M. cymela* from June – August 2004. Recapture rates for each species were roughly 20% (Table 2). Of recaptures, 44.3% of *S. cybele* and 68.9% of *M. cymela* were observed within the same prairie as release. If we consider the scale of subprairies for the smaller *M. cymela*, 39.3% of recaptures occurred in the same subprairie as release. There was no observed difference in movement distance between males and females for either species (*S. cybele*: Mann-Whitney, $z = -0.76$, 70 cases, $P = 0.45$; *M. cymela*: $z = -0.52$, 120 cases, $P = 0.60$), or in movement rates (*S. cybele*: $z = -0.9$, $P = 0.37$; *M. cymela*: $z = -0.077$, $P = 0.94$), so data for males and females were combined in subsequent analyses except where noted. The median movement rate (total distance between captures/time between captures) for *S. cybele* was 105 m/day and 38 m/day for *M. cymela* (Table 2). Although both species exhibited a large range of distances traveled (Fig. 2), the movement rate per day was generally more compact (Fig. 3). Both species exhibited large tails in the latter measure representing highly vagile individuals.

Table 2. Capture, population, and movement statistics observed for *M. cymela* and *S. cybele* at Kuehn Conservation Area. Emigration fraction is calculated as the number of individuals captured in a different prairie than the one in which they were marked, divided by the total number of captures.

	M. cymela	***S. cybele***
Number of captures	883	402
Fraction recaptures (%)	20.7	19.7
Mean/longest period between recaptures (days)	5/16	6/25
First and last sampling dates	June 11-Jul 28	June 11-August 6
Number of sampling dates	19	23
Emigration Fraction E	57/183 (31.1%)	44/79 (55.7 %)
Estimated population	509 (+/- 265)	213 (+/- 136)
Median movement rate (m/day); 10th–90th percentile	38; 6–198	105; 13–775

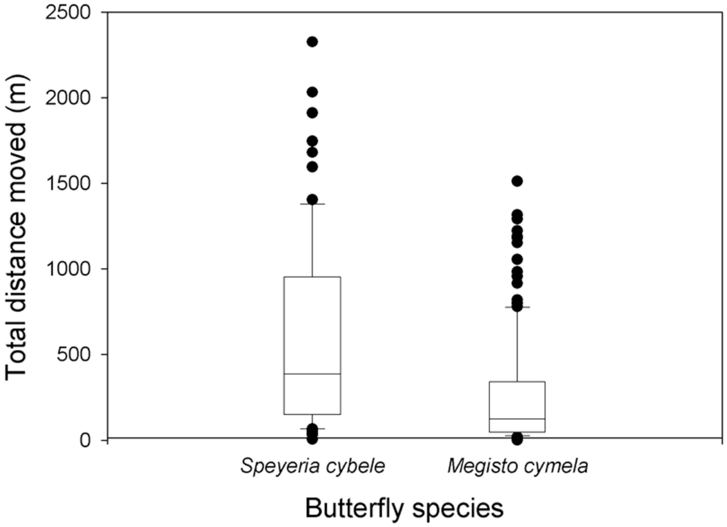

Figure 2: Box and whisker plot of total movement distances (in meters) for recaptured individuals of both species.

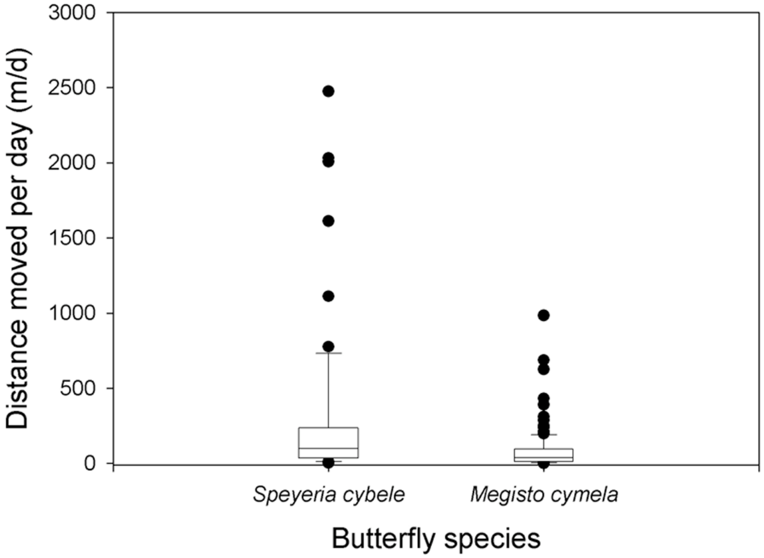

Figure 3: Box and whisker plot of movement rate (in meters per day) for recaptured individuals of both species.

Population estimates for *S. cybele* varied with patch size and ranged from 7 to 54 individuals (Table 3). *S. cybele* population sizes were marginally correlated with prairie size using a simple linear regression model (SAS Institute, 2006) (patch size parameter estimate = 5.01, $P = 0.0577$, $r^2 = 0.64$), with the highest population in the largest prairie, prairie 5, and the smallest in the half-hectare prairie 1. *S. cybele* had the most captures in prairie 2 and the southeast segments of prairies 4 and 5 (Fig. 4). These sites all had abundant *Asclepias sullivantii* A. Gray, *Cirsium arvense* (L.) Scop. (Asteraceae), and other nectar sources, although prairie 2 had a high cover of shrub species as well, including *Cornus* spp.(Cornaceae) and *Salix* spp (Salicaceae). The northwest region of prairie 6 had a large population of *A. syriaca*, but few individuals were ever observed in that area. Although prairie 1 had nectaring opportunities and a few individuals were captured there, during most of our visits there were no *S. cybele* in this prairie. Although significant search time was spent in the northeastern regions of the prairies, very few individuals of either species were found there. The dominance of *P. australis* in these regions left little nectaring opportunity for *S. cybele*, and few suitable egg-laying sites for either species.

We observed a fair amount of interpatch movement for *S. cybele* (Fig. 5a). Prairies 3-6 all exchanged individuals, while individuals were observed to move into prairie 2 only from 3 and 4. Of 8 individuals marked in prairie 1, none were recaptured later, and no marked individuals were recaptured in prairie 1, indicating that most of the interhabitat exchange with prairie 1 was probably with the unsampled area to the west of prairie 1. The largest amount of interaction was between prairies 4 and 5, not surprising because individuals could move between these prairies without entering inter-habitat matrix. If we calculate the per capita emigration (*E*) of various patches (the number of butterflies recaptured in a different prairie from where they were marked, divided by the total number of recaptures from that prairie, from Hill, et al. (1996), we find almost no emigration from prairie 2 (9%; 1/11 individuals). All other prairies had 45% or greater *E*. Very few *S. cybele* were seen in prairie 2 early in the season of study but as time passed the population increased dramatically. Given that this growing population included marked individuals from prairies 3 and 4, it seems likely that much of this population increase was due to immigration from elsewhere (e.g., Fig. 5a). Possible explanations for this movement are: nectaring opportunities were high in this prairie; it may have been too small to support a large larval population, or: eggs might have been destroyed during spring flooding. In either event, butterflies were clearly able to move through the matrix to find this habitat, although we cannot say whether they dispersed again to lay eggs.

Population estimates for *M. cymela* ranged from 4 to 93 individuals (Table 4). *M. cymela* populations were not correlated with patch area ($P = 0.24$) but the highest population estimates were in prairies 1 and 5b. Of 31 individuals marked in 5b, none were recaptured there, while 7 were recaptured in other prairies, perhaps indicating that this patch functioned more as a corridor than as habitat for a stable population. Nearly all individuals were captured along

Table 3. Population estimates for Speyeria cybele observed within each prairie patch at Kuehn Conservation Area. Where the population estimate is based upon a single recapture, the upper bound is recorded as NA.

Prairie #	**1**	**2**	**3**	**4**	**5**	**6**
Area (ha)	0.5	1.1	2.91	4.14	8.41	3.96
Population	7	28	41	53	54	30
Sensitivity	4/NA	26/30	36/48	52/55	52/55	25/38

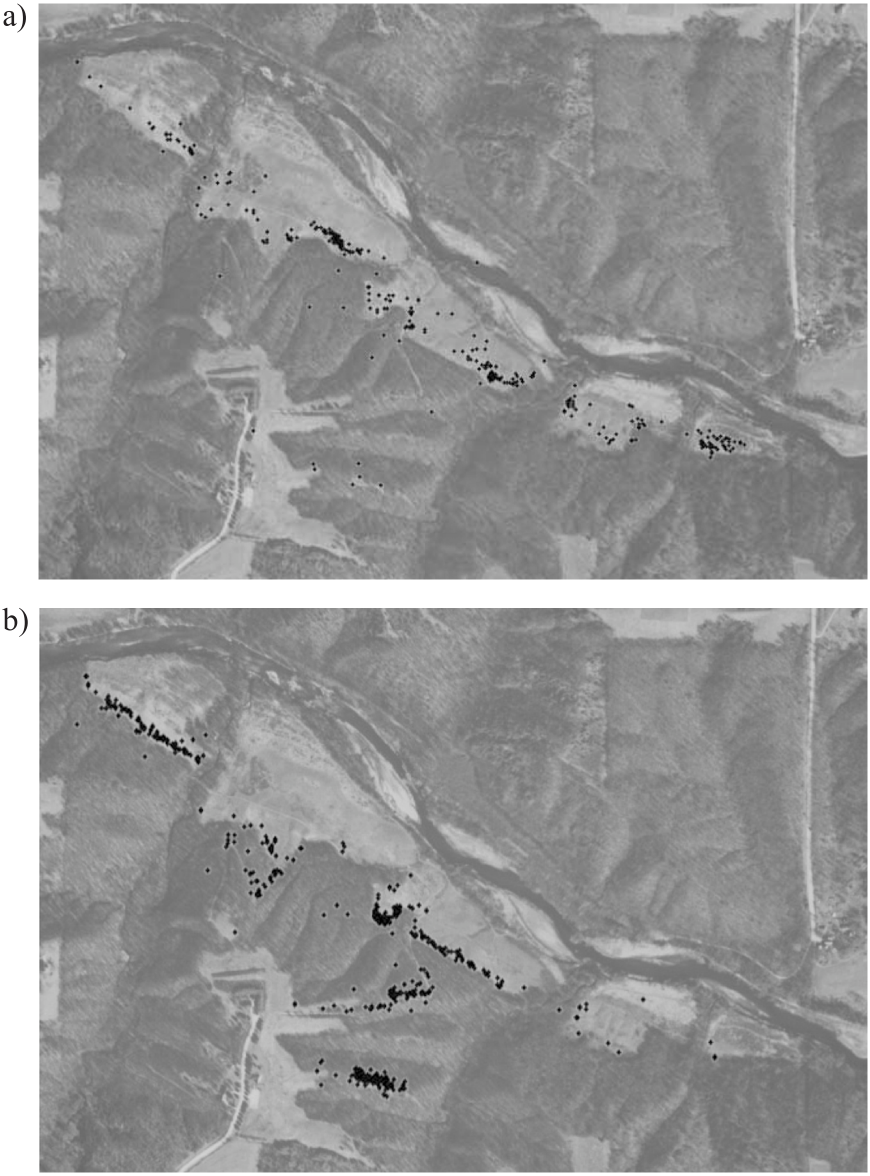

Figure 4: Location of butterfly captures throughout study: a) captures of *S. cybele*. Numerous captures were made in regions of prairies 2, 4, and 5 where nectaring opportunities were high. Very few butterflies were captured in prairie 1 or the western part of 6, although numerous nectaring opportunities existed in these regions as well. Few butterflies were captured in the regions sloping toward the river, even though these sites were visited frequently by researchers; b) captures of *M. cymela*. Nearly all captures were made along the forest edge or within forest matrix. Numerous captures were made in prairie 1, and very few in prairies 2 or 3 (compared with *S. cybele*).

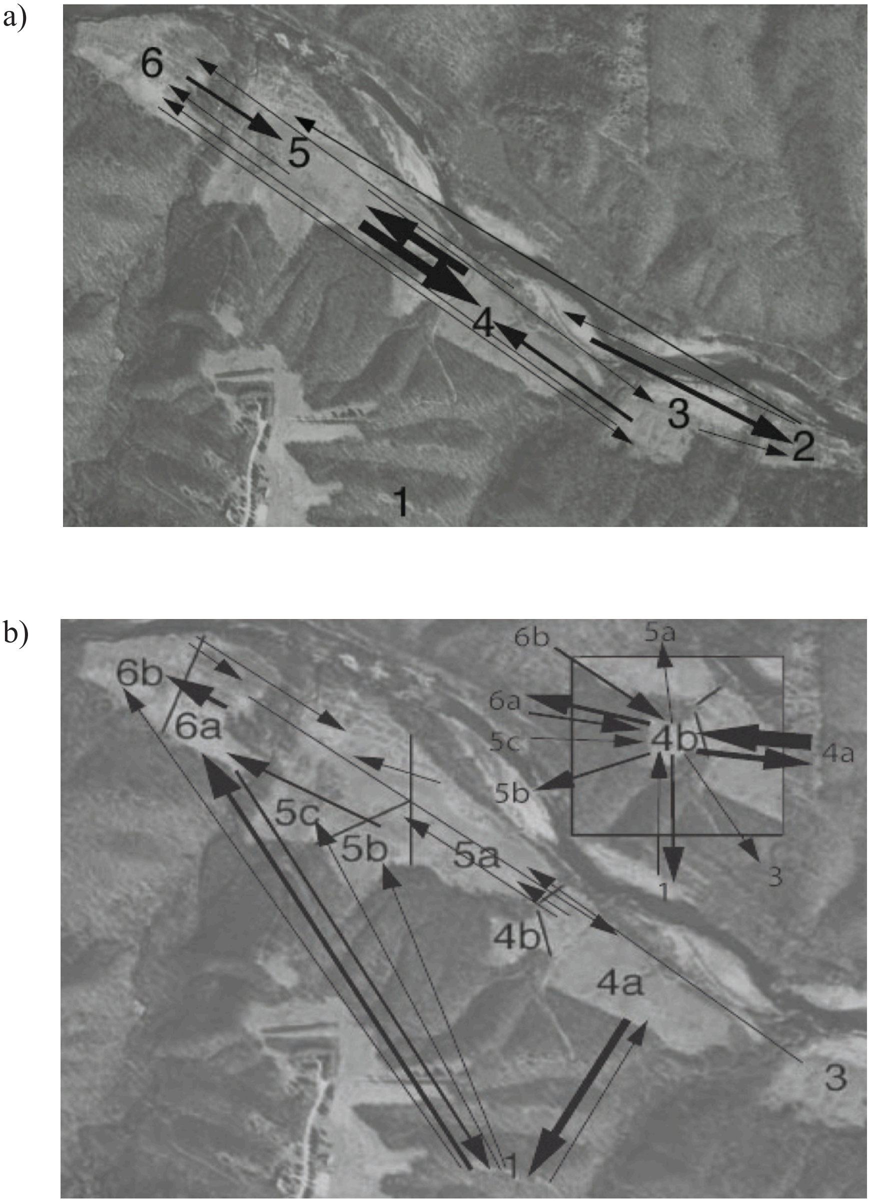

Figure 5: Movement of *S. cybele* (a) and *M. cymela* (b) within the study site. Arrow thickness indicates relative numbers of butterflies observed moving between prairies. In b, subprairie 4b has been separated and added as an inset due to the number of movements in and out of this subprairie patch. The small numbers around this inset indicate which prairies the movement is occurring between but do not indicate actual positions of prairies or subprairies.

Table 4. Population estimates for *M. cymela* in each subprairie patch. GR stands for the long gravel road that moves upslope between prairies 4a and 1. Where a population estimate is impossible, it is recorded as NA. Where a population estimate is based upon a single recapture, the upper bound is recorded as NA.

Prairie #	**1**	**2**	**3**	**4a**	**4b**	**5a**	**5b**	**5c**	**6a**	**6b**	**GR**
Population	93	NA	15	43	50	5	82	4	36	53	71
Sensitivity	91/96	NA	8/NA	41/44	49/51	3/10	54/163	3/6	35/37	44/66	67/76

the southwestern forest edge (Fig. 4b), along the gravel road connecting the visitor's center with subprairie 4a, and in a mown, steeply graded pathway to the southwest of prairies 5b and 5c. We found almost no *M. cymela* in prairie 2 and very few in prairie 3. Prairie 5b started out as a highly populated site in the early spring but became depleted as the season continued. Conversely, as the study progressed, 4b changed from a site with few capture opportunities to one of the two sites with the least amount of time between captures for *M. cymela* (the other being prairie 1). Population density was negatively correlated with patch size ($P = 0.034$) but this effect appears to have been due largely to the very high density in prairie 1 (over twice that of the next-highest density found in prairie 4b). If prairie 1 is left out of the regression, the relationship becomes insignificant ($P = 0.15$).

We find that emigration (E) was lowest in prairie subpatches 6a (31%), 1 (29%), and 4b (25%), indicating that these patches tended to retain individuals. All other subpatches had E above 4a's, which was 59%. In the case of *M. cymela*, there was no obvious reason for the retention within these sites, in terms of abundance of egg-laying sites, shape factor index (sensu Forman 1995), or patch area. Using a linear model, however, for the relationship between butterfly density and the perimeter to area ratio (in meters per hectare), we find that density is positively correlated to perimeter to area ratio, with a slope of 31.8 individuals/ha per m/ha ($P = 0.002$), and an insignificant intercept (-5.8). This suggests that *M. cymela* may seek out, or not exit, prairies dominated by edge habitat, or that preferential movement along edges increases capture frequency.

Megisto cymela were never observed deep in open prairie. Of the 39 individuals for which we followed fine-scale movement and mapped routes traversed, one moved 18 m away from trees and into open prairie before turning back toward the trees, and no others ever moved more than 6 m from the forest edge. The one that ventured the farthest into the prairie may have been exceptional, because it had been following a single row of trees fairly far from the forest edge, and may have been searching for more suitable habitat. On the other hand, numerous individuals were followed into the forest. Movement tended to be along the habitat edge, with 62% (18/29) of those individuals that were tracked at a clearly definable habitat edge having the major axis of their movement along this edge, while only 21% (6/29) moved away from the edge (either into or out of the forest), and 17% (5/29) exhibited no overall bulk movement. This indicates that for *M. cymela*, the presence of edge habitat between larger habitat regions may be useful to encourage population exchange.

DISCUSSION

Our work indicates that *S. cybele* and *M. cymela* exhibit significant movement during the course of a season, with individuals of both species moving between some of the most distant patches in our study site. *S. cybele* is able to cross small amounts of forested matrix habitat in search of nectar sources and tends to aggregate in these areas. As the nectar sources change, or if larval and adult food sources are not locally congruent, we would expect to see net movement of the type observed (Schneider et al. 2003, Auckland et al. 2004, Dennis 2004). In the case of *M. cymela*, the movement is more surprising. As adults are not active feeders, one might expect them to have high patch residence times and remain near emergence sites. While the movement rates recorded in Table 2 may include downward biases due to the nature and scope of the study (mostly related to the fact that highly vagile individuals may leave the limited study area; see Cook et al. 2001, for a discussion and methodological suggestions), it is clear that important redistribution does occur between prairie segments. *M. cymela* was able to cross at least the half-kilometer forested region between prairies 1 and 4, and probably crossed much larger forested regions in moving between prairies 1 and 6. We did not observe marked *S. cybele* crossing more than a few hundred meters of forested area, but this was probably due to the dearth of these captured in the most distant prairie (prairie 1). We did observe some individuals flying into the upper canopy or above it, often as an avoidance behavior. If this is common, it might limit the shade constraint on this species. Numerous individuals were also spotted flying along the gravel pathways and other thin corridors connecting the large grassy area near prairie 1 with the prairies that were part of our study, although these individuals were difficult to capture as they were rarely observed resting in these areas, indicating that *S. cybele* can certainly cross larger expanses of matrix than we observed here. Small pathways may aid this movement as edge effects appear to be important according to Ovaskainen (2004).

The observation that the emigration fraction for *S. cybele* was as low as 10% from prairie 2, and that for *M. cymela* prairie fragments often have emigration fractions on the order of 30%, indicates that prairie management techniques such as burning are likely to destroy the majority of the individuals produced on that patch. *S. cybele* overwinters as unfed 1st instar larvae and *M. cymela* overwinters at the base of grass stems or in the duff as 4th instar larvae (Scott 1986), so fire is likely to result in nearly 100% kill fractions. These kill levels might be tolerable to land managers if: (i) local demes are large and produce at least 25% of their population as emigrants, and; (ii) females indeed move as far as males (Panzer 2003).

Our results indicate that *S. cybele* in the conservation area probably acts as a single population. Only 55% (39/71) of individual recaptures occurred in the same prairie as initial capture and release, indicating that the barriers within the conservation area do not appear to isolate individual subpopulations. The story with *M. cymela* is more complex. If we look at the level of distinct prairie patches separated by inter-habitat matrix or height gradients (i.e. those numbered in Figure 1), 70% of individual recaptures occurred in the same prairie as initial capture and release. This indicates that within the site *M. cymela* may be acting more as a metapopulation, along the continuum between a single population and entirely isolated ones, (Dover 1996, Thomas and Kunin, 1999). It is interesting to note that the two most densely populated patches in our study (1 and 4b) appeared to exhibit a fairly large amount of immigration from most other patches in the study, even though prairie 1 was distant from the others. Both 1 and 4b had small emigration fractions.

Table 5 provides parameters for distance decay curves (frequency of observations versus distance traveled) obtained for both species with a least-squares fit of the negative exponential, as well as a standardized major axis regression for the power function (PROC GENMOD, SAS Institute 2006). These functions were both fit to the inverse cumulative proportion of movement distance per day (Hill et al. 1996). Data are given for males (M), females (F), and both sexes combined. For *S. cybele*, the negative exponential has a higher r^2 than the power function, with values ranging from 0.78 (F) to 0.89 (M) for the negative exponential, and 0.66 (F) to 0.80 (M) for the power function. Hill et al. (1996)

Table 5. Parameter values for least-squares fit of negative exponential and the reduced major axis fit of a power function to the inverse cumulative probability values of movement distances. In the Sex column, C stands for "combined".

	Bin Size		**$I = e^{-kD}$**			**$I = CD^{-n}$**	
	(meters)	**Sex**	k	r^2	C	n	r^2
S. cybele	400	M	8.35x10-4	0.891	18.7	0.823	0.801
		F	4.37x10-4	0.779	2.53	0-Jan	0.657
		C	9.11x10-4	0.866	30	0-Jan	0.738
M. cymele	100						
		M	0.00291	0.839	17.5	1.02	0.946
		F	0.00183	0.688	4.66	0.751	0.813
		C	0.00341	0.904	22.2	1.12	0.971

have suggested that the power function may more accurately predict long-distance colonization for some species, and would indicate that perhaps 1.2% of *S. cybele* might move distances of 5 km or more, while the negative exponential would indicate that about 1.1% would move this distance. For *M. cymela*, both models have fairly good fits, with $r^2 = 0.904$ the negative exponential (males and females combined) and 0.971 for the power function. For both species, the fitted parameters for females result in larger movement distances than for males but the differences were not significant (see above). Similar results, with males moving farther or no significant difference between the sexes, have been reported for butterflies elsewhere (Nieminen 1996, Brommer et al. 1999, Norberg et al. 2002). It is possible that this observation is an artifact of the study scale and that particularly vagile males, for example, were less likely to be resampled as they left the study site.

The power function model would suggest that about 0.16% of *M. cymela* would move distances of 5 km or more while the negative exponential indicates that fewer than 1×10^{-7} would move this far. In either case, the probability of colonization of a distant habitat patch becomes vanishingly small in a state such as Iowa because the likelihood of encountering another habitat patch in a random walk across the landscape is remote.

Thus, our work, coupled with the frequent observation of individuals moving along the gravel road and smaller mowed pathways within the forest, suggests that connectivity will need to be increased in order to improve interactions between isolated populations of similar butterflies in Iowa.

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A FRIEND UNMASKED: NOTES ON *CHAULIOGNATHUS PENSYLVANICUS* (COLEOPTERA: CANTHARIDAE) AND THE NATURE OF NATURAL HISTORY

Andrew H. Williams[1]

ABSTRACT

Data from field observations from 1992 through 2006 and from museum specimens of adult *Chauliognathus pensylvanicus* (DeGeer) from Wisconsin are presented here, with information from the literature. Beetles were found using flowers of 183 species in 29 families growing outside cultivation in Wisconsin and in every Wisconsin county. All evidence supports the characterization of *C. pensylvanicus* as a prairie insect that also lives in other, early successional plant communities.

DEDICATION

This paper is dedicated to the memory of Benjamin D. Walsh, who published basic life history information on *Chauliognathus pensylvanicus* (DeGeer) in “A Friend Unmasked” in 1868. Walsh’s article appeared in *American Entomologist*, the journal he established in partnership with Charles V. Riley that same year.

NOMENCLATURAL NOTE

The beetle usually referred to as *Chauliognathus pennsylvanicus* DeGeer over the past century was first described by DeGeer (1774) as *Telephorus pensylvanicus*. The spelling “*pensylvanicus*” was used by LeConte (1869, 1881), Hubbard (1880), Schwarz (1880) and Riley (1880), though Riley (1869, 1872, 1873) had earlier used the spelling “*pennsylvanicus*”. At the time of DeGeer’s description, “Pensylvania” was a common and apparently acceptable spelling for the colony, so his original spelling should not be considered incorrect. The correct name for this beetle is *Chauliognathus pensylvanicus* (DeGeer).

INTRODUCTION

Chauliognathus pensylvanicus is a distinctive, yellow and black beetle that is commonly found on flowers in late summer over much of the eastern United States (Miskimen 1966, White 1983). This species is often reported to visit flowers of *Solidago* (Table 1). Hentz (1830) noted the modification of their maxillae that facilitates feeding on floral nectar, a subject further discussed by Walsh (1868a). Adults often are covered with pollen of the various flowers they visit (Glover 1856, personal observation), perhaps leading to early reports of their feeding on pollen (Glover 1856, 1869). Such early reports have been passed forward through time in the literature (Riley 1872, 1873, 1880, 1885; Comstock 1879; Dimmock 1884; Lintner 1888; Graenicher 1909; Vestal 1913; Adams 1915; Lutz 1941; Dillon and Dillon 1961; Miskimen 1966; Brown and Brown 1984; Ramsdale 2002), but feeding on pollen warrants confirmation.

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Table 1. Plants bearing flowers visited by adults of *Chauliognathus pensylvanicus*. Citations are provided for previous reports. Original data (presented without citation) comprise 183 species in 29 families growing outside cultivation in Wisconsin. Plant nomenclature generally follows Kartesz (1994).

FAMILY	**SPECIES**	**AUTHORS' COMMENTS**	**CITATION**
Acanthaceae	*Ruellia humilis*		
Agavaceae	*Yucca* sp.	fed upon the pollen	Riley (1873)
Alismataceae	*Sagittaria latifolia*	4 beetles	Robertson (1928)
Apiaceae	*Cicuta maculata*		
	Conium maculatum		
	Daucus carota	15 beetles	Judd (1970)
	Daucus carota	1188 beetles	McCauley and Wade (1978)
	Daucus carota	common	Lago and Mann (1987)
	Daucus carota		Dunn (1996)
	Daucus carota		
	Eryngium yuccifolium		Adams (1915)
	Eryngium yuccifolium		
	Oxypolis rigidior		Robertson (1928)
	Oxypolis rigidior		
	Pastinaca sativa		
	Pimpinella saxifraga		
	Sium suave		Robertson (1928)
	Sium suave		
Apocynaceae	*Apocynum androsaemifolium*		
	Apocynum cannabinum		
Asclepiadaceae	*Asclepias hirtella*		
	Asclepias incarnata	great numbers	Adams (1915)
	Asclepias incarnata	abundant, pollinia on tarsi	Robertson (1928)
	Asclepias incarnata		
	Asclepias syriaca		
	Asclepias tuberosa		
	Asclepias verticillata		

Table 1. Continued.

FAMILY	**SPECIES**	**AUTHORS' COMMENTS**	**CITATION**
Asteraceae	*Achillea millefolium*		
	Achillea sp.		Balduf (1935)
	Ageratina altissima		
	Ambrosia psilostachya		
	Anaphalis margaritacea		
	Arctium sp.		
	Arnoglossum atriplicifolium		
	Aster cordifolius		
	Aster ericoides	frequent	Robertson (1928)
	Aster ericoides		
	Aster lanceolatus	10 beetles	Robertson (1928)
	Aster lanceolatus		
	Aster lateriflorus		
	Aster novae-angliae		
	Aster oolentangiensis		
	Aster pilosus		
	Aster sericeus		
	Aster shortii		
	Aster turbinellus	1 beetle	Robertson (1928)
	Aster umbellatus		
	Aster urophyllus	2 beetles	Robertson (1928)
	Bidens aristosa	abundant, in copula	Robertson (1928)
	Bidens cernua		
	Bidens coronata		
	Bidens laevis	abundant	Robertson (1928)
	Bidens sp.		McLain (1984, 1986)
	Boltonia asteroides	frequent	Robertson (1928)
	Brickellia eupatorioides		
	Carduus acanthoides		Maw (1976)
	Carduus acanthoides		

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Centaurea biebersteinii		
	Cichorium intybus		
	Cirsium altissimum		Johnson (1996)
	Cirsium altissimum		
	Cirsium arvense		Maw (1976)
	Cirsium arvense		
	Cirsium discolor		
	Cirsium muticum		
	Cirsium vulgare	feeding on pollen	Graenicher (1909)
	Cirsium vulgare		
	composites	several hundred beetles	Wheeler (1988)
	Conyza canadensis		McLain (1984)
	Conyza canadensis		
	Coreopsis lanceolata		
	Coreopsis palmata		
	Coreopsis tripteris	1 beetle	Robertson (1928)
	Coreopsis tripteris		
	Crepis tectorum		
	Echinacea purpurea		
	Echinops sphaerocephalus		
	Erechtites hieraciifolia		
	Erigeron annuus		
	Erigeron philadelphicus		
	Erigeron strigosus		
	Eupatorium altissimum		
	Eupatorium coelestinum	1 beetle	Robertson (1928)
	Eupatorium fistulosum	1 dead, due to fungus	Wheeler (1988)
	Eupatorium maculatum		
	Eupatorium perfoliatum		Robertson (1928)
	Eupatorium perfoliatum	1 beetle	Judd (1969)

Table 1. Continued.

FAMILY	SPECIES	AUTHORS’ COMMENTS	CITATION
	Eupatorium perfoliatum		
	Eupatorium purpureum		
	Eupatorium serotinum		Robertson (1928)
	Eupatorium serotinum		
	Eupatorium sessilifolium		
	Eupatorium sp.	many dead, due to fungus	Popenoe and Smyth (1911)
	Eupatorium sp.		McLain (1984, 1986)
	Eupatorium sp.	1000 pairs	McLain (1988)
	Euthamia graminifolia	abundant	Robertson (1928)
	Euthamia graminifolia		Brown and Brown (1984)
	Euthamia graminifolia	large numbers	Wheeler (1988)
	Euthamia graminifolia		
	Gnaphalium obtusifolium	5 beetles	Robertson (1928)
	Gnaphalium obtusifolium		
	Grindelia squarrosa		
	Helenium autumnale	abundant	Robertson (1928)
	Helenium autumnale		
	Helenium sp.	1000 pairs	McLain (1988)
	Helianthus annuus	2 beetles	Robertson (1928)
	Helianthus annuus		Whelan (1936)
	Helianthus annuus		
	Helianthus divaricatus	frequent	Robertson (1928)
	Helianthus giganteus		
	Helianthus grosseserratus		Robertson (1928)
	Helianthus grosseserratus		
	Helianthus x *laetiflorus*		Robertson (1928)
	Helianthus x *laetiflorus*		
	Helianthus maximiliani		
	Helianthus mollis		
	Helianthus occidentalis		

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Helianthus sp.		Bailey et al. (1984)
	Helianthus sp. (*divaricatus* or *strumosus* or both)		
	Helianthus strumosus		Balduf (1935)
	Helianthus tuberosus		Robertson (1928)
	Helianthus tuberosus		
	Heliopsis helianthoides		Robertson (1928)
	Heliopsis helianthoides		
	Heterotheca subaxillaris		McLain (1984)
	Heterotheca villosa		
	Hieracium aurantiacum		
	Hieracium kalmii		
	Ionactis linariifolius		
	Lactuca biennis		
	Lactuca florida	frequent	Robertson (1928)
	Leucanthemum vulgare		
	Liatris aspera		
	Liatris ligulistylis		
	Liatris pycnostachya		
	Liatris spicata	feeding on pollen	Graenicher (1909)
	Liatris spicata		
	Mikania scandens		McLain (1982, 1984, 1986)
	Polymnia canadensis		
	Prenanthes alba		
	Prenanthes aspera		
	Prenanthes crepidinea	frequent	Robertson (1928)
	Ratibida columnifera		
	Ratibida pinnata	feeding on pollen	Graenicher (1909)
	Ratibida pinnata		
	Rudbeckia hirta		
	Rudbeckia laciniata		

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Rudbeckia subtomentosa	2 beetles	Robertson (1928)
	Rudbeckia subtomentosa		
	Rudbeckia triloba	abundant	Robertson (1928)
	Rudbeckia triloba		
	Silphium integrifolium		
	Silphium laciniatum		
	Silphium perfoliatum		
	Silphium terebinthinaceum		Adams (1915)
	Silphium terebinthinaceum		
	Solidago sp.		Walsh (1868a,b)
	Solidago sp.	quite abundant	Riley (1869, 1872)
	Solidago sp.		Riley (1873, 1893)
	Solidago sp.		Smith (1882)
	Solidago sp.		Dimmock (1884)
	Solidago sp.	unusually large numbers	Lintner (1888)
	Solidago sp.	often very large numbers	Smith (1894)
	Solidago sp.		Needham (1898)
	Solidago sp.		King (1914)
	Solidago sp.		Johnson (1915)
	Solidago sp.		Lutz (1921)
	Solidago sp.		Schmucker (1933)
	Solidago sp.	seems preferred host	Miskimen (1966)
	Solidago sp.	900 beetles	Wiener (1974)
	Solidago sp.		Maw (1976)
	Solidago sp.	very common, especially on goldenrod	Headstrom (1977)
	Solidago sp.	large numbers of beetles	Eisner et al. (1981)
	Solidago sp.	454 beetles	Woodhead (1981)
	Solidago sp.		McLain (1982, 1984, 1986, 2005)
	Solidago sp.		White (1983)
	Solidago sp.		Bailey et al. (1984)

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Solidago sp.		Brown and Brown (1984)
	Solidago sp.	476 pairs	McLain (1988)
	Solidago sp.		Downie and Arnett (1996)
	Solidago sp.		Jenkins and Matthews (2003)
	Solidago sp.		Reeves and O'Hara (2004)
	Solidago sp. & allied plants		Blatchley (1910)
	Solidago sp. & allied plants		Rockenbach (1930)
	Solidago sp. & allied plants		Dillon and Dillon (1961)
	Solidago sp. & associated plant species in open fields		Mason (1976, 1980)
	Solidago sp. & other composites		Adams (1915)
	Solidago sp. & other composites		Dunn (1996)
	Solidago sp. & other plants		Mason (1972)
	Solidago sp. & related plants		White (1983)
	Solidago canadensis	abundant	Robertson (1928)
	Solidago canadensis		Brown and Brown (1984)
	Solidago canadensis	large numbers	Wheeler (1988)
	Solidago canadensis		
	Solidago gigantea		
	Solidago juncea		
	Solidago missouriensis		Robertson (1928)
	Solidago missouriensis		Whelan (1936)
	Solidago missouriensis		
	Solidago nemoralis		Robertson (1928)
	Solidago nemoralis		
	Solidago ohioensis		
	Solidago ptarmicoides		
	Solidago riddellii		
	Solidago rigida	abundant	Robertson (1928)
	Solidago rigida		Whelan (1936)
	Solidago rigida		

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Solidago sciaphila		
	Solidago speciosa	frequent	Robertson (1928)
	Solidago speciosa		
	Solidago uliginosa		
	Solidago ulmifolia		
	Sonchus arvensis		
	Synosma suaveolens		
	Tanacetum vulgare		
	Taraxacum offininale		
	thistles		Hentz (1830)
	thistles		Walsh (1868a)
	thistles		Dimmock (1884)
	Verbesina alternifolia	in copula	Robertson (1928)
	Verbesina alternifolia		Jenkins and Matthews (2003)
	Vernonia baldwinii		Johnson (1996)
	Vernonia fasciculata		
Balsaminaceae	*Impatiens pallida*		
Brassicaceae	*Berteroa incana*		
	Brassica nigra		
	Erysimum cheiranthoides		
	Hesperis matronalis		
Campanulaceae	*Campanulastrum americanum*		
	Lobelia siphilitica		
Caprifoliaceae	*Sambucus canadensis*		
Clusiaceae	*Hypericum perforatum*		
Commelinaceae	*Tradescantia ohiensis*		
Convolvulaceae	*Calystegia sepium*		
	Convolvulus arvensis		
Cornaceae	*Cornus amomum*		

Table 1. Continued.

FAMILY	**SPECIES**	**AUTHORS' COMMENTS**	**CITATION**
Cucurbitaceae	cucumber (*Cucumis sativus*)		Balduf (1935)
	Echinocystis lobata		
Dipsacaceae	*Dipsacus fullonum*		
	Dipsacus laciniatus		
Euphorbiaceae	*Euphorbia corollata*		
	Euphorbia dentata		
Fabaceae	*Amorpha canadensis*		
	Chamaecrista fasciculata		
	Dalea candida		
	Dalea purpurea		
	Lespedeza capitata		
	Medicago lupulina		
	Melilotus alba		
	Melilotus officinalis		
	Melilotus sp.		Maw (1976)
	Trifolium hybridum		
	Trifolium pratense		
Lamiaceae	*Agastache nepetoides*		
	Agastache scrophulariifolia		
	Lycopus americanus	abundant	Robertson (1928)
	Lycopus americanus		
	Lycopus sp.		
	Mentha arvensis	abundant	Robertson (1928)
	Mentha arvensis		
	Monarda fistulosa		
	Monarda punctata		
	Nepeta cataria		
	Prunella vulgaris		
	Pycnanthemum tenuifolium		
	Pycnanthemum virginianum		

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Teucrium canadense		
Liliaceae	*Allium cernuum*		
	Allium tuberosum		
Lythraceae	*Lythrum alatum*		
	Lythrum salicaria		
Malvaceae	cotton (*Gossypium* sp.)	great numbers	Glover (1855)
	cotton (*Gossypium* sp.)	up to 6 per bloom	Glover (1856)
	cotton (*Gossypium* sp.)	very common	Glover (1869)
	cotton (*Gossypium* sp.)	abundant	Comstock (1879)
	cotton (*Gossypium* sp.)	quite common	Riley (1880, 1885)
	cotton (*Gossypium* sp.)	abundant	Ashmead (1894-95)
	Napaea dioica		
Onagraceae	*Epilobium angustifolium*		
	Oenothera biennis		
	Oenothera clelandii		
Polemoniaceae	*Phlox glaberrima*		
	Phlox pilosa		
Polygonaceae	*Polygonum cuspidatum*		
	Polygonum hydropiperoides		Robertson (1928)
	Polygonum pensylvanicum		Robertson (1928)
	Polygonum pensylvanicum		
	Polygonum sagittatum		
	Polygonum scandens	1 beetle	Robertson (1928)
	Polygonum scandens		
Ranunculaceae	*Clematis virginiana*		
Rosaceae	*Crataegus* sp.		Balduf (1935)
	Potentilla arguta		
	Rosa sp.		
	Rubus sp.		Riley (1873)
	Rubus sp.		Balduf (1935)

Table 1. Continued.

FAMILY	SPECIES	AUTHORS' COMMENTS	CITATION
	Spiraea alba		
	Spiraea sp.		Riley (1873)
Rubiaceae	*Cephalanthus occidentalis*		
	Galium boreale		
Scrophulariaceae	*Agalinis aspera*		
	Aureolaria pedicularia		
	Linaria vulgaris		
	Mimulus ringens		
	Verbascum thapsus		
	Veronica sp.		Britton (1937)
	Veronicastrum virginicum		
Verbenaceae	*Verbena hastata*	frequent	Robertson (1928)
	Verbena stricta		
	Verbena urticifolia		
GENERAL REPORTS			
	"*trouve dans l'herbe*" (taken in herbaceous vegetation)		DeGeer (1774)
	flowers		Lutz (1941)
	variety of early successional plants		McCauley and Wade (1978)
	flowering plants		Hoffmann and Frodsham (1993)
	wide variety of plants		Ramsdale (2002)
ERRONEOUS REPORTS			
Rosaceae	*Rosa* sp., in May in VA, beetle probably *C. marginatus*		Lintner (1893)
Simaroubaceae	*Ailanthus altissima*, beetle probably *C. marginatus*		Beckwith (1891)
Vitaceae	*Vitis* sp., in May in VA, beetle probably *C. marginatus*		Lintner (1893)

Chauliognathus pensylvanicus is univoltine (Riley 1872, Miskimen 1966). Only Balduf (1935) has suggested this species might be bivoltine, but he likely confused this species with the similar *Chauliognathus marginatus* (Fabricius), adults of which fly earlier in summer (Hentz 1830, Walsh 1868a, Glover 1869). Adults are active fliers, moving from flower to flower gathering food, seeking mates, and avoiding harassment by others of their own kind. Adults show no interest in other species of insects, either as potential predator or prey. This unwary behavior and their aposematic coloration suggest they have chemical defenses, since their mouthparts are ill-suited for defense. Eisner et al. (1981) identified the chemical in their glandular secretions that serves as an antifeedant.

In contrast to the herbivorous adults, larvae are generalist predators (Walsh 1868a, 1868b; Riley 1869, 1873, 1885; Hubbard 1880; Schwarz 1880; Worsham 1909; Vestal 1913; Adams 1915; Carroll 1987; Hoffmann and Frodsham 1993), sheltering in the litter. They hatch and feed, pass the winter in diapause, then feed again in spring before pupating in soil (Riley 1872).

METHODS & MATERIALS

From 1992 through 2006, I collected insects widely throughout Wisconsin, especially in prairie habitat, which is largely restricted to the southern and western parts of the state (Curtis 1959). These specimens are deposited in the Insect Research Collection (IRC) of the Entomology Department of the University of Wisconsin - Madison. By close observation of *C. pensylvanicus* adults in the field I learned things not reported in the literature and this information is presented here. Specimens and specimen records of adult *C. pensylvanicus* in the IRC and the insect collection of the Milwaukee Public Museum were examined. Information winnowed from the literature concerning flower visitation by adults is included in Table 1, together with my field data. Plant nomenclature follows Kartesz (1994).

RESULTS

Prior collection records contributed scant information: some Wisconsin county records. This species has now been collected in every Wisconsin county, though it is much more easily found in the south than in the north of the state. Adults were found using the flowers of 183 species in 29 families growing outside cultivation in Wisconsin (Table 1). Adults were active in the heat of the day, after the vegetation had lost its dew in the morning, which can be as late as 1200 hours in September, and were not found at night. Adults emerge in Wisconsin in the latter half of July and can be found through September.

Predation upon *C. pensylvanicus* was observed: the large araneid spiders *Argiope aurantia* Lucas and *Argiope trifasciata* (Forskal) captured and killed these beetles in their orb webs. The reduviid bug *Sinea diadema* (Fabricius) fed on *C. pensylvanicus* (Williams 2004). Bilsing (1920) reported the capture in a funnel web of this beetle, the captive being consumed by the agelenid *Agelena naevia* Walkenaer. Barrows (1984) reported the mantid *Tenodera aridifolia sinensis* Saussure preying on this beetle.

DISCUSSION

In the literature, *C. pensylvanicus* is reported to visit flowers (Table 1), and is most often reported to use *Solidago*. Some authors broaden this to include “related plants” or “associated plants”, which language is vague -- is this relationship taxonomic or ecological or both? Though these beetles are commonly found on *Solidago*, my simple observational data show they are much more general in their feeding activities.

Flowers of *Solidago* are most often yellow, and these beetles visit other yellow flowers, too, but they also visit flowers of other colors -- white, pale green, cream, orange, pink, majenta, lavender, and blue. They use flowers of a few monocots (*Allium*, *Tradescantia*) and a great many dicots. Most of these 183 plants are herbaceous, but a few are woody or secondarily woody (*Amorpha*, *Cephalanthus*, *Cornus*, *Rosa*, *Sambucus*, *Spiraea*). In Wisconsin, most woody plants bloom before adult beetles emerge.

Most of these flowers are radially symmetrical, but some are bilaterally symmetrical (Fabaceae, Lamiaceae, Scrophulariaceae). Some beetles cannot enter some bilaterally symmetrical flowers (*Linaria*, *Mimulus*). These wander from flower to flower without gaining access to them, but some individuals routinely seek and enter every such flower they find.

Some of these flowers offer only nectar (*Asclepias*), while in others the pollen and nectar are so closely associated that observation fails to show which resource is being used. The abundance of *Ambrosia* growing where this beetle is abundant, coupled with the rare observation of its use of only *A. psilostachya* (four beetles), suggest that nectar, not pollen, is its primary food. This hypothesis is strengthened by my not finding these beetles using the pollen of any grasses, which do not provide floral nectar. That beetles become covered with pollen does not mean they ingest pollen. Even if pollen were ingested, the salient question remains: Is pollen digested? Perhaps any pollen found in the gut is incidental and destined to pass through the beetle. Though various authors have asserted over 150 years that this species feeds on pollen, no proof of this assertion has yet been presented. The specialized mouthparts of this species, the frequent use of only nectar by adult insects generally, and the use by this beetle of *Asclepias* nectar, suggest that nectar is the primary resource these adults actively pursue.

Some of these plants usually bloom before the adults emerge, but late-flowering individual plants were visited (*Galium boreale*, *Phlox pilosa*). Some of these plants start to flower in late summer (*Aster*, *Helenium autumnale*), when the adults have been active for several weeks, yet they find and use these new resources as previously used plants stop flowering.

Some of these plants are abundant here (*Solidago canadensis*) but others are very rare (*Echinops sphaerocephalus*, *Prenanthes aspera*, *Ratibida columnifera*). Some of these plants are native and others are recently arrived exotic species, coming from as nearby as adjacent states (*Coreopsis tripteris*, *Echinacea purpurea*, *Eupatorium serotinum*, *Helianthus maximiliani*, *H. mollis*) or from as far away as Eurasia (*Berteroa*, *Cichorium*, *Dipsacus*, *Melilotus*, *Nepeta*, *Pastinaca*, *Verbascum*).

Chauliognathus pensylvanicus adults visit large flowers (*Aureolaria pedicularia*, *Impatiens pallida*, *Ruellia humulis*) into which a beetle crawls, as well as small flowers that may barely accommodate its mouthparts. Small flowers may be relatively isolated (*Verbena urticifolia*) or tightly bunched with others (Apiaceae, Asteraceae). Beetles use flowers low in the vegetation column (*Euphorbia dentata*, *Mentha arvensis*) and as high as flowers occur in the vegetation column (*Agastache*, *Cirsium*, *Cornus*, *Dipsacus*, *Eupatorium, Helianthus*). I once found many beetles feeding at the bases of corollas on the outside of flowers of *Lobelia siphilitica*, while none of them entered the throats of these flowers. They were probably taking nectar through holes cut in the flowers by some other insects for the same purpose since, on many other occasions, the beetles were sought but not found on these flowers.

Chauliognathus pensylvanicus adults use a wide variety of flowers that are taxonomically and morphologically diverse. The beetles are not overly selective but investigate and use various species of flowers growing in a small area. Individual beetles use flowers of many species, though some fail to exploit particular flowers, as noted above. Based on the diversity of forms used in Wisconsin, there are surely a few more plant species attractive to these beetles that I have not found here, and there must be many other species that these beetles visit elsewhere that have not yet been reported.

The abundance of diverse nectar sources throughout the growing season is much greater in prairies, being open and sunny, than in forests, being shadier (Curtis 1959), and prairies provide abundant litter wherein larvae develop. Unlike many prairie specialist insects, *C. pensylvanicus* is often present in early successional habitats generally, but it is most abundantly evident in prairies. Grasses such as *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Spartina pectinata* are called prairie grasses for this same reason: though they occur in open areas all the way east to the Atlantic shore, they are most successful in prairies. In like fashion, *C. pensylvanicus* is a prairie insect.

Because of its ability to use early successional habitats generally, Miskimen (1966) characterized *C. pensylvanicus* as ruderal -- benefiting from our ecologically disruptive habits. We lay waste to native ecosystems, throwing them into tumult with disturbance and the introduction of exotic species; the survivors of this we term ruderal. That *C. pensylvanicus* survives our activities rather well does not mean these conditions are optimal for the beetle. Rather, this is a prairie insect. Until now, the best characterization of this beetle's habitat was also the first -- DeGeer (1774) wrote that *C. pensylvanicus* was "*trouve dans l'herbe*" (taken in herbaceous vegetation).

Natural history, the study of organisms to generate factual information, primarily through fieldwork and direct observation, tends to reveal this sort of holistic understanding. It shows us the truest nature of a species, its basic ideal or what it is. This sheds light on our understanding of the ecosystems in which species evolved, illuminating the world as it was prior to the ecological disruption associated with our modern way of life. In this way, natural history looks backward and provides spiritual refreshment in glimpses of the world, whole, before we ripped it apart. It reflects our own long experience as hunters and gatherers: over millenia, we honed these same skills, which success made our experiment with modernity possible. Natural history is the foundation of the biological sciences, but it is not anachronistic, as it's often characterized by practitioners of more recent, reductionist, experimental and applied biology. Rather, natural history is as fascinating, as revealing, and as fulfilling today as ever.

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FIRST RECORD OF *HARPALUS OCHROPUS* KIRBY (COLEOPTERA: CARABIDAE) FROM MINNESOTA AND THE CONTERMINOUS UNITED STATES

Foster Forbes Purrington[1] and Richard M. Maxey[2]

The epigeal ground beetle *Harpalus ochropus* Kirby (Coleoptera: Carabidae) has been reported from Alaska and across Canada from British Columbia into Quebec (Bousquet and Larochelle 1993). It is local and rarely collected. Gandhi et al. (2005) surveyed for carabids extensively for several years along the Gunflint Trail and adjacent Boundary Waters Canoe Area in northeastern Minnesota. Their reported New Records for the entire state total 100, but they did not find *H. ochropus*. Lindroth (1968) obtained three specimens on sandy open moraine at Nipigon, Ontario, on the north shore of Lake Superior, which he designated the type locality. For his revision of the genus, Noonan (1991) saw only 13 specimens in addition to the male holotype (in the British Museum of Natural History, London).

We found a single male *H. ochropus* in Superior National Forest on the Gunflint Trail four miles west of Gunflint, Cook County, Minnesota, 7.IV.2003. Our collection of this rare ground beetle represents the first record from the lower 48 contiguous United States as well as its first collection in Minnesota. It is held in the personal collection of the first author.

The collection area in northeast Minnesota is in a transitional zone between the boreal spruce-balsam forest and pine-hemlock forest types (Shelford 1963). It is characterized by scattered black spruce (*Picea mariana* [Miller] BSP.), balsam fir (*Abies balsamea* [L.] Miller and quaking aspen (*Populus tremuloides* Michaux) with occasional paper birch (*Betula papyrifera* Marsh.) and sugar maple (*Acer saccharum* Marsh.).

The somewhat smaller *H. ochropus* adults resemble those of (sympatric) *H. herbivagus* Say but microsculpture on frons and pronotum is less pronounced; the pronotal sides and posterior angles are less rounded. Moreover, the spines of the internal sac fields in the *H. herbivagus* aedeagus are much larger than those of *H. ochropus* (Noonan 1991).

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ADDITIONS AND CORRECTIONS TO THE STONEFLIES (PLECOPTERA) OF IOWA, U.S.A.

Dennis P. Heimdal[1] and Michael W. Birmingham[1]

Until recently, Iowa's stonefly fauna was poorly documented. Heimdal et al. (2004) published a comprehensive report on stonefly distributions within the state, reporting seven families and 43 species. Five species, *Allocapnia pygmaea* (Burmeister) (Capiniidae), *Leuctra tenuis* (Pictet) (Leuctridae), *Amphinemura linda* (Ricker) (Nemouridae), *Nemoura trispinosa* Claassen (Nemouridae), and *Soyedina vallicularia* (Wu) (Nemouridae), were recommended for state protection because of their limited distribution within Iowa. Four species, *Amphinemura delosa* (Ricker), *Isogenoides doratus* (Frison) (Perlodidae), *I. krumholzi* (Ricker), and *I. varians* (Walsh), had limited distributions, but were not listed because their observed habitat preferences appeared common or were difficult to sample and poorly collected. From 2004 to 2006, fifteen county, state, and federal parks and preserves in east and northeast Iowa were sampled during the spring and summer in an effort to find additional locations for these nine species. The surveys yielded new distributional data for five species, including two new state records, and one species deletion, updating the total number of species recorded from Iowa to 44. A discussion for these records and corrections is presented below. Material collected from these surveys was deposited in the University of Iowa Hygienic Laboratory Collection (UHL) and the Illinois Natural History Survey Insect Collection (INHS).

***Leuctra rickeri* James (Leuctridae):** This species was first described from a small stream in Kentucky and most closely resembles *L. ferruginea (Walker)* (James 1976). Adult *L. rickeri* were recently collected in northeast Iowa from a small, cobble-laden creek that starts as two springs emerging from limestone bedrock. Currently, the nearest population of *L. rickeri* is located in the Shawnee and Ozark regions of southern Illinois where it is demonstrably secure, but restricted (DeWalt et al. 2005). Other states that have reported this species include Alabama, Florida, Indiana, Kentucky, Maryland, Mississippi, Ohio, and West Virginia (Grubbs 1997, 2004, Pescador et al. 2000, Stark and Baumann 2006).

New State Record. CLAYTON COUNTY: Mossy Glen Creek, Mossy Glen State Preserve (MGSP), 02 June 2005, 35 ♂, 19 ♀ (UHL); same but 1 ♂ (INHS); same but 26 May 2006, 5 ♂, 3 ♀ (UHL).

***Amphinemura delosa* (Ricker) (Nemouridae):** This species was described by Ricker (1952) from a creek near Spencer, Indiana. It is known from 20 states/provinces (Stark and Baumann 2006), including adjacent Illinois (DeWalt et al. 2005), Missouri (Poulton and Stewart 1991), and Wisconsin (Hilsenhoff 1975). Heimdal et al. (2004) reported this species from only one county previously. Recently, adults have been collected from four new Iowa counties along the Mississippi River. Collection sites consisted of springs and small cold-water creeks, which differs from Ricker's (1952) observations of *A. delosa* frequenting warmer, small streams.

New County Records. ALLAMAKEE COUNTY: French Creek, Churchtown, 16 September 2004, 1 ♂ (INHS); CLAYTON COUNTY: Bear Creek, Bixby State Preserve (BSP), 02 June 2005, 1 ♂, 1 ♀ (UHL); Mossy Glen Creek, MGSP, 02 June 2005, 19 ♂, 30 ♀ (UHL); same but 26 May 2006, 3 ♂, 2 ♀ (UHL); Brownfield Creek, Colesburg, 25 May 2006, 3 ♂, 5 ♀ (UHL); Cow Branch, Driftless Area National Wildlife Refuge (DANWR), 30 May 2006, 2 ♂, 6 ♀ (UHL); DELAWARE COUNTY: Little Turkey River, Hoffman Wildlife Area, 20 May

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2005, 1 ♂ (UHL); Unnamed Spring of Grimes Hollow, Colesburg, 01 May 2004, 3 ♂, 4 ♀ (UHL); DUBUQUE COUNTY: White Pine Hollow Creek, White Pine Hollow State Preserve, 01 June 2005, 20 ♂, 27 ♀ (UHL); FAYETTE COUNTY: Unnamed Creek, Dutton's Cave Park, 03 June 2005, 3 ♂, 5 ♀ (UHL).

***Nemoura trispinosa* Claassen (Nemouridae):** This species was first described from a small creek in central New York (Claassen 1923). It is known from 16 states/provinces of northern North America (Stark and Baumann 2006), including adjacent Illinois (DeWalt et al. 2005), Minnesota (Harden and Mickel 1952), and Wisconsin (Hilsenhoff 1975). In Iowa, *N. trispinosa* was restricted to springs within the northeast counties (Heimdal et al. 2004). Several additional populations have recently been discovered, most commonly in springs with cobble substrate, abundant leaf packs, and discernable flow.

New Location Records: ALLAMAKEE COUNTY: Unnamed Spring of Waterloo Creek, Dorchester, 01 June 2004, 2 ♂, 1 ♀ (UHL); CLAYTON COUNTY: Unnamed Spring of Bear Creek, BSP, 02 June 2005, 1 ♀ (UHL); same but 02 May 2006, 6 nymphs (UHL); Mossy Glen Creek, MGSP, 02 June 2005, 1 ♀ (UHL); Unnamed Spring of Pine Creek, DANWR, 25 April 2006, 2 ♂ (reared and emerged: 05 May 2006), 1 ♀ (UHL); Unnamed Spring of Steele Branch, DANWR, 25 April 2006, 1 ♂ (reared and emerged: 19 June 2006) (UHL); DUBUQUE COUNTY: Unnamed Spring of Middle Fork Little Maquoketa River, Bankston County Park, 28 April 2004, 2 ♂, 2 ♀ (reared and emerged: 03 June 2006 through 17 June 2006) (UHL); FAYETTE COUNTY: Unnamed Spring of Brush Creek, Brush Creek Canyon State Preserve, 02 June 2005, 1 ♂, 9 ♀ (UHL).

***Soyedina vallicularia* (Wu) (Nemouridae):** Wu (1923) gave the first description of this species from Ithaca, New York. Grubbs (2006) studied this species across its range and found little morphological variation. *S. vallicularia* was previously found from a single location within northeast Iowa (Heimdal et al. 2004). Adjacent Illinois (Harris and Webb 1995) and Wisconsin (Hilsenhoff 1975) have also reported this species, along with 12 other states/provinces (Stark and Baumann 2006, Grubbs 2006). Recently, two additional collection sites in northeast Iowa were found along small, hillside, wet areas with little discernable flow.

New County Record: CLAYTON COUNTY: Unnamed Spring of Cow Branch, DANWR, 25 April 2006, 2 ♂, 2 ♀, 3 nymphs (UHL); Unnamed Spring of Pine Creek, DANWR, 25 April 2006, 1 ♀ (UHL).

***Hydroperla fugitans* (Needham and Claassen) (Perlodidae):** Needham and Claassen (1925) described *H. fugitans* from Texas. Adults of this species were recently collected on two separate visits to the Cedar River in east-central Iowa. This collection site is a sixth order stream with a primarily shifting sand and gravel substrate. *H. fugitans* has been reported from seven states (Kondratieff 2004) including adjacent Illinois (Frison 1942) and Missouri (Kondratieff 2004).

New State Record: LINN COUNTY: Cedar River, Cedar Rapids, 18 April 2006, 1 ♀ (UHL); same but 19 April 2006, 1 ♂ (UHL).

***Isogenoides doratus* (Frison) (Perlodidae):** Frison (1942) described *I. doratus* (as *Hydroperla dorata*) from Michigan, and Ricker (1952) later described *I. krumholzi* also from Michigan. Heimdal et al. (2004) reported both from Iowa, including a new state record for *I. krumholzi*. Sandberg and Stewart (2005) recently synonymized *I. krumholzi* with *I. doratus*, thereby removing the former species from Iowa's state list. No additional locations for *Isogenoides* species were discovered throughout the above surveys.

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