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# Pollination Ecology of an Alpine Fell-Field Community in the North Cascades

## Abstract

A study of the pollination ecology of an alpine fell-field located in the Mount Baker area of Washington State was conducted during the summer of 1981. Pollination syndromes (strategies) of the dominant plants were anemophily, generalized entomophily, and specialized entomophily. Insect visitations to plant species were quantified and flowering phenology was determined. The most important pollinators were bumblebees, syrphid flies, and muscoid flies; of lesser importance were butterflies and primitive flies. Plants exhibiting specialized entomophily appeared to minimize competition by separation of flowering times. Many of the plants exhibiting generalized entomophily flowered synchronously, perhaps as an adaptation to attract large numbers of flies by the colorful array of yellow and white flowers.

## Introduction

Pollination ecology is a rapidly growing subdiscipline of "old-fashioned" biology, recently expanding from a primarily descriptive to an experimental science. However, although there are a number of excellent texts, e.g., Faegri and Vander Pijl (1979), Jones and Little (1983), Proctor and Yeo (1973), and Richards (1978), and numerous articles concerning pollination biology, there are few studies that deal specifically with pollination ecology of alpine communities. This is especially true of the North Cascades.

The most commonly cited insect pollinator groups (orders/families) in alpine areas of North America are bumblebees (Hymenoptera/Apidae); syrphid flies (Diptera/Syrphidae); Muscoid flies (Diptera/Anthomyidae, Muscidae, Calliphoridae, Sarcophagidae, Tachinidae); and butterflies (Lepidoptera/Papilionoidea, Lycaenidae, Satyridae, Nymphalidae) (Moldenke 1976, 1979; Moldenke and Lincoln 1979; Levesque and Burger 1982; Bauer, 1983).

Bumblebees are social insects and must forage for colony needs as well as their own. Accordingly they forage very intensively and visit numerous flowers. As a whole, the colony assumes a generalist role, visiting a wide variety of flower types. However, individuals tend to specialize (major) on one or two species at any given time (Heinrich 1976a, 1979). Many plant species are more-or-less dependent on bumblebees for pollination and have developed sequential flowering times (Pojar 1974; Reader 1975; Heinrich 1975, 1976b; Pleasants 1980; Bauer 1983), reducing competition for pollinators. Foraging behavior of flies and butterflies is variable and less well known (Proctor and Yeo 1973, Faegri and Vander Pijl 1979). In general, flies prefer flowers with non-concealed rewards, do not specialize, and appear in alpine communities early in the season. Butterflies prefer tubular flowers with concealed rewards, have a higher level of floral constancy than flies, and appear much later in the season.

For our study an alpine plant community was selected because of its simplicity, lack of disturbance, and, perhaps, more obvious plant-insect coadaptations, i.e., relationship between floral morphology/color and type of insect pollinator. By definition (Douglas and Bliss 1977) the alpine is that area in the mountains above the limit of upright tree growth, characterized by soil and weather extremes (Bliss 1971, Billings 1974). Our study consisted of analyses of flowering phenology and insect visitation. Flowering phenology is an important component of pollination ecology because it determines the availability of resources to animal pollinators and the competitive relationships among plants for these pollinators (Levin and Anderson 1970, Mosquin 1971, Pojar 1974, Heinrich 1975, Proctor 1978, Pleasants 1980). The pattern of pollinator visitation is important because it has a direct effect on the reproductive success and gene flow rate of plants (Macior 1971, Proctor and Yeo 1973, Richards 1978, Faegri and Vander Pijl 1979), and makes it possible to quantitatively assess the importance of specific pollinators within an alpine (in this case) community.

## Methods

The selected study site was an alpine fell-field located near Mt. Baker on Chowder Ridge, a proposed research natural area (Tayor and Douglas 1978) (Figure 1). The ridge is relatively inaccessible and remains undisturbed. The area of sampling consisted of a 20 x 20 m plot on a moderate SE slope at ca. 2041 m elevation. The rocky ridgetop was sparsely vegetated by clumped, cushion plants, a typical fell-field community (Taylor and Douglas 1978). The community structure was determined in August 1980, using the experimental design described by Bliss (1963). In total, sixty 20 x 50 cm quadrats were used for measuring coverage (following Daubenmire 1959, 1968) and frequency. Importance or prominence values were calculated for each plant species by multiplying its mean percent cover by the square root of its frequency. Plants were identified using Hitchcock and Cronquist (1973) and Hitchcock *et al.* (1955-1969).

The pollination study was carried out during the summer of 1981. Plant species of the fell-field community were assigned a floral color class, following the system described by Kevin (1972a). The color class assignment does not relate to the insect visual range, which at least in some cases extends into the ultra-violet spectrum. Following Proctor and Yeo (1973), floral morphology was classified into the following types: (1) open—more-or-less bowl-shaped with exposed rewards; (2) partially exposed—usually some portion of the perianth fused resulting in somewhat difficult access to rewards; (3) closed—flower structured in such a way so as to exclude visitation by non-specialized pollinators; (4) small tubular—flowers with short tubular corollas, e.g., compositae, with little restriction of rewards; (5) large tubular—long tubular flowers requiring long "tongued" insects to reach concealed nectar. On the basis of floral morphology, plant species were assigned pollination strategies: wind (anemophily), generalist (generalized entomophily), specialist (specialized entomophily). See Table 1 for pollination strategies and related characteristics of the predominant plant species of our study.

Within the 20 x 20 m study area, insect group activity was quantified using 20 m transects (randomly selected from meter loci 1 through 20) and 2 m square observation plots (randomly selected from the 100 possible). All insect visits to flower species, including each of multiple visits by single insects, were recorded both while walking slowly along the transects and during 20 minute watch periods of the 2 m square plots. The number of watch periods and transects were limited by time to a maximum of six per day. In addition to the quantitative data collected from the study area, pollinator behavior was noted along the full length of Chowder Ridge periodically during the summers of 1980-1984.

An attempt was made to collect representatives of each discernable flower-visiting insect for identification to genus or family. Identifications were made using Borrer *et al.* (1976) and were confirmed by G. Kraft (Western Washington University).

An analysis of four bumblebees and eight syrphid fly pollen loads was made to supplement constancy determinations based on observed insect behavior. For bumblebees, corbiculae were used; for syrphid flies the entire insect was used, thus counts included pollen within the gut as well as grains attached externally. Percent pollen types was determined for each insect.

Flowering phenology was quantified using four 20 m permanent transects. The location of the transects was established by marking the northern and southern borders of the study area at 1 meter intervals (1-20) and randomly choosing a meter locus (1-4, 6-9, 11-14, 16-19) from within each of the four 5-meter intervals. All open flowers (flower clusters in the case of dense inflorescences, e.g., those of *Oxytropis campestris, Phacelia sericea, Solidago multiradiata,* and *Sedum lanceolatum*) within a one meter swath along the transect were counted. Phenology was recorded once each week throughout the 1981 flowering season.

## Results and Discussion

The plant species of the Chowder Ridge fell-field community are listed in Table 1, along with their prominence value (PV), pollination strategy, floral morphology, floral color, and insect visitors. Dominant plants, based on PVs, were *Oxytropis campestris, Cerastium arvense, Agropyron caninum, Phlox diffusa,* and *Potentilla diversifolia.* Bare ground exceeded 50 percent coverage (69 percent), a characteristic of fell-field communities (Douglas and Bliss 1977). Plants were scattered, typically clumped, and most exhibited a cushion growth form.

Among the principal plant species, the "open" floral morphology was most common, followed in order of decreasing occurrence by "inconspicuous" (graminoids), "small tubular" (compositae), "partially exposed," "large tubular," and "closed." The latter two types were each represented by a single abundant species. Predominant floral colors were yellow and white.

## Flower Visitors

Table 2 presents numbers of insect visits to flowers or inflorescences of principal plant species, as determined by watch periods and transects. Unfortunately, based on supplementary observations, the numbers are biased. During visits to Chowder Ridge prior to July 28, inclement weather (fog, rain, and even snow) restricted insect activity, especially that of bumblebees, butterflies, and syrphid flies. Thus, early flowering species typically pollinated by these insects, e.g., *Phlox diffusa, Silene acaulis, Phacelia sericea, Oxytropis campestris,* and *Potentilla* species, have lower visitation numbers than would be expected. Also, in *Phacelia sericea, Sedum lanceolatum,* and the Compositae, the entire inflorescence was treated as a single unit resulting in comparatively low visitation numbers since insects tended to probe several flowers per inflorescence for each recorded visit.

Major flower-visiting insects, discussed below, were bumblebees, syrphid flies, muscoid flies, butterflies, and primitive flies. Although primitive flies are not generally thought to be important alpine pollinators, Levesque and Burger (1982) listed dance flies (Empididae) among visitors to *Minuartia groenlandica* and Kevan (1972b) considers empids to be important pollinators in the high arctic.

*Bumblebees*—Three bumblebee species were observed visiting flowers within the study community on Chowder Ridge: *Bombus melanopygus, B. flavifrons,* and *B. boleatus,* the latter observed infrequently. These bees preferred the "insect specialist" flowers of *Oxytropis campestris* and *Phacelia sericea* when available early in the season, *Sedum lanceolatum, Solidago multiradiata,* in midseason, and *Aster sibiricus* in late season (see Table 2). The latter three species have "generalist" pollination strategies. Other "generalists" were visited by bumblebees but probably only exploratorily since so few visitations were recorded. Finally, bumblebees were unavailable to take advantage of the early-flowering and very abundant *Phlox diffusa* during the 1981 season (See Table 2). However, we have frequently observed queen bumblebees foraging on *Phlox diffusa* on Chowder Ridge.

Pollen types collected from four bumblebees suggest that those bees were majoring on two species at one time (see Table 3).

*Syrphid flies*—Syrphids, represented by several species, did not become abundant in 1981 until late July. After this time they were frequent visitors to most generalist plants and were observed to visit species with other pollinations strategies, including graminoids (*Carex phaeocephala* and *Poa alpina*) and *Phacelia sericea.* In these cases, the syrphids probably foraged on pollen without contacting stigmas and without effecting pollination.

Pollen samples from eight syrphid flies indicated variable foraging behavior. Some insects fed exclusively on one plant species while others exhibited little constancy (see Table 3). Syrphids had large visitation numbers, as shown in Table 2, suggesting their importance as pollinators in alpine habitats. They preferentially foraged on cushion plants with dense mats of flowers, e.g., *Saxifraga bronchialis* and *Cerastium arvense,* with several flowers typically being sampled from each plant.

*Muscoid flies*—Muscoid flies were represented by numerous species of four families: Anthomyidae, Muscidae, Callophoridae, and Tachinidae, the anthomyids being the most abundant. The muscoids were present in the fell-field community throughout the season and, along with primitive flies, were abundant early in July when other pollinators were unavailable or were inactivated by the cold and inclement weather. Like the syrphids, these flies preferred open, bowl-shaped flowers such as those of *Cerastium arvense, Saxifraga bronchialis,* and *Potentilla* spp., and had high visitation numbers (see Table 2). They also visited the short-tubular flowers of various Compositae.

*Butterflies*—Several species of butterflies (lepidopterids) were observed in the fell-field community, the most abundant being checkerspots and tortoise shells (*Nymphalidae*) and blues (*Lycaenidae*). Other lepidopterids observed were anglewings and fritillaries (*Nymphalidae*), whites

TABLE 1. Prominence values (PVs) and pollination related characteristics[a] of plants in the fell-field community on Chowder Ridge.

| Plant Species | PV | Pollination Strategy | Floral Morphology | Floral Color | Insect Visitors[b] | |
|---|---|---|---|---|---|---|
| | | | | | Major | Minor |
| Oxytropis campestris | 80 | Insect-spec | Closed | Yellow | Bu | — |
| Cerastium arvense | 72 | Insect-gen | Open | White | Sf,Mf | Bu,Bf,Pf |
| Agrophyron caninum | 60 | Wind | Inconspicuous | Not/appl | — | — |
| Phlox diffusa | 57 | Insect-spec | Large-tubular | Pink | Bu,Bf | Sf,Mf |
| Potentilla diversifolia | 46 | Insect-gen | Open | Yellow | Sf,Mf,Pf | Bu,Bf |
| Sedum lanceolatum | 29 | Insect-gen | Open | Yellow | Bu,Bf,Sf,Mf | — |
| Saxifraga bronchialis | 26 | Insect-gen | Open | White | Sf,Mf | Pf,Bf |
| Phacelia sericea | 22 | Insect-spec | Part. exposed | Purple | Bu,Sf | Mf |
| Poa alpina | 16 | Wind | Inconspicuous | Not/appl | — | Sf |
| Achillea millefolium | 10 | Insect-gen | Short-tubular | White | Mf | Sf,Bf |
| Potentilla Villosa | 07 | Insect-gen | Open | Yellow | Sf,Mf,Pf | Bu,Bf |
| Solidago multiradiata | 05 | Insect-gen | Short-tubular | Yellow | Bu,Bf,Sf | Mf |
| Haplopappus lyallii | 02 | Insect-gen | Short-tubular | Yellow | Bu,Bf | Sf |
| Festuca ovina | 02 | Wind | Inconspicuous | Not/appl | — | — |

Table 1 (continued)

| Plant Species | PV | Pollination Strategy | Floral Morphology | Floral Color | Insect Visitors[b] | |
|---|---|---|---|---|---|---|
| | | | | | Major | Minor |
| Aster sibiricus | 01 | Insect-gen | Short-tubular | Purple | Bu,Bf | Mf |
| Carex albonigra | 01 | Wind | Inconspicuous | Not/appl | — | — |
| Carex phaeocephala | 01 | Wind | Inconspicuous | Not/appl | — | — |
| Erigeron compositus | 01 | Insect-gen | Short-tubular | White | Bf,Mf | Sf,Pf |
| Silene acaulis | 01 | Insect-spec | Part. exposed | Red | Bf,Bu | — |
| Anemone multifida | <01 | Insect-gen | Open | White | — | — |
| Antennaria alpina | <01 | Insect-gen | Short-tubular | White | — | — |
| Campanula rotundifolia | <01 | Insect-spec | Large-tubular | Blue | Bu | Sf |
| Draba lonchocarpa | <01 | Insect-gen | Part. exposed | White | — | — |
| Draba paysonii | <01 | Apomixis | Part. exposed | Yellow | — | Pf |
| Sibbaldia procumbens | <01 | Insect-gen | Open | Yellow | — | — |
| Trisetum spicatum | <01 | Wind | Inconspicuous | Not/appl | — | — |

[a]See the methods section for a full description of pollination related characteristics.

[b]Determination of major (primary) and minor (secondary) insect visitors is based on general observations as well as quantitative data given in Table 2.

Bu = bumblebees, Bf = butterflies, Sf = syrphid flies, Mf = muscoid flies, Pf = primitive flies.

TABLE 2. Number of observed insect visits to flowers or inflorescences during 2 meter plot watch periods/transects walks.[a]

| Plant Species[b] | Insect Visitors | | | | |
|---|---|---|---|---|---|
| | Primitive Flies | Syrphid Flies | Muscoid Flies | Butterflies | Bumblebees |
| Aster sibiricus | — | — | — | 1/0 | 19/0 |
| Achillea millefolium | — | 0/1 | — | — | — |
| Cerastium arvense | 10/5 | 134/18 | 63/22 | — | 1/0 |
| Erigeron compositus | 2/1 | 9/3 | 7/1 | 7/0 | — |
| Oxytropis campestris | — | — | — | — | 33/10 |
| Phacelia sericea | — | 56/21 | 3/1 | — | 61/28 |
| Phlox diffusa | — | 3/1 | 1/0 | — | — |
| Potentilla diversifolia | 7/13 | 7/11 | 7/15 | — | 0/1 |
| Potentilla Villosa | 1/0 | 28/10 | 43/12 | — | — |
| Saxifraga bronchialis | — | 224/21 | 105/14 | 0/1 | — |
| Sedum lanceolatum | — | 67/16 | 6/1 | 6/1 | 245/18 |
| Solidago multiradiata | — | 81/4 | 22/1 | 2/0 | 9/0 |
| Total | 20/19 | 609/106 | 257/67 | 18/2 | 368/57 |

[a]The number of visitations to *Achillea* and *Phlox* are lower than expected because peak flowering for *Achillea* was after counts were made and *Phlox* flowered before its major pollinators appeared in the fell-field.

[b]Some species of the fell-field community were not observed to be visited by insects during watch periods or transects and are therefore not included here.

(*Pieridae*), skippers (*Hesperiidae*), swallowtails (*Papilionidae*), alpines (*Satyridae*), and several undetermined moths. The lepidopterids primarily visit tubular flowers such *Phlox diffusa, Silene acaulis* and Compositae, utilizing their long probing/sucking mouth parts to reach concealed nectar. In 1981, however, butterflies were not observed on Chowder Ridge until after 6 August, when *Phlox* and *Silene* had finished flowering (see Figure 3 and Table 2). In subsequent years we have observed butterflies foraging on these cushion plants on Chowder Ridge.

*Primitive flies*—These flies were represented by three families: Mycelophilidae (fungus gnats), Bibionidae (March flies), and Empididae (dance flies). They were abundant early in the flowering season and were most frequently observed on *Potentella diversifolia, P. villosa,* and *Cerastium arvense.*

*Miscellaneous insects*—Other observed flower visitors included ladybird beetles (Coleoptera/Coccinelidae), plant bugs (Hemiptera/Miridae), and solitary bees (Hymenoptera/family undetermined). These insects were not considered to be important pollinators. The bugs and beetles did not fly from flower to flower and lacked pollen carrying capacity, and solitary bees were rare in the community (three individuals observed during two field seasons). However, ladybird beetles were common and were frequently observed with their heads buried in flowers, apparently seeking nectar.

## Pollination Strategies

Three pollination strategies were well represented among the dominant plant species of the fell-field community: wind (*Agropyron caninum* and *Poa alpina*), insect generalist (*Cerastium arvense* and *Potentilla diversifolia*), and insect specialist (*Oxytropis campestris* and *Phlox diffusa*). See Table 1 for a summation of pollination strategies and prominence values. One of the conspicuous species of the fell-field community, *Draba paysonii,* is reportedly agamospermic (Mulligan 1971). This dense cushion plant was the first to flower in the fell-field community and was visited only by primitive flies.

## Flowering Phenology and Pollination Patterns

Figures 2-4 depict the flowering periods of twelve common insect pollinated plants in the fell-field community during 1981. The first of these plants to peak in flowering was *Phlox diffusa.* This

TABLE 3. Pollen types, as percentages of total pollen load, from corbiculae of *Bombus melanopygus* and from whole body analyses of syrphid flies.

| Insect | Date Captured | Host Plant | Pollen Types | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Phacelia | Oxytropis | Sedum | Phlox | Cerastium | Compositae | Potentilla | Saxifraga | Undetermined |
| Bombus 1 | 8/2 | Oxytropis | 60 | 39 | | | | | | | 1 |
| Bombus 2 | 8/2 | Phacelia | 32 | 63 | | | | | | | 5 |
| Bombus 3 | 8/12 | Sedum | | 46 | 42 | | | 5 | | | 6 |
| Bombus 4 | 8/14 | Sedum | | 13 | 80 | | | 7 | | | |
| Syrphid 1 | 8/12 | Phacelia | 19 | | | 19 | | 60 | | | 2 |
| Syrphid 2 | 8/12 | Saxifraga | 2 | | | | 1 | 1 | | 96 | |
| Syrphid 3 | 8/12 | Potentilla | | | | | 32 | 4 | 64 | | |
| Syrphid 4 | 8/13 | Compositae | 4 | | | | 4 | 58 | | 33 | 1 |
| Syrphid 5 | 8/13 | Saxifraga | 1 | | | | 29 | 16 | | 54 | |
| Syrphid 6 | 8/13 | Saxifraga | 26 | | | | 2 | 33 | | 38 | 1 |
| Syrphid 7 | 8/13 | Saxifraga | | | | | 45 | 10 | | 36 | 9 |
| Syrphid 8 | 8/14 | Saxifraga | 31 | | | | 8 | | 29 | 35 | 6 |

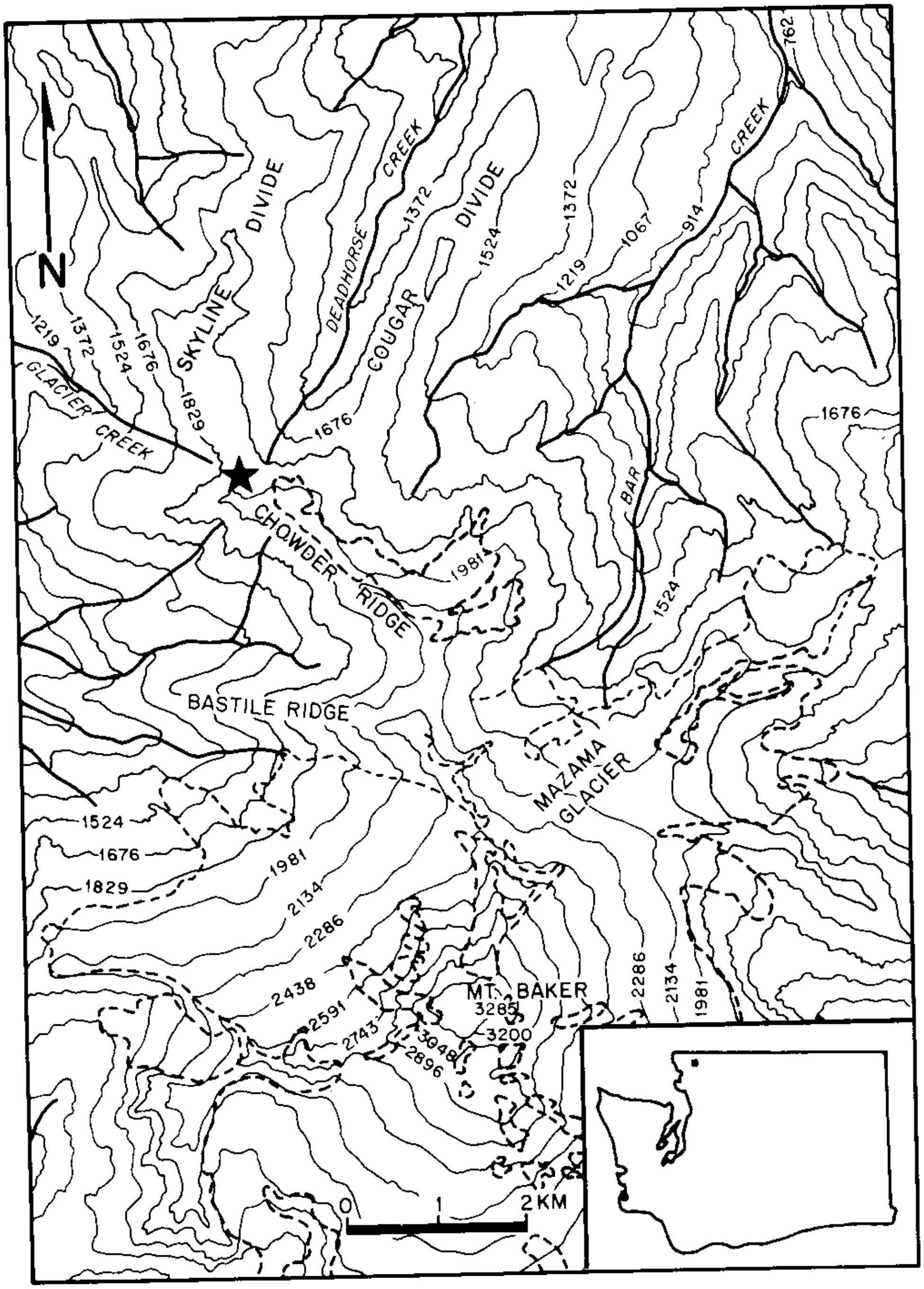
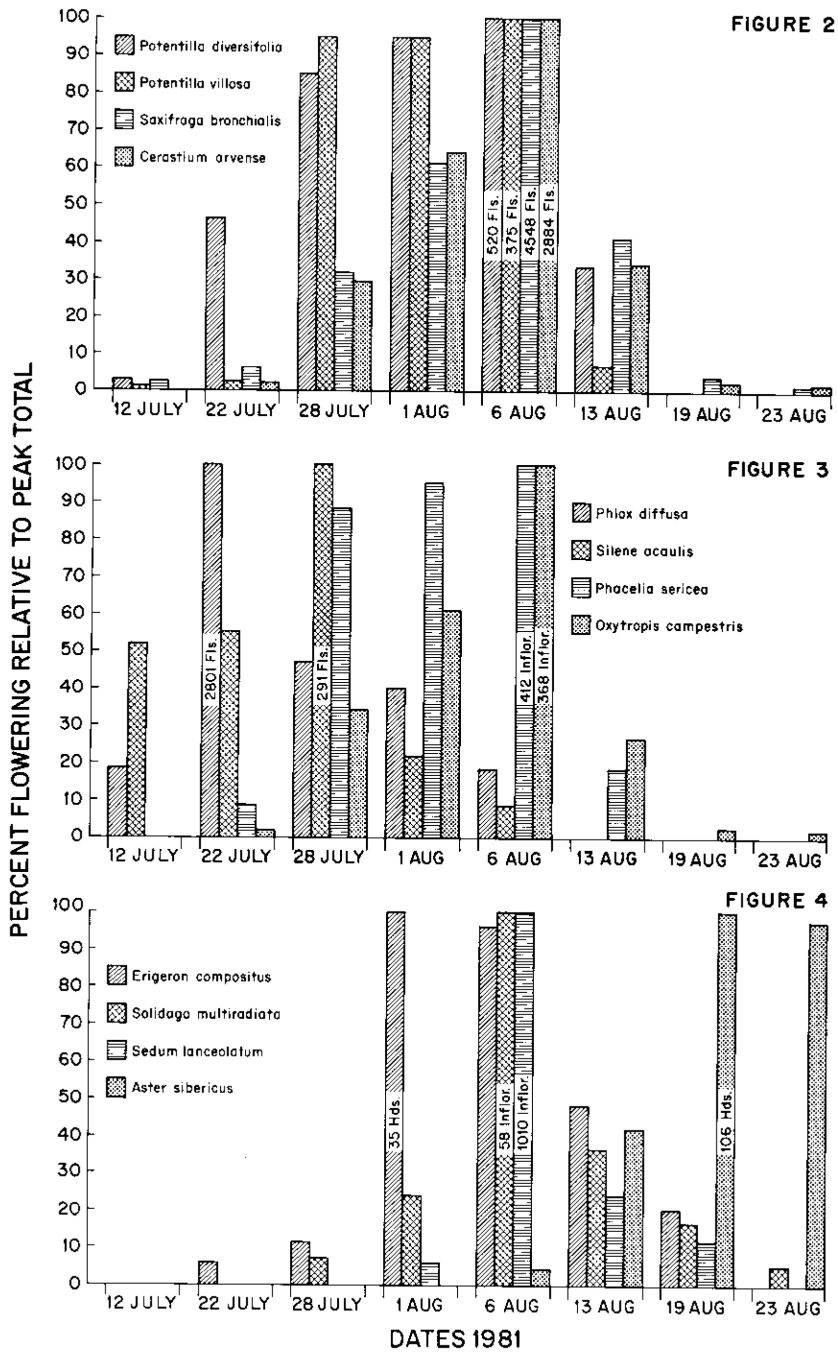



Figure 1. Map showing the location of the study area (star): Chowder Ridge, Mount Baker area, Whatcom County, Washington.




Figures 2-4. Flowering periods of major entomophilous species in the alipine fell-field.
Figure 2: Insect generalist flowers with open floral morphology.
Figure 3: Insect specialist flowers: partially exposed (*Phacelia* and *Silene*), large tubular (*Phlox*), and closed (*Oxytropis*) floral morphology.
Figure 4: Insect generalist flowers: short tubular (compositae) and open (*Sedum*) floral morphology.

early flowering trait seemed non-adaptive since the specialist pollinators were not yet available at this time (see Table 2 and Figure 3). However, in years subsequent to 1981, butterflies and, especially, bumblebees have been observed visiting *Phlox*. *Phlox* is most likely an important nectar source for early season queen bumblebees.

*Potentilla villosa* and *P. diversifolia* flowered synchronously as did *Cerastium arvense* and *Saxifraga bronchialis* (see Figure 2). These four insect generalists had a recorded (1981) peak flowering time of 6 August. This seems at odds with the popular theory that the flowering phenologies of species sharing pollinators tend to diverge, increasing pollination efficiency and reproductive success (Levin and Anderson 1970, Mosquin 1971). However, synchronous flowering may serve to attract greater numbers of potential pollinators to alpine communities, mostly flies in this case, increasing the chance of cross pollination. Macior (1971) suggested this as a possibility in the alpine where topography and climate often limit plant population size. This idea is supported by Williams and Batzli (1982) who showed increased seed set in interspecific stands of *Pedicularis* as opposed to single species stands. A third interpretation is that synchronous flowering is simply a reflection of genetically based opportunism, i.e., of the plants' ability to take advantage of a limited suitable flowering period, and has little to do with coadaptation with insects or with interspecific interaction.

In contrast to those of fly-pollinated plants, peak flowering times of bumblebee majors were spread over several weeks (see Figures 3 and 4). In this respect, the Chowder Ridge fell-field is similar to other communities where bumblebees are important pollinators (Reader 1975, Heinrich 1976b, Pleasants 1980). Again, however, caution should be taken in interpreting these results. The apparent competitive displacement of flowering times as exhibited by bumblebee majors, especially those with generalist pollination strategies, may also simply reflect opportunism, this time on the part of the bees. Since bee colonies depend on a continuous source of floral foods, they necessarily major on species with temporally dispersed phenologies. Species such as *Aster sibiricus* then become bee majors *because* they are available at an opportune time, rather than having evolved separate peak flowering periods in response to competitions for bumblebee pollinators.

Phenological data have not been provided for: *Achillea millefolium*, which achieved peak flowering after 1 September, the date that field analyses were terminated; *Haplopappus lyallii*, which by chance did not occur along the phenology transects; and plants with prominence values of less than 01 (see Table 1).

## Conclusions

Although we cannot quantify the relative importance of pollinators in the Chowder Ridge fell-field community, it is obvious from numbers of flower visitations that bumblebees, syrphid flies, and muscoid flies are all very important, butterflies and primitive flies less so. The relationship between floral morphology and insect visitor was consistent with expectations based on publications cited herein. The results of phenological analyses indicate that plants with generalist pollination strategies tend to flower synchronously, perhaps as an adaptation for greater insect attraction, while those with specialist strategies flower sequentially, perhaps due to competitive displacement. It is suggested, however, that these results may merely reflect opportunism on the part of the plants and specialist pollinators (bees) respectively. Finally, observations of alpine communities on Chowder Ridge over a several year period have resulted in our appreciation of the year to year variation in flowering phenology. The flowering sequence of representative species remains more or less consistent but the time of the flowering peak, the length of the flowering period, and the extent of flowering overlap vary considerably according to vagaries of the weather. Also, the availability of "preferred" pollinators is influenced by the weather, a case in point being the apparent absence of butterflies and bumblebees during the peak flowering period of *Phlox diffusa* in 1981. The alpine communities of Chowder Ridge are especially sensitive to climatic fluctuations because of the south-facing exposure and associated water stress.

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