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Flower Phenology, Bumble Bee Foraging, and Climate Change in North Cascades Mountain Meadows

Running Footer: Bumble Bees In Subalpine Meadows

Three tables and eight figures in article and seven tables and eleven figures in supplement

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This research was conducted within the traditional territory of the Nooksack Indian Tribe.

Abstract

We conducted a five-year study (2015-2019) of flower phenology and insect flower-foraging in Heather Meadows in the northern portion of the North Cascades in Washington State. We recorded 70 species of eudicot forbs and shrubs on seven transects at elevations ranging from 1,260 meters to 1,582 meters. In a typical year, there was continuity of floral resources within each transect and across the elevational gradient for the duration of the growing season. Black huckleberry was a critically important forage resource for post-diapause queens as they established nests in spring, even as 98% of the meadow was under snow. Transects with the highest tree island cover had the largest number of foraging spring queens. The exceptionally early spring of 2015 made it a good analog of climate change predicted for this region toward the end of the century. In 2015, flowering was two to eight weeks early for a majority of species, while the duration of flowering increased for a few species and decreased substantially for others, leading to phenological reassembly. These findings preview the potential impacts of climate change on flowering plants and flower-foraging insects in mountain meadows in the Pacific Northwest and could help guide effective conservation.

Key Words

Subalpine meadows, flower phenology, bumble bees, climate change, phenological reassembly

Introduction

Climate Change Impacts on Alpine and Subalpine Vegetation

Research in mountain meadows around the world has shown that vegetation will likely be sensitive to projected changes in climate (Holtmeier and Broll 2005, Canonne et al. 2007). Photographs taken during the past 100 years in Kootenay National Park in British Columbia have shown significant changes in the treeline (Roush 2009). In some areas, there was a 150 meter increase in the elevation of the treeline. A digital elevation climate model used to predict movement of the treeline over the next 100 years in the mountains of Sweden showed the treeline moving up by 233 to 667 meters, depending on the climate scenario used and location within the mountains (Moen et al. 2004). Treeline movements of this magnitude in these mountains would cause a 75% to 85% reduction in treeless alpine meadows. The remaining meadows would be extensively fragmented (Moen et al. 2004).

In the North Cascades of Washington State (USA), climate change may have significant impacts in mountain meadows (Raymond et al. 2014). Weather stations have shown that snowpack has already declined by 15% to 35% since the 1930s. The current warming trend is expected to continue, with average warming of 2.1 °C by the 2040s and 3.8 °C by the 2080s. Increases in temperature and precipitation will likely reduce overall snowpack and cause earlier snowmelt, leading to earlier spring emergence of plants and flowers and a longer growing season (Grimm et al. 2013 and Harley et al. 2020). Reduced snowpack and a longer growing season will also likely lower environmental constraints on tree establishment in subalpine meadows. Rising treelines and expansion of tree islands may be the most visible impacts related to climate change in mountain meadows (Mote et al. 2005, 2008). Some meadow habitats will almost completely disappear and the total area of meadows will likely decrease significantly (Rogers et al. 2011). The area available for meadow expansion upslope in the North Cascades is limited by the available land area at higher elevations and by the lack of soil development in areas that have been covered by year round snow or glaciers (Smith et al. 2009).

Habitat fragmentation, which can have significant impacts on biodiversity, is another climate change threat in North Cascades meadows (Macarthur and Wilson 1967). Currently, a large contiguous "sky island" of meadow habitat stretches more than 50 kilometers from Mount Baker eastward across the Picket Range to just west of Ross Lake. Figure 1 shows topographic lines at 1,280 meters, the approximate current treeline on north facing slopes, and 1,585 meters across this 'seastar-like' area of contiguous mountain meadows. If north-facing treelines move up 305 meters to the higher elevation line on the map (a reasonable climate change projection), this large sky island will fragment into an archipelago of discontinuous meadows.

Phenological reassembly is also a potential threat to the stability of community interactions in mountain meadows (Forrest et al. 2010, Theobald et al. 2017). The relationship between flower phenology and climate change was quantified in a network of meadows across Mt. Rainier (Washington state, USA). Significant differences were observed in the sensitivity of different plant species to climate drivers (Theobald et al. 2017). This differential sensitivity produced a temporal shift in the co-flowering community at Mt. Rainier under climate change analog conditions in 2015 (earlier snowmelt, shorter snow duration, and warmer growing season).

Bumble Bees in Mountain Meadows

Bumble bees have unique adaptations compared to other pollinators in high elevation habitats (Heinrich 2004, Goulson 2010, Williams et al. 2014). They emerge early in the season, have long body hairs that preserve warmth, shiver their wing muscles to warm their bodies, fly at colder temperatures than most other insects, and have a flower-diverse diet. It is likely some combination of these characteristics has allowed bumble bees to thrive in mountain meadows. However, bumble bees in high elevation meadows may be particularly vulnerable to climate change (Inouye, 2020). Martinet et al. (2020) examined heat stress resistance in 39 species of bumble bees from diverse habitats across the globe and found that those from arctic, boreal, and montane habitats were more vulnerable than temperate and Mediterranean species, and that heat-induced stupor occurred most rapidly in *Bombus melanopygus* Nylander (black tailed bumble bee), the most abundant bumble bee at our Heather Meadows study site in the North Cascades Mountains of Washington State.

Understanding bumble bee foraging is essential for predicting how climate change will impact bumble bee colony survival in North Cascades mountain meadows. Bumble bees have been observed foraging on different plant species as they flower in sequence through the season (Devoto et al. 2013) and collecting pollen and nectar from a wider range of flowering species as altitude increases (Miller-Struttmann et al. 2014). Studies have shown that bumble bee foraging distances increase as available resources decrease (Carvell et al. 2011) and as limited late season floral resources are spread across a broader landscape (Elliott et al. 2009). Foraging workers of *Bombus beaticola* (Tkalcu) have been observed moving between subalpine and alpine sites, with nest sites likely in the subalpine (Tomono and Soto 1997).

Tree Islands in North Cascades Mountain Meadows

Tree islands (clusters of trees with tall shrubs under the tree canopy) are a distinctive feature in North Cascades meadows that have a longer snow free season than surrounding open meadows (Franklin and Dyrness 1973). Tree islands can vary in size from just a few trees to 0.1 hectares (Franklin and Dyrness 1973). Tree islands reduce snow depth through their snow shedding architecture. Additionally, the soil warms faster and snow melts sooner under tall shrub communities (Way and Lapalme, 2021).

Research Objectives

The broadest goal of our five-year study was to create an inventory of flowering plants and flower-foraging insects in the mountain meadows of the North Cascades that could inform current conservation efforts (Strange and Tripodi 2019) and serve as a baseline for future studies examining effects of climate change. The three objectives of our project were to (1) record the abundance and flower phenology of eudicot forbs and shrubs in Heather Meadows, (2) describe the foraging insect community broadly and *Bombus* species more specifically, and (3) understand bumble bee use of meadow habitats, especially nest site selection and foraging. The first year of our study (2015) was marked by the earliest and driest spring in the observational record, with climate conditions approximating those predicted for this region toward the end of this century (Harley et al. 2020). This 2015 anomaly afforded an opportunity to understand how flower phenology in subalpine meadows might shift in response to climate change.

Methods

Study Area

Heather Meadows lies between two snow-capped peaks, Mount Baker (3,285 meters) and Mount Shuksan (2,783 meters). Mount Baker holds the world record for snowfall in a single season (almost 30 meters in 1998). In a typical year, there is substantial snowpack at Heather Meadows (five to ten meters or more) that does not melt until early summer (usually June). The lower elevation continuous forest that borders Heather Meadows ends at approximately 1,280 meters on north facing slopes and 1,585 meters on south facing slopes. Heather Meadows is primarily a shrub meadow with ericaceous heathers and *Vaccinium* species dominating. Lower elevation portions of the meadow are subalpine with numerous tree islands of various sizes, whereas higher elevations are alpine with tree islands absent, very small, or very sparsely distributed.

Mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) is the dominant tree in tree islands, with a scattering of silver fir (*Abies amabilis* Douglas ex J. Forbes). Shrubs under the tree canopy most commonly include black huckleberry (*Vaccinium membranaceum* Douglas ex Torr.) and Cascade blueberry (*Vaccinium deliciosum* Piper). Cascade blueberry, pink mountain heather (*Phyllodoce empetriformis* (Sm.) D. Don), white mountain heather (*Cassiope mertensiana* (Bong.) G. Don), white-flowering rhododendron (*Rhododendron albiflorum* Hook), Sitka mountain ash (*Sorbus sitchensis* M. Roem.), and false azalea (*Rhododendron menziesii* Craven) are commonly found along the margins of tree islands

Monitoring Transects

Monitoring transects were established on a north facing slope across an elevational gradient from 1,260 meters to 1,582 meters. Supplementary Figures 1-7 (online) show locations of transects (aerial photos) and provide information on tree island cover. Seven transects were established: five primary transects each at a different elevation (Picture Lake, Visitor's Center, Austin Pass, Artist's Point, and Huntoon Point) and two supplemental transects at approximately the same elevation as the Visitor's Center transect (Visitor's Center High and Visitor's Center Low). The supplemental transects were added in 2016, 2017, 2018, and 2019 to investigate the effect of tree islands on foraging by bumble bee queens in the spring.

The lowest elevation transect (Picture Lake) was at the treeline, with forest almost completely dominating below this elevation. The highest elevation transect (Huntoon Point) was an open alpine meadow habitat with no tree islands. The locations of intervening transects were guided by an effort to space transects equally with 80 meter increments in elevation between transects. Because the Forest Service asked that all transects be located along existing gravel or paved trails, the elevation increments were only approximately 80 meters. Each transect was 9.10 meters wide and 183 meters long (approximately 0.16 hectares). Transects were centered on the Forest Service trails and extended out 4.55 meters in both directions from the edge of the trails.

Data Collection

Data were collected at Heather Meadows on flower phenology and insects visiting flowers, with a special focus on bumble bees. Fifteen trained citizen science observers associated with the Koma Kulshan Chapter of the Washington Native Plant Society conducted the flower phenology monitoring. The lead study author conducted the assessment of insects visiting flowers.

Flower Phenology -- Phenology was monitored every year in the five primary transects and for four years (2016-2019) in the two supplementary transects. Data were collected from when flowers first appeared (typically June for the lower elevation transects) to when major snowfalls began (typically late September). Teams of volunteers visited the study site every two weeks and monitored each transect for 30 minutes. Phenological stages were categorized based on flower abundance. Since it was not possible to count the total number of flowers for all species present in each transect, flower abundance for each species was estimated and coded as: 0) "absent" (abundance of zero), 1) "uncommon" (abundance of <100 individual flower stalks), 2) "common" (abundance of 100 to 5,000 flower stalks), or 3) "abundant" (abundance of >5,000 flower stalks).

The relationship between climate variables (collected from secondary sources) and flower onset for black huckleberry, Cascade blueberry, and pink mountain heather (the most common early flowering plants in Heather Meadows) was examined in a correlation analysis for the years 2015 to 2019. The Picture Lake transect was designated as our reference transect for the climate analysis. Climate data were obtained from the Natural Resources Conservation Service SNOTEL station at Wells Creek in the North Cascades, the Western Regional Climate Center station in Bellingham, Washington, the Mt. Baker Ski Area, and the Washington Department of Transportation. The SNOTEL station (1,228 meters elevation) is approximately seven kilometers west of the Picture Lake transect (1,260 meters elevation) and is topographically similar to the Picture Lake transect (Figure 1). SNOTEL data includes daily measurements of air temperature (maximum and minimum), snow depth, and wind speed starting in 1997. We used the SNOTEL data as a proxy for climate conditions at the Picture Lake transect. Because the SNOTEL temperature data starts only in 1997, and has some missing data points, we relied on National

Weather Service data for Bellingham to compute the long-term average air temperatures (1945-2005).

Flower Visiting Insects -- The abundance of insects visiting flowers was assessed once every two weeks at all seven transects during 2019. Insect monitoring was conducted separately from flower phenology monitoring. The full length of each transect was monitored for 30 minutes, during a four-hour window from 11:00 a.m. to 3:00 p.m. Insects were counted only if they were observed on a flower. Information on plant species was collected for all insect visits. Other than bumble bees, insects were identified only to order or family level. The two most common bumble bee species (*B. melanopygus* [black tailed bumble bee] and *Bombus flavifrons* Cresson [yellow head bumble bee]) were easily identified to species through observation on flowers. Other bumble bees were observed during monitoring, but not identified to species. These uncommon bumble bees were not captured for identification to species due to concerns about unnecessarily endangering small populations. Information was also collected on bumble bee reproductive caste (i.e., queen, worker, male).

After the first year of monitoring, it became apparent that bumble bee foraging in tree islands is important for understanding the early season relationship between flowering plants and bumble bees at Heather Meadows. Using aerial photographs, we measured the extent of tree canopy cover along each transect by computing the percentage of the length of the transect that was bordered (on one or both sides) by tree canopy. This measure of tree island cover links directly to the 183 meter long transect areas that were monitored for flower phenology and insects. This measure does not reflect the overall size or shape of the tree island.

A small mark and recapture study of bumble bee foraging across the elevational gradient was conducted during the summer of 2021, using methods described by Mola and Williams (2019). We examined the potential for bumble bees to move from lower elevation sites (suspected nesting sites) to higher elevation sites (suspected late summer foraging sites). Bumble bees (not identified to species) were collected at foraging sites near the Artist's Point transect (1,520 meters) and transported to a lower elevation site near the Visitor's Center transect (1,347 meters), where they were marked with fluorescent paint and released. The area between the capture and release sites was open alpine and subalpine meadow. Recapture efforts occurred the following day in the vicinity of the Artist's Point transect where the bees were initially captured (approximately 1,000 meters from the release site).

Results

Flower Phenology

Seventy eudicot forbs and shrubs were identified in transects, of which 62 (89%) were native (Supplementary Table 1, online). The eight non-native species were rare, especially at higher elevations, and most were observed near the Visitor's Center, coincident with the greatest summer tourist traffic. Eight native species accounted for the majority of flowers observed and were designated as focal species (Figure 2). They fell into three phenology categories. 1) Four early-season plants began flowering in June at lower elevations in a typical year: black huckleberry (*Vaccinium membranaceum*), Cascade blueberry (*Vaccinium delisciosum*), pink mountain heather (*Phyllodoce empetraformis*), and white mountain heather (*Cassiope mertensiana*). 2) Three mid-season plants began flowering in July in a typical year: Sitka mountain ash (*Sorbus sitchensis*), Arctic lupine (*Lupinus latifolius* Lindl. Ex J. Agardh), and partridgefoot (*Luetkea pectinata* (Pursh) Kuntze). 3) One late-season plant began flowering in August in a typical year: fireweed (*Chamaenerion angustifolium* (L.) Scop.

Results of the correlation analysis between climate variables and flower onset for early season plants at Picture Lake (black huckleberry, Cascade blueberry, and pink mountain heather) are shown in Tables 1 and 2. There was substantial year-to-year variability for all climate parameters, but the spring deviation in mean daily maximum air temperature correlated strongly (P = 0.01) with flower onset (measured in weeks starting on May 1). May 1 snow depth and total snowfall for the season were weakly correlated with flower onset, while April 1 snow depth and wind speed showed no correlation.

Flower phenology during 2019 for all primary transects is shown in Figure 3 and phenology for all five years is shown in Supplementary Tables 2-6, online. Monitoring during 2019 revealed a consistent and predictable pattern in the sequence of flowering for focal species, with flowering periods overlapping within each transect. The first flowers in Heather Meadows were strongly tied to elevation and the presence of tree islands. The earliest plant to flower was black huckleberry in tree islands at Picture Lake and the three Visitor's Center transects when as much as 98% of the meadow was snow covered. The earliest black huckleberry flowers were recorded at the Visitor's Center Low transect (35% tree island cover), even though this transect was 87 meters higher than the Picture Lake transect (8% tree island cover).

Snowmelt was delayed by a few weeks in open meadows relative to tree islands. Pink mountain heather and white mountain heather flowered soon after snowmelt. They also showed a trend of later flowering with increasing elevation associated with progressive snowmelt. Pink mountain heather flowered for a longer time than most other species, although at relatively lower abundance later in the season (Supplementary Tables 2-6, online). Partridgefoot and Arctic lupine flowered mid- to late-season at higher elevations. Fireweed was observed in all transects. It was especially sensitive to climate variables, flowering in July in 2015 (a year noted for the earliest spring on record); in August in more typical years; and in September in 2017 (a year with a cold spring) (Supplementary Tables 2-6, online).

Combining data on flower abundance from all transects (i.e., elevations) within a single year revealed a continuous and abundant supply of flowers throughout the season (Supplementary Tables 2-6, online). In a typical year (2019) there were seasonal low points in flower abundance for specific transects (for example, early August at Picture Lake), but when flower abundance was combined across transects, we found that abundance was maintained at moderate levels (floral abundance score of 2 or higher) throughout the core three months of the season.

During April 2015 (climate change analog year), mean maximum air temperature was 4.0 ^{0}C higher than the long-term average (Figure 4). Flower onset was accelerated in a majority of species in each transect. At Picture Lake, flowering was advanced in 12 of the 13 most common plant species, compared to a typical year (2019) (Figure 5). There were also shifts in flower phenology in higher elevation transects (Supplemental Figures 8-11, online). The largest acceleration (eight weeks) was observed for fireweed at the Visitor's Center transect.

The duration of the flowering season was reduced in 2015 relative to the 2019 reference year for three lower elevation focal species (black huckleberry, Cascade blueberry, and Sitka mountain ash) and two higher elevation focal species (partridgefoot and Artic lupine) (Supplementary Figures 8-11, online). Cascade blueberry flowering displayed the strongest and most consistent decline in duration for 2015 compared to 2016-2019 (64% at Picture Lake, 53% at Visitor's Center, and 34% at Austin Pass). ANOVA showed duration of Cascade blueberry flowering in 2015 was significantly shorter compared to 2016-2019 (P = 0.0046, t = 5.715, df = 4); while there were no significant differences in the duration of Cascade blueberry flowering within the 2016-2019 period (P = 0.331; F = 1.273; *DFn*, *Dfd* 1.795, 7.181).

The duration of the flowering season increased for several other species in 2015, most notably pink mountain heather and white mountain heather at Picture Lake (Figure 5). This pattern was maintained for pink mountain heather in all transects. Flowering duration at Picture Lake also increased by two to six weeks for subalpine spirea (S*piraea splendens* Baumann ex K. Koch), fireweed (*Chamaenerion angustifolium* (L.) Scop.), subalpine daisy (*Erigeron glacialis* (Nutt.) A. Nelson), and pearly everlasting (*Anaphalis margaritacea* (L.) Benth. & Hook).

The differential flowering response to the early spring in 2015 resulted in phenological reassembly of flowering plants. At Picture Lake, fireweed exceptionally co-flowered with false azalea (*R. menziesii*) (Figure 5). At Artist's Point, black huckleberry and Cascade blueberry co-flowered with Sitka valerian (*Valeriana sitchensis* Bong.), a mid to late-season plant. At Huntoon Point, Arctic lupine co-flowered with the two major early season *Vaccinium* species, instead of the late-season fireweed (Supplementary Figures 8-11, online).

Flower Visiting Insects

A total of 920 insects were observed visiting flowers in Heather Meadows transects during 2019 (Figure 6). They were observed on flowers of 29 species of eudicot shrubs and forbs. The top 20 plant species are shown in Figure 7, of which black huckleberry, Cascade blueberry, pink mountain heather, Sitka mountain ash, and partridgefoot were visited by the largest number of insects. Details on insect visits to all 29 plant species are shown in Supplementary Table 7, online.

Bumble bees were the most abundant insects observed on flowers (67%). Of the 615 bumble bees, *B. melanopygus* was the most abundant (76%), with *B. flavifrons* a distant second (15%) (Figure 6). Identification challenges resulted in 9% of recorded bumble bees being listed as unidentified (Figure 6). European honey bees (*A. melifera*) were the second most abundant insect observed (12%). The source of honey bees was managed hives placed in July along a Forest Service road about 1.8 kilometers northeast of Picture Lake. No honey bees were observed on flowers until the second week of July.

Black huckleberry, Cascade blueberry, and the relatively rare oval-leaved huckleberry (*Vaccinium ovalifolium* Sm.) —all very early flowering shrubs—were the dominant floral resource for post-diapause bumble bee queens (spring queens), with 97% of 63 spring queens visiting these species (Supplementary Table 7, online). We observed queens on these *Vaccinium* flowers in early spring when 98% of the meadow was under snow.

Vaccinium species were particularly dependent on bumble bees for pollination. Bumble bees comprised 94% of all insects observed on these early season plants (Supplementary Table 7, online). Sitka mountain ash, partridgefoot, subalpine spirea, and pearly everlasting were visited frequently by other insects, especially introduced honey bees (112 observed) and syrphid flies (104 observed). Honey bee and bumble bee foraging overlapped primarily on Sitka mountain ash, although partridgefoot and subalpine spirea also served as floral resources for both honey bees and bumble bees (Supplementary Table 7**,** online**)**.

The number of spring bumble bee queens observed at our four lower elevation transects (Picture Lake, Visitor's Center, Visitor's Center High and Visitor's Center Low) increased significantly with tree island cover of transects (linear regression: F = 173.8; *Dfn*, *Dfd* 1, 2; P= 0.0048) (Pearson r = 0.99, two-tailed P= 0.0048) (Figure 8). In contrast, there was no association between numbers of bumble bee workers and tree island cover (F = 6.5; *Dfn*, *Dfd* 1, 2; P = 0.125). There was a striking high abundance of spring queens in the Visitor's Center Low transect, which had the highest proportion of tree island cover (35%), resulting in early snowmelt and early flowering of understory plants. Flowering occurred at this transect earlier than at the lower elevation Picture Lake transect, that had less tree island cover (8%).

The ratio of queens to workers varied substantially between transects and across the season (Table 3). This was especially evident early in the season, when relatively high numbers of queens occurred in transects at lower elevations, but very few at higher elevations and none at the highest transect (Huntoon Point), even after snow had completely melted. Workers were the primary bumble bees at higher elevations (especially during mid and late season). In the small mark and recapture study, four of the 46 bumble bees captured at a higher elevation site (1,529 meters) and transported to a lower elevation site (1,350 meters) for marking and release were recaptured at the same higher elevation site the next day.

Discussion

Our monitoring of the flowering plant community at Heather Meadows in the North Cascades of Washington State revealed abundant and diverse sources of pollen and nectar for foraging insects. For the most part, flowering periods of different species overlapped, such that floral resources were available for an extended time within each transect. The elevational range of the meadow also appeared to be a key factor in maintaining floral resources throughout the season (Figure 3). For example, flower abundance declined to uncommon in the Visitor's Center transect by the end of July, while flowers were still common during the first half of August in the Artist's Point transect, 173 meters higher in elevation.

Flower onset at Heather Meadows for three early season plants (black huckleberry, Cascade blueberry, and pink mountain heather) was best predicted by mean daily maximum air temperature, total annual snowfall, and May 1 snow depth (Table 2). Microhabitats associated with tree islands, somewhat unique landscape features of North Cascades subalpine meadows, were an additional factor that reduced snow accumulation, accelerated snowmelt, and enabled early flowering. In Heather Meadows, black huckleberry began flowering in tree islands when temperatures averaged only 10^0C, and nearly all of the surrounding area was snow covered.

Bumble bees were the major insect visiting flowers throughout the season in all transects at Heather Meadows (Figure 6). The three early flowering *Vaccinium* species in tree islands were visited almost exclusively by bumble bees (94% of all observed insect visits), revealing the importance of bumble bees to *Vaccinium* plants, as well as to higher trophic levels (such as bears) that depend on *Vaccinium* berries for late season calories (Martin et al. 1951). The ability of bumble bee queens to forage in tree islands early in the season when most of Heather Meadows was still snow-covered was remarkable. We observed bumble bee queens foraging on black huckleberry, when no other plants were flowering. Figure 8 shows that the number of foraging spring queens in 2019 was significantly correlated with the percentage of each transect that was covered by tree islands. In an ecosystem where plants and foragers are limited by the duration of the growing season, early season emergence and foraging in tree islands may enable bumble bee queens to get an early start provisioning colonies. The resilience of the early spring *Vaccinium*-bumble bee relationship could be threatened by the effects of climate change on plant or bumble bee phenology. Additional research is needed to determine whether the co-emergence of *Vaccinium* flowers and spring queens in tree islands share a common environmental trigger that will persist through climate change.

Our data suggest that bumble bee nest sites in Heather Meadows were likely within larger subalpine tree islands, since the snowmelt pattern allowed bumble bee queens to access potential nest sites early in the season only within tree islands. Treeless meadows and smaller tree islands were still snow covered when queens were establishing nests. This conclusion was reinforced by visual observations of bumble bee workers later in the season leaving and returning to four nest sites within tree islands. Further research is needed to confirm the hypothesis that bumble bee nest site abundance is correlated with the extent of tree islands. Although tree islands are important for bumble bees, tree island expansion associated with climate change may have to be managed to conserve subalpine meadows. Fully understanding the relationship between tree islands and early season nesting and foraging by post-diapause bumble bee queens will be important for developing effective conservation strategies.

Variation in the observed ratio of queens to workers at different elevations (Table 3) provides clues to how bumble bee foraging may shift across elevations as the season progresses. Queens emerged early and foraged at lower elevations where flowers were abundant early in the season. Workers emerged later in the season. Progressive snowmelt across elevations provided workers with an opportunity to initially forage at lower elevations and then move up slope when lower elevation floral resources began declining and flowers in higher elevations were just peaking. The mark and recapture study confirmed bumble bee workers can move from lower elevation nest sites to higher elevation foraging sites. Although only four of 46 marked bees were recaptured, this can at least partially be explained by the availability of many other foraging sites near the higher elevation recapture site. Further study is needed to better quantify bumble bee foraging across elevational gradients. The observation that bumble bees forage across the elevational gradient reveals a potential vulnerability to climate change in North Cascades meadows. If the elevational range in meadows is constricted due to climate change (i.e., treelines moving up, but limited land available for meadow expansion to higher elevations), bumble bees may lose opportunities to forage at higher elevations later in the season when flower abundance is declining at lower elevations. This could shorten the foraging season and reduce viability of bumble bee colonies in subalpine meadows.

The vulnerability of some bumble bee species to heat stress reveals another potential climate related threat to bumble bees in the North Cascades. *B. melanopygus* (76% of all bumble bees observed at Heather Meadows) showed the lowest heat resistance among 39 species of bumble bees from habitats across the globe that were studied by Martinent et al. (2021). *B. melanopygus* may be exceptionally adapted for the cold temperatures and short growing season in mountain meadows, but these survival traits may not be beneficial under future climate change. An increase in heat waves, such as the record-setting heat in late June and July of 2021 that affected much of the Northwest, is cause for concern even in high elevation meadows.

With severe abiotic conditions in North Cascades meadows, it is conceivable that increased temperatures associated with climate change could benefit plant communities. Record high springtime air temperatures and early snowmelt in 2015 did accelerate flowering in a majority of the most common plant species (Figure 5; Supplemental Figures 1-4, online), however, flower abundance was reduced mid and late season in 2015 (Figure 5, Supplementary Tables 2-6, online). Flower abundance at Picture Lake declined below level 2 (absent or uncommon) for nearly all species by late July. The peak flowering period (range of monitoring periods when flower counts were predominantly at the common [2] or abundant [3] levels) was only eight weeks in 2015 compared to 12 weeks in 2019 (Supplementary Tables 2-6, online). We also observed multiple novel co-flowering patterns at Heather Meadows in 2015.

We did not directly examine whether bumble bee populations at Heather Meadows are limited by floral resource availability. However, it seems likely that floral abundance is more than adequate to support bumble bee colonies during late spring and early summer, when our monitoring revealed abundant flowers (multiple thousands just within study transects). In contrast, floral abundance may be an important limiting factor in early spring when post-diapause bumble bee queens are dependent on *Vaccinium* in tree islands to provision their young nests. Floral abundance may also be a limiting factor for bumble bee populations in late summer and fall, when new queens and males are emerging and flower abundance is declining (especially in years with truncated seasons and reduced flowering, such as 2015). Identifying specific time periods when floral abundance is a limiting factor for bumble bee populations will be important for designing effective conservation programs.

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Tables

TABLE 1. Climate Variables During the Study Period (2015 to 2019). The anomaly in daily mean maximum high temperature was calculated using long-term averages from the Western Regional Climate Center (Bellingham, WA - 60 km from the study site). Snow depth and wind speed records were from the SNOTEL weather station. The total season snowfall data are from Mt. Baker Ski Area and the Washington Department of Transportation.

Study Year	Spring Temp Anomaly (°C)	April 1 Snow Depth (cm)	May 1 Snow Depth (cm)	Total Season Snowfall (m)	Average Spring Wind (km/h)
2015	3.9	25	13	7.7	0.3
2016	0.8	153	104	15.8	2.4
2017	-0.6	195	183	22	2.5
2018	-0.2	265	229	21.4	3.3
2019	0.3	121	99	13.7	1.6
Long-term Mean Baseline (years)	0.0 (1945-2005)	213 (1997-2014)	181 (1997-2014)	16.4 (1970-2010)	1.3 (1997-2014)

TABLE 2. Flower Onset at Picture Lake as a Function of Climate Variables (2015 to 2019). Flower onset (measured in weeks since May 1) for three early flowering species (black huckleberry – *Vaccinium membranaceum*, Cascade blueberry – *V. deliciosum*, pink mountain heather – *Phyllodoce empetriformis*) was the dependent variable in the correlation analysis that included several climate variables.

Dependent Variable	Explanatory Variables				Significant?
		Pearson *r*	R^2	*P*	Alpha=0.05
Flower Onset	Spring Mean Max Temp (^{0}C)[1]	-0.958	0.919	0.01	Yes
	May 1 Snow Depth (cm)[2]	0.887	0.79	0.045	Yes
	Total Season Snowfall (m)[3]	0.991	0.83	0.032	Yes
	Spring Wind Speed (km/h)[2]	0.774	0.599	0.125	No

[1]Deviation from regional long-term mean maximum daily temperature in March-May, using 1949-2005 baseline data from the Western Regional Climate Center for Bellingham, Whatcom County, Washington (https://wrcc.dri.edu/)

[2]From Wells Creek SNOTEL station, US Department of Agriculture (https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=909)

[3]From Mt. Baker Ski Area snow statistics and Washington Department of Transportation

(https://www.mtbaker.us/the-mountain/snowfall-statistics/)

TABLE 3. Ratio of Bumble Bee Queens to Workers Across the Season and Elevational Gradient (All Bumble Bee Species).

Transect	May	June	July	August	September
Huntoon Point 1,582 m	0 : 0	0 : 0	0 : 18	0 : 8	0 : 2
Artist's Point 1,520 m	0 : 0	2 : 2	1 : 31	1 : 61	2 : 4
Austin Pass 1,445 m	0 : 0	4 : 10	2 : 72	0 : 0	0 : 0
Visitor's Center High 1,350 m	0 : 0	7 : 5	0 : 65	1 : 8	1 : 4
Visitor's Center 1,347 m	1 : 0	6 : 12	0 : 61	0 : 4	0 : 14
Visitor's Center Low 1,327 m	8 : 0	24 : 28	0 : 38	0 : 1	0 : 0
Picture Lake 1,260 m	1 : 0	8 : 28	0 : 49	3 : 15	0 : 3

Main Text Figures

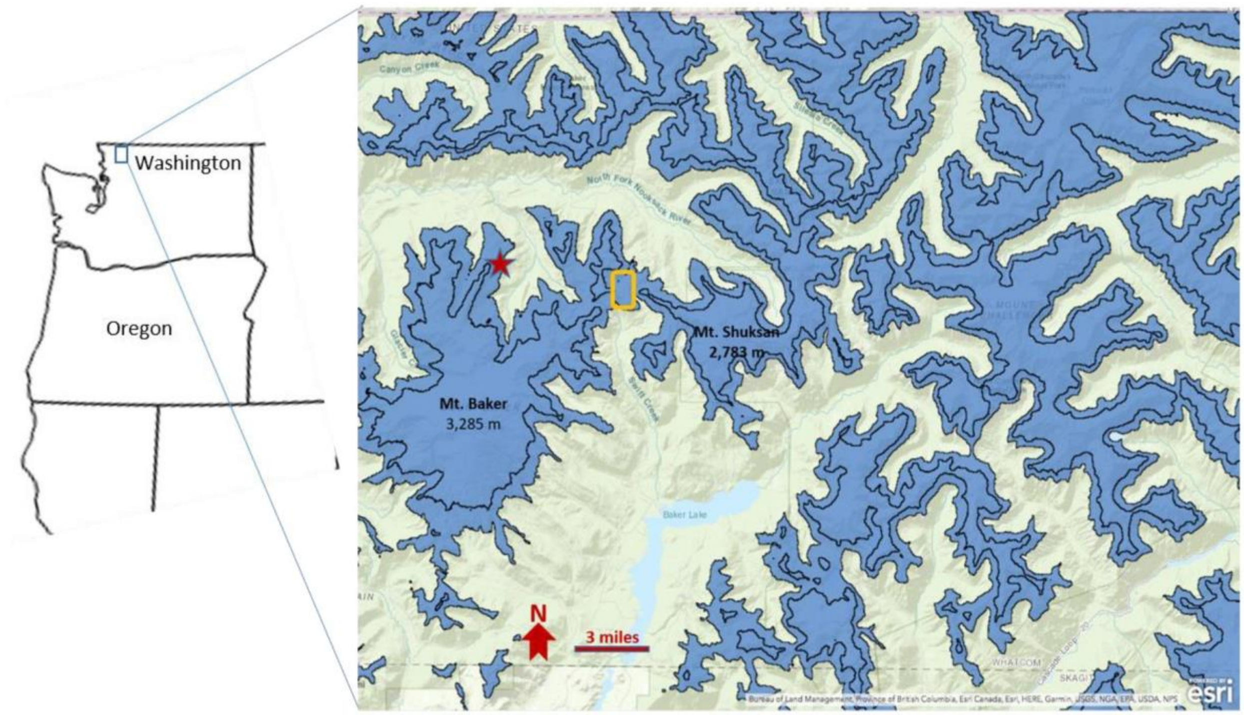


Figure 1. Study transects were located in Heather Meadows (yellow rectangle) in the Mt. Baker-Snoqualmie National Forest in the North Cascades of Washington. The red star marks the location of the SNOTEL weather station at Wells Creek. Areas shaded blue are at or above the 1,280 meters line (approximate treeline on north facing slopes in the northern portion of the North Cascades). The higher elevation line within the blue-shaded region lies at 1,585 meters.

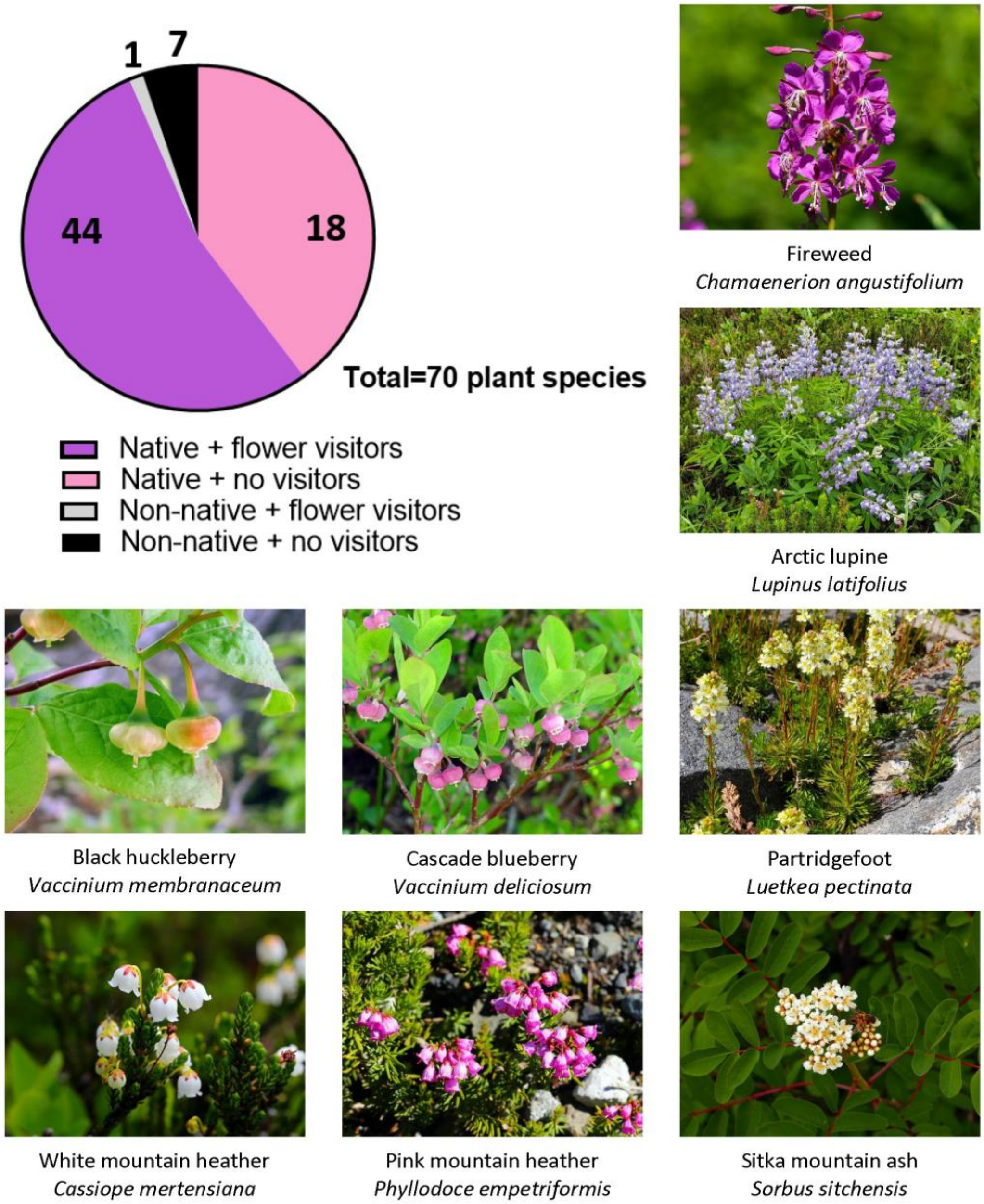


Figure 2. The pie chart shows the total number of flowering plant species observed, broken out by native/non-native status and whether foraging insects were observed on flowers. Photos show the eight focal flowering plant species that were most commonly observed.

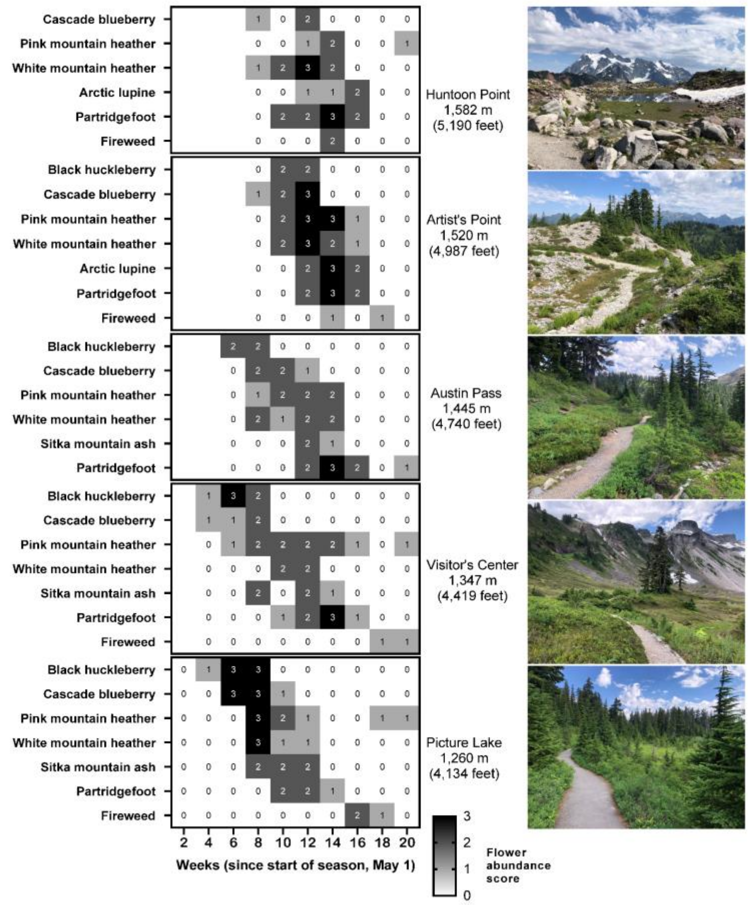


Figure 3. The tables show flower phenology and abundance during 2019 for the eight focal species at the five primary transects. Not all species were found at every transect. Photos show habitat characteristics of each transect.

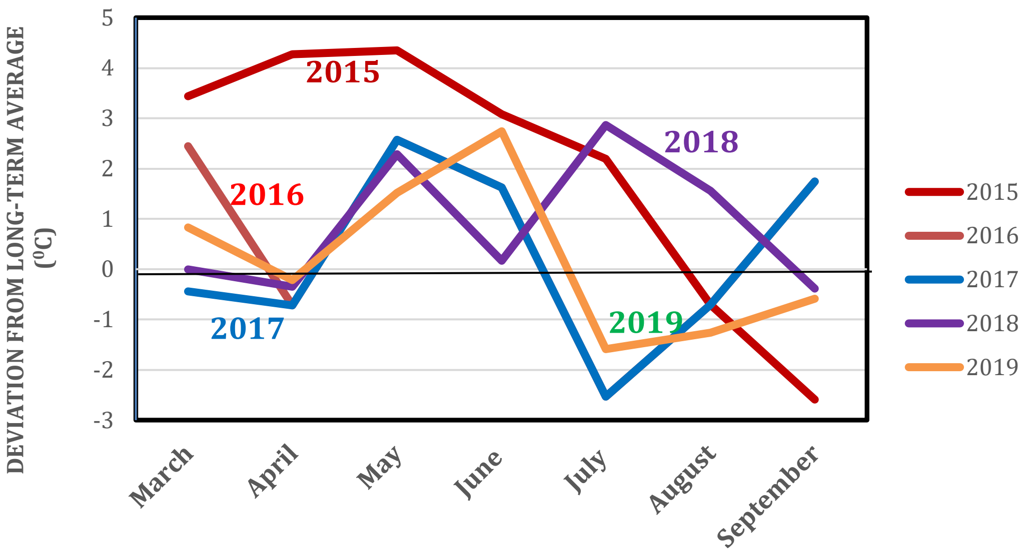


Figure 4. Air temperature deviations from long-term averages during March through September are compared between 2015 (anomalous year) and the other four years (2016-2019).

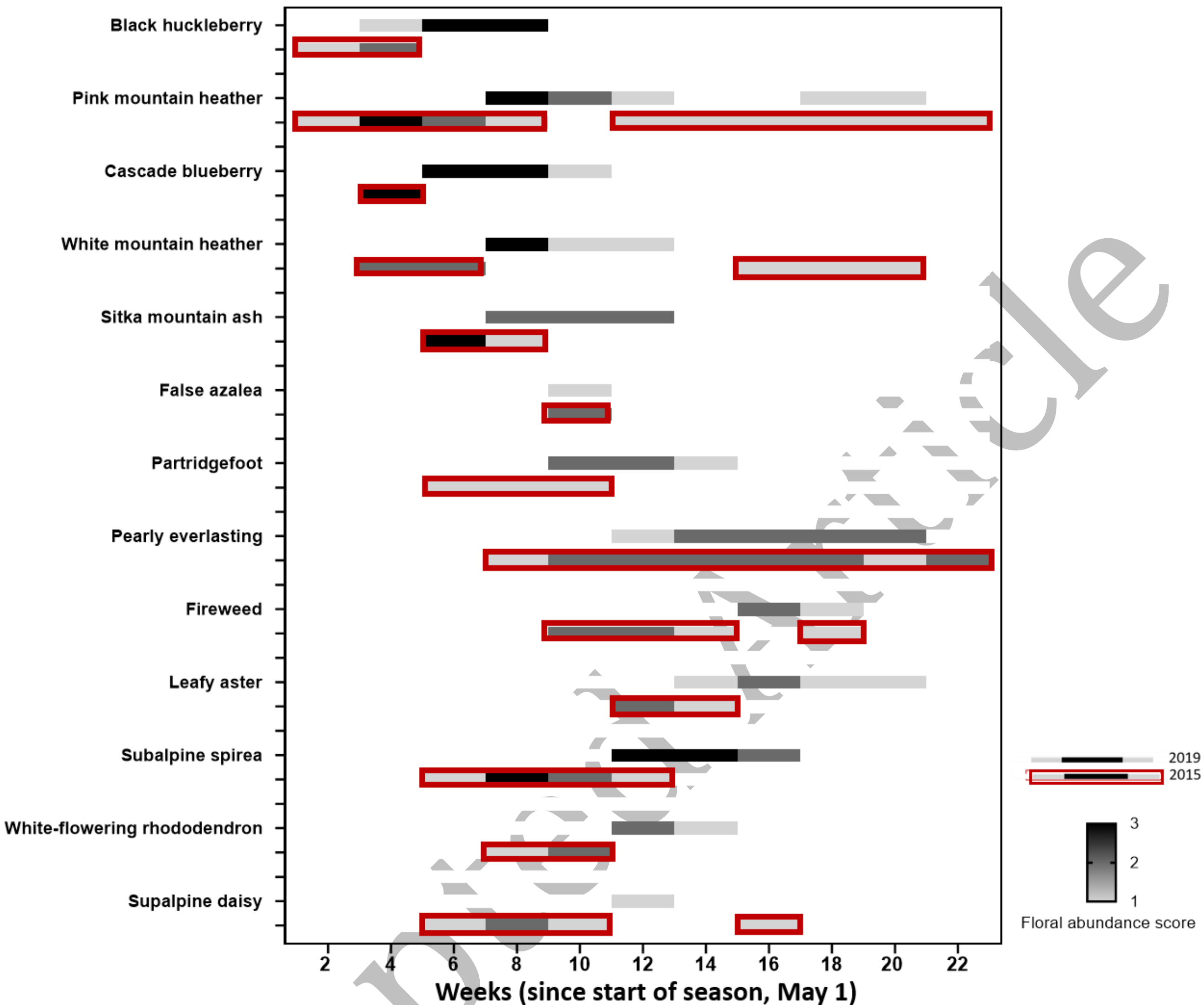


Figure 5. Flower bloom periods at Picture Lake for 13 plant species across 11 monitoring dates are contrasted between 2015 (anomalous year) and 2019 (typical year).

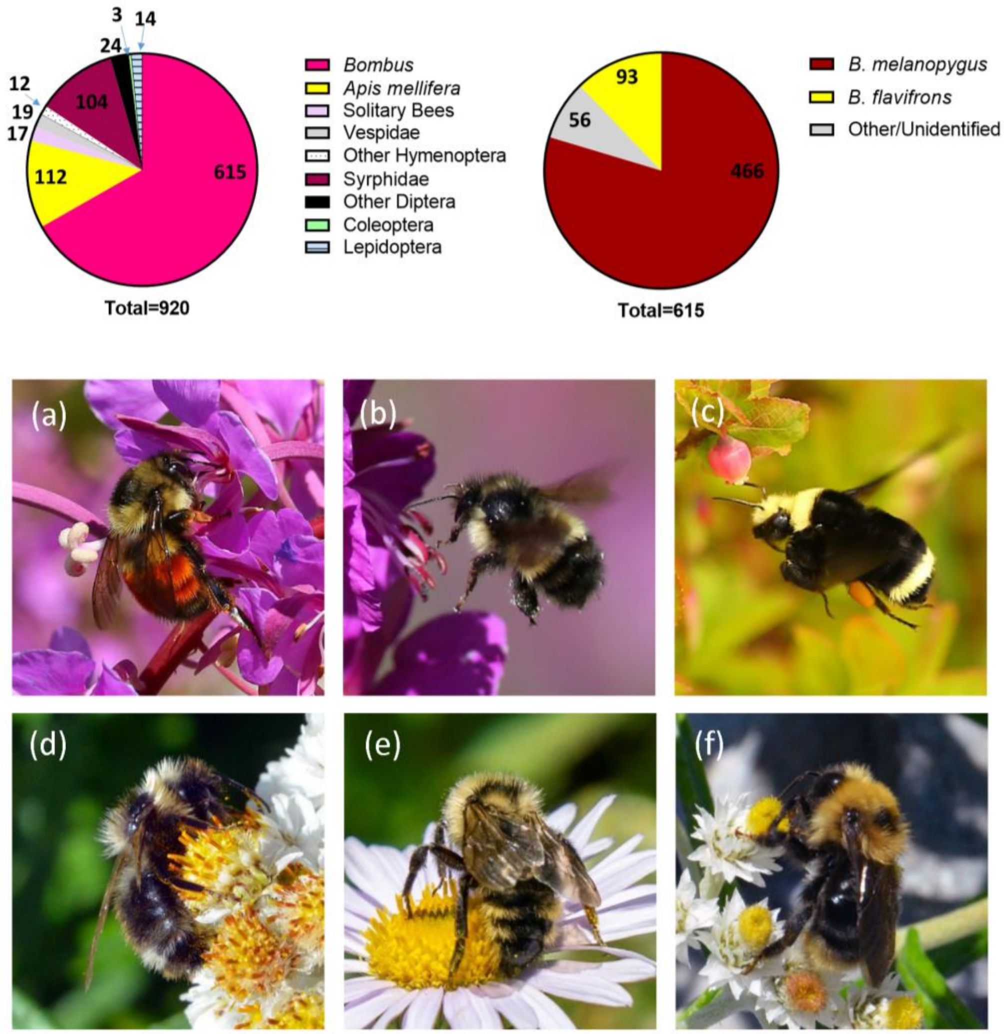


Figure 6. The first pie chart shows the proportion of flower visiting insects during 2019 belonging to different taxonomic groups: the second shows the percent of observed bumble bees belonging to the two main species. Photos illustrate the different bumble bee species recorded at Heather Meadows: (a) *B. melanopygus*, (b) *B. flavifrons,* (c) *B. vosnesenskii*, (d) *B. vancouverensis / B. bifarius* complex, (e) *B. insularis*, and (f) *B. flavidus*.

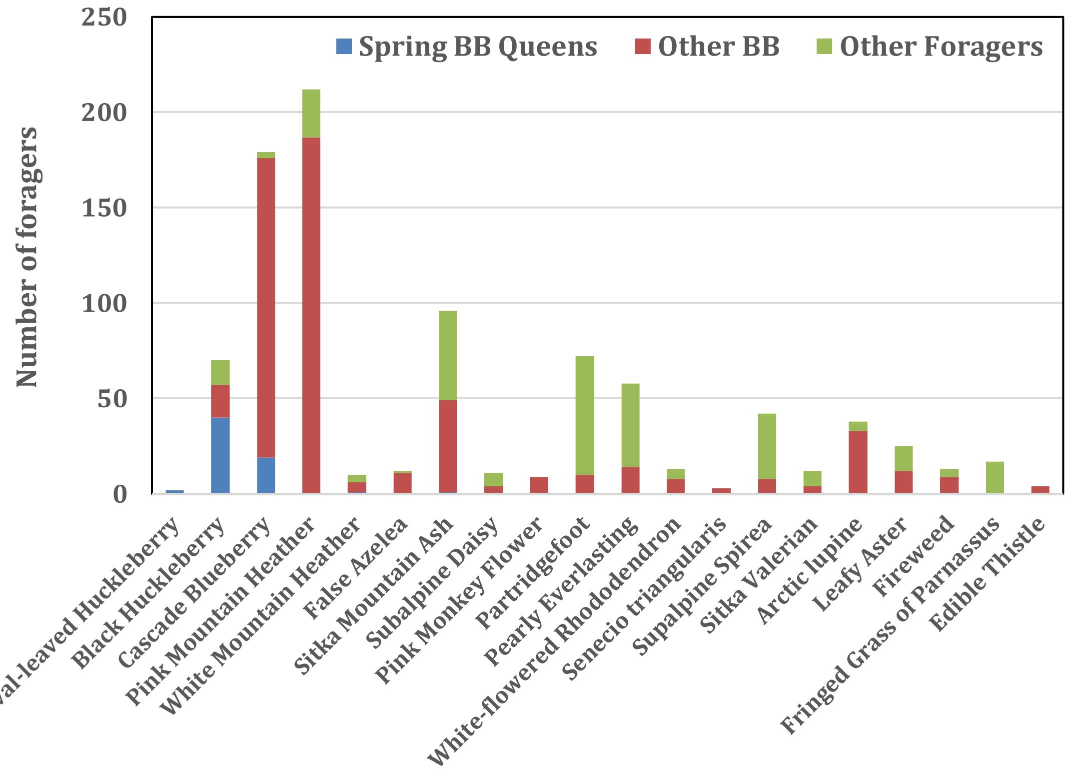


Figure 7. Flower visitation by insects on the top 20 flowering plant species are shown for 2019. Plant species are listed in the order of their bloom phenology (early season on the left). Visits by spring bumble bee queens are distinguished from visits by other bumble bees (workers, fall queens, and males) and other foraging insects.

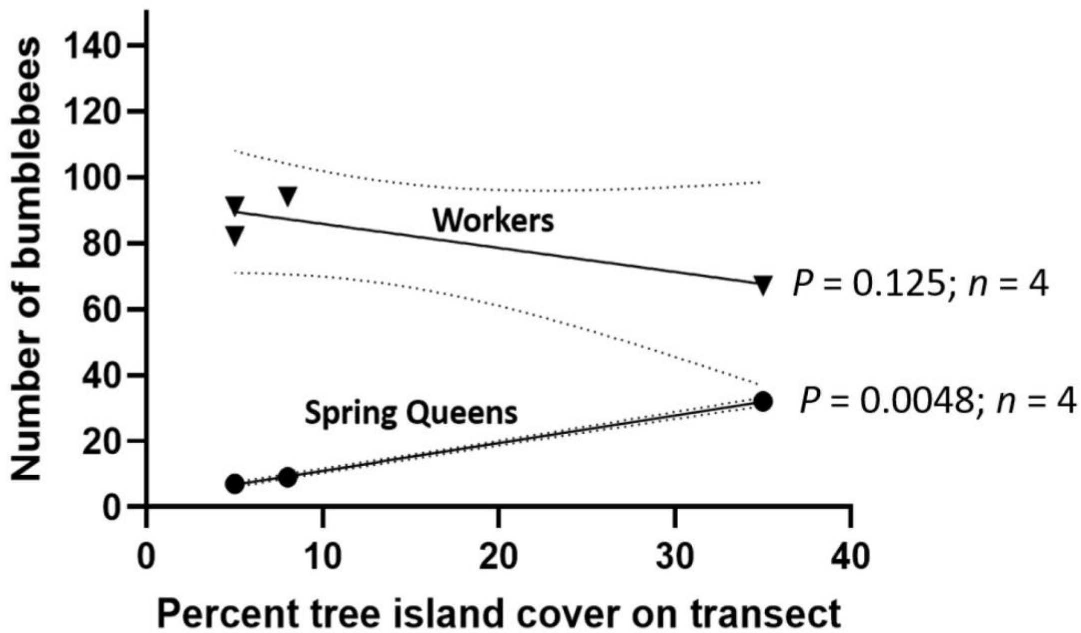


Figure 8. The relationship between tree island cover and the abundance of spring queens and workers at four lower elevation transects (Picture Lake, Visitor's Center, Visitor's Center Low, and Visitor's Center High) is demonstrated in a correlation analysis (GraphPad Prism 9, P = 0.125 for workers and P = 0.0048 for queens). Dotted lines show the 95% confidence intervals. For spring queens, this confidence interval is very narrow on the scale of this graph, and therefore more difficult to discern.

Davis JR, Lloyd TA, Singh-Cundy A. 2024. Flower phenology, bumble bee foraging, and climate change in North Cascades mountain meadows. Northwest Science 97(3): *in press*.

Supplementary Materials

Figure 1. Picture Lake Transect Aerial Photo. This transect (elevation 1,260 meters and near the treeline) is a moist lakeside meadow with multiple small tree islands covering approximately 8% of the transect length. This transect is mostly level, and includes a number of fens. The shrub vegetation includes black huckleberry, Cascade blueberry, pink mountain heather, white mountain heather, white-flowering rhododendron, and Sitka mountain ash. Fireweed (*Chamerion angustifolium*) and leafy aster (*Symphyotrichum foliaceum*) bloom late in the season (August, in a typical year).

Figure 2. Visitor Center Transect Aerial Photo. This transect (elevation 1,347 meters) is undulating and well-drained. It includes open meadows, as well as small patches of tree islands (5%). The dominant shrub vegetation includes black huckleberry, Cascade blueberry, pink mountain heather, white mountain heather, and partridgefoot (*Luetkea pectinata*). Among the forbs, fireweed is a prominent late-season floral resource, along with leafy aster and pink monkey flower (*Erythranthe lewisii*).

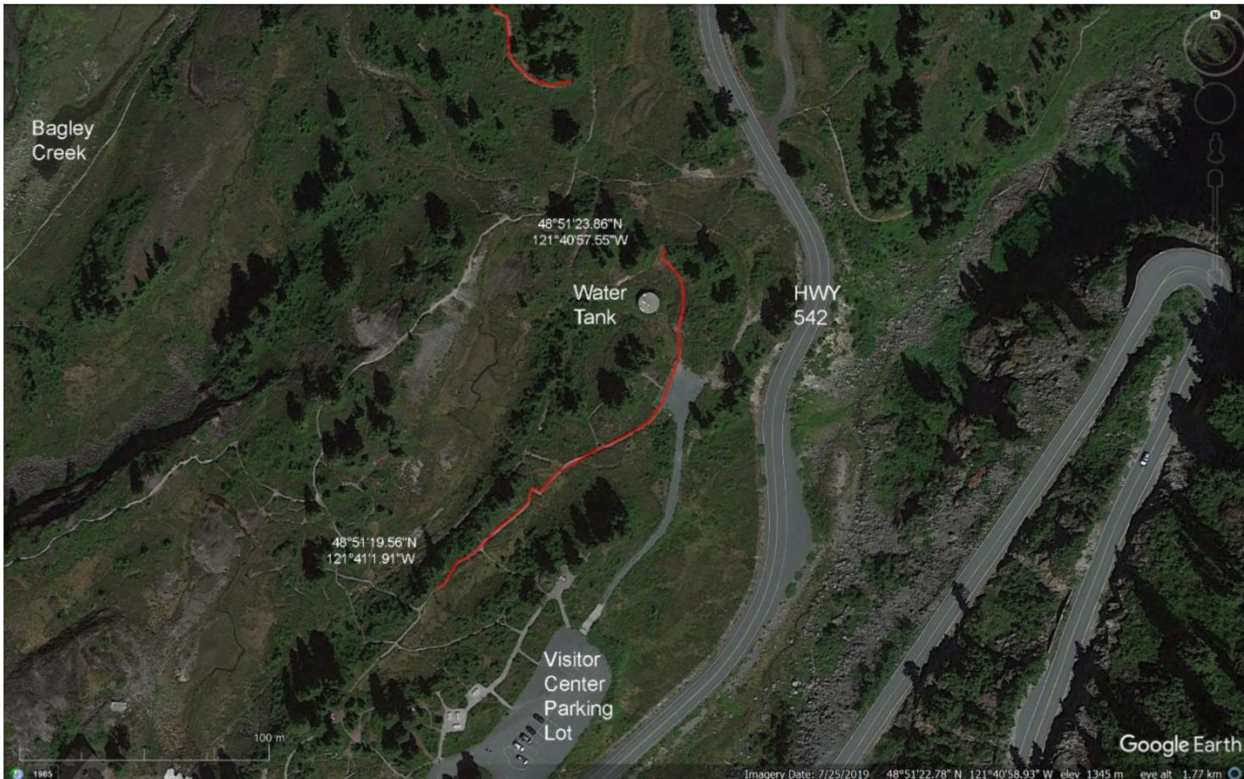


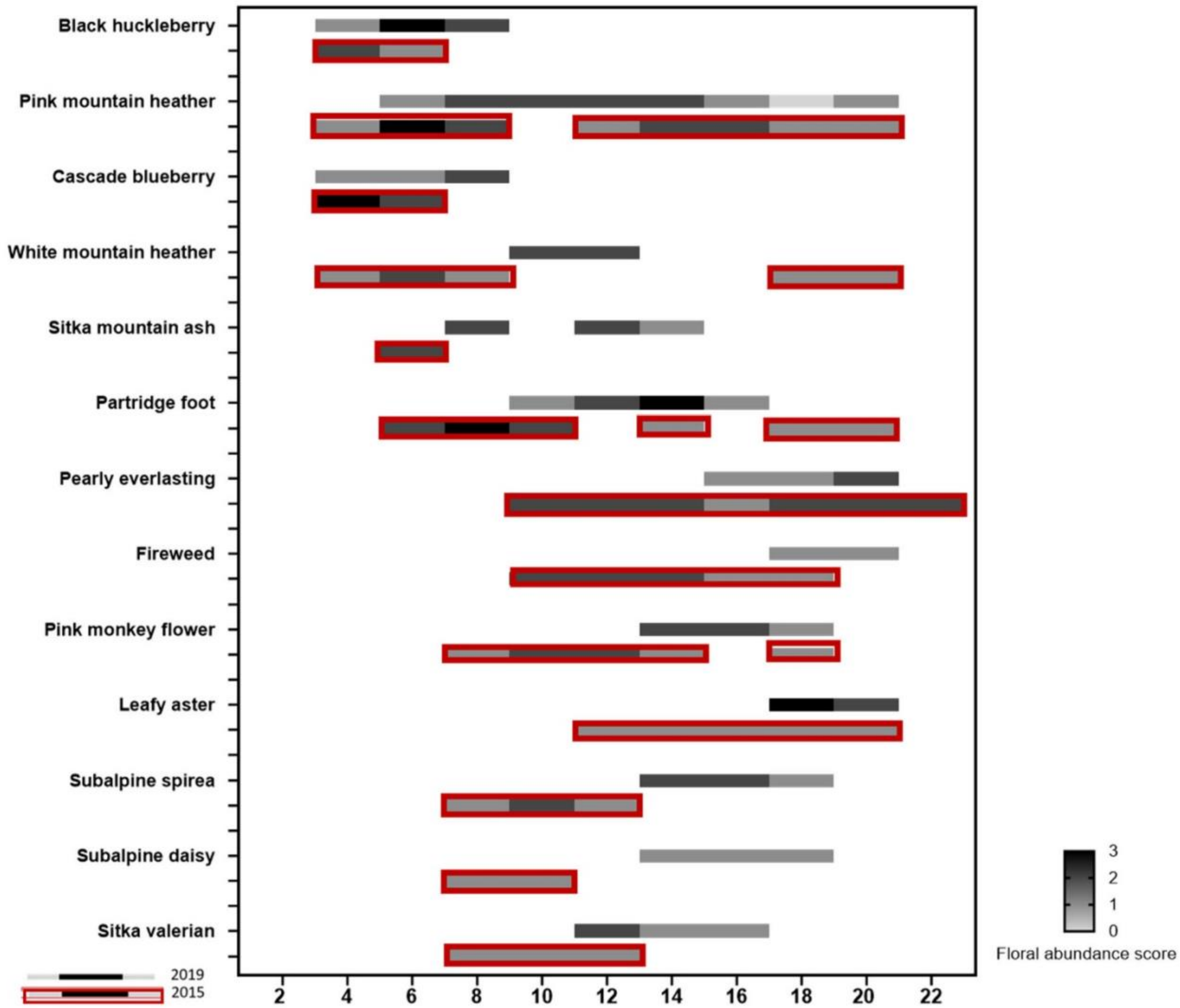
Figure 3. Visitor Center High Transect Aerial Photo. This transect (elevation 1,350 meters) is primarily open meadow with only 5% tree island cover. Dominant shrub vegetation includes pink mountain heather, white mountain heather, and Cascade blueberry. Pink monkey flower and partridgefoot are also common.

Figure 4. Visitor Center Low Transect Aerial Photo. This transect (elevation 1,327 meters) has 35% tree island cover (the largest of all the transects). Dominant vegetation includes black huckleberry, Cascade blueberry, and false azalea in the core of the tree island. Cascade blueberry, pink mountain heather, white mountain heather, and white flowering rhododendron are common along the margins of the tree island. Pink mountain heather and white mountain heather dominate the open meadows adjacent to the tree islands.

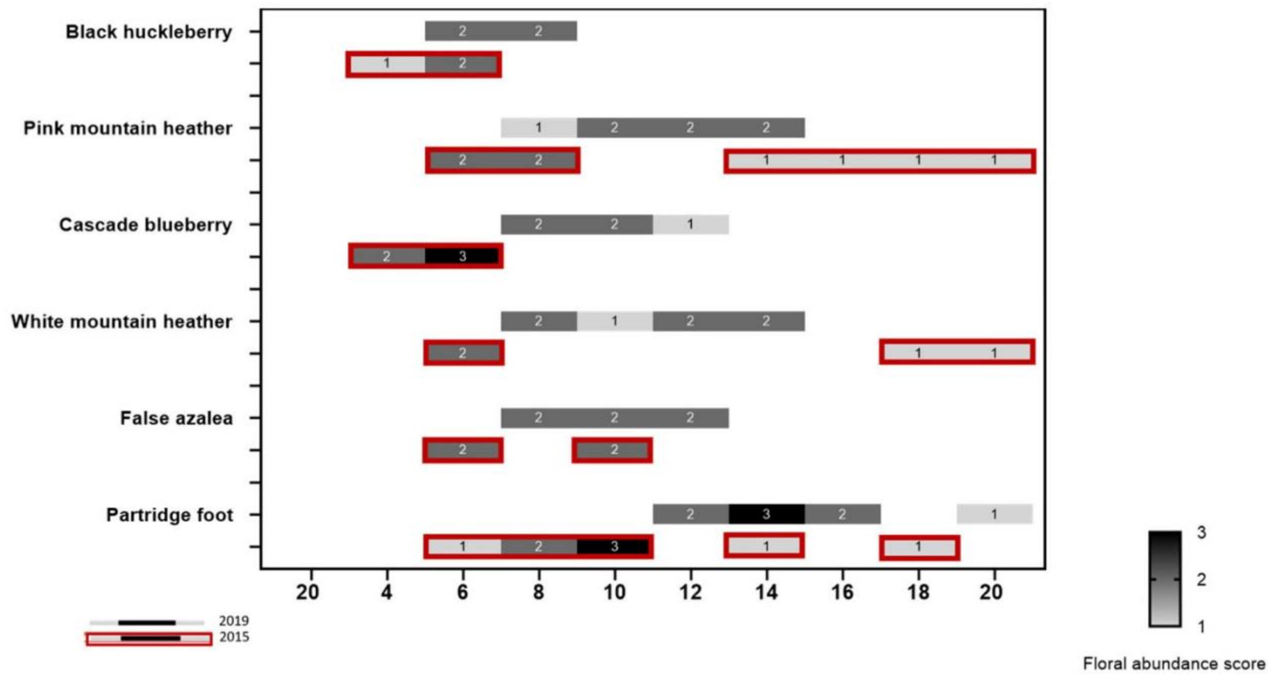
Figure 5. Austin Pass Transect Aerial Photo. This transect (elevation 1,445 meters) is mostly level, but has steep slopes on either side. Tree islands occupy 25% of the transect. The shrub vegetation includes black huckleberry, Cascade blueberry, pink mountain heather, white mountain heather, partridgefoot and Arctic lupine (*Lupinus latifolius*). Two late season flowers, leafy aster and pink monkey flower, were absent from this transect, and there were only small amounts of fireweed, another late-season bloomer.

Figure 6. Artist's Point Transect Aerial Photo. This transect (elevation 1,520 meters) is located on an alpine ridge. Tree islands are not present in this transect. The shrub vegetation includes black huckleberry and Cascade blueberry, along with the three mountain heather species. Among the forbs, Arctic lupine is widespread, along with partridgefoot and Sitka valerian (*Valeriana sitchensis*). Fireweed and leafy aster bloom late in the season in this transect (August, in a typical year).

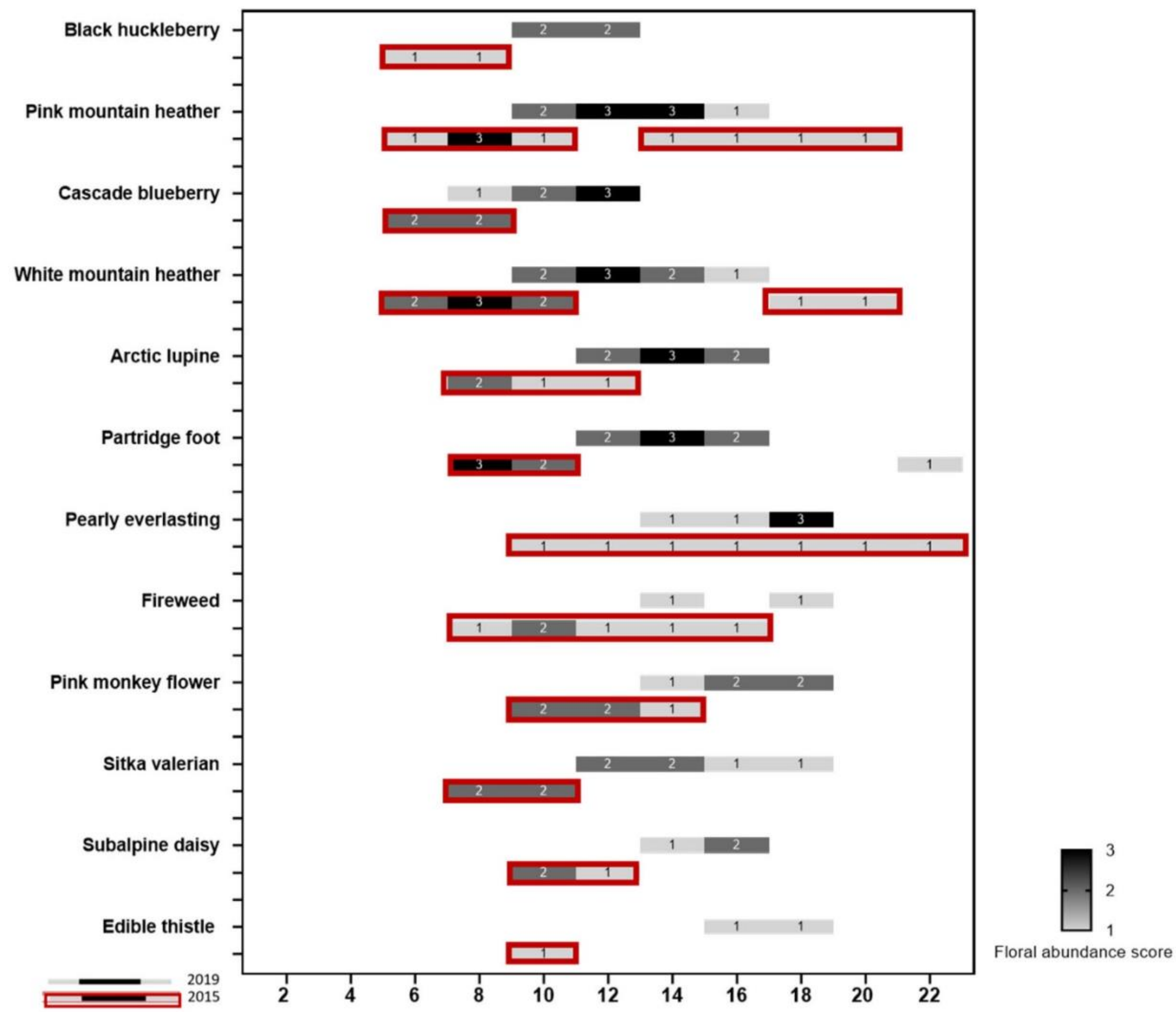
Figure 7. Huntoon Point Transect Aerial Photo. This transect (elevation 1,582 meters) lies on a high alpine ridge, with exposed low-lying vegetation dominated by mountain heathers. There are no tree islands in this transect. Cascade blueberry, Artic lupine, and partridgefoot are also present. Fireweed and leafy aster bloom late in the season (August, in a typical year).



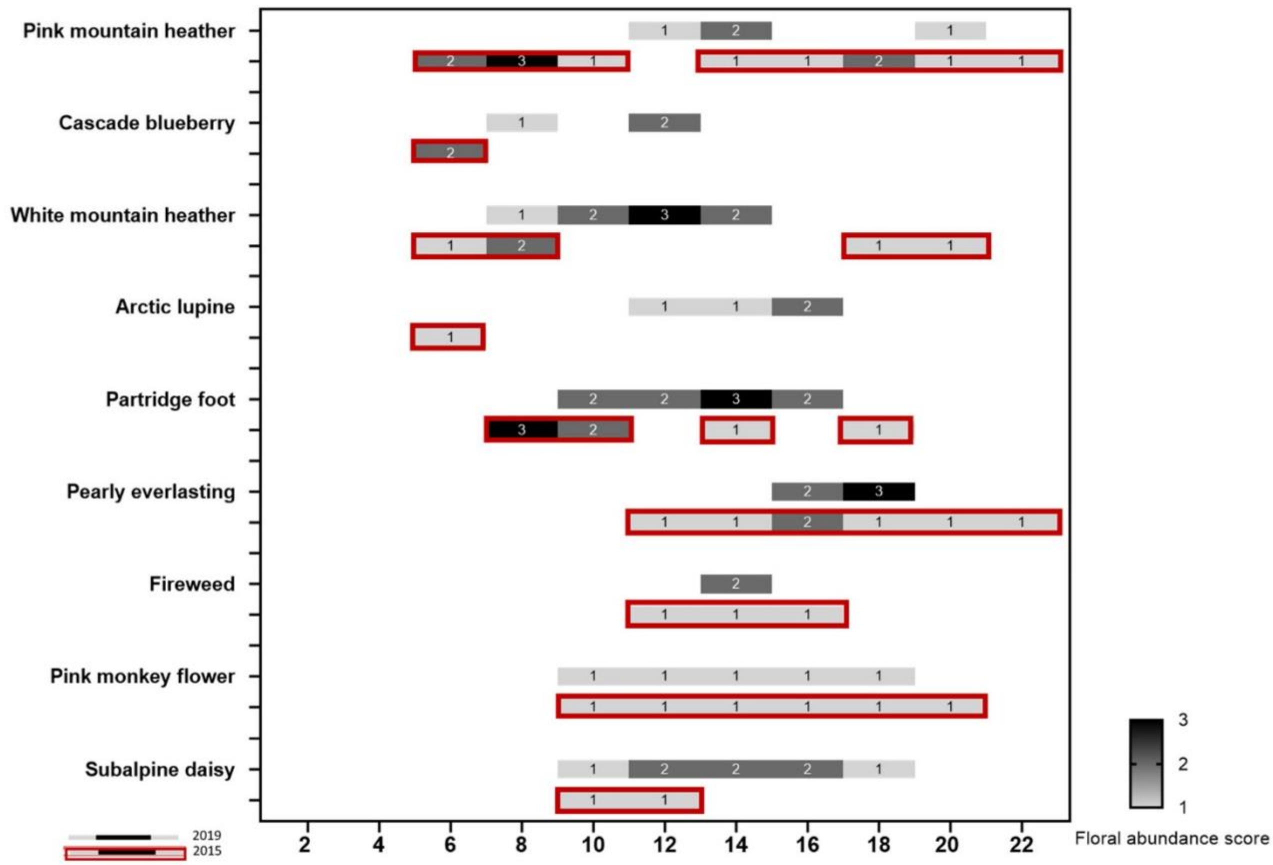
Supplement Figure 8. Phenological reassembly at Visitor's Center. In the climate analog year (2015), the bloom season advanced in 11 out of the 13 species at this transect, compared to their phenology in a more typical year (2019). Bloom duration was curtailed for Cascade blueberry and Sitka mountain ash. The differential response to the warm and dry early spring in 2015 generated a shift in co-flowering patterns. For example, fireweed does not normally co-flower with partridge foot at this site, but it did in 2015.



Supplement Figure 9. Phenological reassembly at Austin Pass. In the climate analog year (2015), the bloom season advanced in all six species compared at this transect, relative to their phenology in a more typical year (2019). Bloom duration was curtailed for Cascade blueberry and false azalea. The differential response to the warm and dry early spring in 2015 generated a shift in co-flowering patterns. For example, partridge foot does not normally co-flower with black huckleberry at this site, but it did in 2015.



Supplement Figure 10. Phenological reassembly at Artist's Point. In the climate analog year (2015), the bloom season advanced in all 12 species compared at this transect, relative to their phenology in a more typical year (2019). Bloom duration was curtailed for Cascade blueberry and Sitka valerian. The differential response to the warm and dry early spring in 2015 generated a shift in co-flowering patterns. For example, fireweed does not normally co-flower with black huckleberry or Cascade blueberry at this site, but it did in 2015.



Supplement Figure 11. Phenological reassembly at Huntoon Point. In the climate analog year (2015), the bloom season advanced in seven out of nine species compared at this transect, relative to their phenology in a more typical year (2019). Bloom duration was curtailed for Cascade blueberry and Arctic lupine. Phenological reassembly was least pronounced at this transect, which is the highest of the five primary transects. Almost all the study species co-flower late in the season at this high elevation site.

TABLE 1. Plant Checklist for Healther Meadows Transects (2015-2019)

Scientific Name	Common Name / Transects	Picture Lake	Vis. Cen.	Vis. Cen. H	Vis. Cen. L	Austin Pass	Artist's Pt.	Huntoon Pt.
Anaphalis margaritacea	Pearly Everlasting		X	X	X		X	X
Arnica latifolia	Mountain Arnica	X	X	X			X	X
Aruncus dioicus	Goats Beard			X		X		
Cassiope mertensiana	White Mountain Heather	X	X	X	X	X	X	X
Castilleja species	Paintbrushes							X
Chamaenerion angustifolium (syn. Epilobium a.)	Fireweed	X	X	X	X	X	X	X
Cirsium edule	Edible Thistle						X	X
Claytonia lanceolata	Spring Beauty			X	X			
Elliottia pyroliflora (syn. Cladothamnus p.)	Copper Bush						X	
Epilobium anagallidifolium	Alpine Willowherb	X	X	X	X	X	X	X
Epilobium luteum	Yellow Willowherb	X	X					
Other *Epilobium species* (small pink flower)	Willowherb	X	X	X		X	X	X
Erigeron glacialis (syn. E. peregrinus)	Subalpine Daisy	X	X	X	X		X	X
Erythranthe caespitosa (syn. Mimulus c.)	Subalpine Monkey Flower	X	X	X				
Erythranthe lewisii (syn. Mimulus l.)	Pink Monkey-Flower		X	X	X		X	X
Erythronium grandiflorum	Yellow Glacier Lily	X						
Erythronium montanum	Avalanche Lily	X						
Geum macrophyllum	Large Leaf Avens							X
Haplopappus species	Haplopappus						X	
Heuchera glabra	Smooth Alumroot		X					X
Hieracium albiflorum	White-Flowered Hawkweed	X	X		X		X	
Hieracium gracile	Slender Hawkweed	X	X	X	X	X	X	X
Hippuris montana	Mountain Mare's-Tale			X				
Kalmia microphylla	Bog Laurel	X						
Leptarrhena pyrolifolia	Leatherleaf Saxifrage		X		X			
Leucanthemum vulgare *	Oxeye Daisy	X					X	
Luetkea pectinata	Partridgefoot	X	X	X	X	X	X	X
Luina hypoleuca	Silverback Luina							X
Lupinus latifolius	Arctic Lupine					X	X	X
Maianthemum racemosum (syn. Smilacina r.)	False Solomon Seal				X			
Micranthes ferruginea (syn. Saxifraga f.)	Alaska Saxifrage		X	X	X	X	X	X
Micranthes mertensiana (syn. Saxifraga m.)	Mertens Saxifrage			X				
Micranthes tolmiei (syn. Saxifraga t.)	Tolmie's Saxifrage					X	X	X
Mycelis muralis * *(syn. Lactuca m.)*	Wall Lettuce		X					
Oreostemma alpigenus (syn. Aster a)	Alpine Aster							X
Osmorhiza berteroi	Mountain Sweet Cicely			X				X
Parnassia fimbriata	Fringed Grass of Parnassia		X					
Petasites frigidus (syn. P. palmatus)	Palmate Coltsfoot		X		X			
Phyllodoce empetriformis	Pink Mountain Heather	X	X	X	X	X	X	X
Phyllodoce glanduliflora	Yellow Mountain Heather					X	X	X
Potentilla flabellifolia	Fan Leaf Cinquefoil	X	X	X	X			X
Prunella vulgaris *	Self Heal							X
Ranunculus acris *	Meadow Buttercup	X	X	X	X			X
Ranunculus repens *	Creeping Buttercup			X				
Ranunculus uncinatus	Small-Flowered Buttercup			X				X
Rhododendron albiflorum	White-Flowered Rhododendron	X		X	X		X	
Rhododendron menziesii (syn. Menziesia ferruginea)	False Azelea	X	X	X	X	X		X
Rubus pedatus	Five Leaved Bramble	X		X	X	X		
Salix species	Willow	X	X		X			
Senecio triangularis	Arrow Leaf Groundsel	X						
Other *Senicio species*	Senecio	X						X
Sibbaldia procumbens	Sibbaldia					X		
Solidago multiradiata	Northern Goldenrod							X
Sorbus sitchensis	Sitka Mountain Ash	X	X	X	X	X		X
Spiraea splendens (syn. S. densiflora)	Subalpine Spirea	X	X	X	X			
Symphyotrichum foliaceum (syn. Aster foliaceus)	Leafy Aster	X	X	X	X		X	X
Tanacetum vulgare *	Common Tansy				X			
Taraxacum officinale *	Common Dandelion			X				
Tiarella trifoliata	Foam Flower		X					
Trifolium species *	Clover	X						
Vaccinium alaskaense	Alaskan Huckleberry	X						
Vaccinium deliciosum	Cascade Blueberry	X	X	X	X	X	X	X
Vaccinium membranaceum	Black Huckleberry	X	X	X	X	X	X	X
Vaccinium ovalifolium	Oval-Leaved Huckleberry	X	X	X	X	X		
Valeriana sitchensis	Sitka Valerian		X	X	X		X	
Veratrum viride	Indian Hellebore	X	X		X		X	
Veronica americana	American Brooklime						X	X
Veronica wormskjoldii	Alpine Speedwell		X	X	X			X
Viola orbiculata	Roundleaf Violet	X			X			
Viola adunca	Early Blue Violet	X						
Native Species (62) / Non-Native Species (8)	Total Species in Each Transect	35	34	34	32	19	27	35

X = Presence of species. * Non-native species. Highlighted species were visited by at least one forager across the five year study period.

Table 2. Heather Meadows Flower Phenology and Abundance 2015

Transect	Flowering Plant	5/11	5/25	6/8	6/22	7/6	7/20	8/2	8/17	8/31	9/14	9/28	
Huntoon Point (5,189')	Black Huckleberry			1	0	0	0	0	0	0	0	0	
	Pink Mountain Heather			2	3	1	0	1	1	2	1	1	
	Cascade Blueberry			2	0	0	0	0	0	0	0	0	
	White Mountain Heather			1	2	0	0	0	0	1	1	0	
	Sitka Mountain Ash			0	0	0	0	0	0	0	0	0	
	Artic Lupine			1	0	0	0	0	0	0	0	0	
	Partridgefoot			0	3	2	0	1	0	1	0	0	
	Fireweed			0	0	0	1	1	1	0	0	0	
	Total # of 2s and 3s			2	3	1	0	0	0	1	0	0	
Artist's Point (4,986')	Black Huckleberry			1	1	0	0	0	0	0	0	0	
	Pink Mountain Heather			1	3	1	0	1	1	1	1	0	
	Cascade Blueberry			2	2	0	0	0	0	0	0	0	
	White Mountain Heather			2	3	2	0	0	0	1	1	0	
	Sitka Mountain Ash			0	0	0	0	0	0	0	0	0	
	Artic Lupine			0	2	1	1	0	0	0	0	0	
	Partridgefoot			0	3	2	0	0	0	0	0	1	
	Fireweed			0	1	2	1	1	1	0	0	0	
	Total # of 2s and 3s			2	5	3	0	0	0	0	0	0	
Austin Pass (4,741')	Black Huckleberry		1	2	0	0	0	0	0	0	0	0	
	Pink Mountain Heather		0	2	2	0	0	1	1	1	1	1	
	Cascade Blueberry		2	3	0	0	0	0	0	0	0	0	
	White Mountain Heather		0	2	0	0	0	0	0	1	1	0	
	Sitka Mountain Ash		0	0	0	0	0	0	0	0	0	0	
	Artic Lupine		0	0	1	0	0	0	0	0	0	0	
	Partridgefoot		0	1	2	3	0	1	0	1	0	0	
	Fireweed		0	0	0	0	0	0	0	0	0	0	
	Total # of 2s and 3s		1	4	2	1	0	0	0	0	0	0	
Visitor's Center (4,419')	Black Huckleberry		2	1	0	0	0	0	0	0	0	0	
	Pink Mountain Heather		1	3	2	0	1	2	2	1	1	0	
	Cascade Blueberry		3	2	0	0	0	0	0	0	0	0	
	White Mountain Heather		1	2	1	0	0	0	0	1	1	0	
	Sitka Mountain Ash		0	2	0	0	0	0	0	0	0	0	
	Artic Lupine		0	2	0	0	0	0	0	0	0	0	
	Partridgefoot		0	2	3	2	0	1	0	1	1	0	
	Fireweed		0	0	0	2	2	2	1	1	0	0	
	Total # of 2s and 3s		2	6	2	2	1	2	1	0	0	0	
Picture Lake (4,126')	Black Huckleberry	1	2	0	0	0	0	0	0	0	0	0	
	Pink Mountain Heather	1	3	2	1	0	1	1	1	1	1	1	
	Cascade Blueberry	0	3	0	0	0	0	0	0	0	0	0	
	White Mountain Heather	0	2	2	0	0	0	0	1	1	1	0	
	Sitka Mountain Ash	0	0	3	1	0	0	0	0	0	0	0	
	Artic Lupine	0	0	0	0	0	0	0	0	0	0	0	
	Partridgefoot	0	0	1	1	1	0	0	0	0	0	0	
	Fireweed	0	0	0	0	2	2	1	0	1	0	0	
	Total # of 2s and 3s	0	4	3	0	1	1	0	0	0	0	0	
Combined Transects	Black Huckleberry	0	2	1	0	0	0	0	0	0	0	0	
Number of Monitoring	Pink Mountain Heather	0	1	4	4	0	0	1	1	1	0	0	
Events with 2s and 3s	Cascade Blueberry	0	3	4	1	0	0	0	0	0	0	0	
	White Mountain Heather	0	1	4	2	1	0	0	0	0	0	0	
	Sitka Mountain Ash	0	0	2	0	0	0	0	0	0	0	0	
	Artic Lupine	0	0	1	1	0	0	0	0	0	0	0	
	Partridgefoot	0	0	1	4	4	0	0	0	0	0	0	
	Fireweed	0	0	0	0	3	2	1	0	0	0	0	
	Total # of 2s and 3s	0	7	17	12	8	2	2	1	1	0	0	50

Davis JR, Lloyd TA, Singh-Cundy A. 2024. Flower phenology, bumble bee foraging, and climate change in North Cascades mountain meadows. Northwest Science 97(3): *in press*.

Table 3. Heather Meadows Flower Phenology and Abundance 2016

Transect	Flowering Plant	5/16	5/30	6/15	6/27	7/11	7/25	8/8	8/22	9/5	9/19		
Huntoon Point (5,189')	Black Huckleberry					0	0	0	0	0	0		
	Pink Mountain Heather					1	2	2	2	0	0		
	Cascade Blueberry					2	1	0	0	0	0		
	White Mountain Heather					0	2	0	2	1	0		
	Sitka Mountain Ash					0	0	0	0	0	0		
	Artic Lupine					0	0	0	0	0	0		
	Partridgefoot					0	2	2	0	2	0		
	Fireweed					0	0	0	0	0	1		
	Total # of 2s and 3s					1	3	2	2	1	0		
Artist's Point (4,986')	Black Huckleberry					0	1	0	0	0	0		
	Pink Mountain Heather					0	2	2	1	1	0		
	Cascade Blueberry					0	2	0	0	0	0		
	White Mountain Heather					0	2	2	2	1	0		
	Sitka Mountain Ash					0	0	0	0	0	0		
	Artic Lupine					0	0	0	1	0	0		
	Partridgefoot					0	2	2	2	0	0		
	Fireweed					0	0	0	1	0	0		
	Total # of 2s and 3s					0	4	3	2	0	0		
Austin Pass (4,741')	Black Huckleberry				2	1	2	0	0	0	0		
	Pink Mountain Heather				1	1	3	3	2	0	0		
	Cascade Blueberry				2	2	2	1	0	0	0		
	White Mountain Heather				0	1	3	2	2	1	0		
	Sitka Mountain Ash				0	0	2	1	0	0	0		
	Artic Lupine				0	0	0	0	0	0	0		
	Partridgefoot				0	0	2	2	2	1	0		
	Fireweed				0	0	0	0	0	1	1		
	Total # of 2s and 3s				2	1	6	3	3	0	0		
Visitor's Center (4,419')	Black Huckleberry		1	1	2	0	0	0	0	0	0		
	Pink Mountain Heather		0	1	2	2	3	2	1	0	0		
	Cascade Blueberry		0	2	2	3	0	1	0	0	0		
	White Mountain Heather		0	0	2	2	2	2	1	0	0		
	Sitka Mountain Ash		0	0	0	2	2	1	0	0	0		
	Artic Lupine		0	0	0	0	0	0	0	0	0		
	Partridgefoot		0	0	0	1	3	3	2	1	0		
	Fireweed		0	0	0	0	0	0	0	2	2		
	Total # of 2s and 3s		0	1	4	4	4	3	1	1	1		
Picture Lake (4,126')	Black Huckleberry	1	1	1	2	0	0	0	0	0	0		
	Pink Mountain Heather	0	0	1	2	2	2	0	0	0	1		
	Cascade Blueberry	0	0	3	3	2	0	0	0	0	0		
	White Mountain Heather	0	0	0	2	3	2	0	0	0	0		
	Sitka Mountain Ash	0	0	0	1	2	2	0	0	0	0		
	Artic Lupine	0	0	0	0	0	0	0	0	0	0		
	Partridgefoot	0	0	0	0	1	3	1	0	0	0		
	Fireweed	0	0	0	0	0	0	0	2	2	1		
	Total # of 2s and 3s	0	0	1	4	4	4	0	1	1	0		
Combined Transects	Black Huckleberry	0	0	0	3	0	1	0	0	0	0		
Number of Monitoring	Pink Mountain Heather	0	0	0	2	2	5	4	2	0	0		
Events with 2s and 3s	Cascade Blueberry	0	0	2	3	4	2	0	0	0	0		
	White Mountain Heather	0	0	0	2	2	5	3	3	0	0		
	Sitka Mountain Ash	0	0	0	0	2	3	0	0	0	0		
	Artic Lupine	0	0	0	0	0	0	0	0	0	0		
	Partridgefoot	0	0	0	0	0	5	4	3	1	0		
	Fireweed	0	0	0	0	0	0	0	1	2	0		
	Total # of 2s and 3s	0	0	2	10	10	21	11	9	3	0		66

Table 4. Heather Meadows Flower Phenology and Abundance 2017

Transect	Flowering Plant	5/15	5/29	6/12	6/26	7/10	7/24	8/7	8/21	9/4	9/18		
Huntoon Point (5,189')	Black Huckleberry						0	1	0	0	0		
	Pink Mountain Heather						2	3	3	2	0		
	Cascade Blueberry						2	0	0	0	0		
	White Mountain Heather						2	3	3	1	0		
	Sitka Mountain Ash						0	2	0	0	0		
	Artic Lupine						0	1	1	0	0		
	Partridgefoot						2	2	3	0	0		
	Fireweed						0	0	0	1	1		
	Total # of 2s and 3s						4	4	3	1	0		
Artist's Point (4,986')	Black Huckleberry						0	1	0	0	0		
	Pink Mountain Heather						2	2	2	2	0		
	Cascade Blueberry						2	2	0	0	0		
	White Mountain Heather						1	2	3	2	0		
	Sitka Mountain Ash						0	0	0	0	0		
	Artic Lupine						0	2	3	3	1		
	Partridgefoot						2	2	1	1	1		
	Fireweed						0	0	0	1	1		
	Total # of 2s and 3s						3	5	3	3	0		
Austin Pass (4,741')	Black Huckleberry					2	2	1	0	0	0		
	Pink Mountain Heather					1	2	2	2	1	0		
	Cascade Blueberry					1	3	0	0	0	0		
	White Mountain Heather					1	2	2	2	2	0		
	Sitka Mountain Ash					0	0	2	1	0	0		
	Artic Lupine					0	0	0	0	0	0		
	Partridgefoot					0	1	2	1	1	1		
	Fireweed					0	0	0	1	3	0		
	Total # of 2s and 3s					1	4	4	2	2	0		
Visitor's Center (4,419')	Black Huckleberry				2	1	1	0	0	0	0		
	Pink Mountain Heather				0	2	3	2	1	0	0		
	Cascade Blueberry				2	2	3	1	0	0	0		
	White Mountain Heather				0	2	2	3	1	0	0		
	Sitka Mountain Ash				0	1	2	1	0	0	0		
	Artic Lupine				0	0	0	0	0	0	0		
	Partridgefoot				0	0	1	2	2	2	1		
	Fireweed				0	0	0	0	3	3	0		
	Total # of 2s and 3s				2	3	4	3	2	2	0		
Picture Lake (4,126')	Black Huckleberry				1	2	2	0	0	0	0		
	Pink Mountain Heather				0	2	3	1	0	0	0		
	Cascade Blueberry				0	3	3	0	0	0	0		
	White Mountain Heather				0	2	3	2	0	0	0		
	Sitka Mountain Ash				0	1	3	2	1	0	0		
	Artic Lupine				0	0	0	0	0	0	0		
	Partridgefoot				0	0	0	2	0	0	0		
	Fireweed				0	0	0	0	0	2	3		
	Total # of 2s and 3s				0	4	5	3	0	1	1		
Combined Transects	Black Huckleberry				1	2	2	0	0	0	0		
Number of Monitoring	Pink Mountain Heather				0	2	5	4	3	2	0		
Events with 2s and 3s	Cascade Blueberry				1	2	5	1	0	0	0		
	White Mountain Heather				0	2	4	5	3	2	0		
	Sitka Mountain Ash				0	0	2	3	0	0	0		
	Artic Lupine				0	0	0	1	1	1	0		
	Partridgefoot				0	0	2	5	2	1	0		
	Fireweed				0	0	0	0	1	3	1		
	Total # of 2s and 3s				2	8	20	19	10	9	1		69

Table 5. Heather Meadows Flower Phenology and Abundance – 2018

Transect	Flowering Plant	5/13	5/27	6/10	6/24	7/8	7/22	8/5	8/19	9/3	9/17		
Huntoon Point (5,189')	Black Huckleberry					0	1	0	0	0	0	0	
	Pink Mountain Heather					0	2	2	1	0	0	0	
	Cascade Blueberry					0	2	0	0	0	0	0	
	White Mountain Heather					1	2	2	2	0	0	0	
	Sitka Mountain Ash					0	0	0	0	0	0	0	
	Artic Lupine					0	0	1	1	0	0	0	
	Partridgefoot					0	1	2	2	2	1	0	
	Fireweed					0	0	0	0	2	2	1	
	Total # of 2s and 3s					0	3	3	2	2	1	0	
Artist's Point (4,986')	Black Huckleberry					0	2	0	0	0	0	0	
	Pink Mountain Heather					0	2	2	1	1	0	0	
	Cascade Blueberry					0	2	0	0	0	0	0	
	White Mountain Heather					0	2	2	2	1	0	0	
	Sitka Mountain Ash					0	0	0	0	0	0	0	
	Artic Lupine					0	0	3	2	2	1	0	
	Partridgefoot					0	1	3	2	2	2	0	
	Fireweed					0	0	0	0	1	1	1	
	Total # of 2s and 3s					0	4	4	3	2	1	0	
Austin Pass (4,741')	Black Huckleberry				1	3	3	0	0	0	0	0	
	Pink Mountain Heather				0	0	2	3	2	0	0	0	
	Cascade Blueberry				1	2	3	0	0	0	0	0	
	White Mountain Heather				0	0	0	3	2	0	0	0	
	Sitka Mountain Ash				0	0	1	2	0	0	0	0	
	Artic Lupine				0	0	0	0	0	0	0	0	
	Partridgefoot				0	0	0	0	2	1	0	0	
	Fireweed				0	0	0	0	1	1	0	0	
	Total # of 2s and 3s				0	2	3	3	3	0	0	0	
Visitor's Center (4,419')	Black Huckleberry			0	2	0	0	0	0	0	0	0	
	Pink Mountain Heather			0	0	1	3	2	0	1	0	0	
	Cascade Blueberry			0	2	1	3	0	0	0	0	0	
	White Mountain Heather			0	0	1	3	0	0	0	0	0	
	Sitka Mountain Ash			0	0	0	1	2	0	0	0	0	
	Artic Lupine			0	0	0	0	0	0	0	0	0	
	Partridgefoot			0	0	0	1	0	2	1	0	0	
	Fireweed			0	0	0	0	2	2	0	1	1	
	Total # of 2s and 3s			0	2	0	3	3	2	0	0	0	
Picture Lake (4,126')	Black Huckleberry			0	2	0	0	0	0	0	0	0	
	Pink Mountain Heather			0	1	3	3	0	0	0	0	0	
	Cascade Blueberry			0	3	3	1	0	0	0	0	0	
	White Mountain Heather			0	0	1	3	0	0	0	0	0	
	Sitka Mountain Ash			0	0	1	3	1	0	0	0	0	
	Artic Lupine			0	0	0	0	0	0	0	0	0	
	Partridgefoot			0	0	0	1	0	0	0	0	0	
	Fireweed			0	0	0	0	1	2	0	0	0	
	Total # of 2s and 3s			0	2	2	3	0	1	0	0	0	
Combined Transects Number of Monitoring Events with 2s and 3s	Black Huckleberry			0	2	1	2	0	0	0	0	0	
	Pink Mountain Heather			0	0	1	5	4	1	0	0	0	
	Cascade Blueberry			0	2	2	4	0	0	0	0	0	
	White Mountain Heather			0	0	0	4	3	3	0	0	0	
	Sitka Mountain Ash			0	0	0	1	2	0	0	0	0	
	Artic Lupine			0	0	0	0	1	1	1	0	0	
	Partridgefoot			0	0	0	0	2	4	2	1	0	
	Fireweed			0	0	0	0	1	2	1	1	0	
	Total # of 2s and 3s			0	4	4	16	13	11	4	2	0	54

Table 6. Heather Meadows Flower Phenology and Abundance 2019

Transect	Flowering Plant	5/14	5/28	6/11	6/25	7/9	7/23	8/6	8/20	9/3	9/17	9/30	
Huntoon Point (5,189')	Black Huckleberry				0	0	0	0	0	0	0		
	Pink Mountain Heather				0	0	1	2	0	0	1		
	Cascade Blueberry				1	0	2	0	0	0	0		
	White Mountain Heather				1	2	3	2	0	0	0		
	Sitka Mountain Ash				0	0	0	0	0	0	0		
	Artic Lupine				0	0	1	1	2	0	0		
	Partridgefoot				0	2	2	3	2	0	0		
	Fireweed				0	0	0	2	0	0	0		
	Total # of 2s and 3s				0	2	3	4	2	0	0		
Artist's Point (4,986')	Black Huckleberry				0	2	2	0	0	0	0		
	Pink Mountain Heather				0	2	3	3	1	0	0		
	Cascade Blueberry				1	2	3	0	0	0	0		
	White Mountain Heather				0	2	3	2	1	0	0		
	Sitka Mountain Ash				0	0	0	0	0	0	0		
	Artic Lupine				0	0	2	3	2	0	0		
	Partridgefoot				0	0	2	3	2	0	0		
	Fireweed				0	0	0	1	0	1	0		
	Total # of 2s and 3s				0	4	6	4	2	0	0		
Austin Pass (4,741')	Black Huckleberry			2	2	0	0	0	0	0	0		
	Pink Mountain Heather			0	1	2	2	2	0	0	0		
	Cascade Blueberry			0	2	2	1	0	0	0	0		
	White Mountain Heather			0	2	1	2	2	0	0	0		
	Sitka Mountain Ash			0	0	0	2	1	0	0	0		
	Artic Lupine			0	0	0	0	0	0	0	0		
	Partridgefoot			0	0	0	2	3	2	0	1		
	Fireweed			0	0	0	0	0	0	0	0		
	Total # of 2s and 3s			1	3	2	4	3	1	0	0		
Visitor's Center (4,419')	Black Huckleberry		1	3	2	0	0	0	0	0	0		
	Pink Mountain Heather		0	1	2	2	2	2	1	0	1		
	Cascade Blueberry		1	1	2	0	0	0	0	0	0		
	White Mountain Heather		0	0	0	2	2	0	0	0	0		
	Sitka Mountain Ash		0	0	2	0	2	1	0	0	0		
	Artic Lupine		0	0	0	0	0	0	0	0	0		
	Partridgefoot		0	0	0	1	2	3	1	0	0		
	Fireweed		0	0	0	0	0	0	0	1	1		
	Total # of 2s and 3s		0	1	4	2	4	2	0	1	0		
Picture Lake (4,126')	Black Huckleberry	0	1	3	3	0	0	0	0	0	0		
	Pink Mountain Heather	0	0	0	3	2	1	0	0	1	1		
	Cascade Blueberry	0	0	3	3	1	0	0	0	0	0		
	White Mountain Heather	0	0	0	3	1	1	0	0	0	0		
	Sitka Mountain Ash	0	0	0	2	2	2	0	0	0	0		
	Artic Lupine	0	0	0	0	0	0	0	0	0	0		
	Partridgefoot	0	0	0	0	2	2	1	0	0	0		
	Fireweed	0	0	0	0	0	0	0	2	1	0		
	Total # of 2s and 3s	0	0	2	5	3	2	0	1	0	0		
Combined Transects Number of Monitoring Events with 2s and 3s	Black Huckleberry	0	0	3	3	1	1	0	0	0	0		
	Pink Mountain Heather	0	0	0	2	4	3	4	0	0	0		
	Cascade Blueberry	0	0	1	3	2	2	0	0	0	0		
	White Mountain Heather	0	0	0	2	3	4	3	0	0	0		
	Sitka Mountain Ash	0	0	0	2	1	3	0	0	0	0		
	Artic Lupine	0	0	0	0	0	1	1	2	0	0		
	Partridgefoot	0	0	0	0	2	5	4	3	0	0		
	Fireweed	0	0	0	0	0	0	1	1	0	0		
	Total # of 2s and 3s	0	0	4	12	13	19	13	6	0	0		67

Table 7. Pollinator Preference for Flowers in Heather Meadows (2019)

Plant Species	Spr BB Que	Fall BB Que	BB Worker	BB Unk Stage	Honey Bee	Sol. Bee	Vespid	Oth. Hym.	Syrphid	Oth. Dip.	Lepid.	Coleop.	Total
Artic Lupine		1	29	3	1				4				38
Black Huckleberry	40		15	2			11		1	1			70
Cascades Blueberry	19		156	1		1				1	1		179
Copper Bush			1										1
Creeping Buttercup			1		1				8				10
False Azelea			11				1						12
Fireweed		3	6		1				3				13
Grass of Parnassus						1		11	1	4			17
Leafy Aster			13		3	1			9				26
Meadow Buttercup										1			1
Mountain Arnica			1										1
Oval-leaved Huckleberry	2												2
Partridgefoot			5	5	33	5			18	6			72
Pearly Everlasting		3	11		1	1	1		29		9	3	58
Pink Heather			187		4	3	3		12		3		212
Pink Monkey Flower		1	8										9
Potentilla									2				2
Senecio			3										3
Silverback Luina			1										1
Sitka Mountain Ash	1		48		33	4		1	2	7			96
Sitka Valerian			3	1	6				1	1			12
Solidago			2										2
Subalpine Daisy			4		2				2	2	1		11
Supalpine Spirea			8		24	1			8	1			42
Thistle			4										4
White Flowering Rhododendron			8		3	1	1						13
White Mountain Heather	1		5			1			3				10
Willow									1				1
Yellow Heather			2										2
Total	63	8	532	12	112	19	17	12	104	24	14	3	920