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SPHINX MOTH POLLINATORS FOR THE ENDANGERED WESTERN PRAIRIE FRINGED ORCHID, *PLATANTHERA PRAECLARA* IN MANITOBA, CANADA

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ABSTRACT. The western prairie fringed orchid, *Platanthera praeclara* (Sheviak & Bowles), is an endangered species in North America. In Manitoba orchids produce lower numbers of seed capsules than more southern populations. Exploration of the pollination biology for *P. praeclara* is critical to preserve this endangered species. This study identified the pollinators of *P. praeclara* using cone and malaise traps and tested the effectiveness of marking pollinators with traces of Day-Glow® orange marker powder. Although Lepidoptera were numerous in orchid plots during daily observation periods, including day flying Sphingidae, none were pollinators for *P. praeclara*. Among the 5856 insects from 49 families captured over 45 trapping days, six sphinx moths, two specimens of *Hyles gallii* (Rottenburg) and four specimens of *Sphinx drupiferarum* J.E. Smith (Sphingidae), were found with two or more orchid pollinia attached to their eyes and were confirmed as pollinators of *P. praeclara*. *S. drupiferarum* is uncommon in southern Manitoba and *H. gallii* appears to be a less efficient pollinator than *S. drupiferarum*. Proboscis length, eye width and flight period may influence the efficiency of biotic pollination of the orchid.

Additional key words: Sphingidae, pollinia, pollination, *P. praeclara*, *S. drupiferarum*, *H. gallii*.

The western prairie fringed orchid, *Platanthera praeclara* (Sheviak & Bowles 1986), occurs in areas of remnant tall grass prairie in southeastern Manitoba. Prior to its discovery in the mid 1980's near Tolsoi, Manitoba, *P. praeclara* was not known to exist in Canada (Johnson 1985, 1991). The Manitoba population, at its maximum has consisted of approximately 21,000 individual plants (although the population may fluctuate widely from year to year) and it is the largest of four metapopulations (over 300 plants) in North America. The remaining populations occur in North Dakota, South Dakota, Minnesota, Kansas, Nebraska, and Iowa (Sheviak & Bowles 1986, Bjugstad & Fortune 1989, Bray & Wilson 1992, Bjugstad-Porter 1993, Pleasants & Moe 1993, Davis 1994, Sieg & King 1995, U.S. Fish & Wildlife Service 1996, Hof et al. 1999).

The orchid is protected under Manitoba's Endangered Species Act and has been placed on the endangered species list in both Canada and United States (Collicutt 1993, Davis 1995). In Manitoba, *P. praeclara* often has low fruit set and subsequent seed production (Borkowsky 1998). Although the western prairie fringed orchid will produce a vegetative form, there is little evidence that vegetative reproduction occurs in *P. praeclara* (Bowles 1983, Sather 1991, Sieg & King 1995, Hof et al. 1999). A plant may also go dormant, as is typical in other species of orchids (Nilsson 1992). Therefore, the recruitment of new plants is dependant primarily upon successful pollination and subsequent seed production. In surveys of over 1000 plants Borkowsky (1998) found that only 2.1% of orchid stems produced one or more seed capsules annually in Manitoba between 1994 and 1998. In more southern orchid populations the percent of stems that produce seed capsules can range up to 49% (Bowles 1983, Sheviak & Bowles 1986, Cuthrell 1994). The authors have hypothesized that reduced seedpod production may be linked to low pollination success in Manitoba. The level of pollination success for *P. praeclara* and the identity of the orchid pollinators are unknown in Manitoba.

Pollination is the process in which pollen grains are transferred to the stigma, which is followed by fertilization of the ovules and development of seeds (Proctor et al. 1996). Many orchids require a biotic organism (a pollination agent or pollen vector) to transport the pollen to the stigma (van der Pijl & Dodson 1966, Faegri & van der Pijl 1979). In *P. praeclara* the most striking visual characteristic of the flower is a large, deeply fringed, tri-lobed lower lip and a long, slender spur containing nectar that suspends backward from the flower (Figs. 1, 2). The nectar spur may be 36–55 mm long with a maximum diameter of 2.7 ± 0.5 mm (Sheviak & Bowles 1986). Orchids grow to 38–85 cm tall (Sheviak & Bowles 1986) with the determinant inflorescence containing 7 to 12 flowers (Sheviak & Bowles 1986, Pleasants 1993). The pollinium (Fig. 1) is a specialized structure that consists of pollen, a column and viscidium (Nilsson 1992). In *P. praeclara* the minute grains of pollen are arranged into subunits called massulae (Pleasants & Moe 1993). These subunits form a bi-lobed mass that is attached to the column, which is secured to the viscidium (the entire structure is termed the pollinium). The pollinium is sheathed, with the exception of the viscidium, which is exposed and adapted to cement itself to the pollinator (Bowles 1983). Each flower has one pollinium located on either side of the stigmatic surface. This allows for a 6 to 7 mm separation between each viscidium (Sheviak & Bowles 1986). The opening to the nectar spur is located immediately below the stigmatic surface.

The small opening to the nectar spur restricts the

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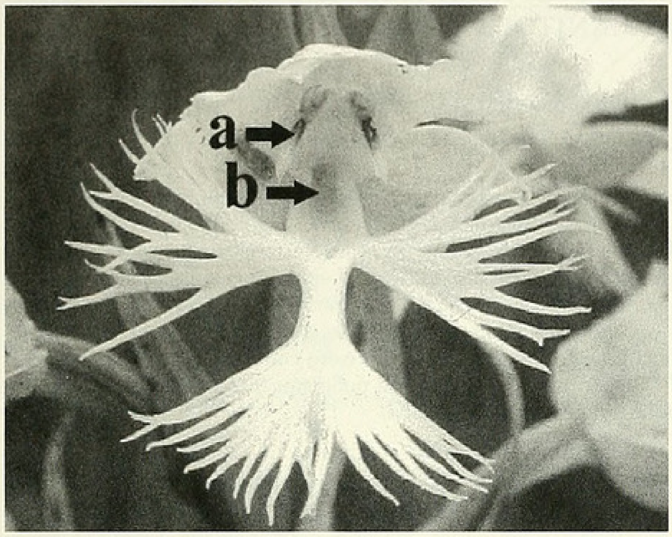

FIG. 1. *Platanthera praeclara* flower, anterior view, showing pollinium (a), and the opening to nectar spur (b).

FIG. 2. *Platanthera praeclara* flower, lateral view, showing nectar spur (a).

position of a potential nectar seeking insect, and increases the likelihood that one or both viscidia will come into contact with a likely pollinator. The pollinium is pulled from the sheath when a pollinator contacts the viscidium and then withdraws from the flower (Darwin 1904, Dressler 1981, 1993).

Orchids also produce a scent or fragrance which may be weak or absent in the daytime, increases in intensity at dusk and may remain strong until sunrise depending on the age and condition of the flower (Sheviak & Bowles 1986). The relationship between the attractiveness of the fragrance to pollinators and the intensity of the scent is unknown in *P. praeclara*.

To be identified as a pollinator and to rule out indiscriminate visitors to the flower, the organism must make regular visits to the flowers during its lifetime and effectively deposit the pollen on the stigma (Faegri & van der Pijl 1979). The flower–pollinator relationship may also be controlled by pollinator behavior, mouthpart morphology or taxonomy and by flower morphology (Faegri & van der Pijl 1979, Wyatt 1983). Wyatt (1983) identified nine forms of biotic pollination in orchids including sphingophily (Sphingidae—hawkmoths), phalaenophily (small moths), psycophily (butterflies), melittophily (bees), myophily (syrphid and bee flies), sapromyophily (carrion and dung flies), cantharophily (beetles), ornithophily (birds) and chiropterophily (bats).

The potential pollinators for *P. praeclara* in Manitoba are not known. Although the literature suggests that night-flying members of the Sphingidae may be key pollinators of *P. praeclara*, other members of this orchid genus and several closely related genera may be pollinated by butterflies, other moth species, certain Diptera, Coleoptera or Hymenoptera (van der Pijl & Dodson 1966, Patt et al. 1989, Robertson & Wyatt 1990, Bowles et al. 1992, Larson 1992).

The floral characteristics of *P. praeclara* indicate a moth pollination method (Faegri & van der Pijl 1979, Sheviak & Bowles 1986, Luyt & Johnson 2001), most likely sphingophily or phalaenophily. *P. praeclara* has no developed landing platform on the flowers, therefore hovering pollinators are favored and butterflies may be excluded (van der Pijl & Dodson 1966, Dressler 1981). To retrieve nectar, the insect must correctly align itself with the flower as it inserts its proboscis, which increases the likelihood that the pollinator will contact one or both of the viscidia which will adhere to the proboscis or eyes of the insect (Sheviak & Bowles 1986). Considering the length of the nectar spur of *P. praeclara* and position of the viscidia, the list of potential pollinators is further reduced to Lepidoptera with a very long proboscis (e.g., moths belonging to the Sphingidae or hawkmoth family). Few, if any, observations of pollination of fringed orchids by hawkmoths have been made in the field (Bowles 1983, Sheviak & Bowles 1986, Pleasants & Moe 1993). Based on proboscis length, Sheviak & Bowles (1986) suggested that the following species of moths could be potential pollinators of *P. praeclara* in the United States: *Eumorpha achemon* (Drury), *Hyles lineata* (F.), *Sphinx drupiferarum* J.E. Smith and *Sphinx kalmiae* J.E. Smith. Cuthrell (1994) collected two specimens, one each of *Sphinx drupiferarum* and *Eumorpha achemon* with viscidia from *P. praeclara* attached to the head, from a light trap adjacent to a field of orchids in the United States.

To better understand the pollination biology of *P. praeclara* in Manitoba diurnally active Lepidoptera including day flying Sphingidae, nocturnally active

Lepidoptera and other insect Orders were surveyed as potential pollinators of *P. praeclara*. Several types of passive traps were tested to capture *P. praeclara* pollinators, and a method to mark individual pollinators was investigated.

STUDY SITE AND METHODS

Five field experiments were established between 1997 and 1999 to determine the identity of *P. praeclara* pollinators. Three study plots were located in the Manitoba Tall Grass Prairie Preserve, near Tolsoi, Manitoba (49°05′N, 96°49′W) and two additional moth light trapping sites were located near Lonesand, Manitoba (approximately 21 km east of the Preserve) and near Grunthal, Manitoba (approximately 26 km northwest). The climate is a boreal continental regime with mean temperatures of 19.6°C and –18.8°C for July and January, respectively. Fifty-five percent of the annual precipitation (mean 579.1 mm) falls during the period of May through August (Canadian Climate Program 1993). Drainage in much of the prairie is poor with soil composed of lacustrine parent material, sandy loam to clay loam upper horizons and a thin organic surface layer. Stones, rocks and occasionally boulders are also scattered across the prairie (Canada Soil Inventory 1989, Moore & Fortney 1994).

The Tall Grass Prairie Preserve has an abundance of grasses, including Big bluestem (*Andropogon gerardii* Vitman) and Little bluestem (*Schizachyrium scoparium* (Michx.) Nash) (Gramineae) and is interspersed with bluffs of various deciduous tree species, including willow (*Salix* spp.) and poplar (*Populus* spp.) (Henne & Diehl 2002).

Three 50 × 50 m plots were established in fields were orchids were numerous. Each plot contained a minimum of 25 orchids. Plots were separated by a distance of 500 to 1000 m. To establish that there were no day flying insects pollinating the orchids, 15 individual orchids were tagged in each of the three plots (total of 45 plants) in 1997 and 1998. Each orchid was visually observed for 15 minutes on at least three separate days during the flowering period in 1997 and 1998 between 1100 h to 1500 h to determine if insects contacted plants and were responsible for removal of one or more of the pollinium from the flowers, either by accident or for the purpose of obtaining nectar or pollen. The number and identity of potential pollinators (Order, Family and Genus/species if known) landing or crawling on the orchids was recorded.

Inverted cone insect traps were used to sample potential pollinators from individual orchids. Cone traps were constructed from light gauge steel tubing and wire and covered in fine mesh screen. Cone traps were approximately 40 cm in length and 25 cm in diameter. An inverted wire mesh cone was placed at the base of the trap (much like a minnow trap) and a hinged trap door placed on the top of the trap. Three legs attached to the bottom of trap allowed it to be placed over an individual orchid. The legs were of sufficient length that they could be pushed into the ground around the orchid, allowing the mouth of the inverted cone to be suspended approximately 5 to 10 cm above the terminal flower of the orchid. Traps were emptied daily between 0630 h and 0830 h and again between 1900 h and 2030 h. Captured insects were identified and examined for presence of orchid pollinia. One cone trap was placed in each of the three plots and rotated between plants during the flowering period. Cone traps were placed over orchids that had the most flowers open with intact pollinia available. Traps remained in place over an individual orchid for 24–48 hours and were placed in the plots between 1 July and 15 July in 1997, 1998 and 1999.

Malaise insect traps (Bioquip® Equipment Specialities) were to used to sample for potential pollinators over a groups of orchids (generally five or more individual plants). Each trap was approximately 2 m in height with a glass container at the top to collect trapped insects. A piece of Vapona® insecticide strip (0.2 cm^2) was placed at the end of the collecting cylinder to kill captured insects. One malaise insect trap was placed within each of the three plots and rotated among groups of orchids during the flowering period. Traps were emptied daily between 0630 h and 0830 h and again between 1900 h and 2030 h. Insects were identified and examined for presence of orchid pollinia. Traps were placed in the field between 1 July and 15 July in 1997, 1998 and 1999. Traps were rotated within the plot to new groups of orchids every three to five days.

In 1999, five orchids in each plot under a malaise trap or one orchid under a cone trap were chosen to test the effectiveness of Day-Glow® orange marker dye powder in identifying potential pollinators. A small amount of Day-Glow® orange marker dye powder was applied with a extra fine nylon brush to the centre of each flower of the orchids chosen. Insects captured in the traps were identified and examined for presence of pollinia removed from the orchids and also examined in a dark room under an ultra-violet light for the presence of the Day-Glow® powder. Insects with marker particles adhering to their bodies were considered to have come in contact with the treated flowers.

To determine moth flight periods, two Wards all-weather insect traps® (Wards Natural Science) were placed approximately 1 km to the west of the orchid plots and 5 km to the south of the plots. Two additional Ward's all-weather insect traps® were located at Lonesand and Grunthal, Manitoba to augment moth captures at the Tall Grass Prairie Preserve. Traps were operated from 1 May to 31 August, 1997–1999. Traps had an eight watt ultra-violet fluorescent bulb as an attractant. The traps were used to survey nocturnal Lepidoptera and determine the flight periods of potential orchid pollinators. Flight periods were considered to include the period between date of first and last capture in each year. Traps in the Tall Grass Prairie Preserve were placed in open areas surrounded by mature trees and were not visible from orchid plots. Lepidoptera captured in traps were sorted, pinned and identified to species.

The flowering period for orchids in plots was recorded during the study. Flowering period was defined as the period between the appearance of the first flower and last flower in a plot and peak flowering date was defined as the date when the most flowers were fully open in a plot. The mean overlap in days between moth species flight period and orchid flowering period for all years was calculated. Mean overlap flight period data was square root transformed to satisfy assumptions of normality and heterogeneity of variance for analysis of variance (ANOVA) (SPSS Inc. 1999). Where ANOVA was significant a least-significant difference (LSD) test was used to determine the differences between means ($\alpha = 0.05$) because of its consistency (Saville 1990). To determine if potential pollinators would fit pollinia distance separation requirements and nectar spur depth requirements of *P. praeclara*, measurements were made on a minimum of five individuals from all sphinx moth species collected in the various trap types. Pinned moths were softened in a relaxing chamber and the length of the proboscis, the distance between the outer margins of the compound eyes and distance between the inner margins of compound eyes where measured in mm under a dissecting microscope. For data analysis the proboscis length was square root transformed and distance between outer eye edges and distance between inner eye edges were log transformed to satisfy assumptions of normality and heterogeneity of variance. Morphological measurements between species were subject to ANOVA and where ANOVA was significant differences between means were identified using a LSD test. To examine the relationship between proboscis length and ability of pollinators to retrieve nectar, the length of nectar spurs and the depth of nectar within the spur (distance from distal end of spur to top of nectar line) was measured for orchids in each of the three plots.

TABLE 1. Number and identity of insect Orders and Families collected in cone and malaise traps 1997–1999.

Order	Family/Subfamily	n
Ephemeroptera	Baetidae	1
	Heptageniidae	1
Odonata	Coenagrionidae	3
Orthoptera	Acrididae	5
Plecoptera	Perlidae	1
Hemiptera	Miridae	21
	Reduviidae	2
	Pentatomidae	2
Homoptera	Cercopidae	5
	Cicadellidae	13
Neuroptera	Mantispidae	2
	Chrysopidae	9
Coleoptera	Carabidae	8
	Scarabaeidae	5
	Elateridae	2
	Lampyridae	12
	Cleridae	5
	Coccinellidae	8
	Tenebrionidae	1
	Chrysomelidae	5
	Curculionidae	3
Mecoptera	Panorpidae	2
Trichoptera	Limnephilidae	6
Diptera	Tipulidae	26
	Culicidae	55
	Chironomidae	24
	Simuliidae	15
	Tabanidae	4450
	Syrphidae	45
	Muscidae	546
	Calliphoridae	228
	Sarcophagidae	11
Lepidoptera	Pyralidae	14
	Pterophoridae	2
	Tortricidae	34
	Gelechiidae	40
	Geometridae	18
	Arctiidae	3
	Noctuidae	34
	Lasiocampidae	15
	Sphingidae	6
	Hesperiidae	10
	Nymphalidae	5
	Satyridae	2
Hymenoptera	Ichneumonidae	23
	Vespidae	2
	Sphecidae	3
	Megachilidae	2
	Apidae	19

Identification of insects was based upon Hodges (1971), Rockburne and Lafontaine (1976), Morris (1980), Hodges et al. (1983), Covell (1984), Borror et al. (1989), Klassen et al. (1989), Layberry et al. (1998) and Handfield (1999).

RESULTS

Observational survey. In 1997 and 1998 orchids were observed between 1100 h and 1500 h for approximately 70 hours. Although numerous insects (many

TABLE 2. Summary of six Sphingidae collected from cone and malaise traps with attached pollinia 1997–1999.

Date	Species	Type	# of pollinia	Pollinia location	Marker powder
11 July 1997	*Hyles gallii*	cone	2	head	n/a
11 July 1997	*Sphinx drupiferarum*	malaise	5	head	n/a
15 July 1998	*Sphinx drupiferarum*	malaise	11	head	n/a
15 July 1998	*Sphinx drupiferarum*	malaise	3	head	n/a
20 July 1998	*Sphinx drupiferarum*	cone	7	head	n/a
6 July 1999	*Hyles gallii*	cone	2	head	present

belonging to pollinating families or genera) frequented the plots during the daily observation periods no individuals were observed to seek nectar or pollen from the orchids, to use the flowers as a resting platform or to sun themselves on the orchids. Individuals of the sphinx moths *Hemaris thysbe* (Fabricus) (16 individuals) and *Hemaris diffinis* (Boisduval) (28 individuals) were observed in the orchid plots during the observation periods but they were not attracted to orchids, despite repeatedly visiting nearby flowering herbs for nectar.

Trapping experiments. Between 1997 and 1999 the cone and malaise traps caught 5856 individual insects from 49 families over 45 trapping days (Table 1). The only insects found to have pollinia attached to their bodies belonged to the family Sphingidae (Table 2). Six sphingid moths, two specimens of the Bedstraw hawkmoth, *Hyles gallii* (Rottenburg), and four specimens of the Wild cherry sphinx, *S. drupiferarum* were collected with two or more pollinia attached to the eyes (Figs. 3, 4). *H. gallii* had 2 pollinia per moth, while *S. drupiferarum* had 3 to 11 pollinia per moth.

Marking experiment. In 1999 one sphinx moth, *H. gallii*, was collected from a cone trap with traces of Day-Glow® orange marker dye powder on both eyes and the proboscis. Both pollinia attached to the eyes also had traces of powder, primarily on the massulae and viscidium.

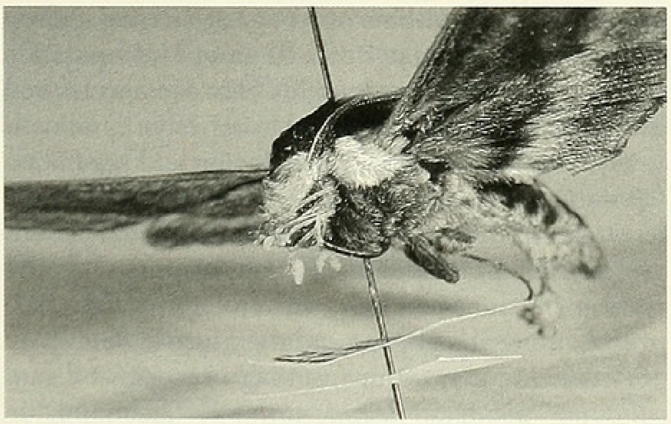

FIG. 3. Anterior/lateral view, *Sphinx drupiferarum* J. E. Smith with pollinia from *Platanthera praeclara* attached to eyes.

Flight period. The flight periods for sphingid species found in the vicinity of the Tall Grass Prairie Preserve were based on the catches from the four black light traps during the period of 1997 to 1999 (Table 3). Flowering dates for *P. praeclara* are also shown in Table 3. Generally the moths collected were most abundant in the first several weeks of the orchid flowering period. The flight periods of *S. drupiferarum* and *H. gallii* overlapped with orchid flowering by 34.6% and 45.3% respectively.

Morphological measurements. The proboscis length, width across the eyes and distance between the inner eye margins were measured for the 15 species of Sphingidae collected in the vicinity of the Tall Grass Prairie Preserve (Table 4). The mean orchid nectar spur length was 45.27 mm (n = 1016, SE = 0.134) and the mean depth of nectar within the spur was 12.44 mm (n = 1016, SE = 0.201).

DISCUSSION

The results confirm observations by Faegri and van der Pijl (1979), Sheviak and Bowles (1986), Cuthrell (1994) and Luyt and Johnson (2001) that *P. praeclara* is pollinated by nocturnal Lepidoptera confined to the family Sphingidae. It appears that there are no diurnally active insects that seek nectar or pollen from *P.*

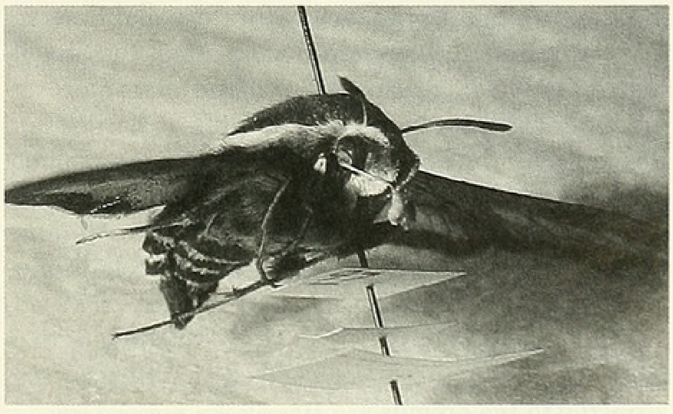

FIG. 4. Anterior/lateral view, *Hyles gallii* (Rottenburg), with pollinia from *Platanthera praeclara* attached to eyes. Note the large viscidium cemented to lower-center of eye, with massulae projected forward.

TABLE 3. Flight period dates, orchid flowering periods, number of individual sphinx moths collected in black light traps and percent overlap between flight and flowering dates in the vicinity of the Tall Grass Prairie Preserve and for orchids 1997–1999.

	Date				% Overlap of flight period & flowering period days ± SE
	1997	1998	1999	n[1]	
Peak orchid flowering date	2 July	4 July	7 July		
Orchid flowering dates	22 June–16 July	19 June–20 July	23 June–19 July		
Sphingidae–flight period dates					
Ceratomia undulosa Harris	12 June–12 July	7 June–18 July	9 June–31 July	14	92.0 ± 4.9c[2]
Sphinx chersis (Hubner)	31 May–2 July	11 July	absent	6	14.1 ± 13.9a
Sphinx kalmiae J.E. Smith	1–26 July	5–24 June	10 June–18 July	8	58.0 ± 23.2abc
Sphinx luscitiosa Clemens	absent	20 May–30 June	19 June–11 July	7	34.6 ± 19.9abc
Sphinx drupiferarum J.E. Smith	11 July	1 June–25 July	24 June	5	34.6 ± 32.7abc
Smerinthus cerisyi Kirby	28 May–27 June	21 May–29 July	16 May–25 July	58	73.7 ± 26.3bc
Smerinthus jamaicensis (Drury)	25 May–30 June	1 June–10 July	29 May–18 July	123	65.3 ± 18.2bc
Poanes excaecatus (J.E. Smith)	3 June–20 July	11 June–15 July	5 June–20 July	37	94.6 ± 9.2c
Poanes myops (J.E. Smith)	11–28 June	9 June–4 July	1–27 June	34	29.3 ± 16.9abc
Cressonia juglandis (J.E. Smith)	absent	8–30 June	absent	5	11.7 ± 11.6a
Pachysphinx modesta (Harris)	27 May–28 June	11 June–5 Aug	9 June–9 July	61	63.0 ± 20.8bc
Hemaris thysbe (Fabricus)[3]	31 May–25 June	5–28 June	4 June–2 July	16	25.3 ± 6.9abc
Hemaris diffinis (Boisduval)[4]	21 May–2 July	10 June–10 July	1 June–13 July	28	62.0 ± 10.4bc
Darapsa myron (Cramer)	absent	15 May–6 July	absent	5	18.0 ± 16.0a
Hyles gallii (Rottenburg)	15 June–31 July	31 May–29 June	6 July	18	45.3 ± 28.5abc
					$p = 0.040$
					$F_{14,44} = 2.086$

[1] Number of moths collected 1997, 1998 & 1999.
[2] Means within each column followed by the same letter are not significantly different (Fisher's LSD, $p > 0.05$).
[3,4] *H. thybe* and *H. diffinis* collected by sweep net in the vicinity of the Tall Grass Prairie Preserve.

praeclara. The presence of pollinia on one *H. gallii* specimen and four *S. drupiferarum* specimens and the marker powder and pollinia on another specimen of *H. gallii* confirm these species as pollinating agents of *P. praeclara* in Manitoba. Despite the larger size of the malaise trap covering more orchids, there was little difference in the capture rates of moths with pollinia between trap types. The Day-Glow® orange marker dye powder successfully marked one pollinator.

Pollinia were attached to the center of each eye on both moth species. *S. drupiferarum* had more pollinia per specimen. The distance between the outer edges of the eyes was greater in *S. drupiferarum* than *H. gallii* (Table 4), but it is unknown if this small difference in eye separation (0.43 mm) would affect the attachment of pollinia. Perhaps *S. drupiferarum* is more aggressive at retrieving nectar and presses harder into the centre of the orchid thus capturing more pollinia. Alternately *H. gallii* may visit the orchids less frequently resulting in fewer opportunities to remove pollinia, or be discouraged from visiting orchids once several pollinia have been attached to the eyes. *H. gallii* is more numerous in the vicinity of the orchids than *S. drupiferarum*, thus it seems likely that they are less attracted to the orchids.

Cuthrell (1994) described two specimens of *S. drupiferarum* (one caught by light trap and one a museum specimen) and one specimen of *E. achemon* (Drury) (collected by light trap) with *P. praeclara* pollinia attached to the eyes. The present study adds *H. gallii* to this list of pollinators while *E. achemon* does not occur in Manitoba.

The mean proboscis lengths for *S. drupiferarum* and *H. gallii* captured in this study were 38.40 mm and 33.50 mm, respectively. Subtracting the mean nectar depth from total nectar spur length provides a distance of 32.83 mm, thus it appears that a proboscis length of 30–35 mm is required to reach the nectar in *P. praeclara*. Based on proboscis length, *Sphinx chersis* (Hubner) and *S. kalmiae* may also be potential pollinators in Manitoba (Table 4). These species had a significantly longer proboscis than all other species collected (Table 4), with no other species having a mean proboscis length greater than 23 mm. The separation of inner and outer eye margins between species was less distinct with some species having a short proboscis yet still having similar eye positioning and separation (Table 4).

Orchid flowering periods and moth flight periods are restricted in terms of overlap in Manitoba. The overlap in more southern areas of the range of *P. praeclara* may be greater and therefore higher levels of pollination may occur resulting in more seed capsules per plant. *S. drupiferarum* is uncommon in southern Manitoba and the most numerous sphingid species in the Tall Grass Prairie Preserve do not possess

TABLE 4. Length of proboscis, the distance between the outer margins of the compound eyes and distance between the inner margins of compound eyes for Sphinx moths collected in the vicinity of the Tall Grass Prairie Preserve, Manitoba.

	n[1]	Mean proboscis length (mm ± SE)	Mean distance between outer eye margins (mm ± SE)	Mean distance between inner eye margins (mm ± SE)
Ceratomia undulosa Harris	7	9.14 ± 0.76c[2]	5.05 ± 0.05h	2.04 ± 0.02d
Sphinx chersis (Hubner)	5	40.32 ± 0.48h	5.89 ± 0.03k	2.40 ± 0.11ef
Sphinx kalmiae J.E. Smith	5	33.64 ± 1.31g	5.31 ± 0.17bi	2.05 ± 0.18d
Sphinx luscitiosa Clemens	5	22.56 ± 0.17f	4.46 ± 0.05ef	2.34 ± 0.01bc
Sphinx drupiferarum J.E. Smith	5	38.40 ± 0.97h	5.59 ± 0.06i	2.34 ± 0.02e
Smerinthus cerisyi Kirby	8	2.21 ± 0.06a	4.76 ± 0.13g	1.88 ± 0.03c
Smerinthus jamaicensis (Drury)	8	1.73 ± 0.75a	3.85 ± 0.03c	1.70 ± 0.02b
Poanes excaecatus (J.E. Smith)	7	2.89 ± 0.03b	4.63 ± 0.05fg	2.09 ± 0.03d
Poanes myops (J.E. Smith)	7	1.87 ± 0.04a	4.07 ± 0.03d	1.83 ± 0.06bc
Cressonia juglandis (J.E. Smith)	5	2.10 ± 0.05a	3.31 ± 0.08a	1.37 ± 0.53a
Pachysphinx modesta (Harris)	8	1.95 ± 0.17a	5.73 ± 0.07j	2.53 ± 0.02f
Hemaris thysbe (Fabricus)	8	12.75 ± 0.52d	3.88 ± 0.02c	1.88 ± 0.08c
Hemaris diffinis (Boisduval)	8	9.48 ± 0.20c	3.58 ± 0.06b	1.89 ± 0.03c
Darapsa myron (Cramer)	5	17.68 ± 0.18e	4.28 ± 0.09e	2.12 ± 0.04d
Hyles gallii (Rottenburg)	8	33.50 ± 0.96g	4.88 ± 0.03gh	2.44 ± 0.02ef
		$p = 0.001$ $F_{14,98} = 37.1$	$p = 0.001$ $F_{14,98} = 35.2$	$p = 0.001$ $F_{14,98} = 40.1$

[1] Number of moths measured.
[2] Means within each column followed by the same letter are not significantly different (Fisher's LSD, $p > 0.05$).

a proboscis of sufficient length to take nectar from *P. praeclara*. *H. gallii* populations fluctuate greatly from year to year in southern Manitoba, often with very few individuals appearing in some years. Therefore, low pollinator populations may be restricting seed production in some years for orchids in Manitoba.

The Tall Grass Prairie Preserve is surrounded by agricultural lands, a mixture of intensively farmed grains and oilseeds and livestock production. The larval host plants for *S. drupiferarum* can very regionally and include *Malus* spp., *Prunus* spp. and lilac, *Syringa vulgaris* L. (Hodges et al. 1983). These plants are present in the vicinity but their distribution is patchy. It is unknown whether insecticide usage (Suzán et al. 1994) on adjacent farmlands may restrict the population of larval forms of *S. drupiferarum* and *H. gallii* or if weed control may restrict access to host plants. *S. drupiferarum* may be a more efficient pollinator than *H. gallii*, but the number of *S. drupiferarum* adults frequenting the orchid fields was low in this study. There may be considerable competition between nectar sources given the amount of intensively managed lands adjacent to the Tall Grass Prairie Preserve, which would further reduce the time spent by moths pollinating orchids. Strong light sources from farms surrounding the orchid fields may also attract moths, preventing them from visiting orchids. *S. drupiferarum* occupies the northernmost extension of its range in Manitoba, which may also contribute to sporadic population occurrence and lower pollination rates of *P. praeclara*.

Baker (1961) stated that sphingophilous flowers often have a low frequency of pollinator visitation and compensate by producing numerous seeds. Further research is required to determine if other sphinx moth species are pollinating orchids and if the current level of seedpod production is abnormally low or normal for *P. praeclara* in Manitoba.

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LITERATURE CITED

BAKER, G. E. 1961. The adaptation of flowering plants to nocturnal and crepuscular pollinators. The Quarterly Review of Biology 38:64–71.

BJUGSTAD, A. J. & W. FORTUNE. 1989. The western prairie fringed orchid (*Platantherapraeclara*): monitoring and research, pp. 197–199. *In* Bragg, T. B. & J. Stubbendieck (eds.), Proceedings of the Eleventh North American Prairie Conference. University of Nebraska, Lincoln. 292 pp.

BJUGSTAD-PORTER, R. 1993. The western prairie fringed orchid (*Platanthera praeclara*): its response to burning and associated fungi. M.Sc. (Range Management) Thesis. Range Management Department, University of Wyoming, Laramie, Wyoming. i–vii + 116 pp.

BORKOWSKY, C. L. 1998. Manitoba Tall Grass Prairie Preserve—natural resources inventory III. Critical Wildlife Habitat Program. 30 pp.

BORROR, D. J., TRIPLEHORN, C. A. & N. F. JOHNSON. 1989. An introduction to the study of insects. 6th ed. Saunders College Publishing, Toronto. 875 pp.

BOWLES, M. L. 1983. The tallgrass prairie orchids *Platanthera leucophaea* (Nutt.) Lindl. and *Cypripedium candidum* Muhl. *ex* Willd.: some aspects of their status, biology, and ecology, and implications towards management. Natural Areas Journal 3:14–37.

BOWLES, M. L., R. FLAKNE & R. DOMBECK. 1992. Status and population fluctuations of the eastern prairie fringed orchid (*Platanthera leucophaea* (Nutt.) Lindl.) in Illinois. Oregano 12:26–40.

BRAY, T. E. & B. L. WILSON. 1992. Status of *Platanthera praeclara* Sheviak & Bowles (western prairie fringed orchid) in the Platte River Valley in Nebraska from Hamilton to Garden counties. Transactions of the Nebraska Academy of Science 19:57–62.

CANADA SOIL INVENTORY. 1989. Soil landscapes of Canada—Manitoba. Land Resource Research Center, Research Branch, Agriculture Canada, Ottawa, Ontario. Agric. Can. Publ. 5242/b. 22 pp. 1:1 million scale maps compiled by Canada-Manitoba soil survey.

CANADIAN CLIMATE PROGRAM. 1993. Canadian climate normals: 1961–1991. Minister of Supply and Services. Rpt. No. 56-61/2-1993. 266 pp.

COLLICUTT, D. R. 1993. Status report on the western prairie white fringed orchid *Platanthera praeclara* in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 39 pp.

COVELL, C. V., JR. 1984. A field guide to the moths of eastern North America. Houghton Mifflin Co., Boston. 496 pp.

CUTHRELL, D. L. 1994. Insects associated with the prairie fringed orchids, *Platanthera praeclara* Sheviak & Bowles and *P. leucophaea* (Nuttall) Lindley. MSc. Thesis, North Dakota State University, Department of Entomology. 76 pp.

DARWIN, C. 1904. The various contrivances by which orchids are fertilized by insects. 2nd ed. John Murry, London. 300 pp.

DAVIS, S. K. 1994. Manitoba Tall Grass Prairie Preserve—natural resources inventory I. Critical Wildlife Habitat Program. 48 pp.

———. 1995. National recovery plan for the western prairie fringed orchid, *Platanthera praeclara*. Canadian Nature Federation, Endangered Plant and Invertebrates of Canada Project. 23 pp.

DRESSLER, R. L. 1981. The orchids: natural history and classification. Harvard University Press, Cambridge, Massachusetts. 332 pp.

———. 1993. Phylogeny and classification of the orchid family. Dioscorides Press, Portland, Oregon. 314 pp.

FAEGRI, K. & L. VAN DER PIJL. 1979. The principles of pollination ecology. Pergamon Press, New York. 244 pp.

HODGES, R. W. 1971. The moths of America north of Mexico. Fascicle 21. Sphingoidea. E.W. Classey Ltd. & R.B.D. Publications Inc., London. 158 pp. + color plates.

HODGES, R. W., T. DOMINICK, D. R. DAVIS, D. C. FERGUSON, J. G. FRANCLEMONT, E. G. MUNROE & J. A. POWELL. 1983. Check list of the Lepidoptera of America north of Mexico. National Museum of Natural History. MRC-127, Washington, D.C., U.S.A. 284 pp.

HANDFIELD, L. 1999. Les guide des Papillons du Quebec. Broquet Inc. 657 pp.

HENNE, D. C. & J. K. DIEHL. 2002. Notes on the Nevada buck moth, *Hemileuca nevadensis* (Saturniidae) in southern Manitoba. J. Lepid. Soc. 56:112–114.

HOF, J., C. H. SIEG & M. BEVERS. 1999. Spatial and temporal optimization in habitat placement for a threatened plant: the case of the western prairie fringed orchid. Ecological Modeling 115:61–75.

JOHNSON, K. L. 1985. Rare plant alert: another new orchid: the prairie white fringed orchid (*Platanthera leucophaea*). Manitoba Naturalists Bulletin 8:12–13.

———. 1991. Marking News, Botanical Survey of Manitoba, Newsletter #6. Manitoba Museum of Man and Nature, Winnipeg, Manitoba. 6 pp.

KLASSEN, P., A. R. WESTWOOD, W. B. PRESTON & W. B. MCKILLOP. 1989. Butterflies of Manitoba. Manitoba Museum of Man and Nature. 1989 Winnipeg, 290 pp.

LARSON, R. J. 1992. Pollination of *Platanthera dilatata* var. *dilatata* in Oregon by the noctuid moth *Discestra oregonica*. Madroño 39:236–242.

LAYBERRY, R. A., P. W. HALL & J. D. LAFONTAINE. 1998. The butterflies of Canada. NRC Research Press. University of Toronto Press, Toronto. 280 pp.

LUYT, R. & S. D. JOHNSON. 2001. Hawkmoth pollination of the African epiphytic orchid *Mystacidium venosum*, with special reference to flower and pollen longevity. Plant Syst. Evol. 228:49–62.

MOORE, J. R. & G. FORTNEY (EDS.). 1994. Management plan for the tall-grass prairie preserve in Manitoba. Critical Wildlife Habitat Program. 36 pp. + appendices.

MORRIS, R. F. 1980. Butterflies and moths of Newfoundland and Labrador: the Macrolepidoptera. Research Branch, Agriculture Canada. Publication 1691. 407 pp.

NILSSON, L. A. 1992. Orchid pollination biology. Trends in Ecology and Evolution 7:255–259.

PATT, J. M., M. W. MERCHANT, D. R. E. WILLIAMS & B. J. D. MEEUSE. 1989. Pollination biology of *Platanthera stricta* (Orchidaceae) in Olympic National Park, Washington. Amer. J. Bot. 76(8):1097–1106.

PLEASANTS, J. M. 1993. Pollination ecology of the western prairie fringed orchid, *Platanthera praeclara*. North Dakota Parks and Tourism Department. 24 pp. + figures.

PLEASANTS, J. M. & S. MOE. 1993. Floral display size and pollination of the western prairie fringed orchid, *Platanthera praeclara* (Orchidaceae). Lindleyana 8:32–38.

PROCTOR, M., P. YEO & A. LACK. 1996. The natural history of pollination. Timber Press, Portland, Oregon. 479 pp.

ROBERTSON, J. L. & R. WYATT. 1990. Reproductive biology of the yellow-fringed orchid, *Platantera ciliaris*. Amer. J. Bot. 77(3):388–398.

ROCKBURNE, E. W. & J. D. LAFONTAINE. 1976. The cutworm moths of Ontario and Quebec. Research Branch, Canada Dept. of Agriculture. Publication 1593. 164 pp.

SATHER, N. 1991. Recovery plan for western prairie fringed orchid (*Platanthera praeclara* Sheviak & Bowles). Unpublished Report. St. Paul, Minnesota.

SAVILLE, D. J. 1990. Multiple comparison procedures: the practical solution. The American Statistician 44(2):174–180.

SHEVIAK, C. J. & M. L. BOWLES. 1986. The prairie fringed orchids: a pollinator-isolated species pair. Rhodora 88:267–290.

SIEG, C. H. & R. M. KING. 1995. Influence of environmental factors and preliminary demographic analyses of a threatened orchid, *Platanthera praeclara*. Am. Midl. Nat. 134:307–323.

SPSS INC. 1999. SPSS, version 10.0.0 for Windows. Chicago: SPSS Inc.

SUZÁN, H., G. P. NABHAN & D. T. PATTEN. 1994. Nurse plant and floral biology of a rare Night-Blooming Cereus, *Peniocereus striatus* (Brandegee) F. Buxbaum. Conservation Biology 8:461–470.

U.S. FISH & WILDLIFE SERVICE. 1996. *Platanthera praeclara* (western prairie fringed orchid) recovery plan. U.S. Fish and Wildlife Service, Ft. Snelling, Minnesota. vi + 101 pp.

VAN DER PIJL, L. and C. H. DODSON. 1966. Orchid flowers: their pollination and evolution. University of Miami Press, Coral Gables, Florida. 214 pp.

WYATT, R. 1983. Pollinator-plant interactions and the evolution of breeding systems, 51–95 pp. *In* Real, L. (ed.), Pollination biology. Academic Press, Inc., Orlando, Florida. 338 pp.

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