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Introduction

Eastern prairie fringed orchid (*Platanthera leucophaea* [Nuttall] Lindley) is a federally threatened species known from approximately 55 populations in seven Midwestern states, primarily Wisconsin, Illinois, and Michigan (Bowles 1993). Although this may seem like an adequate number of populations within a reasonable range of the Midwest, the majority of these populations are small, unprotected, and erratic in their persistence. In addition, few occurrences are in good quality habitat. At present, only four legally protected populations in the U.S. are considered to have high viability (Bowles 1993).

Platanthera leucophaea was formerly widespread in prairies and wetlands east of the Mississippi River (Bowles 1993). Its historic range included 13 states extending from eastern Missouri and Iowa to northwest Pennsylvania, western New York, and southern Ontario, with disjunct populations in Oklahoma, New Jersey, Virginia, and Maine (Bowles 1993). In the U.S., *Platanthera leucophaea* has declined more than 70% from original county records due to habitat destruction from agriculture, wetland drainage, and natural succession (Bowles 1993). This drastic decline led the U.S. Fish and Wildlife Service to list *Platanthera leucophaea* as a federally threatened species in 1989 (U.S. Fish and Wildlife Service 1989).

In Michigan, Eastern prairie fringed orchid was known from 21 counties historically (Case 1987). Currently there are a total of 14 extant populations from nine counties (Natural Heritage Biological and Conservation Data System, 1999). The species has been listed as a state endangered species by the Michigan Department of Natural Resources since the inception of the Endangered Species Act in 1974. The populations are found in two main habitat types: lakeplain prairies and bogs.

In Ohio, *Platanthera leucophaea* is presently known to occur in four northern

counties (Holmes, Lucas, Sandusky, and Wayne) and one west-central county (Clark). It has been listed as a state threatened species by the Ohio Department of Natural Resources, Division of Natural Areas and Preserves, since 1986 (ODNAP 1986). Prior to 1986, it was listed first as extirpated in 1980 and then as endangered from 1982-1985 following the discovery of the Lucas and Wayne county populations. Historic records from Ottawa County (North Bass Island-1980), Auglaize County (1901), Erie County (1916), and Montgomery County (1800s) have not been relocated, despite recent surveys. There are also literature references to historic occurrences in Champaign and Franklin counties (Braun 1967) as well as Fairfield County (Schaffner 1932). None of the extant populations occur in counties where there are historic records or references.

A necessary step in the recovery of *Platanthera leucophaea* is obtaining specific knowledge about its reproductive biology including information regarding its pollinators. Important information such as the role of pollinators in relation to seed-set and their role in maintaining viable orchid populations is lacking. Hawkmoths (Lepidoptera: Sphingidae) have been identified as primary pollinators of *Platanthera leucohaea* in Illinois and Wisconsin (Robertson 1893, Bowles 1983, and Cuthrell 1994), however little is known of their population or habitat status. To our knowledge, no *Platanthera leucophaea* pollinator studies have previously been conducted in Ohio or Michigan.

Pollinator loss or decline can affect plants in several ways including most obviously the loss of, or reduced, seed-set (Tepedino 1979). The production of less vigorous offspring is also possible due to effects of inbreeding depression resulting from a higher percentage of seed-set through self-pollination (Kearns and Inouye 1997). Pollinators may be threatened by habitat alteration including destruction of larval and

adult food sources, introduction of alien pollinators, and/or the use of pesticides.

The identification and status of pollinators of Eastern prairie fringed orchid has been identified as a priority research task in the Federal Recovery Plan for this species (Bowles 1993). This study was conducted in order to begin to identify the pollinators of Eastern prairie fringed orchid in Michigan and Ohio.

Orchid Pollination

The floral biology of the Orchidaceae has fascinated biologists for many years because of the pollination mechanism exhibited by members of this group (Cole and Firmage 1984). Two orchid genera that have attracted considerable attention are *Platanthera* L.C. Richard and *Habenaria* Willdenow, which together comprise more than 800 species of orchids (Nilsson). Most of these orchids possess adaptations that indicate lepidopteran pollination (van der Pijl and Dodson, 1966; Catling and Catling 1991), although other insect taxa have been reported as pollinators for some species (Thien and Utech, 1970; Cole and Firmage 1984; Patt et al. 1989).

Most orchid species within these two genera can be categorized as either moth-pollinated or butterfly-pollinated species based on specialized plant morphologies and adaptations linked with their primary pollinator groups (van der Pijl and Dodson, 1966). Several species of Lepidoptera are known to be important pollen vectors for *Platanthera*. Pollinator specificity is dictated by the placement and positioning of pollinia (packets of pollen) on the vector. Removal of pollinia by attachment to the eyes is one way that pollination takes place in *Platanthera* and *Habenaria* (Smith 1975; Smith and Snow 1976, Catling 1984; Inoue 1985; Robertson and Wyatt, 1985, 1990, and Cuthrell 1994). Orchid spur length and

distance between the viscidia (sticky pads at the base of the pollinia that become attached to the pollen vector) become important plant characters by governing pollinator position in relation to various floral parts during floral visitation (Inoue 1985, 1986). Moths with a long proboscis may be able to reach nectar without affecting pollination and are therefore labeled pollen “thieves”. Pollinia attachment at the proboscis and the dorsal thorax appears to be the usual situation for pollen vectors of North American orchids (Catling and Catling 1991). For example, in *P. bifolia* (L.), the viscidia are spaced close together and adhere to pollen vectors at the base of the proboscis. This type of pollinia attachment allows for a greater number and more diverse set of pollinators, and pollinator morphologies are not quite as important (Nilsson 1983).

Eastern prairie fringed orchid ranges from 20-100 cm tall, producing a terminal and determinate inflorescence with between 5 and 40 flowers comprised of three creamy-white petals backed by three pale green sepals. The lower petal is modified into a broad lip which is deeply 3-lobed. Each of the lobes is deeply incised which produces the fringed appearance. The lower lip also bears a slender, curving spur that extends up to 5 cm and contains a supply of nectar. The flower also produces a sweet fragrance most pronounced at dusk when the hawkmoths are beginning their feeding flights.

These orchid morphologies are adapted to pollination by Lepidoptera. The white, nocturnally fragrant flowers help pollinators to locate the plants. Once in close proximity to the flowers, the white-fringed lip directs approaching moths to the spur and the nectar. The close spacing of the viscidia allow moths to pick up pollinia at the base of their tongue. Only those moths with compatible tongues (length and width) can function as pollinators.

Materials and Methods

Study Sites

Two sites were selected for this study, one in northern Ohio along the shores of Lake Erie, and one in the Saginaw Bay region of Michigan. These two sites were chosen as they both support relatively large flowering populations of the orchid, thus the likelihood of encountering and capturing pollinators would be optimized.

Pickerel Creek Wildlife Area, Sandusky County, Ohio

The Pickerel Creek Wildlife Area prairie includes lakeplain wet prairie and lakeplain wet mesic prairie and is located in Sandusky County along the shores of Sandusky Bay. The approximately 20 acre site is located just inland of an extensive marsh complex, and consists of an open, seasonally wet

prairie dominated by early successional species such as reed canary grass (*Phalaris arundinacea*), bluejoint (*Calamagrostis canadensis*), Canada goldenrod (*Solidago canadensis*), and dogwoods (*Cornus* spp.). An associated species list is provided in Table 1.

The site is threatened by several species which are invasive and/or non-native (e.g. dogwood, purple loosestrife, reed canary grass). Parts of the area are subject to shallow flooding when levels of adjacent Lake Erie are high. Flooding episodes usually occur in the spring and may last several days. Aerial photographs indicate the area was farmed from at least 1950 to the early 1970's. The area was acquired by the Ohio Department of Natural Resources, Division of Wildlife in 1986.

Table 1. Associated Plant Species at Pickerel Creek Wildlife Area.

<i>Allium vineale</i>	<i>Cornus racemosa</i>	<i>Lysimachia ciliata</i>
<i>Ambrosia artemisiifolia</i>	<i>Cuscuta</i> sp.	<i>Lythrum salicaria</i>
<i>Asclepias incarnata</i>	<i>Cyperus strigosus</i>	<i>Openothera biennis</i>
<i>Aster ericoides</i>	<i>Dipsacus sylvestris</i>	<i>Phalaris arundinacea</i>
<i>Aster novae-angliae</i>	<i>Epilobium coloratum</i>	<i>Rorippa palustris</i> var. <i>palustris</i>
<i>Calamagrostis canadensis</i>	<i>Geum laciniatum</i>	<i>Rosa palustris</i>
<i>Carex cristatella</i>	<i>Glyceria</i> sp.	<i>Rosa setigera</i>
<i>Carex granularis</i>	<i>Hibiscus moscheutos</i>	<i>Rumex crispus</i>
<i>Carex scoparia</i>	<i>Hordeum jubatum</i>	<i>Scirpus pendulus</i>
<i>Carex tribuloides</i>	<i>Hypericum punctatum</i>	<i>Solidago canadensis</i>
<i>Carex vulpinoidea</i>	<i>Impatiens capensis</i>	<i>Spheopholis obtusata</i>
<i>Cirsium</i> sp.	<i>Juncus dudleyi</i>	<i>Stachys palustris</i> var. <i>homotrichia</i>
<i>Cornus ammomum</i>	<i>Leersia oryzoides</i>	<i>Trifolium hybridum</i>
<i>Cornus drummondii</i>	<i>Lobelia siphilitica</i>	<i>Vitis riparia</i>

Huron County #1 Site, Michigan

This Huron County site includes lakeplain wet mesic prairie and lakeplain wet prairie (Comer et al. 1995) and is located along the shore of Saginaw Bay.

The prairie is located just inland of an extensive Great Lakes marsh in the bays behind a residential and recreation area. The best prairie lies adjacent to the shore, with lower quality prairies occurring behind the primary beach ridges, the latter of which are

now closed canopy due to fire suppression. Much of the inland area appears to have been farmed at some time but is reverting to prairie vegetation. The Huron County #1 prairie is a 10-15 acre portion of a large lakeplain prairie, Great Lakes marsh, and lakeplain oak opening complex. Prior to European settlement, this complex reached from the mouth of the Saginaw River in Bay County to the Wildfowl Bay Islands in Huron County and extended inland from 0.3-5 km (Comer et al. 1995).

The adjacent marsh is dominated by narrow-leaved cat-tail (*Typha angustifolia*), hard-stemmed bulrush (*Scirpus acutus*), and soft-stemmed bulrush (*S. validis*). Inland and upland of the prairie is a mature forest supporting bur oak (*Quercus macrocarpa*), swamp white oak (*Q. bicolor*), and occasional individuals of northern white cedar (*Thuja occidentalis*), with an

understory dominated by prickly ash (*Zanthoxylum americanum*). There are also areas of abandoned agricultural land that contain assemblages of prairie vegetation, which, if properly managed, may be restored to prairie communities.

The high quality wet prairie (Comer et al. 1998) is dominated by sedges (*Carex stricta*, *C. lasiocarpa*, *C. buxbaumii*, and other taxa.), twig-rush (*Cladium mariscoides*), prairie cordgrass (*Spartina pectinata*), Ohio goldenrod (*Solidago ohioensis*), and the exotic Kentucky bluegrass (*Poa pratensis*). Other common plants include shrubby cinquefoil (*Potentilla fruticosa*), marsh blazing star (*Liatris spicata*), bluejoint (*Calamagrostis canadensis*), and Canada rush (*Juncus canadensis*). An associated species list is included in Table 2.

Table 2. Associated Plant Species at Huron County # 1 Site, Huron County, Michigan, 1998.

<i>Andropogon gerardii</i>	<i>Comandra umbellata</i>	<i>Potentilla fruticosa</i>
<i>Andropogon scoparius</i>	<i>Cornus amomum</i>	<i>Pycnanthemum virginianum</i>
<i>Asclepias hirtella</i>	<i>Cornus foemina</i>	<i>Salix bebbii</i>
<i>Asclepias incarnata</i>	<i>Cornus stolonifera</i>	<i>Salix discolor</i>
<i>Aster ericoides</i>	<i>Euthamia graminifolia</i>	<i>Salix exigua</i>
<i>Cacalia plantaginea</i>	<i>Hypericum kalmianum</i>	<i>Solidago altissima</i>
<i>Calamagrostis canadensis</i>	<i>Leersia oryzoides</i>	<i>Solidago canadensis</i>
<i>Carex aquatilis</i>	<i>Linum medium</i>	<i>Solidago ohioensis</i>
<i>Carex buxbaumii</i>	<i>Lysimancia quadrifolia</i>	<i>Solidago</i> spp.
<i>Carex lanuginosa</i>	<i>Lythrum salicaria</i>	<i>Sorghastrum nutans</i>
<i>Carex lasiocarpa</i>	<i>Populus deltoides</i>	<i>Ulmus americana</i>
<i>Carex stricta</i>	<i>Populus tremuloides</i>	

Pollinator Activity

Pollinator activity was monitored by visual inspection of orchids for pollinators and light trapping. In Ohio, the Pickerel Creek study site was sampled from 24 June to 26 June 1998. In Michigan, the Huron County prairie site was sampled from 30 June to 3 July 1998. Observations were conducted from 0.5 hour before dusk until ambient light conditions became too low for continued observations. Dense clusters of flowering *Plantathera leucophaea* were selected before dusk for pollinator studies.

Observations were made at a distance of 2.0 to 0.5 meters while standing very still and holding an aerial net. When moths were observed or heard hovering near orchids, attempts were made to capture the moths with the aerial net. No mosquito or other insect repellants were used until after the observations were completed and the blacklights were turned on.

Light trapping consisted of standard mercury-vapor and UV lights, powered by a portable Honda generator. A 2 x 2 meter metal conduit frame supporting a large white

sheet was used as a collecting surface. This frame was placed in the field in a central location with flowering orchids on all sides to maximize the likelihood of collecting moths carrying pollinia. This technique attracted a large sample of nocturnal insects that could be examined for *Platanthera leucophaea* pollinia.

Fruit Set

Fruit set was monitored on 2 October 1998 at the Huron County site in Michigan. The total number of *Platanthera leucophaea* plants monitored included 16 individuals.

The number of flowers and number of fruit pods were recorded for each plant. Census results were based only on 16 orchids that could be relocated and thus results should be interpreted cautiously. Fruit set data were acquired from 14 plants at the Pickerel Creek study site in Ohio on 6 October, 1998. Although there were many flowering plants (1065), very few were found with seed capsules, which may have been a result of the late season sampling period. Many plants were grazed or otherwise damaged.

Results

A total of 53 hawkmoth specimens were recorded during the 1998 pollinator inventory with 14 different species represented. At the Pickerel Creek site in Ohio, 19 specimens represented by 11 different species were collected (Table 3). At the Huron County #1 prairie in Michigan, 34 specimens represented by 9 different species were recorded (Table 4).

At the Pickerel Creek site in Ohio on 25 June 1998, two specimens of *Manduca sexta* were observed visiting flowers of *Platanthera leucophaea* between 2322 and 2329 EST but upon capture and close inspection neither moth was carrying pollinia. On 26 June 1998, two specimens of hawkmoths were collected carrying several pollinia attached to their tongue. One *Eumorpha pandorus* (Figure 1) was taken at 2340 EST and one *Eumorpha*

achemon (Figure 2) was recorded at the sheet 15 minutes later at 2355.

At Huron County #1 Prairie in Michigan on 1 July 1998, at 2150 EST, one *Sphinx eremitus* was collected after the senior author heard a buzzing near one of the flowering orchids. This particular specimen was not carrying *P. leucophaea* pollinia but on 2 July at 2222 EST, at the same site, a specimen of *Sphinx eremitus* (Figure 3) was collected at the light sheet with one pollinium attached to its proboscis.

In summary, a total of three species of hawkmoths were collected with *Platanthera leucophaea* pollinia attached to their proboscis. Two species were recorded from Ohio: the Pandorus sphinx, *Eumorpha pandorus*, and the Achemon sphinx, *Eumorpha achemon*. One species, the Hermit sphinx, *Sphinx eremitis*, was recorded from Michigan.

Table 3. Hawkmoths Recorded from Pickerel Creek State Wildlife Area, Sandusky County, Ohio, 1998.

Species	Date	Time EST	Comments
<i>Ceratomia undulosa</i>	24-Jun-98	2305	
<i>Lapara</i> sp. prob. <i>bombycoides</i>	24-Jun-98	2330	
<i>Smerinthus cerisyi</i>	24-Jun-98	2345	
<i>Cressonia juglandis</i>	24-Jun-98	2355	
<i>Cressonia juglandis</i>	25-Jun-98	04	
<i>Paonias excaecatus</i>	25-Jun-98	215	
<i>Eumorpha achemon</i>	25-Jun-98	2315	
<i>Darapsa myron</i>	25-Jun-98	2315	
<i>Manduca sexta</i>	25-Jun-98	2322	seen visiting EPFO
<i>Manduca sexta</i>	25-Jun-98	2329	seen visiting EPFO
<i>Manduca sexta</i>	25-Jun-98	2330	
<i>Ceratomia amyntor</i>	26-Jun-98	031	
<i>Darapsa pholus</i>	26-Jun-98	158	
<i>Darapsa pholus</i>	26-Jun-98	220	
<i>Paonias myops</i>	26-Jun-98	345	
<i>Eumorpha achemon</i>	26-Jun-98	2210	
<i>Eumorpha pandorus</i>	26-Jun-98	2340	carrying EPFO pollinia
<i>Eumorpha achemon</i>	26-Jun-98	2350	
<i>Eumorpha achemon</i>	26-Jun-98	2355	carrying EPFO pollinia

EPFO = Eastern prairie fringed orchid

Table 4. Hawkmoths Recorded from Huron County # 1 Site, Huron County, Michigan, 1998.

Species	Date	Time EST	Comments
<i>Paonias myops</i>	30-Jun-98	23:15	
<i>Ceratomia amyntor</i>	30-Jun-98	23:40	
<i>Ceratomia undulosa</i>	30-Jun-98	23:40	
<i>Ceratomia amyntor</i>	30-Jun-98	23:42	
<i>Eumorpha pandorus</i>	1-Jul-98	0:10	
<i>Sphinx eremitus</i>	1-Jul-98	21:50	visiting EPFO
<i>Darapsa myron</i>	1-Jul-98	22:05	
<i>Ceratomia undulosa</i>	1-Jul-98	22:35	
<i>Paonias myops</i>	1-Jul-98	23:14	
<i>Paonias myops</i>	1-Jul-98	23:18	
<i>Ceratomia undulosa</i>	2-Jul-98	0:02	
<i>Ceratomia undulosa</i>	2-Jul-98	0:06	
<i>Ceratomia undulosa</i>	2-Jul-98	0:10	
<i>Ceratomia undulosa</i>	2-Jul-98	0:10	
<i>Smerinthus cerisyi</i>	2-Jul-98	0:12	
<i>Ceratomia undulosa</i>	2-Jul-98	0:15	
<i>Ceratomia undulosa</i>	2-Jul-98	0:25	
<i>Paonias myops</i>	2-Jul-98	0:25	
<i>Paonias excaecatus</i>	2-Jul-98	1:05	
<i>Paonias myops</i>	2-Jul-98	1:20	
<i>Paonias excaecatus</i>	2-Jul-98	1:30	
<i>Paonias myops</i>	2-Jul-98	1:33	
<i>Ceratomia undulosa</i>	2-Jul-98	1:37	
<i>Paonias myops</i>	2-Jul-98	2:46	
<i>Paonias excaecatus</i>	2-Jul-98	2:50	
<i>Paonias myops</i>	2-Jul-98	3:17	
<i>Paonias excaecatus</i>	2-Jul-98	3:18	
<i>Sphinx eremitus</i>	2-Jul-98	22:22	carrying EPFO pollinia
<i>Ceratomia undulosa</i>	2-Jul-98	22:22	
<i>Ceratomia undulosa</i>	2-Jul-98	22:51	
<i>Sphinx kalmiae</i>	3-Jul-98	0:05	
<i>Ceratomia undulosa</i>	3-Jul-98	0:21	
<i>Ceratomia undulosa</i>	3-Jul-98	0:42	
<i>Ceratomia undulosa</i>	3-Jul-98	0:42	

EPFO = Eastern prairie fringed orchid

Figures 1-3



Figure 1. *Eumorpha pandorus* carrying EPFO pollinia, Sandusky County, OH, June 26, 1998



Figure 2. *Eumorpha achemon* carrying EPFO pollinia, Sandusky County, OH, June 26 1998.



Figure 3. *Sphinx eremitis* specimen carrying EPFO pollinia, Huron County, MI, July 1, 1998

Discussion

Both Michigan and Ohio contain a diversity of hawkmoth species, many of which are resident species with a few regular, nonbreeding migrant species (Tables 5 and 6). Eleven of 38 (29%) resident hawkmoths were recorded from this study from Ohio and 9 of 32 (28%) from Michigan. Others have tried to document the pollinators for *P. leucophaea* and have had varying degrees of success (Table 7). Our study establishes baseline information on the pollination ecology of the Eastern prairie fringed orchid in Ohio and Michigan. However, because our study was limited to two sites over a 6-day period, it is very likely that other pollinators will be documented in the future.

Eastern prairie fringed orchid pollinators

As a result of this study, a newly discovered pollinator for the Eastern prairie fringed orchid was recorded. The Pandorus sphinx, *Eumorpha pandorus*, was collected carrying several orchid pollinia (Figure 1). This species is known from Nova Scotia and Maine, west through southern Wisconsin to central Kansas; south to southern Florida and southern Texas. The larvae feed on grape species (*Vitis* spp.) and Virginia creeper (*Parthenocissus* spp.) in the north and porcelain berry vine (*Ampelopsis*) in the south (Hodges 1971). Full grown larvae pupate in shallow chambers in the soil. Adults fly at dusk and nectar on a variety of flowers including petunia (*Petunia hybrida*), bouncing bet (*Saponaria officinalis*), and white campion (*Lychnis alba*), to name a few (Fleming 1970).

Two other hawkmoth species (*E. achemon*, *Sphinx eremitis*) (Figures 2, 3) were reconfirmed as pollen vectors. While *Eumorpha achemon* has been implicated in the pollination of *P. leucophaea* in the past (Cuthrell 1994), it seems remarkable that the moths were carrying so many pollinia. In a previous pollinator study by the senior

author, the captured sphingid pollinators were carrying far fewer (in most cases only one) pollinia. It appears that both of these species are adept at visiting several flowers and potentially several orchid plants.

The Achemon sphinx, *Eumorpha achemon*, is widely distributed in the Eastern United States from Florida north to Massachusetts and west to North Dakota and Arizona. Host plants of the larva include grape (*Vitis* spp.) and porcelain berry vine (*Ampelopsis* spp.) (Hodges 1971). Adult nectar sources include flowers of Japanese honeysuckle (*Lonicera japonica*), petunia (*Petunia hybrida*), mock orange (*Philadelphus coronarius*), evening primroses (*Oenothera* spp.), and phlox (*Phlox* spp.) (Fleming 1970).

The third confirmed pollinator species, the Hermit sphinx, *Sphinx eremitis*, is reported to occur from Maine south to North Carolina, west to Manitoba, South Dakota, and Missouri. Larval food plants include various species of beebalm (*Monarda*), mints (*Mentha*), bugleweed (*Lycopus*) and sage (*Salvia*) (Hodges 1971). Adults have been reported to nectar on Japanese honeysuckle (*Lonicera japonica*), bouncing bet (*Saponaria officinalis*), petunia (*Petunia* spp.) and catalpa (*Catalpa speciosa*) (Fleming 1970).

A fourth species of hawkmoth, the Tersi sphinx (*Xylophanes tersa*) has been confirmed by other researchers as a pollen vector for *P. leucophaea* (Robertson 1893, Hapeman, 1996). *X. tersa* is not a resident of Michigan or Ohio but routinely occurs in the northern parts of the United States far removed from its larval food plants which include smooth buttonplant (*Spermacoce glabra*), starclusters (*Pentas* spp.), *Borreria*, *Catalpa*, and *Manettia* spp. Adults likely visit several species but are only reported visiting honeysuckle (*Lonicera* spp.). No *X. tersa* were recorded during this study.

Table 5: The Sphingidae of Ohio (the Ohio Survey of Lepidoptera sponsored by The Ohio Lepidopterists. Compiled by Eric H. Metzler, 1999.)

*Pink-spotted hawkmoth (<i>Agrius cingulata</i>)	Huckleberry sphinx (<i>Paonias astylus</i>)
Carolina sphinx (<i>Manduca sexta</i>)	Walnut sphinx (<i>Laothoe juglandis</i>)
Five-spotted hawkmoth (<i>Manduca quinquemaculata</i>)	Modest sphinx (<i>Pachysphinx modesta</i>)
Ash sphinx (<i>Manduca jasminearum</i>)	*Giant gray sphinx (<i>Pseudosphinx tetrio</i>)
Rustic sphinx (<i>Manduca rustica</i>)	*Ello sphinx (<i>Erinnyis ello</i>)
Pawpaw sphinx (<i>Dolba hyloeus</i>)	*Obscure sphinx (<i>Erinnyis obscura</i>)
Elm Sphinx (<i>Ceratomia amyntor</i>)	*No common name (<i>Erinnyis domingonis</i>)
Waved sphinx (<i>Ceratomia undulosa</i>)	*Fadus sphinx (<i>Aellopos fadus</i>)
Catalpa sphinx (<i>Ceratomia catalpae</i>)	*Titan sphinx (<i>Aellopos titan</i>)
Hagen's sphinx (<i>Ceratomia hageni</i>)	Hummingbird clearwing (<i>Hemaris thysbe</i>)
Plebeian sphinx (<i>Paratreia plebeja</i>)	Slender clearwing (<i>Hemaris gracilis</i>)
Hermit sphinx (<i>Sphinx eremitus</i>)	Snowberry clearwing (<i>Hemaris diffinis</i>)
Great ash sphinx (<i>Sphinx chersis</i>)	Achemon sphinx (<i>Eumorpha achemon</i>)
Canadian ash sphinx (<i>Sphinx canadensis</i>)	*Banded sphinx (<i>Eumorpha fasciata</i>)
Franck's sphinx (<i>Sphinx franckii</i>)	Pandorus sphinx (<i>Eumorpha pandorus</i>)
Laurel sphinx (<i>Sphinx kalmiae</i>)	Abbott's sphinx (<i>Sphecodina abbottii</i>)
Apple sphinx (<i>Sphinx gordius</i>)	Lettered sphinx (<i>Deidamia inscripta</i>)
Clemen's sphinx (<i>Sphinx luscitiosa</i>)	Nessus sphinx (<i>Amphion floridensis</i>)
Wild cherry sphinx (<i>Sphinx drupiferarum</i>)	Virginia creeper sphinx (<i>Darapsa myron</i>)
Southern pine sphinx (<i>Lapara coniferarum</i>)	Azalea sphinx (<i>Darapsa pholus</i>)
Northern pine sphinx (<i>Lapara bombycoides</i>)	Galium sphinx (<i>Hyles gallii</i>)
Twin-spotted sphinx (<i>Smerinthus jamaicensis</i>)	White-lines sphinx (<i>Hyles lineata</i>)
One-eyed sphinx (<i>Smerinthus cerisyi</i>)	*Tersa sphinx (<i>Xylophanes tersa</i>)
Blinded sphinx (<i>Paonias excaecatus</i>)	
Small-eyed sphinx (<i>Paonias myops</i>)	*= Stray, nonbreeding in OH

Table 6: The Sphingidae of Michigan (Opler et al. 1995)

*Pink-spotted hawkmoth (<i>Agrius cingulata</i>)	Modest sphinx (<i>Pachysphinx modesta</i>)
*Cluentius sphinx (<i>Neococytius cluentius</i>)	*Ello sphinx (<i>Erinnyis ello</i>)
Carolina sphinx (<i>Manduca sexta</i>)	*Tantalus sphinx (<i>Aellopos tantalus</i>)
Five-spotted hawkmoth (<i>Manduca quinquemaculata</i>)	*Mournful sphinx (<i>Enyo lugubris</i>)
Pawpaw sphinx (<i>Dolba amyntor</i>)	Humming bird clearwing (<i>Hemaris thysbe</i>)
Elm sphinx (<i>Ceratomia undulosa</i>)	Slender clearwing (<i>Hemaris gracilis</i>)
Waved sphinx (<i>Ceratomia undulosa</i>)	Snowberry clearwing (<i>Hemaris diffinis</i>)
Catalpa sphinx (<i>Ceratomia catalpae</i>)	Pandorus sphinx (<i>Eumorpha pandorus</i>)
Hermit sphinx (<i>Sphinx eremitus</i>)	Achemon sphinx (<i>Eumorpha achemon</i>)
Great ash sphinx (<i>Sphinx chersis</i>)	*Gaudy sphinx (<i>Eumorpha labruscae</i>)
Canadian sphinx (<i>Sphinx canadensis</i>)	Lettered sphinx (<i>Deidamia inscripta</i>)
Laurel sphinx (<i>Sphinx kalmiae</i>)	Nessus sphinx (<i>Amphion floridensis</i>)
Poecila sphinx (<i>Sphinx poecila</i>)	Hydrangea sphinx (<i>Darapsa versicolor</i>)
Clemen's sphinx (<i>Sphinx luscitiosa</i>)	Virginia creeper sphinx (<i>Darapsa myron</i>)
Wild cherry sphinx (<i>Sphinx drupiferarum</i>)	Azalea sphinx (<i>Darapsa pholus</i>)
Northern pine sphinx (<i>Lapara bombycoides</i>)	*Tersa sphinx (<i>Xylophanes tersa</i>)
Twin-spotted sphinx (<i>Smerinthus jamaicensis</i>)	Bedstraw hawkmoth (<i>Hyles gallii</i>)
One-eyed sphinx (<i>Smerinthus cerisyi</i>)	White-lined sphinx (<i>Hyles lineata</i>)
Blinded sphinx (<i>Paonias excaecatus</i>)	
Small-eyed sphinx (<i>Paonias myops</i>)	
Walnut sphinx (<i>Laothoe juglandis</i>)	* = Stray, non-breeding in MI

Table 7. A summary of pollinator activity recorded for *Platanthera leucophaea* (bold indicates known pollinators).

Hawkmoth Species	Study Location	Date	Time EST	Seen visiting EPFO	Pollinia attached	Source of Information
<i>Xylophanes tersa</i>	NA	1893	NA	Yes	?	Robertson 1893
<i>Xylophanes tersa</i>	South-central WI	July 1994	NA	?	Yes	Hapeman 1996
<i>Eumorpha achemon</i>	NA	1893	NA	Yes	?	Robertson 1893
<i>Eumorpha achemon</i>	Faville Prairie, WI	14 July 1993	NA	No	Yes	Cuthrell 1994
<i>Eumorpha achemon</i>	Pickerel Creek	26 June 1998	2355	No	Yes	This study
<i>Eumorpha pandorus</i>	Pickerel Creek	26 June 1998	2340	No	Yes	This study
<i>Sphinx eremitus</i>	Illinois		NA	?	Yes	Bowles 1983
<i>Sphinx eremitus</i>	Huron County #1 Prairie	1 July 1998	2150	Yes	No	This study
<i>Sphinx eremitus</i>	Huron County #1 Prairie	2 July 1998	2222	No	Yes	This study
<i>Manduca sexta</i>	Illinois		NA	Yes	No	Bowles 1983
<i>Manduca sexta</i>	Pickerel Creek	25 June 1998	2329	Yes	No	This study
<i>Manduca sexta</i>	Pickerel Creek, OH	25 June 1998	2322	Yes	No	This study
<i>Manduca quinquimaculata</i>	Illinois		NA	Yes	No	Bowles 1983
small moths	Michigan	1964	NA	Yes	?	Case 1964

Non-pollinators

Several species of sphingids have reduced or non-functioning tongues and some do not even feed as adults, therefore we can eliminate these as pollinators for the orchid (Fleming 1970). Our list of collected species includes: *Ceratomia undulosa*, *C. amyntor*, *Paonias myops*, *Smerinthus cerisyi*, *Paonias excaecatus*, *Cressonia juglandis*, and *Lapara* sp. These hawkmoths were present in the area and were drawn into our light source.

Unlikely pollinators

Another set of hawkmoths can be categorized as unlikely pollinators based on their shorter proboscis lengths (14.7 mm-22 mm) which would limit their ability to reach nectar within the long nectar spur of the orchid. These species include: *Darapasa myron* and *Darapasa pholus*. Neither of

these were observed visiting the orchid but were collected at the light.

Pollen thieves

A third category of moths would be those moths that have been observed visiting the orchids but which upon close inspection were not carrying pollinia. Two such species with extremely long tongues include *Manduca sexta* and *Manduca quinquimaculata*. These two moths have not been observed carrying Eastern prairie fringed orchid pollinia. A few explanations as to why these species do not affect pollination may include the angle in which they visit the orchid, or because their tongues are too fine at the proximal end and do not come into contact with the orchid viscidia.

Hawkmoth behavior

Hawkmoths are known for their ability to fly long distances. *Xylophanes tersa* (a

pollen vector for the Eastern prairie fringed orchid) and *Eumorpha labuscae* (a subtropical member of the genus) regularly occur hundreds of miles outside the ranges of their host plants. Hawkmoth dispersal in terms of capability to fly to an orchid population is not a barrier. However, insect behavior may play a significant role. Separate activities of a given insect (which tend to be synchronized in a population) include feeding, dispersal, mate finding, and host plant finding. Each of these activities

elicits different flight behaviors in moths and may affect their attraction to lights.

It must also be stated that while the orchid is adapted for and dependent upon a hawkmoth for pollination, there is not a species of hawkmoth that is known to be dependent upon the Eastern prairie fringed orchid. No hawkmoth larvae are known to feed on the orchid and adult hawkmoths nectar from a variety of flowering plants.

Conclusions and Recommendations

As outlined previously, *P. leucophaea* once ranged widely in Eastern North America from Oklahoma to southern Ontario. Land conversion and associated human activities have caused this species to become severely diminished, with fewer than 60 populations now known, most of which have relatively poor viability (Bowles 1993). Central to the perpetuation of viable populations of Eastern prairie fringed orchid is an understanding of its breeding system and the identification and role of its required pollinators, the hawkmoths.

Our study reconfirmed the role of two of the three previously documented pollinators of *Platanthera leucophaea* (*Eumorpha achemon* and *Sphinx emeritus*). It also resulted in the identification of a previously unknown pollinator (*Eumorpha pandorus*), a highly significant finding for one of North America's most imperiled orchid species.

Other than for a few notable pest species, very little information in the literature is currently available providing detailed data on hawkmoth distributions, life histories, or specific habitat requirements. Life history studies constitute an especially critical need for those species that have been documented as pollinators. Specifically, habitat requirements and larval ecology studies are required to assess the impacts of landscape fragmentation and pesticides on

hawkmoth populations. Studies to determine if resident or migratory hawkmoth populations are responsible for pollination are also an important need. Conservation of Eastern prairie fringed orchid may ultimately constitute considerably more than the protection and management of lakeplain prairie habitats, particularly if pollinators are influenced by factors well beyond the local environs of orchid populations.

This study can be considered only an initial step in ascertaining the identities of pollinators, from which more directed efforts can be made to compile relevant natural history data. An area of further investigation includes determining the population size of resident hawkmoths. In addition to the ongoing monitoring of orchids and orchid fruit set, it is extremely important to start monitoring the hawkmoth pollinators associated with these sites. We may be able to detect trends in orchid fruit set if we assess the numbers of pollinators present at a site during the flowering period.

While we have been successful in reconfirming two hawkmoth species as pollinators and discovering a new hawkmoth pollen vector for the Eastern prairie fringed orchid, much work remains to fully understand the pollination biology of this unique and rare orchid. When enjoying the

splendors of a meadow full flowering
Eastern prairie fringed orchids, remember

the unsung heroes who made this all
possible--the hawkmoths.

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Appendix I

Platanthera leucophaea abstract for Michigan

Orchidaceae

Orchid Family

Legal status: State Endangered, Federal Threatened

Global and state rank: G2/S1

Other common names: White fringed-orchid, prairie white fringed-orchid.

Synonyms: *Habenaria leucophaea* (Nutt.) A. Gray

Taxonomy: Formerly included within the genus *Habenaria* by Correll (1950), this species, in addition to several other Michigan taxa, is widely recognized as appropriately belonging to *Platanthera* (Case 1987). Western populations of what had once been considered *P. leucophaea*, comprising most populations west of the Mississippi River, have been distinguished by Sheviak and Bowles (1986) as *P. praeclara* (western prairie fringed-orchid) based on significant differences in morphology, pollination mechanism, and geographic distribution.

Total range: Centered about the Great Lakes, *P. leucophaea* occurs east to Virginia and along the St. Lawrence drainage to Maine, ranging west into the Great Plains to the Dakotas and Iowa, and south in the Mississippi drainage to Missouri and Oklahoma. Now near extinction throughout much of its range, most populations are concentrated in the southern Great Lakes region, occurring primarily in southern Wisconsin, Illinois, Ohio, and southern Lower Michigan. This species is considered rare in Illinois (S2-rank), Iowa (S2), Maine (S1), Missouri (S1), Ohio (S1), Oklahoma (S1), Virginia (S1), Wisconsin (S1), and Ontario. It is considered extirpated in Indiana, New Jersey, and Pennsylvania, and is known only from historical records in New York and South Dakota.

State distribution: *Platanthera leucophaea* was once known from more than 20 counties, primarily in southern Lower Michigan, with one anomalous disjunct locality documented in Cheboygan County. Extensive habitat modification and destruction has caused this species to severely decline. It is now extant in fewer than 10 counties, persisting mostly in the remnant lakeplain prairies of Saginaw Bay and western Lake Erie. The relatively high numbers of plants observed in 1984 declined markedly following years of high lake levels and drought. An exhaustive 1990 inventory of this species' remaining strongholds in Michigan found approximately 1100 plants total, with few populations supporting large numbers of plants in good quality, viable habitat.

Recognition: Prairie fringed-orchid is a tall, striking plant. It produces single stems that range from approximately 20 cm to 1 m or more in height, bearing long, narrow, sharp-pointed leaves that become progressively reduced upward. The leaves are strongly sheathing, becoming bract-like beneath the inflorescence. Relatively wide, showy racemes of up to 40 or more creamy white, stalked flowers terminate the stems. Each flower has a long (2-5 cm), slender, downward-curving nectar spur behind and a **three-parted, prominently fringed lower lip, the fringe up to about half the length of the lip.** The small, wedge-shaped upper petals are rounded with **toothed or**

ragged margins, forming a loose bonnet arching over the column. *Platanthera blephariglottis* and *P. lacera* are superficially similar species that can be easily distinguished. *Platanthera blephariglottis*, which occurs only in sphagnum bogs in Michigan, bears white flowers with fringed lower lips that are tongue-shaped and undivided. *Platanthera lacera* is a more common, widespread species of a variety of habitats; it bears white to greenish-white flowers with three-parted lower lips deeply divided into slender, thread-like segments, and upper petals that are linear.

Best survey time/phenology:



Habitat: *Platanthera leucophaea* occurs in two distinct habitats in Michigan--wet prairies and bogs. It thrives best in the lakeplain wet or wet-mesic prairies that border Saginaw Bay and Lake Erie. These communities have relatively alkaline, lacustrine soils, and are dominated by *Carex aquatilis*, *C. stricta*, and *Calamagrostis canadensis*, as well as several prairie grasses and forbs. Common associates include *Andropogon scoparius* (little bluestem) and *A. gerardii* (big bluestem), *Spartina pectinata* (prairie slough grass), *Potentilla fruticosa* (shrubby cinquefoil), *Liatris spicata* (blazing star), *Linum medium* (flax), *Cornus stolonifera* and *C. amomum* (dogwoods), *Pycnanthemum virginianum* (mountain mint), *Gentianopsis crinita* (fringed gentian), *Solidago riddellii* (Riddell's goldenrod), *Cladium mariscoides* (twig-rush), *Typha latifolia* (cattail), *Juncus* spp. (rushes), and *Scirpus acutus* (hardstem bulrush). Prairie fringed-orchid frequently persists in degraded prairie remnants, and will frequently colonize ditches, railroad rights-of-way, fallow agricultural fields, and similar habitats where artificial disturbance creates a moist mineral surface conducive to germination.

Open or semi-open bog mats of *Sphagnum* and *Carex*, with slightly acidic, neutral, or somewhat alkaline lake water also support small populations of this orchid. Associates in these sites include *Thelypteris palustris* (marsh fern), *Sarracenia purpurea* (pitcher-plant), *Chamaedaphne calyculata* (leatherleaf), *Drosera rotundifolia* (sundew), *Potentilla fruticosa* (shrubby cinquefoil), *Larix laricina* (tamarack), *Betula pumila* (bog birch), and *Toxicodendron vernix* (poison sumac). Farther west and to the south, Eastern prairie fringed-orchid occurs in mesic and wet mesic black soil prairies, or rich, wet, sandy prairies, while to the east of Michigan, occurrences are generally restricted to bogs or sandy or peaty lakeshores.

Biology: Unlike many other *Platanthera* species, *P. leucophaea* is long-lived, with individuals documented to live more than 30 years (Case 1987). According to Case (1987), this perennial produces a bud on one of its roots that develops a new set of roots or tubers, becoming next season's new plant. The development and viability of this bud is highly dependent on the vigor of the old plant. In Michigan, flowering occurs during late June through early July. Case reports that the white blossoms produce a heavy fragrance at dusk and attract many moths, including the large Sphinx moths responsible for pollination. Sphinx moths are probably co-adapted pollinators, since their tongues are long enough to reach the nectar that lies deep in the spur of the flower (M. Bowles, pers. comm.). Capsules mature in September, releasing hundreds of thousands of airborne seeds. Plants do not flower every year, frequently producing only a single leaf above ground (M. Bowles, pers. comm) and possibly even becoming dormant when conditions are unsuitable, such as the onset of drought. Fire is thought to help break dormancy and stimulate flowering (Sheviak 1974), although its role in Michigan *Platanthera* sites is highly uncertain.

Conservation/management: Competitive encroachment by native shrubs, especially dogwoods and willows, and pernicious exotics such as *Lythrum salicaria* (purple loosestrife) pose one of the greatest threats to Michigan's remaining prairie fringed-orchids. The large-scale destruction of lakeplain prairie habitat, primarily through alteration by ditching and diking, the conversion of areas for agricultural use, and other land settlement activities have rendered this species particularly vulnerable to extinction. In its last remaining viable sites, Eastern prairie fringed-orchid is best protected by maintaining the natural hydrological cycles of the lakeplain wet prairies. Protection can only be adequately afforded when sufficient refugia are available during periods of high lake levels. Unfortunately, few natural areas are left that provide the necessary landward habitat. Where refugia are available, this species is able to seed inland during high water cycles, advancing shoreward again as lake levels recede (Case 1987). This natural fluctuation along the lakeshores maintains the required open, wet prairie habitat, preventing closure and shading by highly competitive woody plants such as dogwoods (*Cornus* spp). In sites where active management may be required, shrub removal is of primary importance. Although fire is frequently recommended as a management tool (Bowles 1983), its role in Michigan's prairie fringed-orchid habitat is poorly understood. Case (pers. comm.) recommends great caution with the consideration of fire management, noting that the orchid's shallow subterranean buds can be easily damaged during spring or fall burns. At present, fire should be employed only as a very selective experimental tool, to be used in testing alongside other approaches, such as mechanical brush removal and soil disking. Prescribed burns may be desirable when brush removal and soil scarification enhance the vulnerability of populations to exotics such as purple loosestrife and other invasives. Lastly, one of the greatest recognized threats to this elegant species is poaching and trampling by orchid enthusiasts, photographers, and others. At least one Michigan colony has been obliterated by poachers, and thus great caution must be taken with regard to remaining sites. Based on the aforementioned threats and the great vulnerability of this species, Case (1987) considers Eastern prairie fringed-orchid to be possibly the most "severely endangered orchid of our region".

Comments: According to an early report, *P. leucophaea* once grew so abundantly near the bath houses on Belle Isle Park, Detroit, that visitors there gathered it in bouquets (Foerste 1882). Several decades ago, this species also grew in abundance along Saginaw Bay. These are, however, scenarios unlikely to be witnessed again.

Research needs: Important research areas include pollination and breeding system studies, and especially the role of various management techniques required to sustain viable populations and restore functioning lakeplain prairie communities and landscapes.

Key words: Lakeplain prairie, lakeplain wet prairie.

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