

- Rypstra, A., P. E. Carter, R. A. Balfour, and S. Marshall. 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology* 27:371–377. URL http://www.americanarachnology.org/JoA_free/JoA_v27_n1/arac_27_01_0371.pdf.
- Sikes, D. S., M. L. Draney, and B. Fleshman. 2013. Unexpectedly high among-habitat spider (Araneae) faunal diversity from the Arctic Long-Term Experimental Research (LTER) field station at Toolik Lake, Alaska, United States of America. *The Canadian Entomologist* 145:219–226. doi:10.4039/tce.2013.5.
- Slowik, J. 2006. A Survey of the spiders (Arachnida, Araneae) of Chichagof Island, Alaska, USA. *Journal of the Entomological Society of British Columbia* 103:61–70. URL <https://journal.entsocbc.ca/index.php/journal/article/view/115>.
- Slowik, J., and G. A. Blagoev. 2012. A survey of spiders (Arachnida: Araneae) of Prince of Wales Island, Alaska; combining morphological and DNA barcode identification techniques. *Insecta Mundi* 0251:1–12. URL <https://digitalcommons.unl.edu/insectamundi/768>.
- Ubick, D., N. Dupérré, P. E. Cushing, and V. D. Roth. 2005. *Spiders of North America: An Identification Manual*. American Arachnological Society, Poughkeepsie, New York.
- Uetz, G., J. Halaj, and A. Cady. 1999. Guild structure of spiders in major crops. *Journal of Arachnology* 27:270–280. URL http://www.americanarachnology.org/JoA_free/JoA_v27_n1/arac_27_01_0270.pdf.
- Young, O. O., and G. B. Edwards. 1990. Spiders in United States field crops and their potential effect on crop pests. *Journal of Arachnology* 18:1–27. URL http://www.americanarachnology.org/JoA_free/JoA_v18_n1/JoA_v18_p1.pdf.

Pollination, pilfering, and predation in an orchid pollinator network in the Juneau area of Southeast Alaska

by Marlin Bowles¹ and Robert Armstrong²

Summary

We studied insect pollinators and other visitors to 14 native orchids of the Juneau area of Southeast Alaska. At least 15 insect pollinators, a pollen consumer, and 4 spiders were found among ten orchid species. New North American records included pollination of *Coeloglossum viride* by march flies (Bibionidae), visitation and possible pollination of *Listera cordata* by *Dryomyza* flies, pollen transfer on *Corallorhiza trifida* by dance flies (Empididae) and pollination of *Corallorhiza mertensiana* by a *Bombus* species. New pollinators of *Platanthera dilatata* included the hawkmoth *Hyles gallii*, the butterfly *Pieris marginalis* and several new Noctuidae species. We observed for the first time the bee mimic *Eristalis anthophorina* foraging on *Spiranthes romanzoffiana*. A complex network occurred among these orchids and insects. Some orchids had multiple pollinators, while some insects pollinated multiple orchids. Several insects were nectar thieves, including one pollinator. Noctuidae moths pollinate *Platanthera dilatata*, but they appear to be nocturnal nectar thieves of two other orchid species (*Goodyera oblongifolia* and *S. romanzoffiana*) that are diurnally pollinated by *Bombus* species. Plume moths (*Amblyptilia* sp.) are nectar thieves on *G. oblongifolia* and *P. dilatata* but do not pollinate other orchids. More work is needed to understand interactions among these orchids and their pollinators and nectar thieves.

¹Juneau, Alaska, mbowles@mortonarb.org

²Juneau, Alaska, bob@discoverysoutheast.org

Table 1: Pollinators and insect visitors observed on orchids of the Juneau area.

Common name	Scientific name	Pollinators (literature)	Observed pollinators and insect visitors
Northern bracted orchid	<i>Coeloglossum viride</i>	Europe: Coleoptera, Hymenoptera, <i>Formica</i> (Claessens and Seiffert, 2017)	Bibionidae (<i>Bibio vestitus</i> ?) bearing pollinia
Western fairy slipper	<i>Calypso bulbosa</i> var. <i>occidentalis</i>	<i>Bombus</i> sp. (Ackerman, 1981)	none
Western coralroot	<i>Corallorhiza mertensiana</i>	none	<i>Bombus</i> sp.
Early coralroot	<i>Corallorhiza trifida</i>	self-pollinating (Catling, 1983)	Empididae sp.
Giant rattlesnake plantain	<i>Goodyera oblongifolia</i>	<i>Bombus</i> sp. (Ackerman, 1975)	<i>Bombus</i> sp., Noctuidae (nectar thief), <i>Amblyptilia pica</i> (nectar thief)
Northwestern twayblade	<i>Listera banksiana</i>	none	Dryomyzidae (non-pollinating)
Heart-leaved twayblade	<i>Listera cordata</i>	Mycetophilidae, Sciaridae (Ackerman and Mesler, 1979)	Sciaridae, rove beetle <i>Eusphalerum pothos</i> (consuming pollinia)
Blunt-leaved orchid	<i>Platanthera obtusata</i>	Culicidae (Gorham, 1976)	Empididae (probing for nectar)
Bog adder's mouth	<i>Malaxis paludosa</i>	Mycetophilidae (Reeves and Reeves, 1984)	none
Chamisso's orchid	<i>Platanthera chorisiana</i>	self-pollinating (Catling, 1984), Coleoptera (Inoue, 1981)	none
Slender bog orchid	<i>Platanthera stricta</i>	Geometridae, Empididae, <i>Bombus</i> sp. (Patt et al., 1989)	Geometridae, Empididae (bearing pollinia)
Two-leaved (Aleutian) adders's mouth	<i>Malaxis diphylos</i>	none	none
White bog orchid	<i>Platanthera dilatata</i>	Noctuidae (Larson, 1992)	Noctuidae spp., <i>Hyles gallii</i> , <i>Pieris marginalis</i> , <i>Bombus</i> sp., <i>Amblyptilia</i> sp.
Hooded ladies' tresses	<i>Spiranthes romanzoffiana</i>	<i>Bombus</i> sp. (Larson and Larson., 1987; Larson and Larson, 1990)	<i>Bombus melanogypus</i> , <i>Eristalis anthophorina</i> , Noctuidae (nectar thief)

Introduction

Orchid species are well known for their specialized adaptations to insect pollinators (e.g., Darwin, 1862; Argue, 2012a,b). Their floral structures include a showy modified petal (lip) that attracts insects and directs them toward a food reward as well as pollen masses (pollinia) and the stigma. Nectar is usually located in recessed spurs, at the base of the lip, or in floral tubes, where the ability of an insect to access nectar is often determined by the length of its proboscis (we use tongue interchangeably), or their body structure. This is particularly evident in the rein orchids (*Platanthera* spp.), which use flower color and nectar spur

length to partition moth and butterfly pollinator species by their color preferences and tongue lengths (Hapeman and Inoue, 1997). A few species, such as *Calypso* (*Calypso bulbosa*) are pollinated by deceit, as they falsely advertise a food reward, and attach pollinia to insects as they exit the flower. Self-pollination (autogamy) has evolved independently among different orchid groups, though they may maintain flower structure that allows pollinia removal and outcrossing (Catling, 1983). Some orchid species may be pollinator generalists, or insect species may be versatile pollinators among different orchids. Given the array of adaptations to different pollinators among different types of orchids, these assemblages may display structure or

modularity similar to other plant-pollinator networks (e.g., Olesen et al., 2007).

Objectives

Despite the wealth of investigations into orchid pollination biology, pollinators have not been determined for many North American species (Argue, 2012a,b), which represents a major gap in knowledge about their reproductive requirements. Southeast Alaska has at least 27 native orchid species or varieties (e.g., Hultén, 1968; Brown, 2006). For more information and orchid nomenclature see Bowles and Armstrong (2019). The Juneau area of Southeast Alaska has 14 native orchids with populations accessible for field study. Only eight of these species have pollinators reported in the North American literature (Table 1). In this paper we report on the results of a multi-year effort to catalog pollinators of these species. We sought to determine if orchids in this region are pollinated by insects known from the literature, and whether new pollinators could be identified. We also asked whether other insects may function as nectar thieves or flower consumers, and whether insect predators, such as spiders, use these orchids and impact pollinating insects. Finally, we asked whether pollinators and orchid species groups could be identified that suggested structure

in the network of orchids and their insect pollinators in our study area.

Study area, and orchid species and known pollinators

Juneau is located in the Central Panhandle Climate Zone of Southeast Alaska, which has warmer winters, cooler summers and greater precipitation than interior Alaska (Bie-niek et al., 2012). Vegetation is predominantly coastal rain-forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), as well as open fen and muskeg bog with scattered shore pine (*Pinus contorta* var. *contorta*) and mountain hemlock (*Tsuga mertensiana*). Early successional uplift meadows may occupy coastal areas, while alpine vegetation also occurs on coastal mountains.

A single orchid species, the bracted orchid or frog orchid (*Coeloglossum viride* var. *viride*), occurs in alpine meadows. Its short inflorescence of green flowers appears in early summer. It produces nectar in short spurs as well as at the lip base. No North American pollinators have been reported. In Europe it is pollinated by many alpine insects, including five beetle (Coleoptera) species and four Hymenoptera species as well as the ant *Formica exsecta* (Claessens and Seiffert, 2017).



Figure 1: Motion-sensitive trail cam positioned to record visitors to *Platanthera dilatata*.



Figure 2: A dark-winged fungus gnat (Sciaridae) on flowers of the twayblade *Listera cordata*.

Seven species occupy rainforest habitat. Calypso (*Calypso bulbosa* var. *occidentalis*) is restricted to small forested islands. In early spring it produces small showy pink slipper-like flowers that lack a food reward. This orchid is pollinated by queen bumble-bees (*Bombus* spp.) that switch foraging to other nectar-producing plant species, resulting in low seed pod production.

Three forest species flower in late spring and early summer, producing short inflorescences of small green flowers. The heart-leaved twayblade (*Listera cordata*) and western twayblade (*L. banksiana*) are frequent in old-growth forests, while the blunt-leaved orchid (*Platanthera obtusata*) is rare in coastal forests. *Listera cordata* produces nectar at the lip base, and is pollinated by fungus gnats (Mycetophilidae and Sciaridae) (Ackerman and Mesler, 1979). However, no pollinators are reported for *L. banksiana*. *Platanthera obtusata* has a nectar spur and is pollinated primarily by mosquitoes (Culicidae) (Gorham, 1976).



Figure 3: A geometrid moth (left) and a dance fly (Empididae, right) visiting flowers of *Platanthera stricta*. Note settling behavior of geometrid and pollinia on proboscis of dance fly.



Figure 4: *Autographa corusca* (left) and *Actebia fennica* (right) foraging on *Platanthera dilatata*. Note settling behavior, length of proboscis and presence of pollinia. Right photo by Gwen Baluss

The early coralroot (*Corallorhiza trifida*) and the western coralroot (*C. mertensiana*) often occur with twayblades in near-coastal forests. They are less common and tend to flower later, producing leafless stalks bearing small green and white flowers in *C. trifida* or larger purple and white flowers in *C. mertensiana*. *Corallorhiza trifida* has a reduced nectar spur and has been shown to be autogamous, forming seed pods in enclosures (Catling, 1983). The open structure and longer nectar spur of *C. mertensiana* flowers suggest insect pollination (Freudenstein, 1997); however, no pollinators are reported. The giant rattlesnake plantain (*Goodyera oblongifolia*) is restricted to near-coastal forest. It flowers in late summer, producing a tall spike of white flowers from an evergreen basal rosette of dark green leaves. Nectar is produced at the base of a short floral tube, and it is bumble bee (*Bombus*)-pollinated (Ackerman, 1975).

Six species occur in muskeg bogs and uplift meadows. The bog adder's mouth (*Malaxis paludosa*) occupies muskeg, while the Aleutian adder's mouth (*M. diphyllus*) occurs in bogs and meadows. They produce short spikes of minute green flowers from basal leaves in mid-summer, and are rare and inconspicuous. Both *Malaxis* species produce small amounts of nectar at the base of the lip, and are probably pollinated by fungus gnats (Reeves and Reeves, 1984), though they have not been confirmed for *M. diphyllus*. They can co-occur with the equally rare Chamisso's orchid (*Platanthera chorisiana*), which produces short inflorescences bearing small green flowers. This species is reported as autogamous in Canada (Catling, 1984); but, in Japan it produces nectar in a short spur and is pollinated by the beetle *Oedemeronia lucidicollis* (Inoue, 1981).



Figure 5: The bumble bee *Bombus melanogynus* foraging on *Spiranthes romanzoffiana*.

The slender bog orchid (*Platanthera stricta*) occurs in muskeg, muskeg-forest borders and roadsides. It begins flowering in early summer, producing tall leafy stalks with spikes of small green flowers with short nectar spurs. This orchid appears to be a pollinator generalist, as it is pollinated by moths (Geometridae), dance flies (Empididae spp.), and *Bombus* species (Patt et al., 1989). The white bog orchid (*Platanthera dilatata* var. *dilatata*) grows in open muskeg, meadows, and along roadsides. It begins flowering in mid-summer, producing tall leafy stalks with spikes of fragrant white flowers with long nectar spurs. Only

Noctuidae moths are reported as pollinating this species (Larson, 1992). Noctuidae are termed settling moths with respect to *Platanthera* pollination, as they may alight or partially hover while grasping flowers and do not hover in the same manner as Sphingidae (Hapeman and Inoue, 1997). These longer-tongued hawk moths have been suggested as pollinators as well, especially of *P. dilatata* var. *leucostachys*, which has longer nectar spurs than the typical variety (Sheviak C., 2002). The ladies' tresses orchid (*Spiranthes romanzoffiana*) flowers in late summer in muskeg and along lakeshores. Although less common, it often occurs with *P. dilatata*; its inflorescences reach maturity as those of the latter species are senescing. It produces a short spike of fragrant white flowers with nectar at the base of the floral tube, and is pollinated by *Bombus* spp. (Larson and Larson, 1987).



Figure 6: A March fly (Bibionidae) pollinating *Coeloglossum viride*. Note pollinia at the front of the head and partly opened flowers.

Methods

Much of this work was conducted using motion-sensitive or time-lapse trail cams with flash and close focus capabilities. They could be left unattended to determine, and sometimes quantify, diurnal and nocturnal visitation by insects that were sensitive to human presence (Figure 1). We also recorded video, time-lapse and other photographic images on still cameras with macro capabilities. A black-light was used to capture moths foraging on *Goodyera oblongifolia*. Links to videos and slides from this work are provided in the videos and slide shows section (page 24). The working conditions for this project were not conducive for collecting voucher insect specimens. Often only a single individual was observed carrying pollinia, and its collection would have disrupted pollination. Many other visitors were observed only in video camera outputs, and could not be accessed for precise identification. As a result, we relied upon field observation or identification from pho-

tographs for species identities, and many pollinators could not be identified below the family level. For several orchid species, we used insect exclosures to determine whether they were autogamous, and we also quantified seed pod production to assess the effectiveness of pollinators. All photos are by the authors except as noted.



Figure 7: A *Dryomyza* fly (Dryomyzidae) on flower of *Listera banksiana*.



Figure 8: Sequence showing a dance fly (Empididae) entering and leaving a flower of *Corallorhiza trifida* while bearing pollinia on its thorax.

Results and Discussion

We observed 15 or more insect taxa visiting ten orchid species that were either pollinators or appeared likely to be pollinators (Table 1). They represented the Hymenoptera, Lepidoptera, and Diptera. These insects represented five of the seven taxa reported in the North America literature as pollinators and about eight newly recorded pollinators for the study orchids. The Noctuidae were particularly dif-

ficult to identify as species. Other insects included one pollen consumer and two nectar thieves (Inouye, 1980), which consistently visited some orchid species. At least four spider taxa occurred on the orchids, including three web-spinning species and one ambushing species, as well as several predatory wasp species.

Confirmation of reported pollinators

Among forest species, fungus gnats were observed repeatedly on *Listera cordata*; however, none were bearing pollinia. One species (Figure 2) appears to be a dusky-winged fungus gnat (Sciaridae). We made a single observation of a *Bombus* species visiting *Goodyera oblongifolia*.

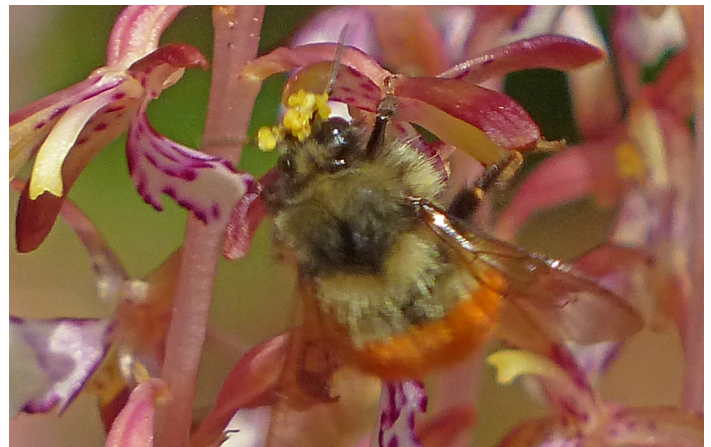


Figure 9: *Bombus* species pollinating *Corallorhiza mertensiana*. Note pollinia positioned below eyes.

In fen, meadow and muskeg habitats, we recorded pollinators on three orchid species. On *Platanthera stricta* we observed a dance fly (Empididae sp.) bearing pollen on its proboscis as well as a moth species (Geometridae) foraging for nectar (Figure 3). On *Platanthera dilatata*, several Noctuidae moth species (probably *Autographa corusca* and *Actebia fennica*) were found bearing pollinia on their tongues while foraging for nectar (Figure 4). On *Spiranthes romanzoffiana*, we recorded visits by the black-tailed bumble bee (*Bombus melanogynus*) (Figure 5). As this orchid flowers in late summer, they were probably male drones. *Goodyera oblongifolia* is also late-flowering, and may have been visited by this *Bombus* species as well.

Newly reported pollinators or visitors

In alpine, *Coeloglossum viride* was pollinated by march flies (Bibionidae, possibly *Bibio vestitus*). These flies entered and exited flowers while bearing multiple pollinia at the base of their heads below the eyes (Figure 6). They often force into newly opening flowers, apparently to access nectar. This insect appears to be an important pollinator of this orchid

in the alpine zone of our study area. More work is needed to determine whether additional insects, such as those in European alpine, pollinate this species in North America.



Figure 10: The hawkmoth *Hyles gallii* pollinating *Platanthera dilatata*. Note hovering behavior and pollinia on the proboscis.



Figure 11: The butterfly *Pieris marginalis* nectaring on *Platanthera dilatata*. Note pollinia on proboscis.

In forest habitats we recorded new pollinators (or apparent pollinators), for three orchid species. Although no pollinators or other insect visitors have been reported for *Listera banksiana*, we observed *Dryomyza* flies (*Dryomyza* sp.) visiting this orchid (Figure 7). They appeared to be

foraging for a food reward on the orchid lip; however, none of the insects were observed carrying pollinia. The *Dryomyza* fly oviposits on bear scat and salmon carcasses, and might be attracted to this orchid if it emits a similar odor. Most individuals of *L. banksiana* produced seed pods, and those we excluded from pollinators did not produce seed pods. This suggests that *L. banksiana* is obligately insect-pollinated; but, more work is needed to confirm pollinating species. Although *Corallorhiza trifida* may be autogamous, we observed dance flies (Empididae sp.) entering their flowers and exiting bearing pollinia on their upper thorax (Figure 8). These visits could provide occasional outcrossing in this apparently self-pollinating orchid. Dance flies were also observed probing flowers of *Platanthera obtusata* but did not extract pollinia and may not pollinate this species. Nevertheless, they appear to be versatile pollinators as one was observed bearing pollinia from *Platanthera stricta* on its proboscis. We recorded pollination of *Corallorhiza mertensiana* by a *Bombus* species. Multiple pollinia were deposited at the base of the head below the eyes of this bee while it foraged for nectar (Figure 9). Our data suggest that bees may be efficient pollinators of this coralroot. Open-pollinated plants at two sites averaged 50–80% of flowers forming seed pods, while inflorescences that were bagged to exclude pollinators did not produce seed pods. This suggests that *C. mertensiana* is an obligate insect-pollinated species.



Figure 12: The bee-mimic *Eristalis anthophorina* foraging on *Spiranthes romanzoffiana*.

In muskeg and meadow habitats, we recorded new pollinators for two species. In addition to expected visits by Noctuidae moth species, we recorded diurnal and nocturnal visits by the hawkmoth *Hyles gallii* to *Platanthera di-*

latata (Figure 10). In contrast to the low number of pollinia carried by Noctuidae, *H. gallii* carried large numbers of pollinia on its proboscis. It appeared to be a very efficient pollinator even though its proboscis length greatly exceeded nectar spur length. We also observed occasional visits by the margined white butterfly (*Peris marginalis*) to this orchid, during which it extracted pollinia on its proboscis (Figure 11). This butterfly may be a rare and inefficient pollinator of *P. dilatata* in our region. *Bombus* species also occasionally visited this orchid, but it is unlikely that they were able to access nectar held in its comparatively long nectar spurs. We suggest that as with *P. stricta*, *P. dilatata* is a generalist with regard to pollinators, but that they vary in pollination efficiency. Although *Spiranthes romanzoffiana* is reported as bee-pollinated, we also observed a bee-mimic Syrphidae (*Eristalis anthophorina*) on this orchid. It foraged in the same manner as *Bombus* species by moving upward on the inflorescence while probing flowers with its proboscis (Figure 12). Although we could not detect presence of pollinia on its proboscis, it may function as a pollinator.



Figure 13: The plume moth *Amblyptilia pica* foraging on *Goodyera oblongifolia*. Note slender proboscis relative to size of floral tube.

Nectar thieves

Species belonging to two different families appeared to function as nectar thieves on *Goodyera oblongifolia*. In early fall, numerous geranium plume moths (*Amblyptilia pica*) were observed visiting late-flowering plants of *G. oblongifolia* (Figure 13). These insects easily inserted their long slender proboscis into the comparatively short floral tube of the orchids. None were observed bearing pollinia, and the plants they visited did not produce seed pods. This species overwinters as an adult, and the nectar from *G. oblongifolia* may be quite beneficial to these insects, as no other flowering plant species occurred in the area occupied by the orchids. We have observed such visitation at multiple sites over multiple years. We also observed a plume moth (*Amblyptilia* sp.) nectaring on *P. dilatata* without removing pollinia. Likewise, *A. pica* has been recorded as a probable nectar thief on *P. orbiculata* in New Hampshire (Bergum et al., 2018).



Figure 14: Nocturnally foraging *Autographa corusca* on *Goodyera oblongifolia*. Note proboscis inserted into floral tube.

Goodyera oblongifolia was also visited by a second apparent nectar thief, Noctuidae moths that may be *Autographa corusca* (Figure 14). Over a fifteen day period, 24 hour time-lapse videos (at one minute intervals) revealed an average of 8.7 visits per night among 15 plants. However, no diurnal visitors were recorded, and no seed pods were formed on these plants. In an area 0.15 km away where plants were not video monitored, 62% of 178 flowers produced seed pods among 17 plants. Although we do not know if Noctuidae visited the adjacent area, they did not pollinate

plants at the first site, and their repeated visits suggest that they were removing nectar from these plants. Their proboscis length is greater than the floral tube, which may have facilitated nectar thievery. Several of these moths that were captured by blacklight also did not bear pollinia. *Goodyera oblongifolia* is reported to have naturally low levels of seed pod production, and spreads by rhizomes (Ackerman, 1975). Nectar thieves can influence reproductive fitness by influencing behavior of pollinators (Zhang et al., 2014). If the high visitation rate we observed for Noctuidae species reduced nectar availability, it might have contributed to reduced visitation by *Bombus* and the low reproduction that we observed. If widespread, this process could provide selective pressure for the development of vegetative spread as an alternate use of reproductive resources by *G. oblongifolia*. More work is needed to test this hypothesis.



Figure 15: Nocturnally foraging Noctuidae on *Spiranthes romanzoffiana*.

We also video-recorded nocturnal visits by Noctuidae moths to a second *Bombus*-pollinated orchid, *Spiranthes romanzoffiana* (Figure 15). This orchid is closely related to *Goodyera*, and Noctuidae species may function as nectar thieves on this species as well. However, it differs from *G. oblongifolia* by having relatively high levels of *Bombus*

visitation and seed pod production (Larson and Larson, 1987). The greater level of reproduction for *S. romanzoffiana* could be related to habitat conditions, as this orchid occurs in open vegetation where its inflorescences may be highly visible (Larson and Larson, 1990), while coastal *G. oblongifolia* populations occupy dense shaded spruce forests (Ackerman, 1975).

Although not reported in the literature, our results indicate that Noctuidae species that pollinate *Platanthera dilatata* may function as nocturnal nectar thieves on two *Bombus*-pollinated orchid species with overlapping flowering periods. *Platanthera dilatata* flowers from late June through late July in our region, while *Spiranthes romanzoffiana* and *Goodyera oblongifolia* usually flower from mid-July through August. More work is needed to determine the number of Noctuidae species involved in visitation to these orchids and whether individual Noctuidae species overlap in their visits. The Noctuidae species we have observed appear to have proboscis lengths that exceed the nectar spur length of *P. dilatata* as well as the floral tube lengths of *S. romanzoffiana* and *G. oblongifolia*. However, these species differ in their manner of pollinia placement (Argue, 2012a,b). *Platanthera dilatata* positions its pollinia on either side of the nectar spur entrance, which facilitates pollinia deposition on the proboscis. The latter species position their pollinia within the floral tube on its dorsal side, which are attached to the proboscis of nectar-seeking species. The pollinia may be less likely to contact the slender proboscis of Noctuidae moths (Figure 14). Also, as their flowers mature, the pollinia are moved upward to expose the stigma (Argue, 2012a,b). In *G. oblongifolia*, the pollinia lose their adhesive ability as the flower matures, making them less likely to adhere to an insect proboscis.

Pollinator network

The orchids and insect visitors in our study area comprise a complex network in which orchids may have multiple pollinators or may share pollinators and nectar thieves (Figure 19). To some extent, pollinator types appear to be structured among different orchid groups. For example, orchids with smaller flowers and more easily accessible nectar resources display adaptation to Diptera species that have comparatively small bodies and short tongues. In contrast, orchids with more showy larger flowers that maintain nectar in recessed spurs show adaptation to Lepidoptera species. Moreover, proboscis lengths of *Platanthera* pollinators in this network correspond to orchid nectar spur lengths, supporting the idea that orchids partition pollinator resources by adapting their spur lengths to proboscis lengths (Hapeman and Inoue, 1997). *Bombus* species, which have intermediate proboscis lengths, visit orchids with intermediate flower sizes and nectar resources maintained in shorter floral tubes or nectar spurs. One species, *Calypso*

bulbosa, attracts *Bombus* species by advertising a false reward. Longer-tongued *Bombus* species that would access greater floral diversity may occur in our area, but we have no information on this group. The additional pollinator-nectar thief relationship among the Lepidoptera-pollinated *Platanthera dilatata* and the *Bombus*-pollinated *Goodyera oblongifolia* and *Spiranthes romanzoffiana* suggests that interactions become more complex in association with larger orchids with greater nectar resources. However, we may lack comparative information on interactions among the smaller orchids and pollinators.



Figure 16: The rove beetle *Eusphalerum pothos* consuming pollen of *Listera cordata*.

Pollen consumers

A rove beetle species (*Eusphalerum pothos*) was recorded consuming pollen on the twayblade orchid *Listera cordata* (Figure 16). Rove beetles are well known pollenophagous feeders (Sayers et al., 2019). Although we have limited data, we found no difference in seed pod production between plants attacked by rove beetles and those that did not have rove beetles. While foraging for pollen, these beetles occasionally had pollinia attached to their heads, but they did not appear to pollinate plants.

Insect predation

We observed insect predation by four different spider taxa. However, predation of pollinators appeared to be rare. Two web-spinning spiders, the silver long-jawed orb weaver (*Tetragnatha laboriosa*) and the six-spotted orb weaver (*Araniella displicata*) were observed on the slender

bog orchid (*Platanthera stricta*). The former species had captured a biting midge (Ceratopogonidae), while the latter species appears to have captured a wasp (Hymenoptera) as prey (Figure 17). As this orchid can occupy muskeg borders where shrubs are present, this may have facilitated web building by these spiders. A cobweb spider (Theridiidae) was observed with a captured fungus gnat on the western twayblade (*Listera cordata*) (Figure 18). This orchid routinely produces a large number of seed pods in our area, and it is unlikely that pollinator predation affects its levels of seed production.



Figure 17: The orb weaver *Araniella displicata* with captured wasp on *Platanthera stricta*.



Figure 18: A cobweb spider (Theridiidae) with fungus gnat prey item on *Listera cordata*.

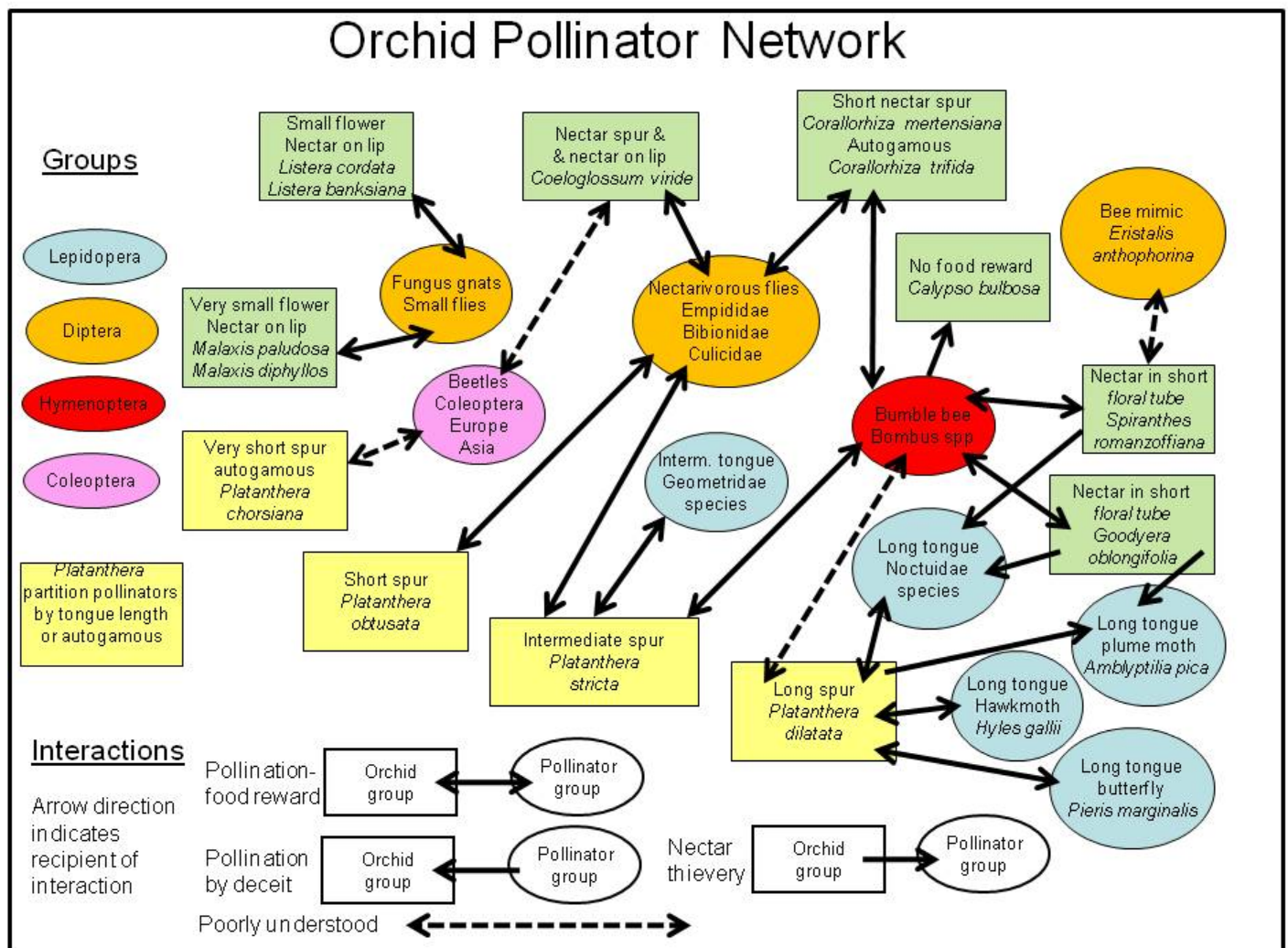


Figure 19: Relationships in an orchid pollinator network in the Juneau area of Southeast Alaska. Squares represent orchid species or species groups with similar morphological features. The *Platanthera* group is color-coded. Circles represent insect pollinators, or pollinator groups with similar morphological features, which are color coded by order. Arrow directions represent recipients of plant-pollinator interactions. Double-headed arrows indicate both pollination and food reward, single headed arrows indicate either pollination or food reward by nectar thievery. Dashed arrows indicate poorly understood relationships due to lack of information. Tongue is used interchangeably for proboscis in labeling modules.

Crab Spiders (Thomisidae) which hunt by ambush-ing prey on flowers, were observed on *Platanthera dilatata*. Their prey included a biting midge, crane fly (Tipulidae), and horse fly (Tabanidae) (Figure 20). None of these insects are known pollinators of *Platanthera* species and it is unknown whether crab spiders impact true pollinators of these orchids.

Yellow jackets (Vespiniae) are occasional visitors to *Platanthera dilatata*. We do not know whether they are foraging for insect prey, or perhaps seeking nectar. An Ichneumonid wasp (Ichneumonidae) was also observed on *Listera cordata*, but its activity could not be determined.

Conclusions

This work confirmed published pollination (or flower visitation) of at least five different insect taxa to seven orchid species in the Juneau area of Southeast Alaska. We also recorded eight new North America pollinators or visitors for six orchid species. This included pollination of *Coeloglossum viride* by march flies (Bibionidae), visitation and possible pollination of *Listera cordata* by *Dryomyza* flies, pollen transfer on *Corallorhiza trifida* (which is thought to be autogamous) by dance flies (Empididae) and pollination of *Corallorhiza mertensiana* by *Bombus* species. We

also recorded new pollination of *Platanthera dilatata* by the hawkmoth *Hyles gallii*, the butterfly *Pieris marginalis* and several new Noctuidae species. The *H. gallii* would be expected to pollinate orchids with much longer nectar spurs. However *P. dilatata* appears to be adapted to multiple species with a wide range of proboscis lengths. We also observed for the first time the bee-mimic syrphid fly *Eristalis anthophorina* foraging on *Spiranthes romanzoffiana* in the same manner as its identified *Bombus* pollinator.



Figure 20: A female goldenrod crab spider (*Misumena vatia*) with a horse fly (Tabanidae) on *Platanthera dilatata*.

Nectar thievery is well known among flowers and insects, but a complex relationship among multiple orchid and insect species has not been reported from North America. We established that while Noctuidae moths function as adapted pollinators of *Platanthera dilatata*, they appear to be nocturnal nectar thieves of two other orchid species (*Goodyera oblongifolia* and *S. romanzoffiana*) that are diurnally pollinated by *Bombus* species. Further, *G. oblongifolia* is also visited by a second nectar thief, the geranium plume moth (*Amblyptilia pica*), which overwinters as an adult and may rely on this local nectar resource. We also observed a plume moth acting as a nectar thief on *P. dilatata*.

Acknowledgments

We are grateful to the many people who contributed to this study. Derek Sikes and Joey Slowik (University of Alaska Museum of the North), identified difficult insects and spiders, respectively. Bob Biagi, Robbin McLeod and Bill Dean (BugGuide.net), also identified Bibionidae, Noctuidae and Syrphidae species, respectively. John Hudson assisted with additional insect identification and provided blacklight capture of Noctuidae moths, and Gwen Baluss contributed

an additional Noctuidae. Rita Hassert (The Morton Arboretum), provided essential library assistance. We are also grateful to Don Kurz and Mary Willson for reviewing the manuscript, and to Lisa Wallace for comments on the pollinator network model.

References

- Ackerman, J. D. 1975. Reproductive biology of *Goodyera oblongifolia*. *Madroño* **23**:191–198. URL <http://www.jstor.org/stable/41424024>.
- Ackerman, J. D. 1981. Pollination biology of *Calypso bulbosa* var. *occidentalis* (Orchidaceae): a food-deception system. *Madroño* **28**:101–110. URL <http://www.jstor.org/stable/41424311>.
- Ackerman, J. D., and M. R. Mesler. 1979. Pollination biology of *Listera cordata* (Orchidaceae). *American Journal of Botany* **66**:820–824. doi:10.1002/j.1537-2197.1979.tb06288.x.
- Argue, C. L. 2012a. The Pollination Biology of North American Orchids: Volume 1: North of Florida and Mexico. Springer-Verlag, New York. doi:10.1007/978-1-4614-0592-4.
- Argue, C. L. 2012b. The Pollination Biology of North American Orchids: Volume 2: North of Florida and Mexico. Springer-Verlag, New York. doi:10.1007/978-1-4614-0622-8.
- Bergum, M., N. Cleavitt, and D. Matthews. 2018. An unexpected visitor. *Frontiers in Ecology and the Environment* **16**:502–502. doi:10.1002/fee.1968.
- Bieniek, P. A., U. S. Bhatt, R. L. Thoman, H. Angeloff, J. Partain, J. Papineau, F. Fritsch, E. Holloway, J. E. Walsh, C. Daly, M. Shulski, G. Hufford, D. F. Hill, S. Calos, and R. Gens. 2012. Climate divisions for Alaska based on objective methods. *Journal of Applied Meteorology and Climatology* **51**:1276–1289. doi:10.1175/JAMC-D-11-0168.1.
- Bowles, M. L., and R. Armstrong. 2019. Native Orchids in Southeast Alaska. URL <https://www.naturebob.com/sites/default/files/Bowles-Armstrong-2019-Native-Orchids-in-Southeast-Alaska.pdf>.
- Brown, P. M. 2006. Wild Orchids of the Pacific Northwest and Canadian Rockies. The University Press of Florida. The University Press of Florida, Gainesville, Florida.
- Catling, P. M. 1983. Autogamy in eastern Canadian Orchidaceae: a review of current knowledge and some new observations. *Le Naturaliste Canadien* **110**:37–53.

- Catling, P. M. 1984. Self-pollination and probable autogamy in Chamisso's orchid (*Platanthera chorisiana* (Cham.) Reichb.F. *Le Naturaliste Canadien* **111**:451–453.
- Claessens, J., and B. Seiffert. 2017. Significant ant pollination in two orchid species in the Alps as adaptation to the climate of the alpine zone? *Tuexenia* **37**:363–374. doi:10.14471/2017.37.005.
- Darwin, C. 1862. The various contrivances by which orchids are fertilised by insects. John Murray, London. doi:10.5962/bhl.title.37883.
- Freudenstein, J. V. 1997. A monograph of *Corallorhiza* (Orchidaceae). *Harvard Papers in Botany* **1**:5–51. URL <http://www.jstor.org/stable/41761525>.
- Gorham, J. R. 1976. Orchid pollination by *Aedes* mosquitoes in Alaska. *The American Midland Naturalist* **95**:208–210. doi:10.2307/2424249, URL <http://www.jstor.org/stable/2424249>.
- Hapeman, J. R., and K. Inoue. 1997. Plant-pollinator interactions and floral radiation in *Platanthera* (Orchidaceae). Pp. 432–454 in T. J. Givnish and K. J. Sytsma, editors. *Molecular Evolution and Adaptive Radiation*. Cambridge University Press, New York.
- Hultén, E. 1968. *Flora of Alaska and neighboring territories*. Stanford University Press, Stanford, California.
- Inoue, K. 1981. Beetle pollination of *Platanthera chorisiana* (Orchidaceae). *Journal of Japanese Botany* **56**:213–218. URL <https://ci.nii.ac.jp/naid/10010456333/en/>.
- Inouye, D. W. 1980. The terminology of floral larceny. *Ecology* **61**:1251–1253. doi:10.2307/1936841.
- Larson, K. S., and R. J. Larson. 1990. Lure of the locks: showiest ladies-tresses orchids, *Spiranthes romanzoffiana*, affect bumblebee, *Bombus* spp., foraging behavior. *Canadian Field-Naturalist* **104**:519–525.
- Larson, R. J. 1992. Pollination of *Platanthera dilatata* var. *dilatata* in Oregon by the noctuid moth *Discestra oregonica*. *Madroño* **39**:236–242.
- Larson, R. J., and K. S. Larson. 1987. Observations on the pollination biology of *Spiranthes romanzoffiana*. *Lindleyana* **4**:176–179.
- Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of Sciences* **104**:19891–19896. doi:10.1073/pnas.0706375104.
- Patt, J. M., M. W. Merchant, e. R. E. Williams, and B. J. D. Meeuse. 1989. Pollination Biology of *Platanthera stricta* (Orchidaceae) in Olympic National Park, Washington. *American Journal of Botany* **76**:1097–1106. doi:10.1002/j.1537-2197.1989.tb15093.x.
- Reeves, L. M., and T. R. Reeves. 1984. Life history and reproduction of *Malaxis paludosa* in Minnesota. *American Orchid Society Bulletin* **53**:1880–1291.
- Sayers, T. D. J., M. J. Steinbauer, and R. E. Miller. 2019. Visitor or vector? The extent of rove beetle (Coleoptera: Staphylinidae) pollination and floral interactions. *Arthropod-Plant Interactions* **13**:685–701. doi:10.1007/s11829-019-09698-9.
- Sheviak C., J. 2002. *Platanthera* Richard. Pp. 551–571 in *Flora of North America* Editorial Committee, editors. *Flora of North America North of Mexico*, volume 26, *Magnoliophyta: Liliidae: Liliales and Orchidales*. Oxford University Press, New York.
- Zhang, Y.-W., J.-M. Zhao, and D. W. Inouye. 2014. Nectar thieves influence reproductive fitness by altering behaviour of nectar robbers and legitimate pollinators in *Corydalis ambigua* (Fumariaceae). *Journal of Ecology* **102**:229–237. doi:10.1111/1365-2745.12166.

Videos and slide shows

Below are links to videos and slide shows of insects visiting orchids in the Juneau area. Feel free to download and use however you wish.

Bumblebees

Video: Bumblebees on western coralroot orchids <https://vimeo.com/343560365>

Video: Bumblebee on white bog orchid <https://vimeo.com/342178916>

Video: Bumblebee on bog orchid <https://vimeo.com/280660265>

Video: Bee mimic and bumblebee on ladies-tresses orchid <https://vimeo.com/285643040>

Butterflies

Video: Margined white butterfly on white bog orchid <https://vimeo.com/343845001>

Dance flies

Video: Early coral root orchid with dance fly <https://vimeo.com/337668892>

Video: Dance fly on blunt-leaved orchid (*Platanthera obtusata*) <https://vimeo.com/276573344>

Dryomyza fly

Video: *Dryomyza* fly on northwestern twayblade orchid <https://vimeo.com/430921806>

Video: *Dryomyza* fly on northwestern twayblade orchid on June 17, 2020 <https://vimeo.com/430250286>

Video: *Dryomyza* flies on a northwestern twayblade orchid in the rain <https://vimeo.com/429783758>

Insects

Slides: What comes to a white bog orchid <https://vimeo.com/435323087>

Video: Insect on heart-leaved twayblade orchid flower <https://vimeo.com/421550015>

Video: Insect on a heart-leaved twayblade orchid <https://vimeo.com/420923156>

Video: Insects coming to a heart-leaved twayblade orchid <https://vimeo.com/419786193>

Video: Beetle and flies visit white bog orchid <https://vimeo.com/280590762>

Video: Insects on white bog orchid <https://vimeo.com/343935517> March Fly:

Video: March flies on frog orchids <https://vimeo.com/340916436>

Moths

Slides: Noctuidae moth visits rattlesnake plantain orchid <https://vimeo.com/443394534>

Slides: Owlet moths visit rattlesnake orchids July 28, 2020 <https://vimeo.com/442730723>

Slides: Owlet moth visits to rattlesnake orchids <https://vimeo.com/442134257>

Video: Owlet moth on a white bog orchid <https://vimeo.com/348093863>

Video: Plume moth on white bog orchid at Buckbean Pond <https://vimeo.com/431302940>

Video: Plume moths on rattlesnake plantain orchid <https://vimeo.com/288474762>

Video: Hawkmoth on white bog-orchid <https://vimeo.com/281908716>

Video: Hawkmoth on bog orchid July 17 <https://vimeo.com/280467246>

Video: Noctuidae moth on orchid <https://vimeo.com/279993651>

Video: Noctuidae moth on bog orchid <https://vimeo.com/279969805>

Video: Hawkmoth & Noctuidae moths on white bog-orchid July 20 <https://vimeo.com/281101155>

Rove beetles

Slides & video: Rove beetles on twayblade orchids <https://vimeo.com/422039321>

Spiders

Video: The silver longjawed orbweaver hunting on a slender bog orchid <https://vimeo.com/436958381>

Photography

Slides: Timelapse on white bog orchids <https://vimeo.com/440357095>

Slides: Timelapse on white bog orchid <https://vimeo.com/433273359>

Slides & video: Filming orchids with the Panasonic DMC FZ200 and FZ300 cameras <https://vimeo.com/421616175>