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Pollination of a threatened orchid by an introduced hawk moth species in the tallgrass prairie of North America

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ABSTRACT

The decline of the threatened western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) is associated with destruction of the tallgrass prairie in North America. The role of pollinators in conservation and recovery is not well understood. We studied interactions with hawk moth pollinators in one of the three remaining metapopulations of *P. praeclara*. In an experiment, plants exposed to moths showed three signs of visitation that were associated with production of seed capsules. Plants not exposed to moths failed to produce capsules. The signs of visitation were used to estimate visitation rates at field sites over a four-year period. A majority of plants were visited (89%) and most flowers receiving pollen produced a seed capsule (60%). We discovered two new native hawk moth pollinator species, *Lintneria eremitus* (Hübner) and *Hyles lineata* (Fabricius), giving a total of five pollinators for this *P. praeclara* metapopulation. Only one of the five species was found in each of the nine years of trapping. This was the sole non-native pollinator, *Hyles euphorbiae* L., a Eurasian species introduced to North America to control an invasive weed, leafy spurge (*Euphorbia esula* L.). Given that plants with a greater diversity of pollinators have reduced risk of extinction, conservation and recovery plans should expand the definition of suitable *P. praeclara* habitat to include resources required by native pollinators, including the host plants that feed hawk moth larvae and the nectar plants that feed hawk moth adults before and after the nectar provided by *P. praeclara*.

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1. Introduction

Insect pollinators are essential to maintaining populations of threatened and endangered plants in native habitats (Kearns et al., 1998; Pauw, 2007; Scobie and Wilcock, 2009) but have suffered significant population declines in recent years (National Research Council, 2007; Potts et al., 2010; Menz et al., 2011; Winnfree et al., 2011). Both temperate and tropical orchids suffer from pollen-limited reproductive failure mediated by pollinators (Tremblay et al., 2005; Bernhardt and Edens-Meier, 2010), which is predicted to increase as climate change and habitat conversion and fragmentation alter the relative abundance or species composition of the pollinator fauna (Bernhardt and Edens-Meier, 2010). The western prairie fringed orchid, *Platanthera praeclara* Sheviak & Bowles is an iconic species of the tallgrass prairie that is now listed as a threatened species in both the United States and Canada (United States Fish and Wildlife Service, 1989; Environment Canada, 2006). The conversion of grasslands to agricultural land has made the tallgrass prairie one of the world's most endangered ecosystems (Samson and Knopf, 1996) and has played a key role in the decline of *P. praeclara*. Only three metapopulations remain. All are in the northern part of the orchid's geographic range, a region that has suffered historic flooding during recent years (http://www.ndsu.edu/fargoflood/). Little is known about interactions between *P. praeclara* and its pollinators.

The floral features of the western prairie fringed orchid (Sheviak and Bowles, 1986) comprise the classic pollination syndrome for night-flying hawk moths (Faegri and van der Pijl, 1979; Schiestl and Schlüter, 2009). The large inflorescence is comprised of up to 25 visually conspicuous flowers (Fig. 1A), which emit a fragrance primarily at night. The nectar spur is 30–60 mm long, opening just below the stigma (Fig. 1B). It is explored by the hawk moth's versatile proboscis, which in some species can be over 100 mm long (Krenn, 2010). Above and on either side of the stigma are two structures carrying pollen (Sheviak and Bowles, 1986), the pollinaria (Fig. 1B), which attach to the hawk moth (Fig. 2A) and project in

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front of the head (Fig. 2B), being held on a stalk (caudicle) that is attached, by a sticky pad (viscidium), to the convex surface of the compound eye (Fig. 2C).

Plathanthera praeclara is thought to have a mixed mating system, being self-compatible while also benefiting from outcrossing (Sheviak and Bowles, 1986). Self- movement of pollen from the anther sac to the stigma (autogamy) is thought to be impossible. Anthesis begins in late June or early July and continues for several weeks (Sheviak and Bowles, 1986). The capsule contains 1938–17,028 seeds (mean + SE = 9825 + 4294) resembling finely ground black pepper, which are shed in September (Alexander, 2006; Alexander et al., 2010). *Platanthera praeclara's* status as a protected species (United States Fish and Wildlife Service, 1989) means that estimates of reproductive success are limited to *in situ* measures of capsule length and diameter, which do not predict how many seeds the capsule contains or the proportion of seeds that contain viable embryos (Alexander, 2006; Alexander et al., 2010).

Four hawk moth species have been found carrying orchid pollinia: *Eumorpha achemon* (Drury) and *Sphinx drupiferarum* J.E. Smith (in North Dakota; Cuthrell, 1994), *Hyles gallii* (Rottenburg) (in Manitoba; Westwood and Borkowsky, 2004), and *H. euphorbiae* L. (in North Dakota; Jordan et al., 2006). The first three are native species, while the last is a Eurasian species, deliberately introduced in the 1960s and 1970s to Canada and the USA as a weed biological control agent for leafy spurge, *Euphorbia esula* L. (Tuttle, 2007). The conclusion that the four hawk moth species function as pollinators has not been substantiated experimentally.

Given the importance of pollinators for many orchid species (Bernhardt and Edens-Meier, 2010), we studied interactions between *P. praeclara* and its pollinators in southeastern North Dakota, the location of one of the three remaining orchid metapopulations. The study included nine years of trapping pollinators (2004–2012), four years of direct field observations during anthesis through fruit set (2004–2007), and an experiment that tested cause and effect relationships between native and introduced hawk moth species and seed capsule production (2006–2007). Four hypotheses were addressed. 1. Seed capsules are only produced if a hawk moth is present. 2. Hawk moths leave signs that they have visited flowers. 3. Signs are useful for estimating visitation rates and are strongly associated with capsule production. 4. *Platanthera praeclara* has the ability to recruit additional native hawk moth pollinator species.

2. Materials and methods

2.1. Study area

Research was conducted in southeastern North Dakota on land administered by United States Forest Service (Sheyenne National Grasslands), The Nature Conservancy (Brown Ranch and Pigeon

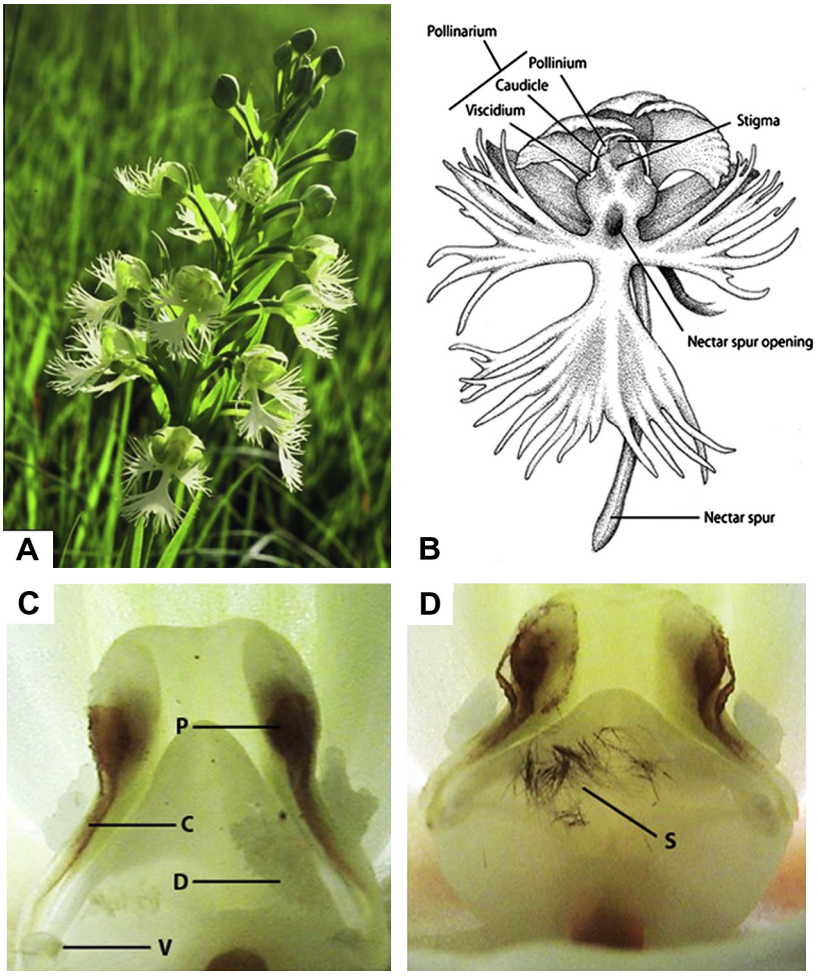

Fig. 1. Features of *P. praeclara* that play a role in pollination. (A) shows the inflorescence, with flowers at the base and buds distally. (B) shows important features of the flower (drawing Meredith Meyer). (C) shows pollen grains deposited (D) on the right side of the stigma, as well as the pollinium (P) sitting inside the anther sac, the stalk or caudicle projecting from the pollinium (C), and ending in the sticky viscidium (V). The dark half circle at the bottom is the opening to the nectar spur. (D) shows moth scales (S) deposited on the stigma.

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