

New pollinators and insect visitors to orchids in Southeast Alaska and the Aleutian Islands, and components of the orchid pollinator network in Southeast Alaska

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Abstract

We provide new records for insects pollinating or foraging on orchids in Southeast Alaska as well as the Aleutian Islands. Bumble bees (*Bombus* spp.) were observed foraging on the ordinarily self-pollinating *Platanthera aquilonis* and on the food-deceptive *Calypso bulbosa* var. *occidentalis*. The latter species is thought to be pollinated by queen *Bombus* species, however we observed *B. melanopygus* workers due to a late spring. We also found *B. melanopygus* pollinating *Goodyera oblongifolia*, and significant variation in pod production between two populations. A Noctuidae moth, apparently *Mniotype tenera* was observed pollinating *Platanthera convallariifolia* in the Aleutian Islands. Other Lepidoptera records include the Nocutuidae *Plusia* spp. on *Platanthera dilatata* and the Geometridae *Antepirrhoe fasciata* and *Rheumaptera subhastata* on *P. stricta*. New Diptera records include mosquito (*Aedes*) species foraging and bearing pollinia on *P. obtusata* as well as the phorid fly *Megaselia* sp. and the dryomyza fly *Dryomyza anilis* foraging on *Neottia banksiana*. We suggest that this orchid may omit a fetid odor that attracts these carrion-feeding insects. These records bring the number of insects pollinating or foraging on Southeast Alaska orchids to at least 20 species among 13 families in the Diptera, Hymenoptera, and Lepidoptera. They also increase the number of orchids with verified pollinators in Southeast Alaska to 17 species. Most of these insects pollinate only 1 or 2 orchid species, indicating the importance of the entire insect community to the orchid population. In contrast, *Bombus* species pollinate at least 5 orchids across the entire flowering season. The spring-flowering *Calypso bulbosa* could be vulnerable to climate warming that causes this species to flower before emergence of queen bumblebees.

Introduction

Given the threat of climate warming to disrupt plant-pollinator synchrony, especially spring flowering plants with specialized pollinators (Kudo and Ida 2013), it is critical to understand these relationships within pollinator networks (Schatz et al. 2020). The Southeast Alaska archipelago and adjacent coastal area support at least 28 native orchid species and varieties (Bowles and Armstrong 2019); at least eight additional species occur in the remaining regions of Alaska. The network of insects that pollinate these orchids is most well known for Southeast Alaska, where 15 pollinating insects have been identified for 14 orchid species, leaving half of the orchid flora with unknown pollinators (Bowles and Armstrong 2021). This paper reports new information on pollinators and other insect visitors to orchids in Southeast Alaska, and one species from the Aleutian Islands. We also examine the relationships between known pollinator families and orchid genera, including several that may be vulnerable to climate warming.

Methods

With two exceptions, this work occurred within the City and Borough of Juneau, Alaska or on adjacent Tongass National Forest land. We used field observations and digital images for insect identification.

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Confirmation was also accessed through online resources such as BugGuide.net, or specimen identification by an authority. We recorded video and time-lapse images to determine presence of insect visitors to several species. We also used bait to attract potential pollinators to one species, and an enclosed terrarium to observe potential pollinators of a second species. All photos are by the authors except as indicated.

Results

Pollinators and visitors to eight orchid species are reported (Table 1).

Table 1: New pollinators and insect visitors to orchid species in Southeast (SE) Alaska and the Aleutian Islands. Insect species are listed by order.

Species	Location and flowering season	Pollination system	Lepidoptera	Hymenoptera	Diptera
<i>Calypso bulbosa</i>	SE Alaska, early spring	pollinator required, food deception		<i>Bombus melanopygus</i> (Apidae)	
<i>Goodyera oblongifolia</i>	SE Alaska, late summer	pollinator required, nectariferous		<i>Bombus melanopygus</i> (Apidae)	
<i>Neottia banksiana</i>	SE Alaska, early summer	pollinator required, nectariferous			<i>Megaselia</i> sp. (Phoridae), <i>Dryomyza anilis</i> (Dryomyzidae)
<i>Platanthera aquilonis</i>	SE Alaska, mid-summer	self-pollinating, nectariferous		<i>Bombus</i> sp. (Apidae)	
<i>Platanthera convallariifolia</i>	Aleutian Islands, mid-summer	pollinator required, nectariferous	<i>Mniotype tenera</i> (Noctuidae)		
<i>Platanthera dilatata</i>	SE Alaska, mid-summer	pollinator required, nectariferous	<i>Plusia putnam</i> , <i>Plusia nichollae</i> (Noctuidae)		
<i>Platanthera obtusata</i>	SE Alaska, early summer	pollinator required, nectariferous			<i>Aedes communis</i> , <i>Aedes excrucians</i> (Cucilidae)
<i>Platanthera stricta</i>	SE Alaska, early summer	pollinator required, nectariferous	<i>Rheumaptera subhastata</i> , <i>Antepirrhoe fasciata</i> (Geometridae)		

Calypso bulbosa var. *occidentalis* (Linnaeus) Oakes (western fairy slipper)

This western variety reaches its northern range limit on forested islands in Southeast Alaska. It is the first native orchid to flower and uses food deception to attract naive queen bumblebees (*Bombus* spp.), which soon switch to spring flowers that provide food resources (Ackerman 1981). The lip of the single flower

is a long-lasting showy slipper, and unpollinated plants may remain in flower for a month. Unlike lady's slipper orchids (*Cypripedium*), which retain pollinia and release pollen grains, entire pollinia are removed from *Calypso* by attachment to the scutellum, a smooth segment on the dorsal surface of the bee (Ackerman 1981). The width of the gap between the orchid column (which holds pollinia) and the lip opening may range from 5 to 10 mm. This variability, in combination with variability in bee species sizes and switching to flowers with food rewards, results in low seed pod production (Ackerman 1981). *Salix* and *Vaccinium* species provided an alternative food source in Finland, where 7% of queen *Bombus* species carried *Calypso* pollinia while foraging on *Salix* (Tuomi et al. 2015), which is visited by *Bombus* species in our study area (Figure 1).



Figure 1: Queen *Bombus* foraging on *Salix* sp. in Southeast Alaska.

In 2023, a late spring in our study area delayed flowering of *C. bulbosa*, allowing overlap with emergence of *Bombus melanopygus* Nylander workers. They were determined to be workers based on their small size and late emergence. *Calypso bulbosa* plants translocated to the Jensen Arboretum, Juneau, were visited by these bumblebees (Figure 2), one of which entered a *C. bulbosa* flower (Figure 3). Though we did not observe pollinia transfer, this is the first report of *Bombus* workers visiting *C. bulbosa* var. *occidentalis*, and demonstrates that a weather-caused shift in flowering may result in asynchrony with foraging queen bumblebees. This orchid could be vulnerable to climate warming that would disrupt this synchrony, thereby reducing pollination and seed production.

***Goodyera oblongifolia* Rafinesque (large rattlesnake plantain orchid)**

This western orchid reaches its northern range limit in near-coastal forests of Southeast Alaska. Extensive populations of plants averaging > 100 rosettes of vegetative and flowering plants per 10 m² area occur where disturbance has reduced shrub cover. Flowering occurs in late summer and extends into early fall. The inflorescence comprises a spike of small white flowers that contain nectar and are reportedly pollinated by *Bombus* species that cause low (< 50%) seed pod production (Ackerman 1975). Our previous monitoring of this species revealed nocturnal visitation by Noctuidae moths, which are apparently nectar thieves that do not contribute to reproduction (Bowles and Armstrong 2021). However, we were unable to document pollination by *Bombus* species.



Figure 2: A *Bombus melanopygus* worker approaching a *Calypso bulbosa* flower.

In 2022, we documented flower visitation by bumblebees resembling *Bombus melanopygus* with time-lapse images and with direct observation. Individuals bearing pollinia approached (Figure 4) and briefly visited (Figure 5) multiple flowers on an inflorescence before moving to neighboring plants. They also appeared to forage especially on higher density patches, quickly moving through orchid populations. We compared percent and total seed capsule production per inflorescence between two sites with different inflorescence densities and sizes, Rainforest and Tee Harbor (Figure 6). Data are from $n = 26$ random 10 m² plots, and from $n = 109$ random inflorescence samples. Tee Harbor had 38% greater average percent seed capsule production, greater flowering plant density, and smaller inflorescences than did the Rainforest population. Average total capsule production was also greater, by 33%, in the Tee Harbor population ($p = 0.013$, Mann-Whitney t -Test). This supports findings that greater flowering plant density enhances bee visitation and pollination at the local scale (Hegland 2014). However, other factors, such as bee population size and nest proximity, as well as orchid population size, could affect visitation rates. Nocturnal foraging by Noctuidae moths might also cause bumble bees to reject inflorescences that have been subject to high levels of nectar thievery (Bowles and Armstrong 2021). More work is needed to test this hypothesis.

***Neottia (Listera) banksiana* (Lindley) Reichenbach (Northwest twayblade)**

This western species reaches its northern range limit in coastal Southeast Alaska forests. Pollination is required for seed pod production, which ranged from 10 to 80% in our study areas. Flowering occurs in late spring, with an inflorescence of up to 20 small green flowers. Most members of the genus are reported to provide small amounts of nectar at the base of the lip, and to attach pollinia to insects as they feed on the nectar. The smaller heart-leaved twayblade *Neottia cordata* (Linnaeus) Richards flowers earlier in similar habitat and is pollinated by fungus gnats, which are attracted to a strong fetid odor (Ackerman and Mesler 1979). *Dryomyza* sp. flies visited *N. banksiana* in previous years, but none were observed accessing nectar nor carrying pollinia (Bowles and Armstrong 2021). *Dryomyza anilis* Fallen feeds on salmon carcasses (Hocking et al. 2009) as well as bear scat. This leads us to hypothesize that *N. banksiana* produces a fetid smell to attract pollinators; however, it does not have a strong odor detectable to humans.



Figure 3: A *Bombus melanopygus* worker foraging in the lip of a *Calypso bulbosa* flower.

In 2023, following van der Niet et al. (2011), we placed pieces of salmon carcass as bait at the base of flowering *N. banksiana* plants to enhance attraction of potential pollinators. This procedure attracted large numbers of *Dryomyza anilis* flies as well as the Phorid fly *Megaselia* sp. Phorid flies also feed on salmon carcasses (Hocking et al. 2009) and pollinate other plants (Rupp et al. 2021). Both insects were observed feeding on the lips of *N. banksiana*, but neither carried pollinia. The *Megaselia* appears to be too small to contact the orchid column (Figure 7), but *Dryomyza* flies appear to be large enough to remove pollinia (Figure 8). Additional work is needed to assess whether this orchid produces a fetid odor detectable by insects, and whether *Dryomyza* flies function as pollinators.

***Platanthera aquilonis* Sheviak (northern green rein orchid)**

This rein orchid was formerly treated with the tetraploid *P. hyperborea*, but was segregated as *P. aquilonis* (Sheviak 2001) as it is diploid and has a more western distribution in northern North America including southeast and south central Alaska. These species self-pollinate or have rain-assisted pollination, but appear to provide nectar in short spurs and may have outcrossing races (Sheviak 2001, Kropf 2015). *Platanthera aquilonis* is also considered one of the diploid progenitors (x *P. dilatata*) of the polyploid *P. huronensis*; however, pollen vectors that would facilitate this cross are not well-known (Wallace 2003). Though classified as a nocturnal moth-pollinated species (Hapeman and Inoue 1997), Kropf (2015) observed *Bombus jonellus* Kirby visiting *P. hyperborea* in Iceland, which suggests that *Bombus* species might facilitate outcrossing in *P. aquilonis* as well.

In 2019 we observed a *Bombus* species foraging on *Platanthera aquilonis* (Figure 9) in a mixed population of this species with *P. dilatata* and *P. huronensis* in an uplift meadow in the Haines area of Southeast Alaska. This observation complements the finding of Kropf (2015). Moreover, as bumble bees also appear to pollinate *P. dilatata* (van der Voort et al. 2022), our observation provides further evidence that *Bombus* species may be pollen vectors between *P. aquilonis* and *P. dilatata*, allowing spontaneous populations of their hybrid *P. huronensis*. More work on potential for pollinia transfer in *P. aquilonis* is needed to verify this process.



Figure 4: *Bombus melanopygus* bearing pollinia on its tongue approaching a *Goodyera oblongifolia* inflorescence.

***Platanthera convallariifolia* Fischer ex Lindley (lily-leaved rein orchid)**

This orchid is native to the Aleutian Islands, eastern Russia (Kamchatka) and northern Japan. Its range extends east through southwest Alaska to Kodiak and the Kenai peninsula, with outposts in coastal Alaska about 150 km west of the western border of Southeast Alaska. It is a polyploid derived from crossing between *P. dilatata* x *P. stricta* (Wettewa et al. 2020).

The flower and inflorescence structure of *Platanthera convallariifolia* suggests a nocturnal settling moth syndrome (as opposed to a hovering moth), where primary pollinators would be members of the Noctuidae or Pyralidae (Hapeman and Inoue 1997). Noctuidae might serve as pollen vectors between *P. dilatata* and *P. stricta*. However, no pollinators had been reported for *P. convallariifolia*. In 2021, we received images from Abi Woodbridge showing a Noctuidae moth pollinating *P. convallariifolia* (Figure 10) at Unalaska, Aleutian Islands. This moth appears to be in the genus *Mniotype*, and resembles *M. tenera* Smith (Figure 11). The type locality of *M. tenera* is Kukak Bay, in the Western Peninsula of Alaska (Dyar 1900).

***Platanthera dilatata* (Pursh) Lindley (white bog orchid)**

This wide-spread orchid ranges from the Aleutian Islands east to Southeast Alaska, north to central Alaska, and east across North America. The flower and inflorescence structure of *Platanthera dilatata* suggests a settling-moth syndrome, and primary pollinators are members of the Noctuidae, including at least 11 such species across North America, as well as several butterflies, bumblebees and a hawkmoth (Wallace and Bowles 2023). In 2022, we observed a day-flying *Plusia* (Noctuidae) species pollinating this orchid, which had not been reported in Bowles and Armstrong (2021). Individuals appear to represent both *P. putnami* Grote (Figure 12) and *P. nichollae* Hampson (Figure 13). In *P. putnami* the basal spot of the stigma extends above the cubital vein in most specimens, giving it a triangular appearance; in *P. nichollae*

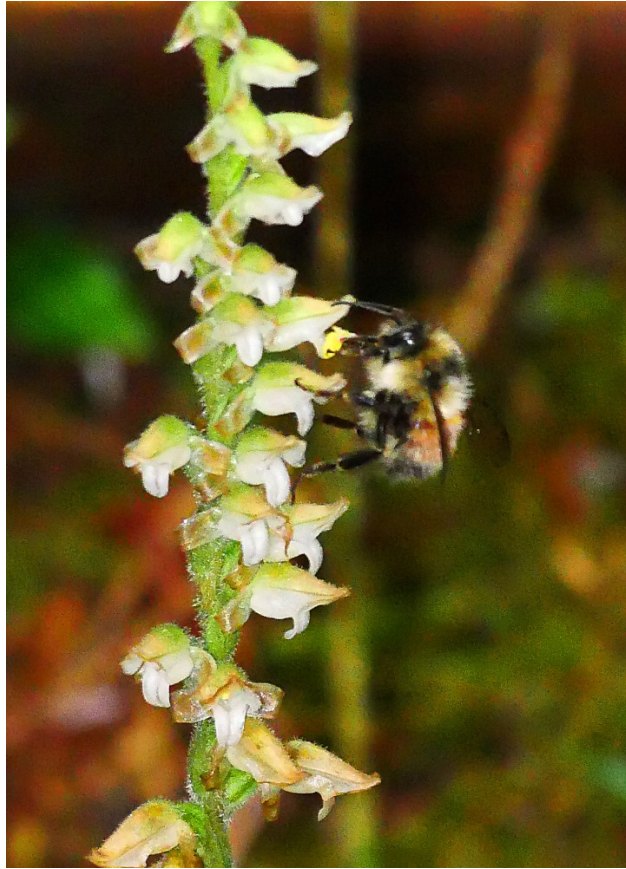


Figure 5: *Bombus melanopygus* bearing pollinia on its tongue while foraging on *Goodyera oblongifolia* flowers.

lae, the more oval basal spot rarely extends above the cubital vein, and in the West the two species are frequently confused (Lafontaine and Poole 1991).

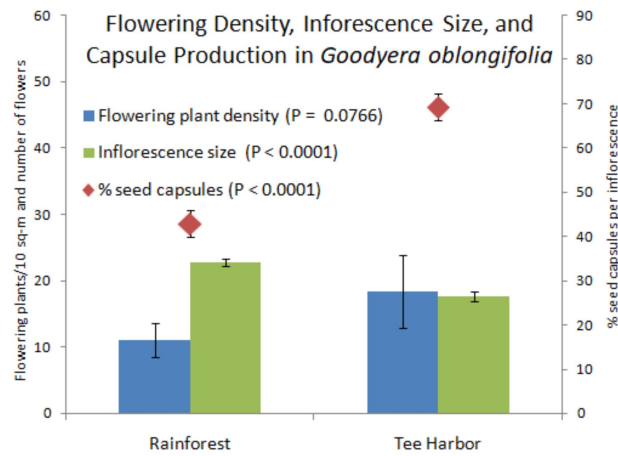


Figure 6: Relationship between flowering plant density per 10 m² plot, seed capsule production, and inflorescence size in *Goodyera oblongifolia*. *p* values are Mann-Whitney *t*-Test probabilities.



Figure 7: *Megaselia* sp. fly foraging on the lip of *Neottia banksiana*. Note relatively small size relative to column height and lack of contact with column.



Figure 8: *Dryomyza anilis* fly foraging on the lip of *Neottia banksiana*. Note relatively large size and head in contact with column.



Figure 9: *Bombus* sp. foraging on an inflorescence of *Platanthera aquilonis*.

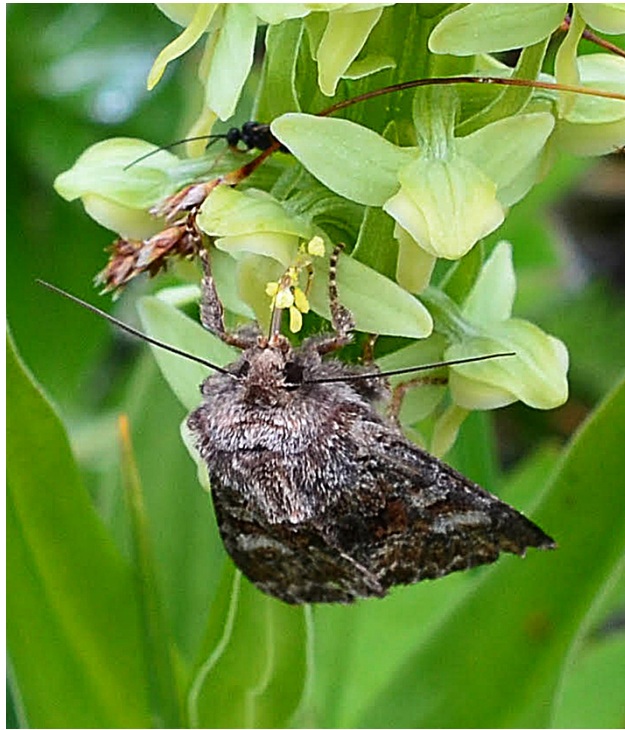


Figure 10: Noctuidae resembling *Mniotype tenera* bearing pollinia on its tongue while foraging on the inflorescence of *Platanthera convallariifolia*. Photo by Abi Woodbridge.



Figure 11: Wing pattern of Noctuidae resembling *Mniotype tenera*. Photo by Abi Woodbridge.



Figure 12: Noctuidae resembling *Plusia putnami* bearing pollinia on its tongue while foraging on *Platanthera dilatata*.



Figure 13: Noctuidae resembling *Plusia nichollae* below an inflorescence of *Platanthera dilatata*. A rear leg of this specimen bears an orchid pollinia.

Table 2: Summaries for orchid genera and numbers of insect species known to pollinate orchid species in an orchid pollinator network in Southeast Alaska. Insects are categorized by order and family, orchids are categorized by genus. Orchid species with known pollinators are based on Bowles and Armstrong (2021), Argue (2012a), Argue (2012b), this paper and references therein. $n_{\text{orchid spp}}$: Number of orchid species. n_{known} : Number of orchid species where pollinators are known. n_{unknown} : Number of orchid species where pollinators are unknown. *: Based in part on literature. **: Includes one or more self-pollinating species that may outcross as well. ***: Pollinia not observed on one or more species. See Table 3 for column totals.

Pollinators	<i>Calypso</i>	<i>Coeloglossum</i>	<i>Corallorhiza</i>	<i>Cypripedium</i>	<i>Goodyera</i>	<i>Malaxis</i>	<i>Neottia</i>	<i>Piperia</i>	<i>Platanthera</i>	<i>Spiranthes</i>
$n_{\text{orchid spp.}}$	1	1	3	3	1	2	4	2	7	1
n_{known}	1	1	2	2*	1	1*	2*	1*	5*	1
n_{unknown}			1**	1**		1	2	1	2**	
Diptera:										
Bibionidae		1								
Cuculidae									2***	
Dryomyzidae							1***			
Empididae			1						1	
Scariidae						1	1*			
Syrphidae										1***
Hymenoptera:										
Apidae	1*		1	1*	1				1*	1
Halictidae				1*						
Andrenidae				1*						
Lepidoptera:										
Geometridae								1*	2***	
Pieridae									1	
Noctuidae									5***	
Sphingidae									1	
Totals	1	1	2	3	1	1	2	1	13	2

Table 3: Table 2 continued. $n_{\text{insect species}}$: Number of insect species. $n_{\text{orchid genera pollinated}}$: Number of orchid genera pollinated.

Pollinators	Totals	Totals
$n_{\text{orchid spp.}}$	25	
n_{known}	17	
n_{unknown}	18	
Diptera:	$n_{\text{insect species}}$	$n_{\text{orchid genera pollinated}}$
Bibionidae	1	1
Cucilidae	2	1
Dryomyzidae	1	1
Empididae	1+	2
Scariadae	1+	2
Syrphidae	1	1
Hymenoptera:		
Apidae	1+	6*
Halictidae	1+	1*
Andrenidae	1+	1*
Lepidoptera:		
Geometridae	3	2
Pieridae	1	1
Noctuidae	5	1
Sphingidae	1	1
Totals	20	21

Platanthera obtusata (Banks ex Pursh) Lindley (blunt-leaved orchid)

The blunt-leaved orchid has a strongly boreal distribution, extending north of the Arctic Circle in Alaska and Canada, and east across North America. This species is known to be pollinated primarily by mosquitoes in the Genus *Aedes*, which are attracted by a specific odor produced by the orchid (Lahondère et al. 2020). Gorham (1976) reported 15 mosquito species and an additional unidentified mosquito as pollinators of *Platanthera obtusata*, including six from north-central Alaska. It is unknown whether these or other *Aedes* species pollinate this species in Southeast Alaska.

We observed and photographed *Aedes* mosquitoes visiting *Platanthera obtusata* in spruce forest near the Mendenhall Glacier, and in an enclosed terrarium to which mosquitoes and flowering stems of *P. obtusata* had been introduced. Mosquitoes were observed bearing pollinia only in the terrarium after a 12 hr overnight period (Figure 14). These mosquitoes belong to the non-band-legged group and appear to be *A. communis* DeGeer but their identity has not been confirmed. Mosquitoes in forest also foraged on flowers (Figure 15). They belong to the band-legged group and appear to be *A. excrucians* Walker but their identity has not been confirmed. A male mosquito was observed on *P. obtusata* in forest but its identity is unknown (Figure 16). *Aedes excrucians* was not reported as a pollinator in Alaska (Gorham 1976). If confirmed, this species may represent a new pollinator of *P. obtusata* in this state.

Platanthera stricta Lindley (slender bog orchid)

This northern rein orchid ranges from the Aleutians east across southern Alaska to western North America, where it may be frequent in open wetlands. Its inflorescence and flower structure suggest that it is pollinated by settling moths, and a wide range of pollinators have been recorded from Washington, including Geometridae moths, Empididae flies, and *Bombus* bumblebees (Patt et al. 1989). We previously reported an unknown Geometridae visiting flowers of *Platanthera stricta*, and an Empididae bearing pollinia



Figure 14: Mosquito resembling *Aedes communis* bearing pollinia on *Platanthera obtusata*.



Figure 15: Mosquito resembling *Aedes excrucians* foraging on *Platanthera obtusata*.

on this orchid (Bowles and Armstrong 2021). We have now found the Geometridae *Antepirrhoe fasciata* Barnes & McDunnough bearing pollinia (Figure 17) and the Geometridae *Rheumaptera subhastata* Nolcken visiting flowers of *P. stricta* (Figure 18). Patt et al. (1989) also recorded *A. fasciata* as a primary pollinator. *Rheumaptera subhastata* may be confused with *R. hastata* Linnaeus, but the former uses *Alnus* (alder) sp as a larval host, while the latter uses *Betula* (birch) (McGuffin 1973) and only *Alnus* occurs in the locality where *R. subhastata* was recorded. Though this moth was not observed bearing pollinia, the proboscis length and foraging behavior of the individual observed suggest that it could serve as a pollinator of *P. stricta*.



Figure 16: Male *Aedes* sp. foraging on *Platanthera obtusata*.



Figure 17: *Antepirrhoe fasciata* bearing pollinia at the base of its tongue while foraging on *Platanthera stricta*.

Components of the pollinator network

This work expands our knowledge of the insect community that forms a pollinator network among South-east Alaska's orchid species. Our observations and other published literature indicate that at least 20 insect species among 3 orders and 13 families may comprise this network (Table 2).

The Diptera order has the greatest number of families (6), with 7 species that appear to pollinate 6 orchid genera and 8 species. These flies are morphologically diverse, matching flower sizes and nectar resources. Minute Scariadae (fungus gnats) feed on nectar at the base of the lip in equally small *Neottia* and *Malaxis*



Figure 18: *Rheumaptera subhastata* foraging on *Platanthera stricta*.

flowers. Larger Bibionidae (March flies) and Dryomyzidae flies feed on nectar in larger *Coeloglossum* and *Neottia* flowers. Empididae (dance flies) and Culicidae (mosquitoes) use longer tongues to feed on nectar in recessed spurs of *Platanthera*. A large Syrphidae (a bee-mimic hover fly) forages on bee-pollinated *Spiranthes*, though we have not seen it carrying pollinia. These insects carry pollinia from different orchid species on their eyes, heads, tongues and backs.

The Lepidoptera order includes 5 families representing 10 species that specialize on only two orchid genera, *Platanthera* and *Piperia* (some authors treat both as *Platanthera*) representing 5 species. These orchids have relatively large volumes of nectar held in recessed spurs adapted to the tongue lengths of their pollinators. Most appear to attach pollinia to the tongues of their pollinators, linking tongue and spur length to reproductive isolation. Noctuidae moths have the greatest number of species, but they may pollinate a single orchid species, *Platanthera dilatata*, in Southeast Alaska, and functionally represent a single pollinator that carries pollinia on its tongue. Noctuidae species also appear to be the only pollinators in this network that also function as a nectar thief on other orchids, feeding on the bee-pollinated *Goodyera oblongifolia* and *Spiranthes romanzoffiana*.

Hymenoptera pollinators contain only three families, the bumblebees (Apidae) and smaller bees in the Andrenidae and Halictidae. Despite low diversity, this group is responsible for pollinating as many orchid genera as the Diptera and at least 6 orchid species. It is the primary group that pollinates slipper orchids (*Calypso* and *Cypripedium*), which use food deception to attract pollinators. *Cypripedium* orchids appear to be pollinated by smaller Bombidae, Halictidae and Andrenidae bees (Bernhardt et al. 2014, Edens-Meier et al. 2018).

The bumblebee *Bombus melanopygus* may be the one of the single most important orchid pollinating insect species. It pollinates across the orchid flowering season, with queens pollinating the spring flowering *Calypso bulbosa* (carrying pollinia on their backs) and workers responsible for mid- to late-summer pollination of *Corallorhiza mertensiana* (carrying pollinia on their heads) and late summer pollination of *Spiranthes romanzoffiana* and *Goodyera oblongifolia* (carrying pollinia on their tongues). Newly emerged queens also forage and may pollinate in early fall.

The bee-pollinated orchids could be particularly vulnerable to climate warming if it causes phenological shifts that lead to asynchrony with foraging bumblebees that pollinate these species. For example, earlier spring flowering lead to asynchrony with bumblebee phenology in the Rocky Mountains (Pyke et al. 2016). Likewise, earlier spring flowering produced phenological asynchrony between *Bombus* queens and *Corydalis* in northern Japan (Kudo and Ida 2013). A similar effect might be expected to occur with the spring-flowering *Calypso bulbosa*.

Climate change effects on late summer or fall flowering plant-pollinator phenologies are poorly under-

stood (Gallinat et al. 2015). Though climate warming might lead to earlier flowering of other bee-pollinated orchids, such a shift would still encounter *Bombus* pollinators as they are active throughout the flowering season. The late-summer flowering *Goodyera oblongifolia* might be most vulnerable, as it currently has little competition for pollinators with other plants. Earlier flowering that encountered greater competition for pollinators, coupled with nectar thievery by Noctuidae and its typical low seed-pod production might lead to reduced reproduction in this species. The study of how climate warming affects plant-pollinator relationships should intensify with ongoing climate change, and should be expected to reveal many additional outcomes that threaten to decouple orchids from their pollinators and reduce their reproduction and survival.

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