Pollination Ecology of an Alpine Fell-Field Community

Chowder Ridge, Mt. Baker, Washington

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MASTER'S THESIS

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POLLINATION ECOLOGY OF AN ALPINE FELL-FIELD COMMUNITY

by

David Carl Shaw

accepted in Partial Completion

of the Requirements for the Degree

Master of Science

Dean of the Graduate School

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Presented to

The Department of Biology

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ABSTRACT - This study, involving an alpine fell-field, was conducted during the summer of 1981. The study site was located on the crest of Chowder Ridge, near Mt. Baker, Washington. Flowering plants of the community were grouped into pollination syndrome types based on floral morphology. Major insect visitors were determined by observations and quantification of insect visits to flowers. Flowering phenology of the dominant plants and insect flight periods of major flower visitors were also determined. Using the above information, in addition to a review of the literature relating to insect characteristics such as flower constancy, behavior, morphological adaptiveness, and energetics, the relative importance of various pollination groups was surmised.

Pollination syndromes of the dominant plants included: anemophily (4 species), polyphilic entomophily (9 species), and specialized entomophily (4 species). The most important pollinators in this community were bumblebees, syrphid flies, muscoid flies, butterflies, and primitive dipterans. Most major pollinator groups visited a wide range of floral types. Exceptions were butterflies which primarily visited composites and primitive dipterans which primarily visited open bowl-shaped flowers.

Differences in flowering phenology appear to minimize competition for pollinators. Plants that are exclusively dependent on flies for pollination bloomed synchronously, an apparent adaption to increase the attraction potential for promiscuous flies by increasing the functional plant population size.

DEDICATION

To my mother and father

ACKNOWLEDGEMENTS

My most sincere thanks go to my wife, Robin, whose support and help made this thesis possible. I would also like to thank Dr. Ronald Taylor, my major professor, who helped crystallize the ideas of this thesis and who encouraged me through to its completion. Thanks, also, go to my committee members, Dr. R. Fonda, who gave me an appreciation of plant ecology and writing, and Dr. G. Kraft, who aided me in the identification and understanding of insects. Special thanks go to Dr. G. Rouse for taking time to teach me pollen analysis and Dr. W. P. Stephen, who identified my bumblebee specimens. I am especially grateful to the Washington Native Plant Society, the Biology Graduate Student Organization, and the Biology Department of WWU for financial support. Thanks also go to the U.S. Forest Service for allowing this study. Additional thanks go to the people of Washington state whose support of the university system makes studies like this possible. Finally, I would like to thank my friends and fellow students who made the last several years some fun.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
DEDICATION	iv
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	vi
LIST OF TABLES	viii
LIST OF FIGURES	ix
INTRODUCTION	1
STUDY AREA	8
Location	8
Geology	8
Climate	10
Plant Community Patterns	11
METHODS	14
Selection of Study Site and Logistical Problems	14
Quantification of Community Structure and Identification of Plants	14
Floral Color, Morphology, Pollination Syndrome, and Rewards	15
Flowering Phenology	17
Collection and Identification of Flower-visiting Insects	18
Observation and Quantification of Insect Activity and Abundance	18
Pollen Analysis	19
Importance as Pollinators	20
RESULTS	21
Plant Community Structure	21

Floral Color, Morphology, Pollination Syndrome, and Rewards 21

Flowering Phenology 25

Flower-visiting Insects 26

Observation and Quantification of Insect Activity and Abundance 31

Pollen Analysis 38

Importance as Pollinators 41

DISCUSSION 43

Floral Strategy 43

Flowering Phenology 44

Importance as Pollinators 47

Bumblebees 47

Syrphid Flies 48

Muscoid Flies 49

Butterflies 50

Primitive Flies 50

Ladybird Beetles 51

Plant Bugs 52

Other Insects 52

Comparison with Other Studies 52

LITERATURE CITED 55

APPENDIX A 58

VITA 60

LIST OF TABLES

Table		Page
1	Vascular plant species, bryophytres, genera of macrolichens, and bare ground of the alpine fell-field community.	22
2	Family, growth form, color class, floral morphology, pollination syndrome, and nectar presence of dominant plants in the fell-field community	24
3	Common name, Order, mouthparts, hair, flower food, major flower types visited, and importance as pollinators for insect groups observed visiting flowers in the fell-field community	30
4	Plants observed to be visited by various insect groups, as a major (M) and minor (m) food source. See Table 1 for varietal names of plant species.	32
5	Number of observed visits by insects to flowers during watch periods	36
6	Number of observed visits by insects to flowers during transects	37
7	Percent pollen types from corbiculae of *Bombus melanopygus*, captured summer 1981	39
8	Percent pollen types from whole body analysis of syrphid flies, captured summer 1981	40

LIST OF FIGURES

Figure		Page
1	Chowder Ridge and vicinity	9
2	Study plot sampling design	16
3	Flowering phenology of plants in the alpine fell-field community. X indicates peak flowering period	26
4	Percent flowering relative to peak flowering total for *Potentilla diversifolia* and *P. villosa*, summer 1981	27
5	Percent flowering relative to peak flowering total for *Saxifraga bronchialis* and *Cerastium arvense*, summer 1981	28
6	Percent flowering rlative to peak flowering total for *Sedum lanceolatum* and *Solidago multiradiata*, summer 1981	29
7	Observed flight periods for pollinator groups on Chowder Ridge, summer 1981. On 9/1 the weather was too severe for insect activity	34

INTRODUCTION

Pollination ecology, as defined by Faegri and van der Pijl (1979), is the study of plants and their pollination vectors: water, wind, and animals. Water pollination is limited to a small number of aquatic species. Wind pollination is the rule among gymnosperms and is well represented among angiosperms. However, animal pollination is the most prevalent mode of pollen transfer among angiosperms, with pollen vectors including birds, bats, and insects, the latter by far the most important. The flower-insect relationship has been the principle force in the origin and adaptive radiation of angiosperms, as has been discussed by numerous authors (see, especially, Baker and Hurd, 1968; and Stebbins, 1973).

Pollination ecology involves such things as floral attractants (odor, morphology, and color) and rewards (nectar and pollen); plant breeding systems; insect behavior and energetics; population biology; community ecology; and co-evolution among flowers and pollinators (Proctor and Yeo, 1972; Faegri and van der Pijl, 1979; Baker and Hurd, 1968; Heinrich and Raven, 1972; and Heithaus, 1974). Recent studies in pollination ecology have emphasized a community approach (Heithaus, 1974; Moldenke and Lincoln, 1979; Arroyo et al., 1982) because the community is the fundamental unit of ecological organization.

Three broad evolutionary syndromes are recognized in the pollination ecology of angiosperms: anemophily, polyphilic entomophily, and specialized entomophily (Proctor, 1978). These syndromes are correlated with corolla morphology and reflect differential selection pressures to ensure reproductive success. In those flowers adapted for anemophily, wind pollination, the corolla is reduced and the anthers and stigma extend beyond confining floral envelopes or bracts, facilitating release of pollen by the anthers into the wind and reception of pollen by the often branched stigmas. Anemophily is predominant in closely clumped, often dominant plants of open, low diversity habitats and cool-temperate forests. Specialized entomophily is reflected in plants with zygomorphic (bilaterally symmetrical) flowers which restrict the range of available pollinators to those with specialized, coadaptive morphologies. Reproductive isolation in these plants is usually closely associated with the flower-insect relationship. Such isolation, based on insect behavior and morphology, is termed external. The polyphilic entomophily syndrome relates to potential pollination by a wide range of common, more or less promiscuous visitors. In this case, reproductive isolation is generally maintained by cytogenetic incompatibilities (internal isolation).

Successful fertilization of a flower may depend on whether the plant is cross-pollinated or not. Cross-pollination is the transfer of pollen from the anther of one flower to the stigma of another flower on a different plant (sometimes defined as different genotype) of the same species (Faegri and van der Pijl, 1979). Self-pollination is the transfer of pollen from the anther of a flower to the stigma of the same flower or another flower on the same plant. Generally, cross-pollination results in higher seed set and more vigorous offspring (Proctor and Yeo, 1972). Whether or not self-pollination will be successful depends on the compatibility of the stigma for the pollen. Self-compatible means that pollen will germinate and grow on the stigma of the same flower or plant and fertilization will be successful. In many plants, self-pollination is prevented by the anther and stigma being structurally separated or maturing at different times. In dioecious species, the plants themselves are unisexual, ensuring cross-pollination.

A broad array of insects, primarily from four Orders, are known as pollinators: Coleoptera--the beetles, Lepidoptera--the butterflies and moths, Diptera--the flies, and Hymenoptera--the wasps, ants, and bees (Proctor and Yeo, 1972; Faegri and van der Pijl, 1979). A list of common families of flower visitors is provided in Appendix A. The importance of any given flower visitor as a pollinator in a community depends on several factors including: 1) its adaptiveness for pollen transfer, especially its hairiness; 2) its constancy, i.e., the repeatibility with which it visits the same species of flower; 3) its abundance in the plant population; 4) its energetics, relating food requirements and, therefore, the number of flowers it must visit to sustain itself; 5) its behavior in regard to manipulation of the flower and potential for cross-pollination.

Recently, considerable interest has been generated in the pollination ecology of alpine and arctic regions. The alpine environment has been defined as that area in the mountains above the limit of upright tree growth (Douglas and Bliss, 1977). Daubenmire (1978) considers the most important factor in delimiting the alpine to be a lack of heat during the growing season. The alpine growing season is short, cold, and variable (Billings, 1974) with considerable fluctuations in temperatures. Wind is also important because it occurs frequently, dessicates plants (Bliss, 1971), physiologically stresses flying insects (Moldenke, 1976), and, in conjunction with topography, determines the pattern of snow accumulation (Billings, 1973). Because of these characteristics, both plant and insect diversity is lower in the alpine than in more mesic habitats (Moldenke, 1976). Plants are predominantly perennials (Bliss, 1971), and include six major growth forms: graminoids, rosette plants, cushion plants, dicotyledonous "forbs" (not rosettes, graminoid, or cushion), prostrate shrubs, and caulescent woody rosette plants (Billings, 1974).

Major community studies in pollination ecology of alpine environments in the Americas include those of Moldenke (1976, 1979a) in California, Moldenke and Lincoln (1979) in Colorado, and Arroyo, et al. (1982) in Chile. Moldenke considered bumblebees (Hymenoptera, Apidae), anthomyiid flies (Diptera, Anthomyiidae), and butterflies (Lepidoptera, Papilionoidea) to be the most important pollinators of the California alpine. Moldenke and Lincoln listed bumblebees, muscoid flies (Diptera, family complex, see Appendix A), syrphid flies

(Diptera, Syrphidae), and butterflies as the most important pollinators in the Colorado alpine. Arroyo, et al., listed bees (Hymenoptera, Apoidea), muscoid flies, syrphid flies, and butterflies as the most important pollinators in the cushion plant zone of the Central Andean alpine.

Pollination ecology in the high arctic has been studied by Hocking (1968) and Kevan (1972a, 1972b). Hocking found that the lower Diptera (Suborders Nematocera and Brachycera), Cyclorrhapha (Diptera, including syrphid and muscoid flies), and the Hymenoptera were the most important pollinators. Kevan listed five pollinating groups, in order of importance, for Camp Hazen on Ellesmere Island (81° 49'N): dance flies (Diptera, Empididae), syrphid flies, Phaoniiae (Diptera, Anthomyiidae), Spilogana spp. (Diptera, Anthomyiidae), and bumblebees. Kevan stated that primitive flies are important in the arctic because the limited diversity of flower species blooming at any one time "forces" flower constancy.

Veno (1979) and Pojar (1974) looked at the pollination ecology of subalpine communities in the Cascade Mountains, on Mt. Rainier and southern British Columbia, respectively. Veno listed bumblebees, syrphid flies, muscoid flies, sawflies (Hymenoptera, Tenthredinidae), and dance flies as the most important pollinators. Pojar cited bumblebees, muscoid flies, syrphid flies, butterflies, bee flies (Diptera, Bombyliidae), and solitary bees (Hymenoptera, family complex, see Appendix A) as important pollinators.

In all North American alpine environments investigated, and in the two subalpine studies of the Cascade Mountains, bumblebees were listed as the most important pollinators. Their importance is based on a combination of several characteristics: they can thermoregulate, maintaining a high (32° C) thoracic temperature necessary for flight, even when ambient air temperatures are near freezing (Heinrich, 1972a); they can conserve energy by allowing their thoracic temperature to drop while on the inflorescence of a plant and then "warm up" again before flight (Heinrich, 1972a); and queen bumblebees normally incubate their brood (Heinrich, 1972b), providing protection against the cold temperatures of the alpine environment. Moreover, bumblebee colonies are present throughout the flowering season, which is longer than the blooming times of individual plant species. To satisfy their food requirements, the bees must, therefore, forage on several species of plants during the flowering season (Heinrich, 1976b). The colony as a whole assumes a generalist role in pollination, since a wide variety of plant species is visited. However, individuals tend to specialize or major on one or two species at any given time, and minor on another less rewarding species (Heinrich, 1976a, 1979a). The minors serve as bridges to new majors when the previous majors are no longer available. In the process of majoring, bumblebees may explore a number of flower types, selecting the one with the greatest reward. The ability to discriminate among flowers and thus major is essential for bumblebees to meet their considerable energy requirements.

Flowering phenology is important not only to bumblebees but also to the entire pollinator spectrum, because it determines the pattern of resource availability. The variety and density of plants blooming at any one time have a direct effect on pollinator diversity and abundance (Moldenke, 1979b). Phenology is controlled primarily by climate (Moldenke, 1979b); but in the alpine, phenology is closely linked with the pattern of snow accumulation and release (Billings, 1973). Within any given community the flowering periods of individual plant species overlap and form a continuum. Mosquin (1971) theorized that the divergence of flowering times in a community is the result of competition for pollinators. When two plant species that are flowering synchronously depend upon the same insects for pollination, reproduction by one or both species may be adversely affected (Levin and Anderson, 1970). Competition for pollinators could then function as a selective force to cause separation of flowering periods. On the other hand, competition could be avoided through specialized floral morphologies, or the need for insect visitation could be reduced through self-pollination or agamospermy. To compete more effectively, a plant species could have large or profuse visual targets with ample nectar and/or pollen rewards (Mosquin, 1971).

Heinrich (1976b) linked flowering phenology and pollination ecology in a study which compared a bog, a woodland, and a disturbed habitat. According to him, each habitat had different selective pressures determining flowering time, and these pressures are exerted in part by life histories of insect pollinators. In the bog, bumblebees were the most important pollinators. The bumblebee colony depended on two or three species of flowers at any one time, and this dependency persisted throughout the growing season. Selection favored an unbroken progression of flowering periods because absence of flowers for a short time may result in death of the bees' colony.

In the Maine woodland, time niches available to flowering plants are much more restricted since the forest canopy shuts out direct sunlight in the summer. Heinrich postulates that pollination of the numerous concurrently flowering species is possible if a variety of specialists, primarily short-lived solitary bees, is available.

Heinrich concluded that in the disturbed habitat, cross-pollinated weedy species cannot rely on the availability of a specific time niche. The species can flower for long durations, since they grow in open habitats; they normally have large available energy supplies; and their pollination strategy is based on opportunism, i.e., pollinators will eventually become available. Within these three habitats, flowering phenologies have been displaced to those times when cross-pollination is optimal.

The questions asked in this study are: 1) What plants are present in and what is the community structure of the selected fell-field? 2) What floral attractants, including colors and morphologies, are present in the community? 3) What is the nature and significance of flowering phenology? 4) What potential insect pollinators are present in the community, when are they present, and for what reward(s) are they foraging in the flowers? 5) Which insect groups appear to be the most important pollinators in this alpine environment?

STUDY AREA

Location

Chowder Ridge (Fig. 1), which has been proposed as a Research Natural Area, is located in the Mt. Baker National Forest on the northwest side of Mt. Baker, within Township 38N and Range 7E. The ridge is oriented northwest-southeast with an exposed southwest slope. The northeast slope is largely buried beneath permanent snow fields and glaciers. Chowder Ridge is approximately five kilometers long and merges with Mt. Baker to the southeast, at the point of contact with Bastile Ridge. Here, the Mazama Glacier covers the north aspect and is continuous with glaciers of Mt. Baker. To the northwest, Chowder Ridge abruptly drops off to Skyline Divine about 150 m below. Elevation of Chowder Ridge varies from 2,031 m at the northwest end to 2,312 m at Hadley Peak, near the southeast end. The study site was located at approximately 2,041 m near the northwest end of the ridge. The site aspect was southeast with a slight slope. The northwestern portion of the ridge tends to be more rounded and level, as was the downhill end of the study site.

Chowder Ridge is accessible from Cougar Divide, a 8.5 km hike, or Skyline Divide, a 12 km hike. From Bellingham, Washington, access is approximately 85 km up the Mt. Baker Highway (St. Rte. 542).

Geology

The North Cascades are characterized by a complex of metamorphic, sedimentary, and igneous rock (McKee, 1972) which exists as the strongly uplifted and deeply eroded northern end of an anticline whose axis of folding is tilted or plunges to the south (Easterbrook and Rahm, 1970). The oldest rocks are crystalline igneous and metamorphic types which are resistant to erosion and persist as the steepest and tallest clusters of peaks (Easterbrook and Rahm, 1970).

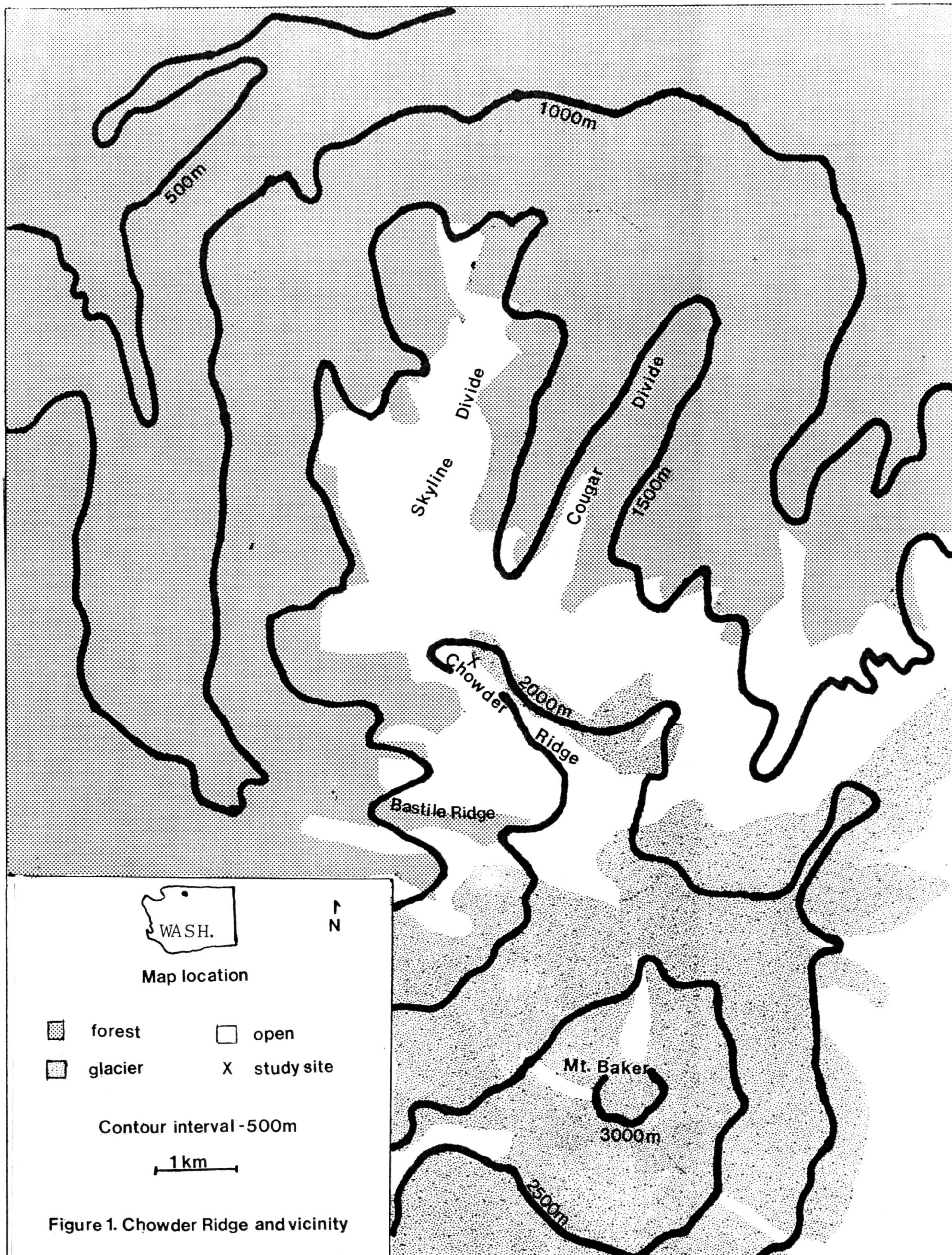

Figure 1. Chowder Ridge and vicinity

Episodes of marine sedimentation and vulcanism occurred in the Jurassic and Cretaceous Periods producing thick sequences of strata (McKee, 1972). Severe orogeny of these strata reached a climax in the Cretaceous Period. This orogeny involved folding, faulting, and severe metamorphism. Saltwater last covered the region during the Cretaceous (McKee, 1972). Mountains arose in the Cretaceous but were eroded to smooth hills by the middle of the Tertiary Period (McKee, 1972). The present mountains were built over the past 10 million years, and Mt. Baker and Glacier Peak are Quaternary volcanoes which are superimposed on existing ridges (Easterbrook and Rahm, 1970).

In the Quaternary, the peaks of the North Cascades spawned large alpine glaciers which moved down valleys and merged with immense glaciers occupying the lowland regions (McKee, 1972). The present form of the range is largely a result of the actions of these past glaciers (Easterbrook and Rahm, 1970). Today, glaciers are limited to the higher peaks.

Mt. Baker is a composite volcano consisting of alternating lava flows and fragmental debris (Easterbrook and Rahm, 1970). Adjacent Chowder Ridge appears to be an arete formed by Pleistocene alpine glaciers (Taylor and Douglas, 1978). Most of the ridge is composed of sedimentary rock of the Nooksack Group (Misch, 1966), consisting of graywackes, siltstones, granite rocks, and limestone boulders of late Jurassic and early Cretaceous age. Marine fossils (presumably clams) of this group are responsible for the name of Chowder Ridge (Taylor and Douglas, 1978).

Climate

The climate of the North Cascades varies from maritime on the western slopes, where Chowder Ridge occurs, to continental on the eastern slopes (Douglas, 1972). The prevailing winds are northwesterly during the spring and summer and southwesterly during fall and winter (Douglas, 1972).

The nearest meteorological station is the Mt. Baker station at Heather Meadows, elevation 1,296 m, located northeast of the mountain approximately 13 km from Chowder Ridge. Mean annual precipitation is 2,790 mm, with only 274 mm occurring during the summer months (June, July, August). The mean annual temperature at this station is 4.4°C, with a July mean of 12.1°C.

Plant Community Patterns

Plant community patterns of the North Cascades were described by Douglas and Bliss (1977), who grouped communities into west, central, and east sections based on species affinities. This west to east gradient is caused by a general shift from the maritime to a more continental climate. Plant communities of the western and central North Cascades have close affinites with species of coastal areas, both to the north and south, while those of the eastern North Cascades have close affinities with species of the Rocky Mountains and far northern regions (Douglas and Bliss, 1977).

Plant communities of Chowder Ridge were described by Taylor and Douglas (1978). The crest and south-facing slope of the ridge are xeric due to light snow cover in the winter, caused by the windblown aspect, and early snowmelt, accentuated by low summer rainfall. Because of these xeric conditions, the flora has species affinities with that of the eastern North Cascades.

The plant communities along the crest of Chowder Ridge include dry graminoid, dwarf shrub, herbfield, vegetation stripe, and fell-field (Taylor and Douglas, 1978). Dry graminoid communities are floristically rich, dominated by sedges and grasses, and occur on well drained slopes. The most extensive of these communities is dominated by an alpine form of *Carex spectabilis*, and includes, especially, *Phlox diffusa*, *Carex breweri*, *Sibbaldia procumbens*, *Solidago multiradiata*, *Antennaria alpina*, and *Festuca ovina*.

Another, more xeric type of dry graminoid community is dominated by Carex phaeocephala. Important components include Phlox diffusa, Solidago multiradiata, and Oxytropis campestris.

Dwarf shrub communites of Salix cascadensis occur in nearly pure mats in slight depressions along the crest of the ridge. Empetrum nigrum often grows adjacent to these Salix mats.

Herbfield communities are characterized by more or less continuous vegetation, with many plants having a cushion or matted habit. Most of these communities cover a limited area. Predominant species include Phlox diffusa, Potentilla diversifolia, Oxytropis campestris, Solidago multiradiata, Carex albonigra, Achillea millefolium, and Poa alpina.

Vegetation stripe communities occur in areas characterized by the downward creep of unstable substrate. The vegetation is arranged in vertical stripes 40-50 cm wide, separated by about 1 m of scree. Plant species include Solidago multiradiata, Phlox diffusa, Oxytropis campestris, Cerastium arvense, Festuca ovina, and Castilleja rupicola.

Fell-field communities are sparsely vegetated, with plants usually in clumps. These communities generally occur on windswept ridgetop areas of gentle slope. Characteristic species include Phlox diffusa, Oxytropis campestris, Carex phaeocephala, Saxifraga bronchialis, Festuca ovina, and Phacelia sericea.

Douglas and Bliss (1977) stated that herbfield, fell-field, and vegetation stripe communities are not discernible on species composition alone, but represent a continuum from the sparse covered fell-field, where cover is less than 50 percent, to the more-or-less complete cover of the herbfield. The vegetation stripe communities occur where the slope becomes steep.

Taylor and Douglas (1978) have shown, through composing an ordination of fifteen alpine stands sampled on Chowder Ridge, that time of snow release is the most obvious factor separating the communities on the ridge. The fell-field communities become released from snow first. Therefore, it would be expected that they would begin flowering earliest in the season. In addition, the fell-field would be affected by summer drought first and end flowering the earliest.

On the southwest slopes below the ridgecrest communities, where conditions are more mesic, mostly lush subalpine communities occur. These lower communities, no great distance from the ridgetop, may represent the source of many insect species observed visiting flowers in the study site, an alpine fell-field.

METHODS

Selection of Study Site and Logistical Problems

During the summer of 1980, five reconnaissance pack trips were made to Chowder Ridge. During these visits, representative pollinators were collected, and the northwest end of the ridge was cruised in search of a suitable study site. The site chosen was a fell-field with a rather homogeneous mix of vegetation. A fell-field community was considered best suited for pollination ecology studies because plant cover is low and observations of insect activity are easier to make than in a high density community.

The major portion of this study was completed during the summer of 1981. Visits to Chowder Ridge were made at least once each week, from June 25 to September 1. If weather permitted, 2-3 days were spent on location during each visit. This maximized the opportunity to collect data.

A major limiting factor in this study was logistics. Early in the year Cougar Divide was entirely snow-covered, and the hike in to Chowder Ridge took several hours. Including the drive from Bellingham, it would take at least half a day to reach the study site. In addition, the weather was unpredictable, often appearing good from Bellingham, but deteriorating rapidly during the hike in. During periods of inclement weather, including high winds, snow, and cold rain, insects were not active, thus the only data that could be collected regarded flowering phenology.

Quantification of Community Structure and Identification of Plants

On August 6, 1980, the selected community was sampled to determine vegetation structure. The methods used were described by Bliss (1963): 20 X 50 cm quadrats were located according to a restricted random technique. The experimental design is shown in Figure 2. The study area was 20 X 20 m square and contained three precisely positioned 8 X 4 m plots. Vegetation was sampled for cover, following the method of Daubenmire (1959, 1968), and frequency, suing 60 quadrats, 20 per 8 X 4 m plot.

Frequency and mean cover were determined for each vascular plant species and for collective groups of macrolichens and bryophytes. These values were then converted to prominence values by multiplying the mean percent cover by the square root of the species frequency. The derived prominence value is a measure of dominance or importance of a species within a stand or community. When determined as described above, it gives more emphasis to percent cover then frequency.

All plants within the 20 X 20 m study plot were identified to species using Hitchcock and Cronquist (1973) and Hitchcock et al. (1955 - 1969). Species and subspecies identifications were confirmed by R. J. Taylor, Biology Department, Western Washington University, and checked against the Chowder Ridge species list of Taylor and Douglas (1978).

Floral Color, Morphology, Pollination Syndrome, and Rewards

Plant species were assigned a color class, on the basis of floral color, following the system described by Kevan (1972b, Table 4). The class assignment does not consider the insect visual range which, at least in some cases, extends into the ultra-violet spectrum.

Floral morphology, based on descriptions of Proctor and Yeo (1927), was classified to one of the following types: open flowers, partially exposed flowers, closed flowers, small tubular flowers, and large tubular flowers. Open flowers are usually bowl-shaped with exposed food rewards. Partially exposed flowers make

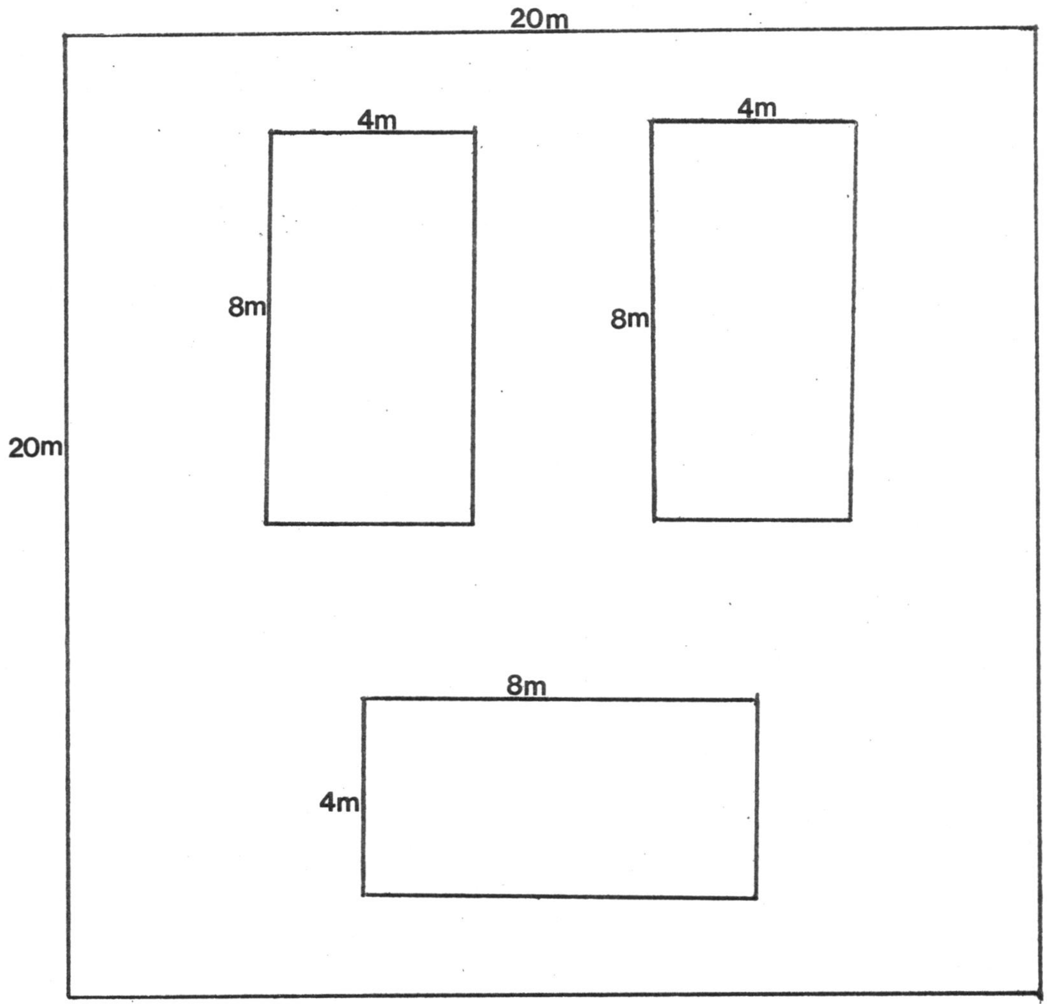

Figure 2. Study plot sampling design.

access by insects semi-difficult and usually have some portion of the perianth fused. Closed flowers have the corolla shaped in such a way as to exclude non-specialized insect visitors. Small tubular flowers are generally associated with composites and do not usually restrict the range of pollinator types. Large tubular flowers require long "tongued" insects to reach the concealed nectar.

Plant species were grouped into pollination syndromes (following Proctor, 1978), based on their perianth morphologies. Open and small tubular flowers are considered to exhibit polyphilic entomophily. Partially exposed, closed, and large tubular flowers are considered to exhibit specialized entomophily. Grasses and sedges are considered to exhibit anemophily.

In all flowers, pollen was considered to be a food reward. No attempt was made to determine nectar constituents of flowers or to quantify nectar, if indeed it was produced. Visual moisture, insect behavior, and literature references were used to determine whether or not any given species provided nectar rewards.

Flowering Phenology

To quantify flowering phenology, four 20 m permanent transects were used. 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 number (a meter locus) from within each of four 5-meter intervals: 1-5, 6-10, 11-15, 16-20.

Within a 1-meter swath along the four transects, those flowers that were in anthesis were counted. However, in graminoids and species with dense flower clusters, e.g., Oxytropis campestris, Phacelia sericea, Solidago multiradiata, and Sedum lanceolatum, the entire inflorescence was counted as a unit.

Phenology was recorded once each week for ten weeks. In addition, flowering patterns were observed and noted in other communities along the crest of the ridge.

Collection and Identification of Flower-visiting Insects

Collection of flower-visiting insects in this fragile ecosystem was minimized for the purpose of this study. In addition, no insects were collected in the study plot, thus avoiding an adverse effect on pollinator abundance and behavior. An attempt was made to collect a series, ten individuals, of each species of flower-visiting insect observed in the fell-field community. Insect species are very difficult to discern in the field, so collections of insect groups were emphasized. In this case, an insect group (see Table 3) may have been a genus (e.g., Bombus), a family (e.g., Syrphidae), or a family complex (e.g., muscoid flies), depending on the difficulty of field recognition. Specimens were identified to family in the laboratory using Borrer et al. (1976), and identifications were confirmed by Dr. Gerald Kraft, Biology Department, Western Washington University.

Observation and Quantification of Insect Activity and Abundance

General observation of visits by various insect groups to plant species along the ridgecrest were made, and notes regarding feeding habits, flower constancy, flower manipulation, type of food sought, and apparent effectiveness as pollinators were taken. At each visit to Chowder, notations were made of all insect groups observed, thus establishing insect flight periods.

Within the 20 X 20 m study plot, insect group activity was quantified using both 20 m transects and 2 m square observation plots. Each transect was chosen at random, from the twenty that were possible, and while walking slowly along a transect, all observed insect visits to flowers, specifically the insect group involved and the plant species visited, were noted. The 2 m observation plots were watched for 20 minute periods. Again, each plot was chosen randomly from a total of 100 plots within the study area. During the 20 minute watch period, insect visits to flowers were scored as described for transects. As many watch periods and transects were carried out as time and weather permitted, generally a maximum of six per field day.

Both watch periods and transects were utilized in this study to quantify relative abundance and activity levels of insect groups. Transects are brief walks over space; therefore, the numbers generated indicate relative abundance of insect groups. Watch periods are obeservations on one plot over time and the numbers generated indicate the relative activity level of insects in the community. In the watch periods an individual insect could be scored more than once if it visited more than one flower in the observation plot. It was unlikely that an individual insect was scored more than once during a walk along a transect.

Weather data and time of day were recorded while insect activity and abundance were being quantified. The weather data consisted of temperature at ground level, cloud level, and estimated wind speed scored as mild, medium, or strong. These data permitted generalizations to be made regarding the relationship between insect activity and environmental factors.

Pollen Analysis

A limited analysis of bumblebee and syrphid fly pollen loads was made to provide some measure of the flower constancy exhibited by these insects. Pollen corbiculae were used from four bumblebees. In the case of syrphid flies, eight of which were collected for analysis, the entire insect was utilized and the pollen counts include those within the gut as well as those grains attacked externally. Percent pollen types was determined for each insect. For the analysis, standard acetolysis preparation was used, the method recommended by G. Rouse (Department of Botany, University of British Columbia, personal communication).

Importance of Pollinators

Pollinator importance in the fell-field community was determined by a variety of characteristics, including insect adaptiveness, abundance, constancy, energetics, and behavior. No one characteristic outweighs all others. Adaptiveness for pollen transfer relates to the morphology of the insect and how this may aid in pollen transfer. Abundance, of course, related to the number of individuals involved in pollen flow within the community. Constancy is a measure of insect fidelity to certain species of plants, i.e., the inverse measure of promiscuity. Energetics determines the number of flowers an insect must visit, i.e., the higher the energetic demand the larger the number of flowers that must be sampled, and the greater the contribution as a pollinator. Behavior relates to the feeding or manipulation strategy of the insect. Insect behavior may or may not lead to successful pollination. For example, some insects may hover above flowers and feed directly from anthers without contacting the stigma.

RESULTS

Plant Community Structure

A species list with cover, frequency, and prominence values is given for the study plot in Table I. No plant species has cover values over ten percent and base ground covers 69.3 percent of the community. Prominence values given by Taylor and Douglas (1978) and Douglas and Bliss (1977) for herbfields indicate much higher values for most species. In addition, Saxifraga bronchialis and Potentilla villosa are not listed as constituents of herbfield communities. Prominence values given by the above authors for fell-fields are more similar to values indicated in Table I, although Cerastium arvense, Potentilla diversifolia, Sedum lanceolatum, Achillea millefolium, and Phacelia sericea are more abundant in the study site than in the other fell-fields sampled.

The study site represents a windblown, ridgecrest community defined by Douglas and Bliss (1977) as a fell-field, with low prominence values, bare ground cover exceeding 50 percent, and Saxifraga bronchialis and Potentilla villosa occurring in significant numbers.

Floral Color, Morphology, Pollination Syndrome, and Rewards

Pollination related characteristics of the dominant plants of the fell-field community are given in Table 2. Of the thirteen entomophilous plants listed, nine have white or yellow flowers. The other four species have floral colors which include purple, pink, and red. Floral morphology-types in this community include open flowers, small tubular flowers, partially exposed flowers, closed flowers (Oxytropis campestris), and large tubular flowers (Phlox diffusa).

Polyphilic entomophily is the most common pollination syndrome, with nine plant species. Anemophily and specialized entomophily are each exhibited in four species.

Table 1. Vascular plant species, bryophytes, genera of macrolichens, and bare ground of the alpine fell-field community.

Plant species	C[a]	F[b]	PV[c]
Oxytropis campestris gracilis	9.0	80	80.5
Cerastium arvense	8.8	67	71.9
Agropyron canimum majus latiglume	8.5	43	60.0
Phlox diffusa longistylus	9.6	35	57.0
Potentilla diversifolia diversifolia	8.1	32	45.8
Sedum lanceolatum lanceolatum	4.1	50	29.0
Saxifraga bronchialis austromontana	5.5	22	25.6
Phacelia sericea sericea	3.5	40	22.1
Poa alpina	3.1	27	16.0
Achillea millefolium lanulosa alpicola	2.6	15	10.1
Potentilla villosa parvifolia	2.1	12	7.2
Solidago multiradiata scopulorum	2.1	7	5.4
Haplopappus lyallii	1.4	2	1.8
Festuca ovina brevifolia	0.6	7	1.5
Carex albonigra	1.0	2	1.4
Carex phaeocephala	0.6	2	0.8
Silene acaulis	0.6	2	0.8
Aster sibiricus meritus	0.3	5	0.7
Erigeron compositus glabratus	0.1	3	0.2
Anemone multifida hirsuta	-[d]		
Antennaria alpina media	-		
Campanula rotundifolia	-		
Draba lonchocarpa	-		

Table I. (continued)

Plant species	C[a]	F[b]	PV[c]
Draba paysonii	-		
Sibbaldia procumbens	-		
Trisetum spicatum	-		
Bryophytes	7.7	70	64.4
Lichens:			
Cetraria	T[e]		
Cladonia	T		
Parmelia	T		
Umbilicaria	T		
Thamnolia	T		
Bare Ground	69.3	100	693.0

[a] Percent cover

[b] Frequency

[c] Prominence value

[d] Plant spp. did not occur in a quadrat

[e] Trace, less than 0.05% of cover

Table 2. Family, growth form, color class, floral morphology, pollination syndrome, and nectar presence of dominant plants in the fell-field community.

Plant species	Growth form	Family	Floral color[a]	Floral morphology[b]	Pollination syndrome[c]	Nectar[d]
Agropyron caninum	graminoid	Graminae	N/A	I	A	N/A
Aster sibiricus	forb	Compositae	purple	Stf	P	Prob
Carex phaeocephala	graminoid	Cyperaceae	N/A	I	A	N/A
Cerastium arvense	forb	Caryophyllaceae	white	O	P	Prob
Draba paysonii	cushion	Cruciferae	yellow	Pe	S	?
Erigeron compositus	cushion	Compositae	white + yellow	Stf	P	No[e]
Festuca ovina	graminoid	Graminae	N/A	I	A	N/A
Oxytropis campestris	forb	Leguminosae	yellow	C	S	Prob
Phacelia sericea	cushion	Hydrophyllaceae	purple	O	P	Prob
Phlox diffusa	cushion	Polemoniaceae	pink	Ltf	S	Yes[f]
Poa alpina	graminoid	Gramineae	N/A	I	A	N/A
Potentilla diversifolia	forb	Rosaceae	yellow	O	P	Yes[f]
Potentilla villosa	cushion	Rosaceae	yellow	O	P	Prob
Saxifraga bronchialis	cushion	Saxifragaceae	white	O	P	Prob
Sedum lanceolatum	forb	Crassulaceae	yellow	O	P	Yes[f]
Silene acaulis	cushion	Caryophyllaceae	red	Pe	S	Yes[e]
Solidago multiradiata	forb	Compositae	yellow	Stf	P	Prob

[a] N/A=not applicable, [b] I=inconspicuous, Stf=small tubular flower, O=open, Pe=partially exposed, C=closed, Ltf=large tubular flower, [c] A=anemophily, P=polyphilic entomophily, S=specialized entomophily, [d] Prob=probably but unconfirmed, [e] Hocking, 1968, [f] Pojar, 1974

Floral rewards can be nectar or pollen, or both. Pollen was present in all flowers, i.e., all species listed are hermaphroditic. Nectar constituents are listed (Table 2) as "probable" for those flowers that appeared to have nectar, and yes or no for those flowers cited in the literature as having or not having nectar. Most entomophilic plants in the fell-field appeared to have nectar.

Flowering Phenology

Flowering phenology of the plants in the fell-field is shown in Figure 3. The wind pollinated plants generally have shorter flowering times than insect pollinated plants. The earliest plants to flower were Draba paysonii and Phlox diffusa, followed by Silene acaulis. These three entomophilous species are all cushion plants (Table 2).

Potentilla diversifolia and P. villosa flowered synchronously (Figure 4) beginning July 12. Saxifraga bronchialis and Cerastium arvense also flowered synchronously (Figure 5) beginning about July 22. These four plants all peaked the week of August 6, and all exhibit polyphilic entomophily.

The earliest composite to begin flowering, on July 28, was Erigeron compositus, followed by Solidago multiradiata, on August 1, and Aster sibericus, on August 13. The most abundant flower on September 1 was Aster sibericus. Sedum lanceolatum flowered synchroneously with the similarly colored Solidago multiradiata (Figure 6).

Flower-visiting Insects

Table 3 lists the flowr visiting insect groups observed on Chowder Ridge in 1981. Included in this table is information on insect characteristics that are important to pollination ecology. The most broadly represented insect Order is the Diptera, which includes the families Mycetophilidae, Bibionidae, Empididae,

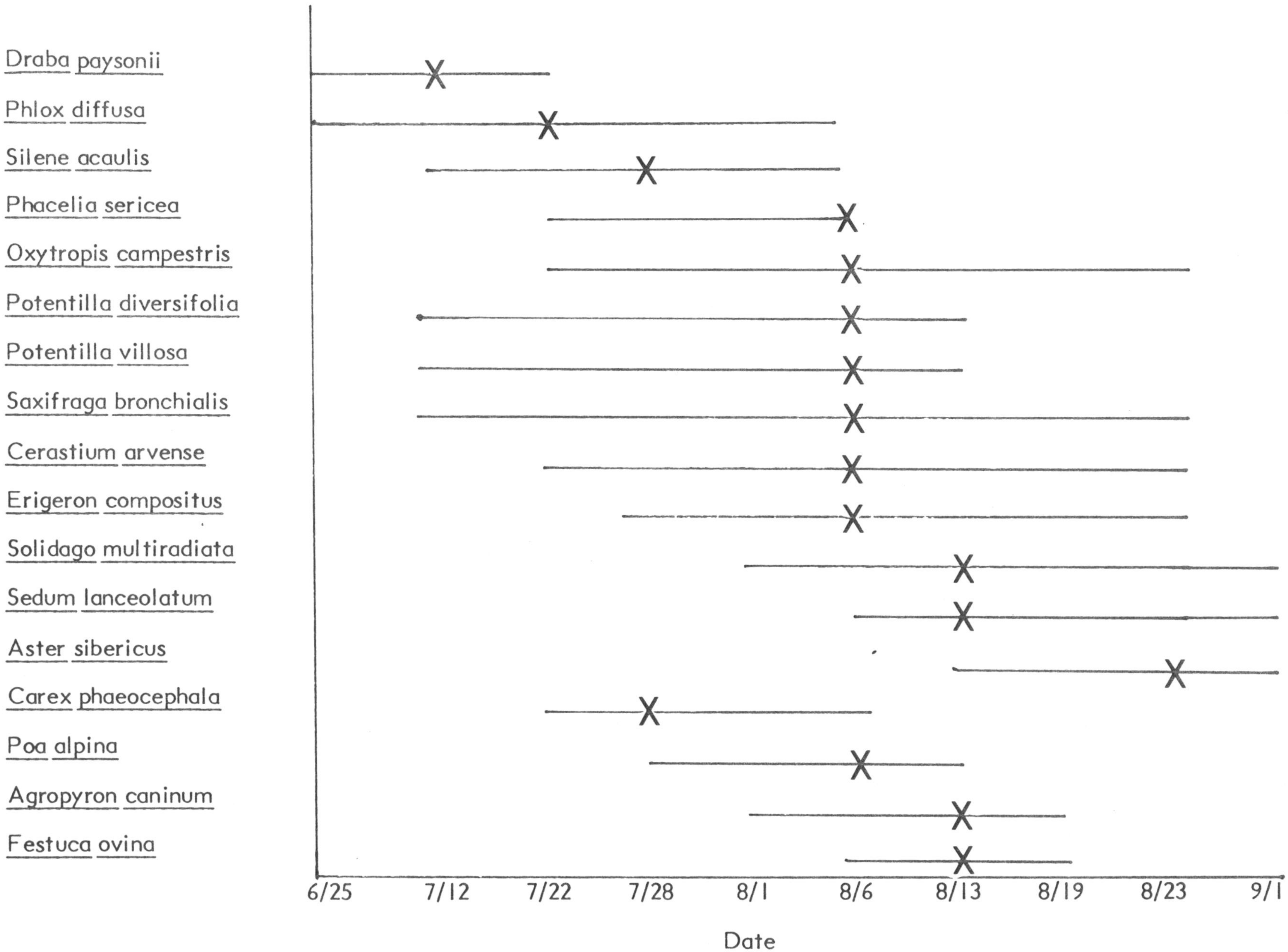

Figure 3. Flowering phenology of plants in the alpine fell-field community. X indicates peak flowering period.

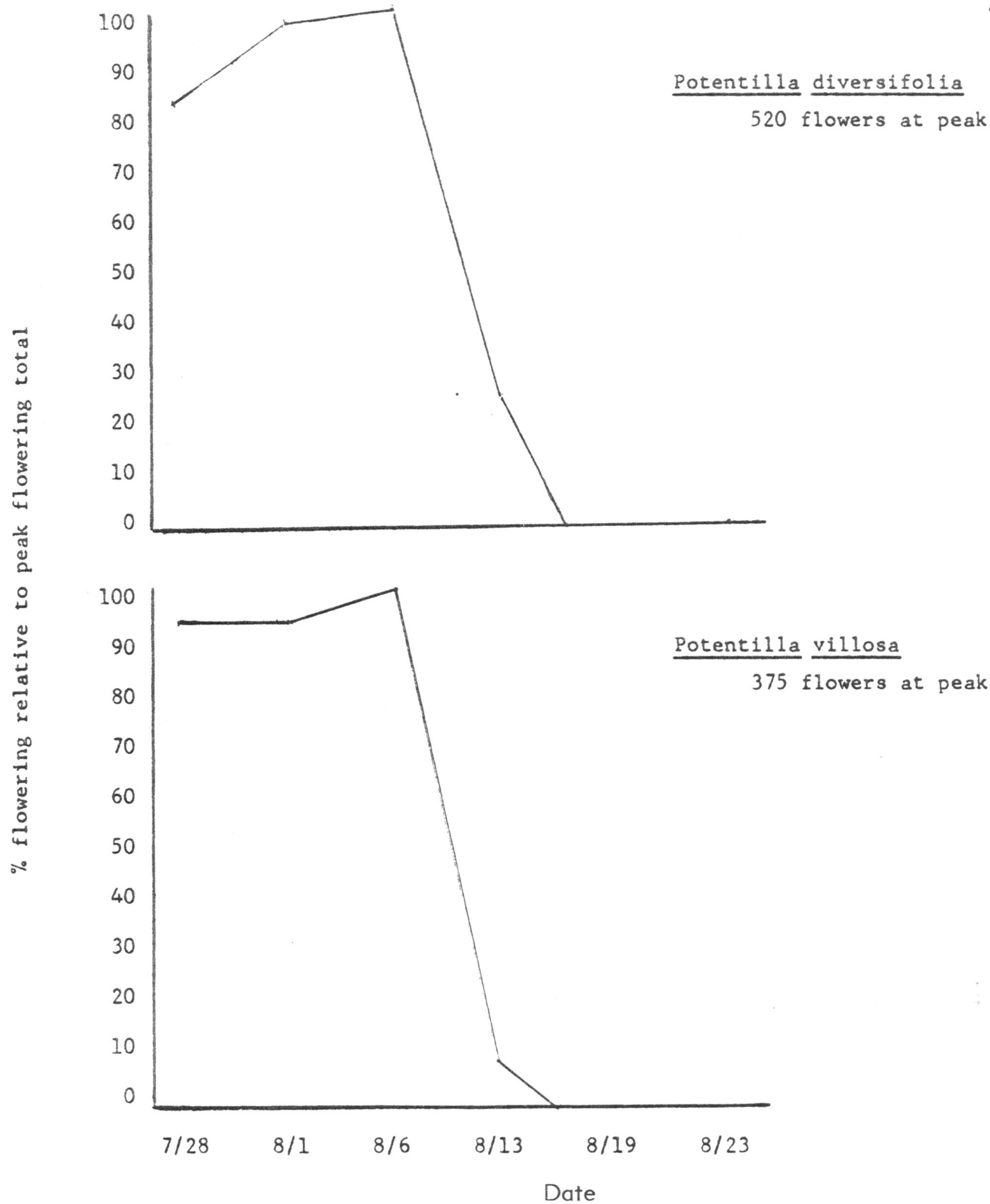

Figure 4. Percent flowering relative to peak flowering total for Potentilla diversifolia and P. villosa, Summer 1981.

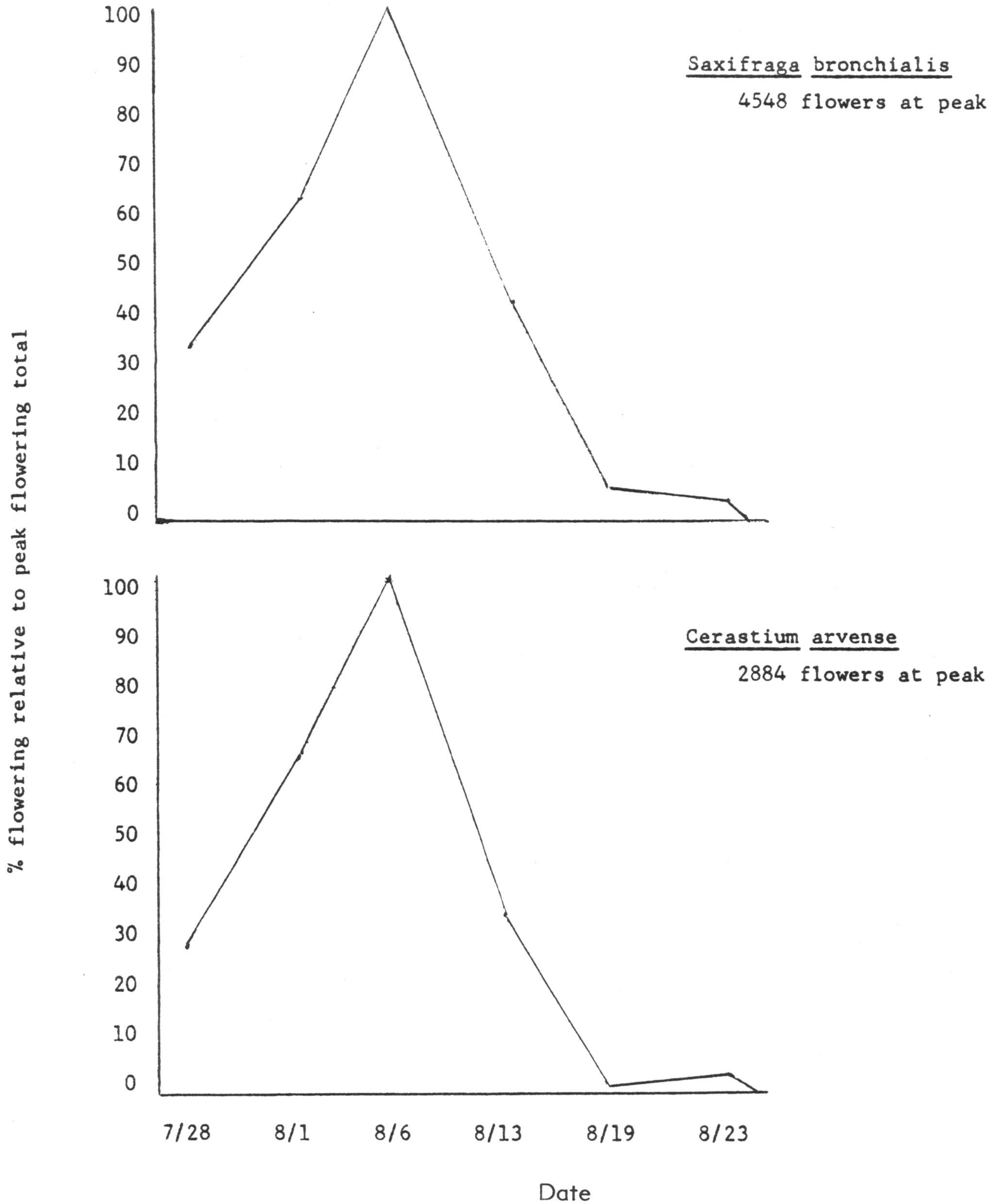

Figure 5. Percent flowering relative to peak flowering total for Saxifraga bronchialis and Cerastium arvense, Summer 1981.

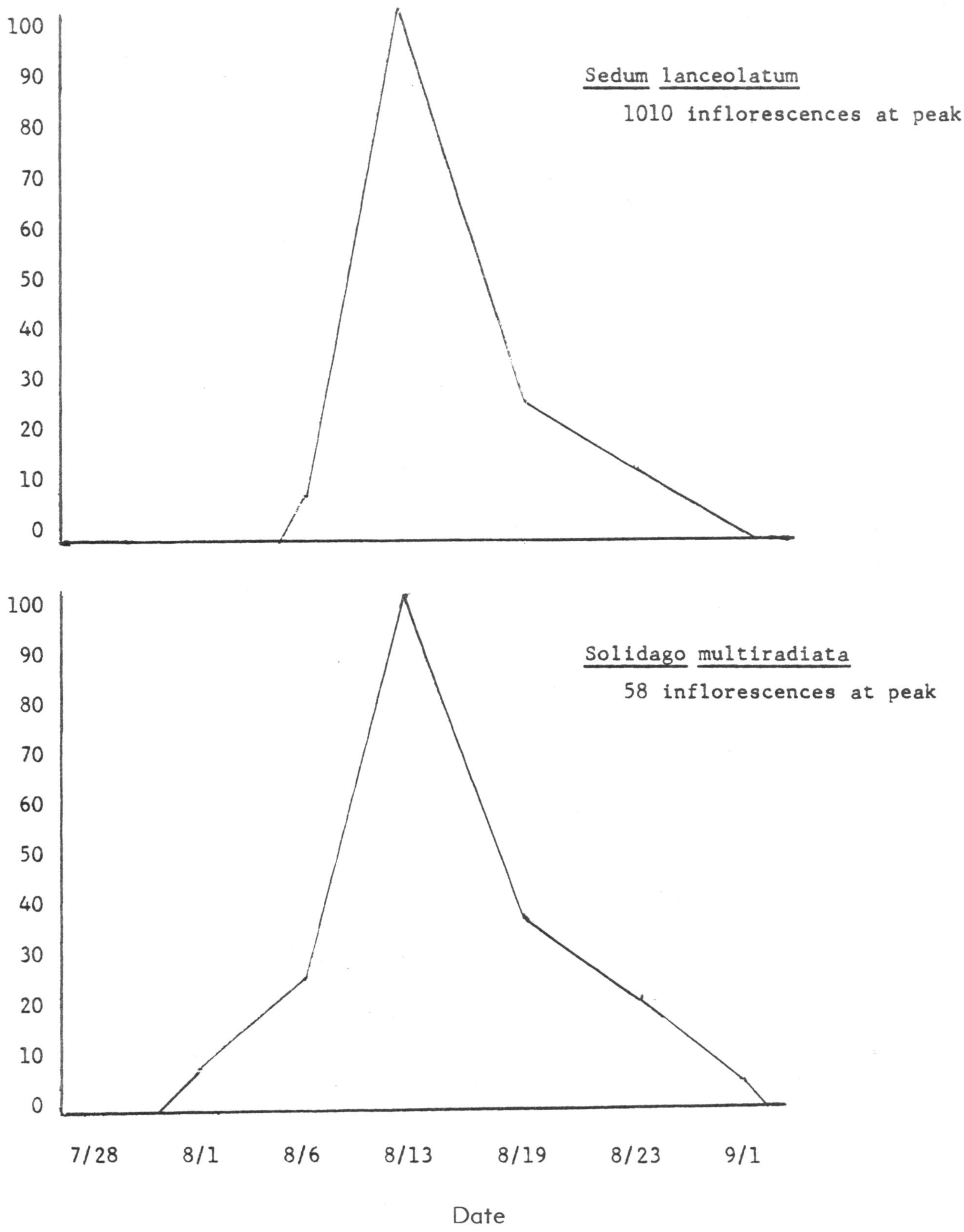

Figure 6. Percent flowering relative to peak flowering total for Sedum lanceolatum and Solidago multiradiata, Summer 1981.

Table 3. Common name, order, mouthparts, hair, flower food, major flower types visited, and importance as pollinators for insect groups observed visiting flowers in the fell-field community.

Insect group	Common name	Order	Mouth-parts	Hair	Flower[a] food	Major flower[b] types visited	Importance[c] as pollinators
Miridae	Plant bug	Hemiptera	piercing sucking	no	N	Stf	no
Coccinellidae	Ladybird beetle	Coleoptera	chewing	no	N,P	O	limited
Mycetophilidae	Fungus gnat	Diptera	primitive sucking	some	N,P	O,Pe	limited
Bibionidae	March fly	Diptera	primitive sucking	some	N,P	O	limited
Empididae	Dance fly	Diptera	primitive sucking	some	N	O	limited
Syrphidae	Hover fly	Diptera	lapping	yes!	N,P	O,Pe,Stf	yes!
Muscoid flies	same	Diptera	lapping	yes!	N,P	O,Stf	yes
Lycaenidae	Gossamer wings	Lepidoptera	sucking	yes!	N	Stf	yes
Nymphalidae	Brush-footed butterflies	Lepidoptera	sucking	yes!	N	Stf	yes
Solitary bees	same	Hymenoptera	lapping	yes!	N,P	O,Pe	no
Bombus	Bumblebees	Hymenoptera	lapping	yes!	N,P	Cl,Pe,Stf	yes!

[a] N=nectar, P=pollen
b Cl=closed, O=open, Pe=partially exposed, Ltf=large tubular flower, Stf=small tubular flowers
[c] !=especially so

Syrphidae, Anthomyiidae, Muscoidae, Calliphoridae, and Tachinidae. The latter four families are muscoid flies, listed in order of their abundance.

The Hymenoptera was represented on Chowder Ridge primarily by two species of bumblebees, Bombus melanopygus and B. flavifrons dimidiatus. Bombus balteatus was also present on the ridge but not as abundantly as the other two species of bumble bees. Solitary bees were observed on the ridge but were very rare. Only one solitary bee was captured; it belonged to the family Andrenidae. Other solitary bees, apparently halictids, were observed but not identified.

Three species of butterflies, belonging to two families, were abundant in the study site. The Lycaenidae was represneted by one species, a blue, and the Nymphalidae by two species, a checkerspot (Euphydryas sp.) and Milbert's Tortoiseshell (Nymphalis milbertii). Other Lepidoptera observed included angelwings and fritillaries (Nymphalidae), white (Pieridae), skippers (Hesperiidae), swallowtails (Papilionidae), alpines (Satyridae), and several undetermined moths.

The families Miridae, Coccinellidae, Mycetophilidae, Bibionidae, Empidiae and Lycaenidae were apparently represented by a single species on Chowder Ridge. Syrphid flies and muscoid flies were represented by the largest variety of species.

Observation and Quantification of Insect Activity and Abundance

Table 4 lists the flowers that insects were observed visiting during the summer of 1981, and indicates whether those flowers appeared to represent a major food source for that insect group. Syrphid flies were the only insects that were observed visiting wind pollinated plants, Poa alpina and Luzula spicata, apparently foraging for pollen which they lapped directly from the anthers.

Table 4. Plants observed to be visited by various insect groups, as major (M) and occasional (m) food source. See Table I for varietal names of plant species.

Plant species	Insect groups B	Bm	C	E	L	M	Mus	My	Sol	Syr
Achillea millefolium							M			m
Aster sibiricus		M			M		m			
Campanula rotundifolia		M				m				m
Cerastium arvense		m	M	m	m		M		m	M
Draba paysonii								M		
Erigeron compositus				m	M		M			m
Haplopappus lyallii		M			M					m
Lupinus lepidus[b]		M								
Luzula spicata[b]										m
Oxytropis campestris		M								
Penstemon procerus[b]		M								m
Phacelia sericea		M	M				m			M
Phlox diffusa		M			m		m			m
Poa alpina										m
Potentilla diversifolia	M	m	M	M	m	m	M	M		M
Potentilla villosa	M	m	M	M		m	M		m	M
Saxifraga bronchialis			M	m	m		M		m	M
Sedum lanceolatum		M	m		M		M		m	M
Silene acaulis		M			m					m
Solidago multiradiata		M	M		M	M	M			M

a B=Bibionidae, Bm=Bombus, C=Coccinellidae, E=Empididae, L=Lepidoptera, M=Miridae, Mus=Muscoid flies, My=Mycetophilidae, Sol=Solitary bees, Syr=Syrphidae

b Species did not occur in study plot

Plants with the fewest types of visitors were those with closed floral morphologies, e.g., Oxytropis campestris which was visited only by bumblebees. Plant species with the greatest variety of insect visitors were those with open floral morphologies, e.g., Potentilla diversifolia, P. villosa, Saxifraga bronchialis, and Cerastium arvense, and those with small tubular flowers, such as the composites.

The insect groups which visited the greatest variety of flower types were syrphid flies, muscoid flies, bumblebees, and butterflies. Fungus gnat and march fly groups were the most restricted in their flower visitations.

Figure 7 shows the flight periods of all the major flower-visiting insect groups. The only group present on June 25 was that of the fungus gnats which were abundant in and on mats of Draba paysonii. The only other plant flowering in the study plot at that time was Phlox diffusa (Figure 3).

The most ephemeral insect group consisted of the march flies which were abundant in Potentilla diversifolia and P. villosa flowers from July 28 to August 1. Plant bugs were observed only on August 23, severe weather made observations on September 1 impossible.

Insect groups present throughout the season, beginning July 12, were bumblebees, syrphid flies, muscoid flies, and ladybird beetles. Bumblebees and ladybird beetles were consistently abundant from week to week. The syrphids appeared to be much more abundant in August after the dry spell set in, with the larger, hairy, swift flying types like Eristalis spp. appearing after the composites began to flower. Muscoid flies were especially abundant in late July and early August when the open, bowl-shaped, generalist flowers were abundant.

Butterflies did not appear in the fell-field until early August (Figure 7), about the time composites and Sedum began flowering (Figure 3). The nymphalids appeared a little earlier than did the lycaenids and were observed on Sedum

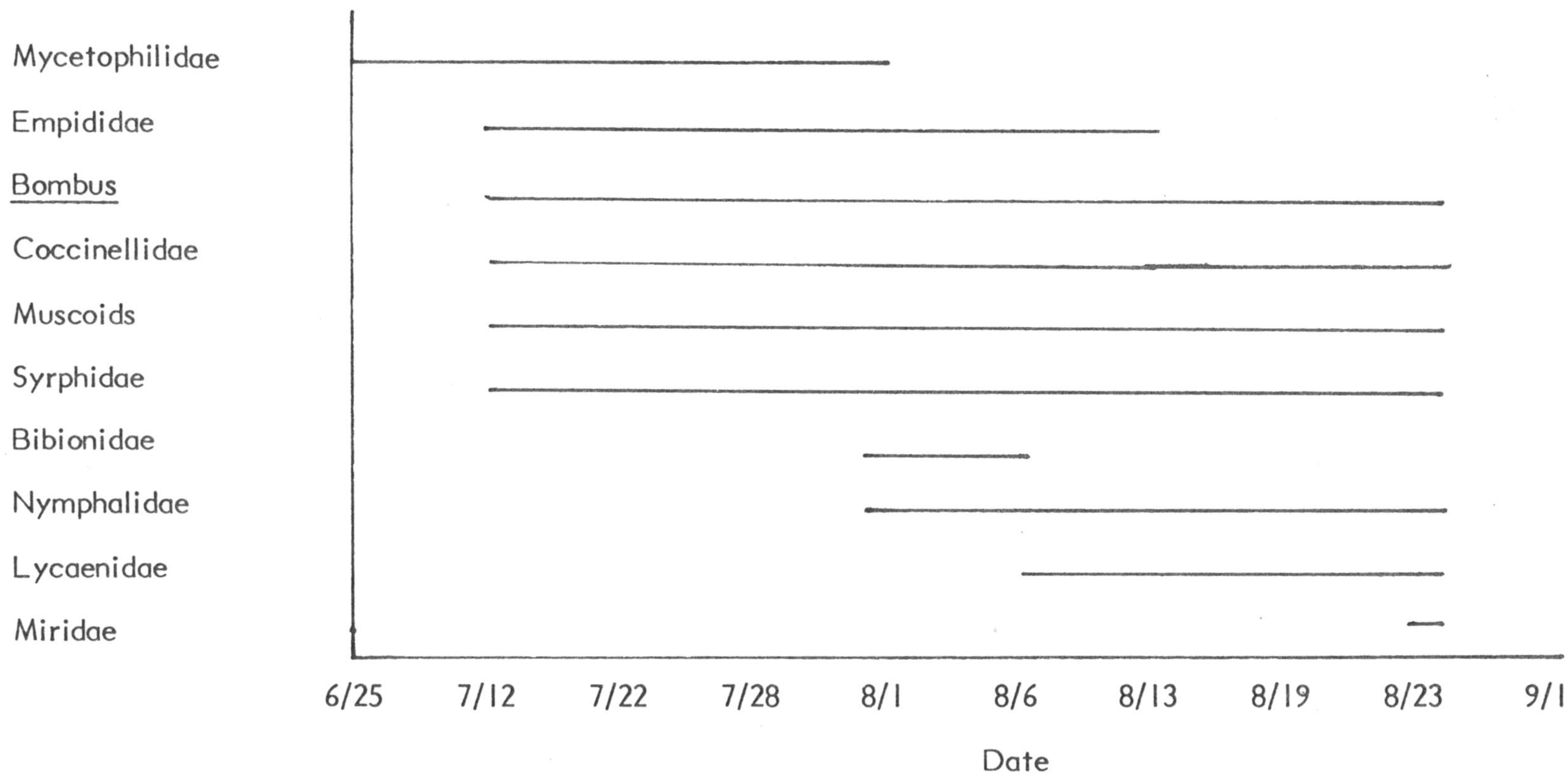

Figure 7. Observed flight periods for pollinator groups on Chowder Ridge, Summer 1981. On 9/1 the weather was too severe for insect activity.

lanceolatum probing with their probosci even before the flowering buds had opened.

Table 5 shows the number of visits by insect groups to flowers during the watch periods. The most active insect groups in the community, based on number of flowers visited, were syrphid flies, bumblebees, muscoid flies, and ladybird beetles. The butterflies are represented by such low numbers primarily because of their wariness of humans.

The majority of the watch periods was carried out in August, because in July research trips were often interrupted by bad weather. March flies, dance flies, and fungus gnats were recorded in low numbers in Table 5 because they were most abundant in July when the weather was often bad or deteriorating and no watch periods could be accomplished. For this same reason no bumblebee visits were recorded to *Silene acaulis* and *Phlox diffusa*. *Potentilla diversifolia* and *P. villosa* flowered primarily in late July and early August (Figure 4); therefore, the numbers shown in Table 5 probably under-represent the true number of visits these plants received from insect groups.

Table 6 depicts the number of observed visits by insects to flowers based on transect data. The most abundant insect groups in the fell-field community were syrphid flies, muscoid flies, bumblebees, and ladybird beetles. Here again, butterflies, march flies, dance flies, and fungus gnats are likely under-represented due to the factors mentioned above.

In general, the information shown for the transects follows the same trends as the watch periods. Muscoid flies and syrphids consistently visited the widest variety of flowers, followed by bumblebees and ladybird beetles. *Potentilla diversifolia* and *P. villosa* were visited by the widest variety of insects, followed by *Saxifraga bronchialis*, *Sedum lanceolatum*, and *Cerastium arvense*. *Oxytropis campestris* was visited only by bumblebees.

Table 5. Number of observed visits by insects to flowers during watch periods.

Plant Species[a]	Insect Group[b]									
	B	Bm	C	E	L	M	Mus	My	Sol	Syr
Aster sibericus		19			1					
Cerastium arvense		1	11	10			63			134
Erigeron compositus				2	7		7			9
Oxytropis campestris		33								
Phacelia sericea		61	11				3			56
Phlox diffusa							1			3
Potentilla diversifolia	1		12	5		1	7	1		7
Potentilla villosa	1		5			3	43		1	28
Saxifraga bronchialis			35				105			224
Sedum lanceolatum		245	4		6		6			67
Solidago multiradiata		9	3		2	17	22			81
Total	2	368	81	17	18	21	257	1	1	609

a This list does not include all the plant species of the community, only those which insects were observed visiting. For varietal status, see Table 1.

b For abbreviations of insect groups, see Table 4.

Table 6. Number of observed visits by insects to flowers during transects.

Plant Species[a]	B	Bm	C	Insect Groups[b] E	L	M	Mus	My	Sol	Syr
Achillea millifolium										1
Cerastium arvense			1	5			22			18
Erigeron compositus				1			1			3
Oxytropis campestris		10								
Phacelia sericea		28					1			21
Phlox diffusa										1
Potentilla diversifolia		1	9	12			15	1		11
Potentilla villosa			10			3	12			10
Saxifraga bronchialis			6		1		14		1	21
Sedum lanceolatum		18			1		1		1	16
Solidago multiradiata							1			4
Total		57	26	18	2	3	67	1	2	106

[a] This list does not include all the plant species of the community, only those which insects were observed visiting. For varietal status, see Table 1.

[b] For abbreviations of insect groups, see Table 4.

Pollen Analysis

Four pairs of pollen corbiculae from Bombus melanopygus individuals were analyzed for percent pollen types. The results are presented in Table 7 and suggest that these four insects were visiting primarily two types of flowers while collecting pollen for the hive. Bombus #185 had 38% Oxytropis campestris and 60% Phacelia sericea pollen while Bombus #186 had 32% Phacelia sericea and 63% Oxytropis campestris pollen in the corbiculae. Bombus #255 was the most one-sided, with primarily Sedum lanceolatum pollen in the corbiculae.

Eight syrphid flies were collected for pollen analysis. The results shown in Table 8 indicate variability among individuals. Cerastium, Saxifraga, Phacelia, and Compositae made up the bulk of these syrphids' diet.

All collections for pollen analysis were made adjacent to the study site in early to mid August. The two Bombus melanopygus individuals collected on August 2 had Phacelia pollen present in their corbiculae while the two individuals collected on August 12 and 14 had none. During this time Phacelia servicea flowers declined significantly in numbers and Sedum lanceolatum increased (Figure 3). The change in the foraging behavior of the bumblebees probably resulted from the decline of one food source, Phacelia, and increase in another, Sedum.

The syphid flies wre all collected on August 12 and 14 when Phacelia flowers were mostly gone from the study site but were occasional in the adjacent areas. Most of the flies had some some amount of Phacelia pollen on them. This indicates the syrphid flies persisted in feeding on the scattered individuals of Phacelia during their foraging or may have had some pollen still stuck between their their hairs from the previous weeks.

Table 7. Percent pollen types from corbiculae of Bombus melanopygus, captured summer 1981.

Insect #	Date captured	Plant visiting	Pollen types,[a] Pha	Oxy	Sed	Com	Tet	Unknown
185	8/2	Oxy	60	39				1
186	8/2	Pha	32	63			3	2
254	8/12	Sed		46	42	5	6	
255	8/14	Sed		13	80	7		

[a] Pha=Phacelia sericea, Oxy=Oxytropis campestris, Sed=Sedum lanceolatum, Com=Composite, Tet=unidentified tetrad (probably Phyllodoce)

Table 8. Percent pollen types from whole body analysis of syrphid flies, captured summer 1981.

#	Date collected	Plant visiting	Pollen types,[a]									
			Cer	Com	Pha	Phl	Pot	Sax	UA	UB	UC	UD
1	8/12	Pha		60	19	19					2	
2	8/12	Sax	1	1	2			96				
3	8/12	Pot	32	4			64					
4	8/13	Com	4	58	4			33			1	
5	8/13	Sax	29	16	1			54				
6	8/13	Sax	2	33	26			38			1	
7	8/13	Sax	45	10				36			9	
8	8/14	Sax	8		31		29	35	6			

[a] Cer=Cerastium type, Com=Compositae, Pha=*Phacelia sericea*, Phl=Phlox type, Pot=Potentilla type, Sax=Saxifraga type, UA=unknown A, UB= unknown B, UC=unknown C, UD=unknown D.

Importance as Pollinators

The most important pollinators in the fell-field community during the 1981 flowering season, listed in the order of presumed importance, were bumblebees, syrphid flies, muscoid flies, and butterflies. Primitive flies (Mycetophilidae, Empididae, and Bibionidae) and ladybird beetles were secondarily important, while plant bugs and solitary bees appeared to have only a minor role as pollinators. An in-depth discussion of insect group characteristics and the relationship of these characteristics to pollination efficiency is reserved for the Discussion Section. Only data from the watch periods, transects, and general observations have been presented in this section.

Bumblebees were present throughout the flowering season (Figure 7) and were very active (Table 5) and abundant (Table 6). They began their activity in the fell-field early in the season by visiting *Silene acaulis* and *Phlox diffusa*, abandoning these species in favor of *Phacelia sericea* and *Oxytropis campestris* when the latter two plants came into flower. Once *Phacelia* and *Oxytropis* flowered-out the bumblebees concentrated their foraging efforts on *Solidago multiradiata* and, especially, *Sedum lanceolatum*. At the end of the season, the bees were commonly observed visiting *Aster sibericus*. Other plants from Table 1 not listed on Figure 3 that bumblebees appeared to major on were *Haplopappus lyallii* and *Campanula rotundifolia*. Bumblebees, then, are important as pollinators to all the entomophilous plants in Table 2, except *Draba paysonii*, *Potentilla diversifolia*, *P. villosa*, *Cerastium arvense*, *Saxifraga bronchialis*, and *Erigeron compositus*.

Syrphid flies were present throughout the season (Figure 7) and were the most active (Table 5) and abundant (Table 6) insect groups in the fell-field community. The syrphids were important visitors to *Potentilla diversifolia*, *P. villosa*, *Cerastium arvense*, *Saxifraga bronchialis*, *Sedum lanceolatum*, and

Solidago multiradiata (Table 5, 6). Their visits to *Phacelia sericea* probably did not result in successful pollination, since they hovered above the flowers feeding on pollen from the exserted anthers.

Muscoid flies were also present throughout the flowering season (Figure 7) and were very active (Table 5) and abundant (Table 6) in the study site. They were especially important flower visitors of *Potentilla diversifolia*, *P. villosa*, *Saxifraga bronchialis*, and *Cerastium arvense*, although they also visited most composites (Table 5, 6).

Butterflies did not emerge until early August (Figure 7) but were fairly abundant after that time. They were important flower visitors to all the composites and were commonly observed on *Sedum lanceolatum*. They were the most important pollinators of *Erigeron compositus*.

The remaining flower-visiting insect groups were of limited or no importance to the fell-field community as pollinators. Ladybird beetles were fairly abundant (Table 6) but were never observed to fly from flower to flower in search of food, and their movements appeared to be more or less random.

DISCUSSION

Floral Strategy

Flowers are colorful and conspicuous in the fell-field community and along the crest of Chowder Ridge, with a strong tendency toward aggregation. Cushion plants like Draba paysonii, Silene acaulis, Phlox diffusa, Potentilla villosa, and Saxifraga bronchialis produce dense mats of flowers, while Oxytropis campestris, Phacelia sericea, Sedum lanceolatum, and Solidago multiradiata have compact inflorescences of numerous flowers. Cerastium arvense and Potentilla diversifolia also produce an abundance of flowers, even though these are individually distinct; and solitary-headed Compositae, Erigeron compositus, Haplopappus lyallii, and Aster sibericus, generally grow in localized populations. Thus, it appears that the severe alpine environment has selected for plants that provide a colorful floral display, attracting insects from considerable distances and enticing them to visit several flowers during a single foraging expedition.

Aggregated flowers are important for insects, especially bumblebees which must maintain high thoracic temperatures at considerable energy expense for flight. The bees can land on an aggregation and allow their thoracic temperatures to drop while they visit numerous flowers (Heinrich, 1972a). Moldenke and Lincoln (1979) have even observed bumblebees walking between cushion plants on cool, cloudy days in Colorado, thus maximizing energy efficiency.

In the Chowder Ridge fell-field community, all entomophilous plants (excepting Antennaria alpina) were hermaphroditic. Relying on insects to visit both male and female flowers of monecious and dioecious plants is not a favorable strategy for such species to survive in this environment. The hermaphroditic condition increases successful pollination with a minimum of repeated visits.

Anemophilous (wind-pollinated) species in this community had shorter flowering periods than did the entomophilous species (Fig. 3). Since anemophilous plants cannot rely on the direct-vector advantage of insect pollination, it is essential that large numbers of plants flower simultaneously. This, of course, results in a compressed phenology.

In the fell-field community of Chowder Ridge, polyphilic entomophily, a generalist strategy, is the predominant pollination syndrome. Even Silene acaulis and Phlox diffusa, which are usually considered specialists, were visited by three or more major groups of pollinators. Only Oxytropis campestris depended on a single pollinator group, the bumblebees (Table 4). Chowder Ridge plant species thus conform to the theory of Moldenke (1976) who found that the generalist strategy predominated among plants and insects of California alpine zones.

Flowering Phenology

The flowering time in the fell-field community lasted approximately ten weeks, beginnning with Draba paysonii and ending with Aster sibericus (Fig. 3). Draba paysonii is agamospermous (Mulligan, 1971) and does not depend on insect pollination. It can therefore flower before conditions are favorable for pollinator activity, as it did on Chowder Ridge.

In the fell-field community, there was a broad divergence of flowering times among plants primarily dependent on bumblebees for pollination; these include, in order of flowering, Phlox diffusa, Silene acaulis, Phacelia sericea, Oxytropis campestris, Solidago multiradiata, Sedum lanceolatum, and Aster sibericus (Fig. 3). Heinrich (1976b) also showed that in a bog community where bumblebees were important pollinators, the plants that are bumblebee "majors" have more or less distinct flowering periods, but they overlap sufficiently to provide a "temporal chain" of food on which the bumblebees depend. This is important since the bees can derive food throughout the season and the plants have dependable pollinator service with minimized competition for that service.

These plants may have diverged their flowering times in response to competition pressures for pollinators, which follows Mosquin's (1971) argument.

In 1981, four dominant plants with open, bowl-shaped flowers all peaked during the same week, 6 August (Fig. 3). Synchronous flowering occured between Potentilla diversifolia and P. villosa (Fig. 4), and between Cerastium arvense and Saxifraga bronchialis (Fig. 5). These four species were equally dependent on syrphid and muscoid flies for pollination, although P. diversifolia and P. villosa were commonly visited by primitive flies. These four species appear to be in direct competition for pollinators and, according to Mosquin's ideas, would be expected to diverge their flowering times. If they are in direct competition for pollinators, why would they flower synchronously? It may be that by so doing, they enlarge the attraction potential of each plant population for promiscous fly pollinators. The selective force for attracting pollinators to the community may be greater than any disadvantage due to competition. For example, in the arctic tundra near Atkasook, Alaska, Williams and Batzli (1982) showed that seed set was higher in Pedicularis species that grew in mixed, synchronously flowering stands than those that grew in isolated pure stands. The authors theorized that the higher density of flowers in the mixed stands serve a greater attractive force for bumblebee pollinators than the single species stands.

It may be that these four plants are primarily self-pollinated without insects, and thus do not seriously compete for pollinators. However, Pojar (1974) considers P. diversifolia to be incompletely self-incompatible and Ugborogho (1977) considers Cerastium arvense to be completely self-incompatible.

In addition, there could be competition for pollinators among communities along the ridge crest. Taylor and Douglas (1978) showed that the alpine communities of Chowder Ridge are generally separated by time of snow release. The sequence of flowering within each community is initiated by snow release. If the open, bowl-shaped flowers within each community along the ridge crest flower synchronously, the promiscuous fly pollinators would have a continual food supply throughout a large part of the season because community release from snow is sequential. This food supply would be locally restricted within each community to make foraging less energetically difficult for the fly pollinators. Competition between communities for fly pollinators, then, may have acted to force open bowl-shaped flowers to bloom synchronously.

Sedum lanceolatum and Solidago multiradiata also flowered synchronously in 1981 (Fig. 6). These two plants share pollinators and may exhibit floral mimicry. Floral mimicry occurs when two unrelated taxa appear to have similar floral color and/or morphology and the flowers are not easily distinguished by pollinators. Macior (1971) cites floral mimicry in the alpine, where topography can limit plant population size, as a means of sustaining pollinator interest in one area by increasing the functional plant population size. Pollinators habituated to foraging on one species may extend their visits to the mimic. The mimic can then expand its population size until it becomes large enough to sustain pollinator interest on its own (Macior, 1971). On Chowder Ridge bumblebees visited Sedum and Solidago indiscriminantly. Since Sedum was much more abundant than was Solidago at peak anthesis (Fig. 6), it appears that Solidago may be benefitting from the floral mimicry relationship. Macior also stated that pollinator sharing, floral mimicry, and synchronous anthesis of sympatric species may reflect convergent evolution, leading to the development of similar pollination mechanisms in unrelated plant taxa.

Importance as Pollinators

Bumblebees

In every regard bumblebees were the most important pollinators in the Chowder Ridge fell-field community. They were abundant (Table 5, 6) and present throughout the growing season (Fig. 7). Their range of food items is strictly limited to floral products (Heinrich, 1979b) and they are morphologically adapted for pollen transfer and collection with a coat of spirally grooved hairs and a pollen collecting apparatus, the corbiculae.

Bumblebees are social insects, each individual belonging to a hive. The hive consists of a queen, workers, and, later in the season, drones and next year's queens. The queens that emerge late in the season are fertilized by the drones and are the only individuals to overwinter. Each queen starts a new colony in the spring and dies at the end of the season. Individuals are constantly foraging for the hive because the larvae are fed a mixture of pollen and nectar. Bumblebees, then, are especially good pollinators because they visit many flowers to satisfy their individual and colony needs.

In addition, bumblebees can activate their thoracic muscles and maintain a body temperature of more than 20°C above ambient air temperature (Lundberg, 1980). Thus they are capable of foraging early in the morning and on cool cloudy days when most other insects are inactive. I observed bumblebees foraging on Silene acaulis and Phlox diffusa at temperatures below 10°C in July, when the entire ridgecrest was in fog! Bumblebees are therefore effective pollinators because cold weather does not necessarily prevent foraging. This is especially important in an alpine environment where weather often limits the activity of insects. Also, the ability to thermoregulate places high emergetic demands on bumblebees. They must visit many flowers to meet these demands which, in turn, increases their effectiveness as pollinators.

Bumblebees almost always contact the stigma and stamens of flowers they visit, primarily because of their large size and the tendency to manipulate flowers into a position where access to nectar or pollen is facilitated. The bumblebees I observed foraging in the fell-field community visited primarily one or two species of plants at any given time. The pollen analysis of corbiculae (Table 7) also indicated that the bees were foraging primarily on two species of plants while collecting pollen.

In the fell-field community, foraging bumblebee queens visited *Silene acaulis* and *Phlox diffusa* in early and mid-July. Then queens and presumably newly emerging workers shifted to *Oxytropis campestris* and *Phacelia sericea* and ignored *Silene* and *Phlox*. By August 13 bumblebees were primarily visiting *Sedum lanceolatum* and *Solidago multiradiata*. At the end of August the bees were visiting *Aster sibericus*. Bumblebees, then, are important pollinators of at least seven of the thirteen dominant entomophilous plants in this community.

Syrphid flies

Syrphid flies are the most important pollinators in the Diptera (Proctor and Yeo, 1972). In the fell-field community on Chowder Ridge, syrphids are important pollinators, primarily because they are so active and abundant (Table 5, 6). In addition, many of syrphids are covered with hairs which aid in the transfer of pollen.

Syrphid flies feed exclusively on nectar and pollen (Proctor and Yeo, 1972). This dependency on floral food adds to their important as pollinators because they must consistently visit flowers to meet their energetic requirements. Behaviorally, they exhibit a wide variety of actions and visit a broad diversity of floral types. On Chowder, some were observed to hover above *Phacelia* flowers and feed directly from the anthers without making contact with the stigma. Others appeared to behave as good pollinators by landing in flowers like Potentilla and crawling over the floral parts while eating nectar and pollen. Still others were observed feeding from anthers of wind pollinated plants, e.g., Poa and Luzula.

Constancy in syrphids varied considerably (Table 8). Some individuals examined for pollen loads had almost all the same type of pollen on their bodies while others had primarily two or three types of pollen. This infers that syrphids may be visiting all the available food sources in their forage area. If syrphids find a large patch of flowers they may spend their time foraging at that patch, be it one, two, or three types of suitable flowers.

Syrphid flies were observed Potentilla diversifolia and P. villosa in July. They also were observed to visit Phacelia sericea, Saxifraga bronchialis, and Cerastium arvense in July through mid August. By mid August the larger, hairy, swift flying syrphids appeared and were observed visiting Sedum lanceolatum and available composites.

Muscoid flies

Muscoid flies are important in the fell-field community because of their abundance. In July through mid August they were commonly observed visiting Potentilla diversifolia, P. villosa, Cerastium arvense, and Saxifraga bronchialis. After mid August they were observed visting available composites.

Muscoid flies do not restrict their diet to nectar and pollen (Proctor and Yeo, 1972). This diminishes their importance as pollinators because pollen from a flower may end up on a variety of non-floral items. For example, I observed a muscoid fly that had been feeding on Potentilla fly directly to scat. However, other food types that would generally attract muscoid flies may be limiting in the alpine and this could force the flies to depend on floral food for their energetic requirements.

Muscoid flies were never observed to hover above flowers while feeding on nectar and pollen. They always landed in the flower and either lapped up pollen and/or nectar from the base of the petals or fed from the anthers directly. Landing in the flowers probably maximizes cross pollination because the flies, at least the larger ones, generally contact the stigma. Some of the small flies can maneuver about within a flower without contacting the stigma. Sizes ranged from 3 to 13 mm in muscoid flies captured on Chowder Ridge.

Butterflies

Beginning in early August, butterflies were important pollinators in the fell-field where they visited, primarily, composites and Sedum lanceolatum. The checkerspot and blue were especially abundant in early-mid August while the tortoiseshell was most abundant in mid-late August.

Most butterflies restrict their feeding entirely to nectar, although some are known to feed on other food items like rotting fruit (Proctor and Yeo, 1972). Their energetic demands are relatively low, as compared to bumblebees, because their lighter body and larger wings allow them to flutter slowly and glide considerably while in flight. They are also able to spend much of their time basking. Butterflies probably do not visit as many flowers in a day as syrphid and muscoid flies, but they constantly visit the same assortment of flowers and are highly adapted for pollen transfer with their thick coat of hairs.

Male checkerspot butterflies are known to defend territory from other males and even other species of butterflies (Pyle, 1974). As a case in point, I observed checkerspots chasing other butterflies. This territoriality is apparently related to mating and may adversely affect pollen flow.

Primitive flies

In the alpine environment, primitive flies, Mycetophilidae, Bibionidae, and Empidadae, played a limited role in pollination during 1981, but their importance could vary from year to year depending on the severity of the weather. These flies are all fairly small and can maneuver in bowl-shaped flowers without actually coming in contact with the stigma and anthers; however, they were often observed directly on the stigmas of Potentilla flowers. Because of their small size, primitive flies don't need to visit many flowers in a day to meet their energy requirements. Although I never observed them flying from flower to flower, they probably do carry some pollen between flowers. Even though they aren't highly adapted for pollen transfer, they may be important in self-pollination, especially in times of bad weather when other insects are not in flight.

Fungus gnats and march flies have primitive sucking mouth parts and feed on both pollen and nectar (Proctor and Yeo, 1972). Dance flies have piercing, sucking mouthparts and are primarily predaceous on smaller insects like fungus gnats and march flies. Dance flies supplement their diet with nectar (Proctor and Yeo, 1972).

None of the primitive flies were present throughout the entire growing season on Chowder Ridge. They were most abundant in July, in the flowers of Potentilla diversifolia and P. villosa. Fungus gnats were the only flower-visiting insects present on June 25, at which time they were abundant on mats of Draba paysonii.

Ladybird beetles

Ladybird beetles were very abundant on Chowder Ridge and were the fourth most frequently observed group visiting flowers (Table 5, 6). On the basis of behavior, energetics, constancy, and adaptiveness--they are not important pollinators. They are primarily predaceous but are known to feed on nectar and pollen in the alpine of Europe, presumably because other prey items, like aphids, are in such short supply (Hodek, 1973). On Chowder, the beetles appeared to clamber randomly over plants in search of available food items, without flying from flower to flower. They may have inadvertently been responsible for some self-pollination.

Plant bugs

Plant bugs were observed only during the week of August 23, when they were especially common on Solidago multiradiata. It is doubtful that they are important as pollinators because they have no long hairs and were not observed to fly. Plant bugs feed primarily on plant juices taken by piercing plant stems and leaves with their long proboscis (Borror, et al., 19776). They are apparently opportunistic in feeding on nectar; their long proboscis aids in extracting nectar from the tubular flowers of composites.

Other insects

Solitary bees are so rare in the alpine that they were not important as pollinators during the time I spent on Chowder Ridge. Conspicuously absent from the alpine were honey bees (Hymenoptera, Apidae) and beeflies, both very important at lower altitudes (Proctor and Yeo, 1972).

Comparison With Other Studies

The four major pollinator groups--bumblebees, syrphid flies, muscoid flies, and butterflies--on Chowder Ridge are also prevalent in alpine areas in Colorado (Moldenke and Lincoln, 1979). In California, however, Moldenke (1976, 1979a) did not include syrphid flies among the important pollinator groups. No other groups were listed as major pollinators for these alpine areas.

In the alpine of Chile (Arroyo, et al., 1982), muscoid flies, syrphid flies, and butterflies are important, but only one species of bumblebee is present. Based on the literature, Anthomyiid flies are the most abundant of muscoid flies in the northern hemisphere, whereas in Chile, Sarcophagidae and Tachinidae are most abundant. Solitary bees constitute the most important bee fauna in Chile.

Moldenke (1979a) stated that solitary bees are present in fair numbers in the Sierras of California but he did not consider them to be a major element of the pollinator fauna in the alpine. The Sierras of California and the Andes of Chile have a mediterranean climate. This may have some important to the distribution of solitary bees which at lower elevations, and to a lesser extent in the alpine, are important elements of the pollinator fauna (Moldenke, 1979b).

In the arctic, primitive flies (Empididae) are the most important pollinators (Kevan, 1972a), apparently because there is a limited diversity of flowers in bloom at any one time. Dance flies in the arctic were flower-constant due to this low diversity. On Chowder Ridge, with greater floral diversity, these insects were only of secondary importance. Muscoid flies (primarily Anthomyiidae), syrphids, and bumblebees are also important in the arctic. Butterflies are secondarily important, as they are not very abundant.

In the subalpine of the Cascades (Veno, 1979; Pojar, 1974) the diversity of pollinators is greater than in the alpine of Chowder Ridge and there is a broader range of important pollinators. Pojar listed bee flies and solitary bees as important pollinators, in addition to bumblebees, butterflies, syrphids, and muscoid flies. Veno considered sawflies and dance flies to be important in her study meadow, in addition to bumblebees, syrphid flies, and muscoid flies. Butterflies were uncommon, which is probably due to local distributional factors (Emmel, 1964), because alpine and subalpine meadows in the Cascades usually have abundant butterflies (Pyle, 1974; Pojar, 1974; personal observation).

Additionally she demonstrated through pollen analysis of surface hairs that bumblebees and syrphid flies can be equally effective in pollen transfer.

Veno (1979) and Moldenke and Lincoln (1979) observed selected communities for several years and found considerable variation from year to year in flower and insect abundance. This variation related to inconsistency of weather factors. My study involved a single year and does not account for potential seasonal variation in pollinator importance. Ehrlich, et al. (1972) documented a case in California where an unusual weather event caused the local extinction of the butterfly Glaucopsyche lygdamus. I feel that any severe weather event or prolonged rainy season through the summer would probably increase the importance of primitive and muscoid flies in the fell-field community of Chowder Ridge. In July, when cool cloudy weather restricted pollinator movements to all but the bumblebees, primitive flies were commonly observed feeding and basking in the open, bowl-shaped flowers. In addition, muscoid flies occasionally were seen but syrphids apparently were absent. If the weather were unseasonably mild for several consecutive seasons, solitary bees could become a major element of the pollinator fauna because of their presence in subalpine meadows where climate is less severe.

In conclusion, the variability of the environment and the patchy distribution of populations in the alpine are major factors in the pollination ecology of the fell-field community. The important pollinators include bumblebees, muscoid flies, syrphid flies, butterflies, and primitive flies. The sequence of flowering and the floral strategies of plants appear to optimize cross-pollination in this environment.

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Appendix A

Selected families known as flower visitors in the four major Orders of insect pollinators. Primarily from Proctor and Yeo (1973). Taxonomy follows Borror et al. (1976).

Coleoptera-the beetles
- Suborder-Polphaga
  - Family- Staphylinidae, rove beetles
    - Cantharidae, soldier beetles
    - Chrysomelidae, leaf beetles

Lepidoptera-the butterflies and moths
- Suborder-Frenatae
  - Division-Microlepidoptera, primarily moths, many with larvae that are economically important
  - Division-Macrolepidoptera,
    - Superfamily- Noctuoidea
      - Family- Noctudiae, noctuid moths
    - Superfamily-Sphingoidea
      - Family-Sphingidae, hawk moths
    - Superfamily-Hesperoidea
      - Family-Hesperiidae, skippers
    - Superfamily-Papilionoidea
      - Family- Lycaenidae, gossamer-winged butterflies
        - Pieridae, whites, sulphurs
        - Papilionidae, swallowtails
        - Satyridae, arctics, alpines
        - Nymphalidae, brush-footed butterlies

Diptera-the flies
- Suborder-Nematocera
  - Family- Tipulidae, crane flies
    - Culicidae, mosquitoes
    - Bibionidae, march flies
    - Mycetophilidae, fungus gnats
- Suborder-Brachycera
  - Family- Bombyliidae, bee flies
    - Empididae, dance flies
- Suborder-Cyclorrhapha
  - Division-Aschiza
    - Family- Syrphidae, hover or syrphid flies
  - Division-Schizophora
    - Family- Anthomyiidae, Muscidae, Calliphoridae, Sarcophagidae, Tachinidae — muscoid flies

Appendix A (continued)

Hymenoptera-the wasps, ants, and bees
Suborder-Symphyta
Family-Tenthredinidae, sawflies
Suborder-Apocrita

Superfamily-	Ichneumonoidea
Family-	Ichneumonidae, ichneumons
Superfamily-	Scolioidea
Family-	Formicidae, ants
Superfamily-	Vespoidea
Family-	Vespidae, paper wasps, yellow jackets, and hornets
	Pompilidae, spider wasps
Superfamily-	Sphecoidea
Family-	Sphecidae, sphecid wasps
Superfamily-	Apoidea, the bees
Family-	Colletidae, Halictidae, Andrenidae, Megachilidae, Anthophoridae — solitary bees
	Apidae, honeybees, bumblebees

VITA

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