Short Communication

DIVERSE FLIES (DIPTERA) LIKELY POLLINATE AN ALPINE DEATH CAMAS, *ANTICLEA ELEGANS* (MELANTHIACEAE)

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Abstract—Several populations of a species of death camas (*Anticlea elegans*) (Melanthiaceae) were found growing and flowering above treeline in the remote Lemhi Mountains of southeastern Idaho USA. The predominant floral visitors were flies representing four families, particularly the Syrphidae. Many individual flies bore visible loads of *Anticlea* pollen. Various native bees were seen foraging in the locale, but all visited flowers other than *Anticlea*. The flies, as well as ants, fed from the tepal nectaries. Despite the plant's common name, no foragers appeared to be impaired by imbibing its nectar. High in a neighbouring mountain range, *A. elegans* was being used as a trysting site by numerous *Tenthredo* sawflies. This is the first report of floral visitors to any *Anticlea* and among the first for any wildflower population above treeline in the vast US Intermountain West.

Keywords—Protandry, Syrphidae, Tenthredinidae, timberline, *Zigadenus*

INTRODUCTION

The death camas genus *Anticlea* is a segregate of *Zigadenus* (also known as death camas) in the Melanthiaceae (formerly part of a larger Liliaceae) (Zomlefer & Judd 2002). Mountain death camas, *A. elegans* (Pursh) Rydberg, is the most widespread member of the genus, growing from Alaska south to Chihuahua. A species of *Toxicoscordion* (another segregate of *Zigadenus*) produces several steroid alkaloids, notably zygacine (Majak et al. 1992). Zygacine renders both its pollen and nectar toxic to all bees but one (Cane et al. 2020), a specialist which is the primary and requisite pollinator of *T. paniculatum* (Nuttall) Rydberg (Cane 2018). Species of *Anticlea* inherited the common name "death camas" from their prior placement in *Zigadenus*, but no toxins have yet been reported.

Few breeding biologies or candidate pollinators are reported for the 170+ species of Melanthiaceae. Four of the five studied species are largely self-incompatible, with autogamy and manual self-pollinations yielding few seeds (Irwin 2001; Vance et al. 2004; Kato et al. 2009; Cane 2018); only *Paris quadrifolia* is fully self-fertile and perhaps anemophilous (Jacquemyn & Brys 2008). Sometimes diverse species of flies and beetles are known to be the primary floral visitors to other Melanthiaceae. These include several species of *Trillium* (Davis, 1981; Tomimatsu & Ohara, 2002), *Veratrum* (Kato et al., 2009), *Xerophyllum* (Vance et al. 2004) and *Zigadenus nuttallii* (Tepedino et al. 1989). Among these, only the nectarless flowers of beargrass (*X. tenax* (Pursh.) Nutt.) are reported to host diverse (13 species) and abundant syrphid flies (Vance et al. 2004).

Many syrphids commonly feed on floral nectar and sometimes pollen, as first reported by Hermann Müller in a detailed letter to Charles Darwin on 23 October 1867 (Darwin Correspondence Project, Univ. Cambridge UK). He also first documented that flies predominate at flowers growing above timberline (Müller 1880), a generalization borne out by some subsequent studies (Warren et al. 1988; Lefebvre et al. 2018). Numerous syrphids and muscoid flies prevail in subalpine (Kearns 1992 and citations therein, David Inouye *personal communication*) and alpine settings (Lefebvre et al. 2018). The mountain ranges of the U.S. Intermountain West have many peaks extending above tree line, but until now, their alpine floral visitors and pollinators have not been reported. This is also the first report of floral visitors for any species of *Anticlea*.

MATERIALS AND METHODS

Two unexpected flowering patches of *A. elegans* were encountered on 31 July 2023 growing above timberline in the remote Lemhi Mountains of southeastern Idaho USA. The sites were accessed via a ten km-long, steep former mining track followed by a three-km cross-country alpine hike. The nearest settlement was 70 km distant. The patches were between Spring and Sheep Mountains (vicinity of 44.38° N x 113.28° W, elev. 3050 m) in small flats below Little Sheep Mountain and the unnamed peak at the head of Bruce Canyon (Fig. 1). Those peaks, as well as Sheep Mountain, are all GLORIA vegetation monitoring sites (https://gloria.ac.at/home). The flats had accumulated some soil, which was damp from snow melt despite the late date. The patches were roughly 0.1 and 0.2 ha in size, each with >1,000 flowering racemes of *A. elegans*. Floral visitors to *A. elegans* were observed, photographed and collected on that day. Flies are vouchered with the California Academy of Sciences, San Francisco.

Collected syrphids were identified using keys to genera (Miranda et al. 2013), and for *Eristalis,* to species (Dankowicz, Z. R. & Dankowicz, E. https://sites.google.com/view/flyguide). Bodily pollen accumulations were viewed by photography and microscopy. Slide mounts for microscopic identification of fresh pollen were made from both surfaces of netted flies as well as directly from the anthers, using both silicon oil (preserves pollen shape) as well as gelatin stained with basic fuchsin.

Figure 1 Population of *Anticlea elegans* below Little Sheep Mountain in the Lemhi Range and its visiting syrphid flies (*Eristalis* above, *Chrysotoxum* below) and unidentified nectaring ants (Formicidae). Note that each fly has extended its proboscis to probe a green bilobed tepal nectary. Yellow *Anticlea* pollen had accumulated on the head and thoracic dorsum of the *Chrysotoxum* fly. Note that the ants bear no bodily pollen, walking well below the plane of the overarching anthers.

Results and Discussion

The only floral visitors seen at *A. elegans* were flies and some nectaring ants (Fig. 1). Flies were quite abundant, as many as 19 flies per 100 racemes. Bumblebees (e.g., *B. fervidus, B. nevadensis*) foraged in the vicinity that day, but they visited flowers other than *Anticlea* (e.g., *Arenaria, Frasera, Lupinus* and *Packera*). Flies visiting *A. elegans* flowers were taxonomically diverse, including species of Syrphidae, Fanniidae, Calliphoridae and Sarcophagidae. Among these, the syrphid species were the most diverse and abundant visitors to *A. elegans.* Their taxa included: one or more *Chrysotoxum* species (Fig. 1); a possible species of *Dasysyrphus; Eristalis tenax* (Fig. 1) and *E.* (*Eoseristalis*) *stipator* (plus a third species); and *Eupeodes volucris.* Among all other Melanthiaceae, only *X. tenax* is known to be visited by any of these syrphid genera, specifically *Chrysotoxum* and *Eupeodes,* albeit in small numbers (Vance et al. 2004). Syrphids and other flies can be prevalent generalist floral visitors and presumably pollinators in other montane habitats, both alpine (Larson et al. 2001; Niu et al. 2017; Lefebvre et al. 2018) and subalpine (e.g. Kearns 1992; Sommaggio et al. 2022), including some of the same syrphid genera (e.g. *Eristalis, Chrysotoxum*) (David Inouye, *personal communication*). Their roles in pollination are typically unknown, however, perhaps because of logistical difficulties accessing remote montane locations.

All flowers of *A. elegans* offered pollen and nectar to foraging pollinators. Nectar accumulates as a thin glistening surface in a shallow central concavity on each tepal's inner (dorsal) surface. My observations and photographs clearly showed the larger flies lapping at these tepal nectaries (Fig. 1). No scent was detected, nor is it mentioned for other *Anticlea* species. No fly was seen daubing the anthers for their pollen, but confirmation was not sought by dissecting their guts, as it would have destroyed the few voucher specimens.

Flowers appeared to be protandrous, with the newest (uppermost) flowers presenting six stamens with explanate anthers that open downward, toward the tepals (Fig. 1). The large pistil divides and elongates into three long, arching styles whose stigmatic tips are in the same plane and radius as the anthers (Fig. 1). This morphological arrangement should serve to enhance chances for pollen transfer from stamens to pollinators to stigmas, reminiscent of *Passiflora* flowers. Protandry and sequential flowering should both promote outcrossing probabilities. The dorsal thoraces of the dark-bodied calliphorids carried so much *Anticlea* pollen that I initially thought that their scutum was yellow, not blue-black. Pollen of *Anticlea* likewise accumulated abundantly on the heads and dorsal thoraces of visiting *Chrysotoxum* syrphids (Fig. 1). Pollen was visible on the thoracic pleura of the larger-bodied *Eristalis* flies. These bodily sites of pollen placement by *Anticlea* seem likely to then contact the stigmas and so effect pollination, but actual single-visit pollen depositions at virgin flowers was not possible owing to the brevity of my visit to this remote site.

Native bees were present nearby at this time near treeline between Sheep and Spring Mountains, visiting other wildflowers on nearby saddles and slopes above 3000m. These included both eight species of *Osmia* (*O. longula, melanopleura, paradisica, raritatis, sculleni, tanneri*) visiting four genera of legumes and, at *Penstemon attenuatus, O. brevis, O. paradisica,* and *O. tristella.* Four species of bumblebee (*Bombus bifarius, californicus, centralis, sylvicola*) were also actively foraging there. Their absence from flowering *A. elegans* underscores flies being its sole prospective pollinators, at least at this location.

A smaller population of *A. elegans* was encountered earlier (28 July 2020) growing at Webber Lakes, another remote, high, roadless, sub-alpine site in a neighbouring mountain range, the Beaverheads, west of Yellowstone National Park (44.37° N x 112.81° W, 2710 m.). Numerous individuals of a sawfly, *Tenthredo* sp. (Tenthredinidae) were actively feeding on its flowers. Species of this massive herbivorous genus (>100 species in North America) are notoriously difficult to identify, with no key to the U.S. fauna. Some pairs of *Tenthredo* at *A. elegans* were mating, suggesting that the flowers served as a trysting as well as a foraging site for these sawflies.

The absence of bees at *Anticlea* flowers here, despite actively visiting other flowers on the same day and in the general locale, could have several reasons. Soil is certainly shallow where present at all, a hindrance to many ground-nesters. However,

some of these bees have long flight ranges (*Bombus*) or nest under flat rocks (e.g., *O. tanneri*), which were numerous at the site. The open floral morphology of *Anticlea* is accessible to bees, and although daubing at flat tepal nectaries might be suboptimal for bees' tongues, there is precedent (Zych et al. 2013). Possibly toxic nectar could explain bees' absence at *Anticlea* flowers. Neurotoxic alkaloids (e.g., zygacine, veratridine) (Bloomquist 1996) are known among a few species in several other genera of the Melanthiaceae. Foraging bees were found dead after visiting flowers of *Toxicoscordion paniculatum* (Hitchcock 1959) and two species of *Veratrum* (Vansell & Watkins 1933; Perepelova 1949). Both adults and larvae of a non-specialist bee died after consuming the floral rewards of *T. paniculatum* or biologically relevant concentrations of its neurotoxin, zygacine (Cane et al. 2020). In contrast, foraging adult *Eristalis tenax* flies avidly ingested its nectar and pollen (Cane 2018). However, species of *Anticlea* remain unstudied for toxins in general and toxicity of floral rewards in particular. Controlled feeding assays with captive adult bees could resolve this question (Cane 2018), given more convenient populations than those studied here.

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Data availability statement

The data used to write this article are available from the corresponding author.

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