AN ABSTRACT OF THE THESIS OF

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Title: Foraging Ecology of Pollinators in the Early Stages
    of Secondary Succession in the Western Hemlock
    (Tsuga heterophylla (Raf.) Sarg.) Zone of the
    Oregon Coast Range

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    The early stages of secondary succession of the
McDonald and Paul Dunn State Forests, Corvallis, Oregon,
were grouped into three stages; herb, herb-shrub, and
shrub, based on vegetation types. Flowers of herbaceous
species and residual shrubs dominated in the early years
after clear-cutting. Woody plants became increasing
abundant in the shrub-dominated period. Flowers of native
plant species were common in the spring, while the
introduced species were abundant in the summer. The
important floral resources for pollinators in the spring
were *Rubus ursinus*, and *Rubus leucodermis*. *Rubus discolor*
and *Cirsium* spp. dominated and contributed to early summer
and late summer flowering peaks, respectively.

    Insect pollinators partitioned floral resources by
foraging at different times of the season or at different

times of the day, or utilizing different sizes of flower patches, or by concentrating on different flower species. Differences in seasonal activity of the bees were due to innate features of the life-histories. Daily activities were strongly influenced by the ambient temperature in early spring, and by resource availability in the summer.

Eighty of the ninety-six species of pollinators were bees. Common native bee genera were *Andrena*, *Bombus*, *Halictus*, *Lasioglossum*, and *Osmia*. The most dominant flower-visitor was the introduced honey bee (*Apis mellifera*). The foraging levels of the honey bees depressed flower visitation of certain wild bee taxa, especially *Bombus*.

The supplementation and removal of the cordovan honey bees during late summer indicated a competitive release on flower visitation by *Bombus*. Competition from *Apis* was probably crucial in the spring, as demonstrated by the increase in visitation rates of *Bombus* when *Apis* were excluded from the flower patches of *Rubus leucodermis*.

FORAGING ECOLOGY OF POLLINATORS IN THE EARLY STAGES OF
SECONDARY SUCCESSION IN THE WESTERN HEMLOCK (TSUGA
HETEROPHYLLA (RAF.) SARG.) ZONE OF THE OREGON COAST RANGE

by

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INTRODUCTION

Pollination biology, or "anthecology" which was named by Charles Robertson in 1904, has become a subject of considerable interest and a fast-growing field during the past two decades. The subject has been recognized since Charles Darwin's time as a model for understanding the relationship of natural selection and evolution. Recently, field biologists realized that pollination systems have potential in providing a good opportunity to test many hypotheses concerning ecological and evolutionary processes.

Angiosperms or flowering plants are the dominant land plants today. There are ca. 200,000-250,000 named species, of which 85 percent are pollinated by insects (Crepet 1984). This correlation would suggest a causal connection between the success of angiosperms and the insects that pollinate them. The most common insect pollinators are in the orders Coleoptera, Lepidoptera, Diptera, and Hymenoptera. These are actively flying adults of neopterous, endopterygote insects. They search for mates, oviposition sites, and food from flowers with the aid of highly developed senses and have evolved the ability to discriminate between floral species. Among

these insects, bees of the superfamily Apoidea (Hymenoptera) are considered to be the most important flower visitors in terms of both number and efficiency. Worldwide, the Apoidea include about 21,000 species of bees in eleven families (Krombein et al. 1979, Michener and Greenberg 1980).

Bees as a group are said to be flower-constant or faithful pollinators in the sense that they tend to visit flowers of the same plant species during a single foraging flight, or often several foraging trips. Bees exhibit many adaptations for the acquisition, manipulation, and transportation of food from flowers to their nests. These include structural, behavioral, and physiological adaptations for collecting pollen, nectar, or other food materials from flowers (see reviews by Thorp 1979, Eickwort and Ginsberg 1980, Kevan and Baker 1983). The general relationships between groups of insects and certain types of flowers or pollination syndromes have been well documented by Proctor and Yeo (1973), and by Faegri and van der Pijl (1978). At the community level, bees have received more scrutiny than other pollinators in terms of their degrees of specialization in various community types, and as biological indicators determining community structure and organization (e.g.: Kevan 1972, Heithaus 1974, 1979, Pojar 1974, Moldenke 1975, 1976, Macior 1978, Proctor 1978, Moldenke and Lincoln 1979). Recently, the concept of a system approach has been

introduced as an alternative for the study of community-level interactions in pollination systems (Thomson 1983).

Foraging ecology of pollinators has gained more interest in recent years. Pollinators have been viewed as optimal foragers in utilizing pollen and nectar from their preferred floral resources. Most current research on foraging of pollinators has been done with bees, especially honey bees (*Apis* spp.) and bumble bees (*Bombus* spp.) (Eickwort and Ginsberg 1980, Kevan and Baker 1983). However, only a relative few studies (Pearson 1933, Sakagami and Fukuda 1973, Ginsberg 1983) have investigated the foraging pattern of an entire assemblage of flower foragers at any one site over long periods. There have been no such studies in the Pacific Northwest of the U.S.

The western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone of the Pacific Northwest is one of the most important forestry areas in North America. Open areas created by clear-cutting in this zone are invaded primarily by herbs and shrubs. In early stages of forest regeneration or secondary succession, flowers of these herbs and shrubs are visited by various kinds of insects, both native and introduced.

The introduced western honey bee (*Apis mellifera* L.) was first brought into Oregon in 1854 (Williams 1975). Later, honey bees became well established both in nature and under domestic conditions. Honey bees are considered to be one of the dominant flower visitors in this zone.

They are found on numerous flower species and often occur in large numbers compared to other entomophilous species. It is suggested that the presence of honey bees as potential competitors on floral resources may have some profound effects on other flower foragers (Inouye 1977, Roubik 1978, 1980, Heinrich 1979, Schaffer et al. 1979, 1983). The presence of potential competitors as well as some plant attributes, such as flower abundance and diversity, have been illustrated as major factors determining foraging patterns of flower visitors (Brian 1957, Inouye 1978).

The overall goal of this research has been to elucidate the guilds of insect pollinators, especially those of bees, in clear-cut forests of the Oregon Coast Range and to investigate the causes of the observed foraging patterns. Specifically, the objectives are as follows: (i) to describe flower diversity and distribution over the study area; (ii) to identify the guilds of bee pollinators; (iii) to examine foraging activities and patterns of resource partitioning of the pollinators in the clear-cut regeneration; and (iv) to evaluate the extent of competition for floral resources between the introduced western honey bee (*A. mellifera*) and the wild bee fauna.

LITERATURE REVIEW

<u>Floral</u> <u>Resources</u>

Plant species, with notes on habitat, abundance, and time of flowering for most taxa in McDonald and Paul Dunn State Forests, have been listed by Hall and Alaback (1982). Vegetation in the Pacific Northwest of America was described by Hitchcock and Cronquist (1973). The early stages of secondary plant succession following logging and burning in the western hemlock zone of Oregon have been reviewed by Franklin and Dyrness (1973). They reported that during the first five years after slash burning, the plant cover is made up of residual species from the original stand, plus some invading herbaceous species such as groundsel (*Senecio sylvaticus* L.), fireweeds (*Epilobium* spp.), and thistle (*Cirsium vulgare* (Savi) Tenore). This successional stage, or so-called weed stage, is followed by a shrub-dominated period. Plant species important as floral resources for insect visitors include vine maple (*Acer circinatum* Pursh), trailing blackberry (*Rubus ursinus* Cham. & Schlecht), and *Rhododendron macrophyllum* G. Don. These shrubs will dominate the site until they are overtopped by the Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). Most research on successional patterns in this zone was limited to the first 5-8 years after clear-cutting. Therefore,

detailed studies for the entire period of forest succession have not been carried out.

The vegetation following logging and burning is typically very heterogeneous. Most of this variability is due to site differences caused by a wide range of types of logging disturbance and degree of burning severity (Dyrness 1965, 1973). Some plant species such as groundsel and fireweed seem to prefer burned areas, whereas the residual species are much more common on unburned sites (Morris 1958, Steen 1966).

A study of nectar and pollen plants of Oregon from the standpoint of honey bee foraging was done by Scullen and Vansell (1942). Plant species which were classified as important honey plants in Oregon, and commonly found in the clear-cuts, include fireweed (*Epilobium angustifolium* L.), big-leaf maple (*Acer macrophyllum* Pursh), vine maple (*A. circinatum*), and Canada thistle (*Cirsium arvense* (L.) Scop.). However, floral resources for pollinators in the early stages of forest regeneration have to date not been evaluated.

Apoidea Fauna

The Apoidea of the world are presently considered to consist of eleven families (Michener and Greenberg 1980). Seven families, i.e. Colletidae, Halictidae, Andrenidae, Melittidae, Megachilidae, Anthophoridae, and Apidae, are

present in northwestern America. Krombein et al. (1979) list 121 bee genera containing approximately 3,500 species in America, north of Mexico. Of these bees, 65 genera, consisting of 879 species, occur in northwestern America (Stephen et al. 1969). The latter authors estimated that 10 percent of the bee species possess some form of social organization, another 10 percent are parasitic, and the remaining 80 percent are solitary bees. They also gave information about the genera and biology of Apoidea in the Pacific Northwest. According to Stephen et al., the most abundant and diverse native bee genera in this area are: *Andrena*, *Nomada*, *Osmia*, *Halictus* s. str., *Perdita*, *Megachile*, *Melissodes*, and *Bombus*. The number of bee species in the Pacific Northwest is relatively low due to unfavorable climatic conditions. This is in contrast to the adjacent Californian region, which is one of the richest areas in bee fauna as indicated by Michener (1979).

Revisions of genera and subgenera of Apoidea in northwestern U.S. up to 1976 were listed in Krombein et al. (1979). Apoid taxa that have been revised after 1976 include many subgenera of the genus *Andrena*. The subgenera *Thysandrena*, *Dasyandrena*, *Psammandrena*, *Rhacandrena*, *Euandrena*, and *Oxyandrena* have been revised by LaBerge (1977). The subgenus *Cnemidandrena* has been revised by Donovan (1977), the subgenus *Melandrena* by

Bouseman and LaBerge (1979), and the subgenus *Andrena* by LaBerge (1980).

Foraging Behavior of Pollinators

The pollinator faunas and their relationships with local floras in northwestern U.S. have not yet been described. Most studies have been done with Apoidea in other areas of North America (e.g. in Florida by Graenicher (1930), in Illinois by Pearson (1933), and in New York by Ginsberg (1983)), and in Japan (Sakagami and Fukuda 1973, Ikudome 1978). Insect-flower relationships in general have been reviewed by Baker and Hurd (1968), Heinrich and Raven (1972), Proctor and Yeo (1973), Faegri and van der Pijl (1978), and Kevan and Baker (1983). Foraging behavior in Apoidea has been reviewed by Eickwort and Ginsberg (1980). Foraging of honey bees is discussed in many texts (e.g.: von Frisch 1967, Free 1970, Michener 1974, Gary 1975, and Seeley 1985). Foraging of bumble bees has been reviewed by Heinrich (1979). Foraging of wild bees in general has been reviewed by Linsley (1958, 1978) and Stephen et al. (1969).

Waddington (1983) proposed a model for studying foraging behavior of pollinators. He suggested that foraging behavior observed in the field is a function of both intrinsic and extrinsic factors. Intrinsic factors include sensory information, memory, learning, and

stereotypic behavior. These attributes are inherited or may be obtained as the result of previous experience. Extrinsic factors are the biotic and abiotic features of the environment, including floral characteristics and climatic conditions. A similar model is found in Ginsberg (1983). Ginsberg's innate characteristics of foraging behavior are equivalent to intrinsic factors. His "local" factors, that vary from site to site, are equivalent to extrinsic factors. However, Ginsberg considered the presence of potential competitors as an extrinsic factor, and he also illustrated this influence on foraging patterns of the bees.

Heinrich and Raven (1972) first emphasized an energetic approach in studying the foraging behavior of pollinators. Most studies were done with bumble bees (*Bombus* spp.) because of their high energy requirements and the relative ease in pursuing the bees during foraging. Recent studies (Heinrich 1976a, 1983, Whitham 1977, Pyke 1978a, 1978b, Hodges 1981) have shown that bumble bees forage for nectar from flowers in an optimal manner. This is not true for bees with low energy requirements such as short-tongued and small, solitary bees. These bees may be severely constrained during foraging by nonenergetic factors such as cold weather, cloud cover, and wind speed (Linsley 1958).

Robertson (1925) pointed out that the relationships between bees and flowers could be recognized on the basis

of pollen collection. He proposed the terms monolecty, oligolecty, and polylecty to apply specifically to the pollen preferences of the bees. Faegri and van der Pijl (1978) amplified the application of these terms to foraging specificity of pollinators. Flower-visitors that visit many different taxa of plants are termed polytropic (polyphagous, or polylectic). Those that restrict themselves to some related taxa of plants are oligotropic (oligophagous, or oligolectic). Flower-visitors which visit only a single or some closely related plant species are called monotropic (monophagous, or monolectic). A host-specific or oligophagous bee is more efficient at harvesting food from its preferred flower than is a polyphagous bee, which lacks preference for any one plant species (Eickwort and Ginsberg 1980). Polyphagy is common among social bees and other bees with activity periods longer than the blooming times of only a relatively few plant species, while oligophagy is essential for solitary bees with generation times shorter than the blooming of preferred plant species (Stephen et al. 1969). Equivalent terms, oligolectic and polylectic, are applied to pollen collecting specificity. Bees generally show greater flower specificity in pollen collecting than in nectar foraging (Linsley 1958, Baker and Hurd 1968, Stephen et al. 1969).

Foraging activity or flight periods of bees can be divided into daily and seasonal flight periods. Five

temporal categories of bees' daily activity were recognized by Linsley and Cazier (1970), i.e. matinal, diurnal, late afternoon, crepuscular, and nocturnal. The daily flight periods usually are associated with pollen and nectar production of the host plants (Linsley and Cazier 1970, Thorp and Estes 1975, Linsley 1978). Schaffer et al. (1979) observed diurnal variation in bee activity on *Agave schottii* in Arizona. They found that the western honey bee (*A. mellifera*) preferred to forage when resources were most abundant, i.e. early morning and late afternoon. Seasonal flight differences among different species of bees probably evolved to avoid competition (Stephen et al. 1969). In temperate North America, most species of the genus *Andrena* are active in the spring (Schemske et al. 1978). Different castes of some social bees forage at different times during the season. For example, queens of social halictines and *Bombus* forage in the spring, while workers are commonly found in the summer (Heinrich 1976b, Macior 1978). However, Sakagami and Fukuda (1973) and Ginsberg (1983) stated that peak seasonal activity of certain bee taxa were often correlated with the periods of maximal presentation of their food sources.

Physical environmental factors influencing foraging activities have been reviewed for solitary bees by Linsley (1958), and for pollinators in general by Kevan and Baker (1983). The most conspicuous factors, as pointed out by

Kevan and Baker, are light and cloudiness. Temperature effects are crucial during cool weather. Strong wind may cause the cessation of foraging activities of pollinators. Humidity affects nectar concentration of flowers, and thus has some indirect effects on foraging.

Resource Partitioning and Competition

Resource partitioning and competition among pollinators for pollen and nectar have been studied over limited areas by Heinthaus (1974), Heinrich (1976b), Macior (1978), and Ginsberg (1983). Partitioning of floral resources among flower-visiting insects might be indicated by foraging at different seasons or at different times of day (temporal partitioning), by visiting different patches of flowers (spatial partitioning), or by exploitation of different flower species (Linsley 1958, 1978, Eickwort and Ginsberg 1980).

Spatial partitioning can be classified into two categories: (i) foraging range, and (ii) differences in the use of patch sizes. Different bee taxa exhibit different patterns in spatial distribution of foraging. Some bees forage along certain paths and repeat the same foraging trips over several days. This behavior is called trap lining, and has been recognized in bumble bees (Heinrich 1976a) and orchid bees or euglossines (Janzen 1971). Most solitary and primitively eusocial bees, such

as halictines, forage within a few hundred meters from their nests (Wille and Orozco 1970). Honey bees (*A. mellifera*) normally forage within 1.0 kilometer of the hive (Free 1970, Gary et al. 1978). Visscher and Seeley (1982), in a study of honey bee colony foraging strategy in a temperate deciduous forest, found that *A. mellifera* routinely foraged within 6.0 kilometers of the colony, with the majority of foraging concentrated within 1.7 kilometers.

Another dimension in which bees can partition their foraging range is that of heighth, as has been documented in the forests of the Neotropical Region by Frankie and his colleagues (Frankie and Coville 1979, Frankie et al. 1976). Frankie and Coville (1979) found that several species of bees in the genera *Centris*, *Xylocopa*, *Eulaema*, and *Euglossa* preferred to forage on *Cassia biflora* shrubs at a high level (4.5 meters high) rather than at ground level.

Many species of the stingless bees in the genus *Trigona*, as well as honey bees, specialize on high-density flower resources (Johnson and Hubbell 1974, 1975, Schaffer et al. 1979, Ginsberg 1983). These bees tend to concentrate on large resource patches, presumably having excess pollen and/or nectar. Johnson and Hubbell (1975) proposed the terms "low and high-density specialists" to describe different foraging strategies of two stingless bees, *Trigona fuscipennis* Friese and *T. fulviventris*

Guerin. *T. fuscipennis*, which forage in large groups, restricted their visits to large, dense patches of *Cassia*. *T. fulviventris*, the low-density specialist, often forage as individuals or in small groups, visiting thinly spread or isolated plants.

Distantly related taxa of pollinators are commonly utilized different flower species. The difference in utilization of floral resources, when it occurs between closely related species or within the same species, is often described as "competition". Competition between pollinators for floral resources has been demonstrated experimentally at both the intraspecific and interspecific levels. Most pollinator competition studies have been done with bumble bees (*Bombus* spp.) (Kevan and Baker 1983). Plowright et al. (1978) compared foraging performance of laboratory-reared *Bombus* colonies in sprayed versus unsprayed areas. The colony performance was significantly better in sprayed areas with reduced numbers of other foragers than in unsprayed areas. In the unsprayed or control areas, pollen-collecting *Bombus* visited nearly twice as many plant species as *Bombus* in the sprayed area in order to obtain the same amount of food.

In interspecific competition, both interference and exploitation among pollinators have been illustrated by observational (Linsley and MacSwain 1959, Heinrich 1976b) and manipulative techniques (Johnson and Hubbell 1974,

Morse 1977, Inouye 1978, Laverty and Plowright 1985). Heinrich (1976b) studied resource partitioning among four common species of bumble bees in central Maine. He inferred that bees competed for nectar, and that competition was mainly exploitative. Overlap in resource utilization among the bees was avoided by differences in tongue length. Interference competition has been reported among stingless bees by Johnson and Hubbell (1974), and between two species of bumble bees by Morse (1977). Experimental demonstration of competition among flower-visiting insects has been demonstrated by using removal experiments on bumble bees by Inouye (1978), and Laverty and Plowright (1985). Both studies found evidence of competitive release in terms of an increase in the number of unremoved foragers and a broadening of flower choice to include more of the abandoned or previously unpreferred flower species.

Competition from _Apis mellifera_

The influence of honey bees on foraging patterns of other bees was reviewed by Eickwort and Ginsberg (1980). They concluded that honey bees do influence the foraging patterns of native bees by competition at resource sites. The impact of honey bees on native pollinators has been studied in different parts of the New World, e.g. in French Guiana by Roubik (1978, 1980), and in southern

Arizona by Schaffer et al. (1979, 1983). Roubik (1978, 1980) introduced hives of africanized honey bees to various locations in French Guiana. The honey bees were able to displace native stingless bees on certain flower species. He also did experiments utilizing artificial feeders instead of flowers. The honey bees again displaced the stingless bees, even though some of the displaced stingless bee species were aggressive. Schaffer et al. (1983) studied competition for nectar between *A. mellifera* and native bees and ants in Arizona. The authors saturated the study site with introductions of several hives of cordovan honey bees, a light-colored strain of *A. mellifera*. When they removed such hives from the area, they were able to observe a gradual increase in the number of darker feral honey bees on the flowers. Interestingly enough, the numbers of bumble bees and small solitary bees first increased and then declined.

Heinrich (1979) gave information on the influence of honey bees on indigenous bumble bees in the United States. He pointed out that a strong hive of honey bees, which collects an average of about 250 kilograms of honey in a season, might reduce the number of bumble bee reproductives by 38,400 individuals. The impact of honey bees on bumble bees also has been indicated by Inouye (1977). He reported that in Europe, where short-tongued *A. mellifera* is native, bumble bees have longer tongues than in North America.

MATERIALS AND METHODS

Study Sites

The study areas were in the McDonald and Paul Dunn State Forests of Oregon State University, Corvallis, Benton County, Oregon. Both forests are in Townships 10 and 11 South from the baseline running east and west near Portland, Range 5 West from the Willamette Meridian, which runs north to south through the Willamette Valley. Their areas are ca. 2,742 hectares for the McDonald Forest, and 1,839 hectares for the Paul Dunn Forest, lying approximately 25 kilometers northwest of Corvallis. The elevation range is from 150 to 540 meters above sea level. Annual rainfall averages 100 to 150 centimeters (Hall and Alaback 1982).

The McDonald and Paul Dunn Forests have a typical soil profile of 130 centimeters of reddish-brown silty clay loam that is sometimes gravelly, underlaid by fractured or partly weathered basalt. Soils are primarily of the Ritner, Price, or Jory series or some combination thereof. These soils are moderately to deeply well drained (Knezevich 1975).

Vegetation in the McDonald and Paul Dunn Forests is representative of that of the eastern foothills of the Oregon Coast Range and the western fringe of the Willamette Valley. Vegetational areas in the study have

been included in the western hemlock or *Tsuga heterophylla* zone by Franklin and Dyrness (1973). This region, which has been called Valley Margin Zone by Juday (1976), is characterized by a heterogeneity of vegetation types and is the most diverse of the Coast Range forest zones. No single tree species dominates this zone, and differs from other Coast Range vegetation zones in the near absence of western hemlock.

The studies were conducted on three 20 hectare clear-cuts at different stages of forest regeneration in the McDonald and Paul Dunn Forests (Figure 1). A clear-cut is a forest area in which all the trees in a stand of timber have been removed. The ages of the clear-cuts, counting from the date of deforestation, range from two to 14 years old. Successional stages are classified on the basis of vegetation types; herb stage (0-6 years old), herb-shrub stage (6-12 years old), and shrub stage (>12 years old). Site 1, which was clear-cut in 1982, is located in Townships 10 South, Range 5 West, Section 15 and 22 (or T10S, R5W, Sec. 15 & 22). It was a two year old clear-cut at the beginning of the study, and the early successional pattern is in the herb stage. Site 2 is in T10S, R5W, Sec. 23. It was clear-cut in 1975 (a 9 year old clear-cut in this study), and is classified as herb-shrub stage. Site 3 is in T11S, R5W, Sec. 17. It was clear-cut in 1970 (a 14 year old clear-cut in this study), and is classified as shrub stage.
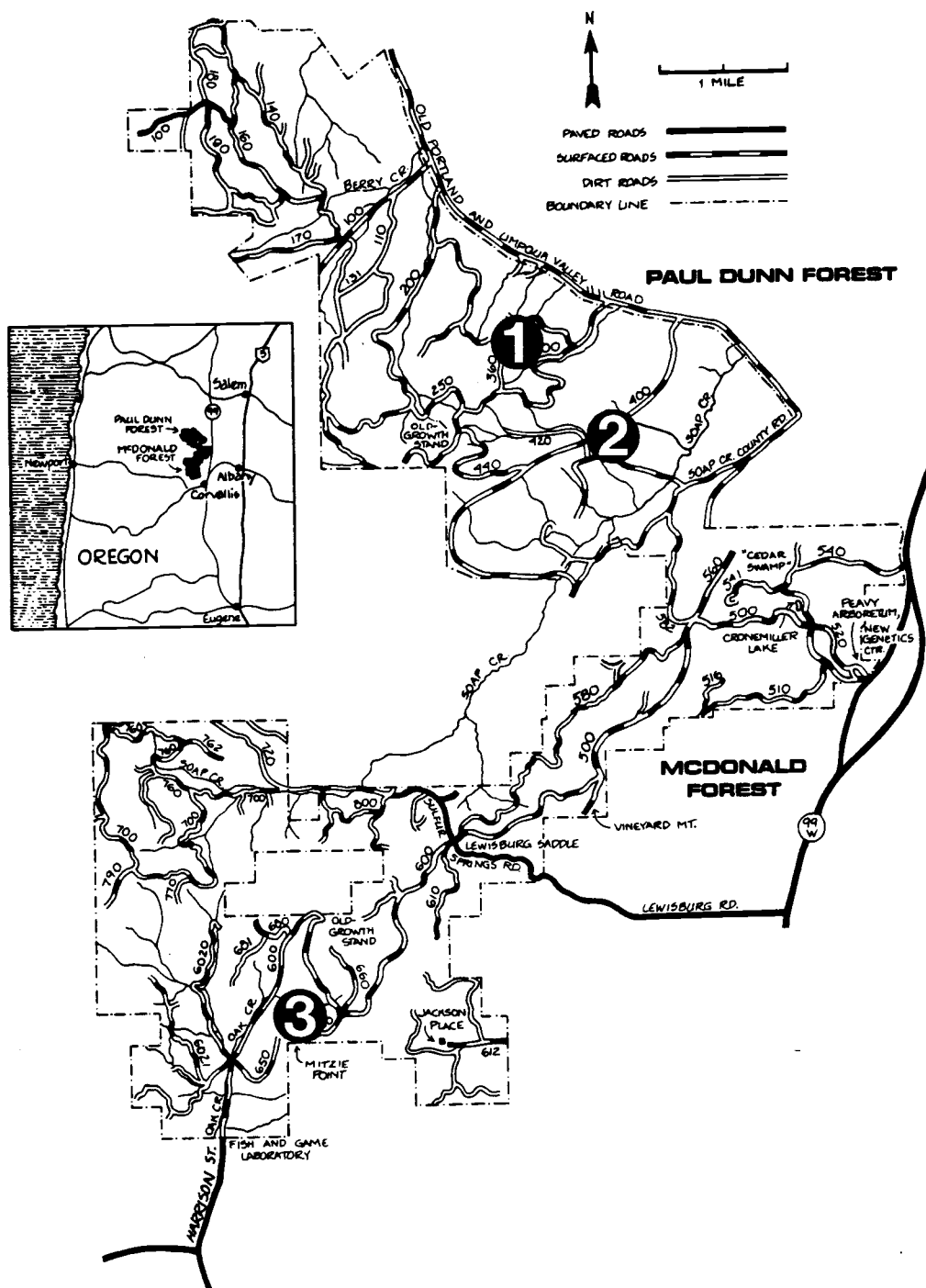
Figure 1. Map of the McDonald and Paul Dunn State Forests,
Corvallis, Oregon (from Hall and Alaback 1982).
The three study sites are shown by the numbers
in dark circles; site 1 (herb stage), site 2
(herb-shrub stage), and site 3 (shrub stage).

Flower Abundance and Insect Pollinators

In each clear-cut site, 5 permanent 20 (2x10) square meter quadrats were randomly selected in order to examine flower abundance and flower-visiting insects. The total sampling area for each clear-cut was 100 square meters. The sampling area was selected to include one quadrat along the roadsides. This was done because some flower species are more abundant along the roadsides compared to those in the clear-cuts. On sampling days I spent approximately 20 minutes per quadrat, identifying and counting both blooming floral units and flower-visiting insects. A floral unit is defined as a single flower or collective flowers in an inflorescence or head such as those of the Compositae. Blooming was judged from the period that nectar and/or pollen were available. Number of flowers was used to obtain an estimate of resources available to pollinators over the season. There are several ways to estimate floral resources in a study of plant-pollinator interactions. The first method is to count the flowers. A second method is to estimate nectar production by each flower species. A third method is to measure the flower abundance of each species by the size of the flower (e.g. Heithaus 1974, Moldenke 1975, and Ginsberg 1983). To count the flowers probably is the least accurate method, but Tepedino and Stanton (1982)

pointed out that the method is appropriate for estimation of resource availability.

The sampling was done once a week during the same time of the day from March 30 to August 14, 1984. Environmental data such as temperature, relative humidity, and wind speed were recorded. The observations were terminated in the middle of August because of the paucity of blooming flowers in the study sites, and it was considered to be the end of the foraging season for pollinator guilds in the clear-cut areas.

Identification of flowering plants in the clear-cuts followed Hall and Alaback (1982) and Hitchcock and Cronquist (1973). Nomenclature of Apoidea followed that of Krombein et al. (1979). Insect pollinators were identified in the field to at least the generic level. Insect specimens were regularly brought back to the lab for further identification to species. Voucher specimens of the insect species were placed in the Entomology Department Museum, Oregon State University.

Foraging Activity

Foraging activity of pollinators was examined for major entomophilous plant species. The important flower species were identified from the standpoint of the frequency of visitation by most kinds of pollinators, or similar to the "cornucopian" species of Mosquin (1971).

The important species are characterized by the following features: 1) they are abundant, and 2) their flowers offer abundant amounts of nectar and/or pollen in a manner convenient to a wide spectrum of pollinators.

Clusters of important flower species in the study sites were mapped for sampling. On the sampling day, a number of flower clusters were randomly selected from the map for examination of daily activity of pollinators. At certain periods of the day from 0800 to 1700, I spent 5-10 minutes at each cluster recording the number of flower-visiting insects. I recorded the number of immigrant insects coming into the investigated flower cluster, and the insects which were already present in the cluster at the beginning of the period. Only the insects that attempted to collect nectar and/or pollen were recorded. Environmental data as well as flower densities were also recorded. Nectar secretion of the flowers was measured by using calibrated microcapillary tubes. A number of flowers of the observed clusters were bagged to exclude nectar foragers. The flower nectar was removed regularly at certain times of the day, and the amount obtained was recorded. For floral nectar of *Ribes sanguineum*, the procedure was done with unbagged flowers. All the extrinsic factors mentioned above, i.e. environmental data, flower densities, and nectar volume, were examined to determine their effects on foraging activity of insect pollinators in the clear-cuts. Studies on foraging

activity of pollinators were carried out in the blooming season of 1984, 1985, and 1986. In the spring of 1984 and 1985, detailed examinations of foraging activity of flower-visiting insects on *Rubus ursinus* were conducted at site 1. Similar studies were performed in the summer of 1985 and 1986 with *Rubus discolor* Weihe & Nees at site 2, and in early spring of 1986 on *R. sanguineum* at site 3.

Resource Partitioning

Studies on resource partitioning among pollinators were done in the flowering seasons of 1984 and 1985. Three kinds of resource partitioning were investigated; temporal partitioning, spatial partitioning, and partitioning of flower species. On sampling days I randomly selected 3-5 different patch sizes of each flower species. The number of flower species which were selected for each study varied from one to five, depending on the season. I spent 5 minutes at each patch identifying bees and recording the number of each taxon (see previous section for sampling criteria). The sampling sequence was repeated at least three times over the day or on two consecutive days if necessary. The observed differences in visitation rates of flower-visiting insects over the day were examined for temporal partitioning. Differences in the uses of patch size and flower species were

illustrated for spatial partitioning and partitioning of flower species, respectively.

In 1984, I examined resource partitioning among pollinators on *Rubus ursinus* and *Rubus leucodermis* Dougl. at site 1, and on *R. discolor*, *Vicia cracca* L., *Cirsium arvense*, *Dipsacus sylvestris* Huds., and two species of Cichorieae (*Hypochaeris radicata* L. and *Taraxacum officinale* Weber) at site 2. In 1985, I did the study on *R. discolor* and *C. arvense* at both site 2 and site 3.

Competition from *Apis mellifera*

Manipulative techniques were employed to test the impact of the honey bee on native pollinators. Combinations of removal, supplementation, and exclusion of *A. mellifera* at the study sites were used to achieve this objective. The studies were done in 1985 and 1986 at all sites. Two hives of cordovan honey bees were used in 1985. The two hives consisted of approximately 32,000 bees with one-fourth to one-third of the population as foragers or about 8,000-10,000 bees. The cordovan line, obtained from a simple recessive mutation, is particularly suitable as a marker, because (1) there is no evidence to indicate that the mutation is in any way harmful, (2) cordovan bees are easily recognized by their light-brown bodies compared to dark-brown to black of the feral honey bees common to the study sites, and (3) the behavior of

cordovan marked bees is considered normal as compared to non-cordovan bees (Taber 1954, Peer 1956).

It was very difficult to exclude honey bees from flowers, especially in the summer at the study sites. However, I performed an equivalent to exclusion by the following approach. Hives of honey bees were introduced into the study sites in order to saturate flower patches with *A. mellifera*. By removing these hives later in the study, the utilization of the flowers by *A. mellifera* was presumed to be temporarily reduced, and thus it was possible to observe whether or not visitation frequency by the native species increased as a result.

In 1985, I supplemented flower foragers at site 2 by introducing the two cordovan hives on June 20. The hives were transferred from site 2 to site 3 on July 3, and then removed from site 3 on July 16. At both study sites, I recorded visitation of flower foragers for three intervals, i.e. before introducing the hives of honey bees, after introduction, and after removal of the hives. At site 2, the study was conducted from June 18 to July 5, 1985. Two clusters of *Rubus discolor* with approximately 100 flowers each were randomly selected on sampling days to determine the level of bee visitation. I spent five minutes at each cluster recording the number of each bee species. The investigated clusters were observed four times over the day, i.e. morning (0800-1000 hours), late morning (1000-1200 hours), noon (1200-1300 hours), and

afternoon (1300-1500 hours). Supplementation of cordovan honey bees at site 3 was carried out from July 2 to July 19, 1985. The observation was done on a large flower patch of *R. discolor* with more than 5,000 flowers. On the sampling day, I randomly selected three areas of the flower patch, and at each area I recorded the number of bees on 50 flowers for five minutes. The sampling was done twice for each investigated area at 1200-1300 hours and 1300-1500 hours.

In May 1986, I performed an exclusion experiment of *A. mellifera* on different patch sizes of *Rubus leucodermis* at site 1. Exclusion of *A. mellifera* was obtained by the combination of two procedures: 1) by using a sweeping net to carefully remove honey bees from the target patch before they attempted to harvest any food, and 2) by chasing the bees with a wooden stick when they landed on any flower in the patch. The procedures were carried out for four hours at each selected patch of *R. leucodermis*. One of the two treatments - either exclusion of *A. mellifera* or no manipulation (control treatment) - was randomly assigned to each patch on any given day. For example, if a flower patch received the exclusion treatment on the first day, it would then receive the control treatment on the next day, and vice versa. Visitation rates of native bees were recorded every hour for 15 minutes over the four-hour period of investigation. Each treatment was replicated 12 times. The observed

differences in visitation of the native bees, especially the bumble bees (*Bombus* spp.), were compared between the two treatments.

RESULTS AND DISCUSSION

Flower Abundance and Insect Pollinators

Seasonal distribution of floral resources

There were 33 entomophilous plant species in the study sites and along the nearby roadsides. The flowering season began in March and ended in August. Individual blooming periods (phenologies) for the 15 common flower taxa are shown in Figures 2, 3, and 4. The first flower species to bloom was red-flowering currant (*Ribes sanguineum*) at site 3 (shrub stage) (Figure 4), followed by other spring-blooming native species such as vine maple (*Acer circinatum*), big-leaf maple (*A. macrophyllum*), strawberry (*Fragaria vesca* L., and *Fragaria virginiana* Duchesne), blackberry (*Rubus ursinus*, and *R. leucodermis*), and black hawthorne (*Cretaegus douglasii* Lindl.). The late-spring and early-summer blooming plants are mostly introduced species, beginning with ox-eyed daisy (*Chrysanthemum leucanthemum* L.), vetch (*Vicia* spp., mainly *Vicia cracca*), snowberry (*Symphoricarpos albus* (L.) Blake), Himalayan blackberry (*R. discolor*), spotted cats-ear (*Hypochaeris radicata*), common dandelion (*Taraxacum officinale*), and St. John's wort (*Hypericum perfoliatum* L.). The summer period, considered in this study, begins with the blooming of *R. discolor*. The midsummer blooming species are fireweed (*Epilobium angustifolium*), Canada
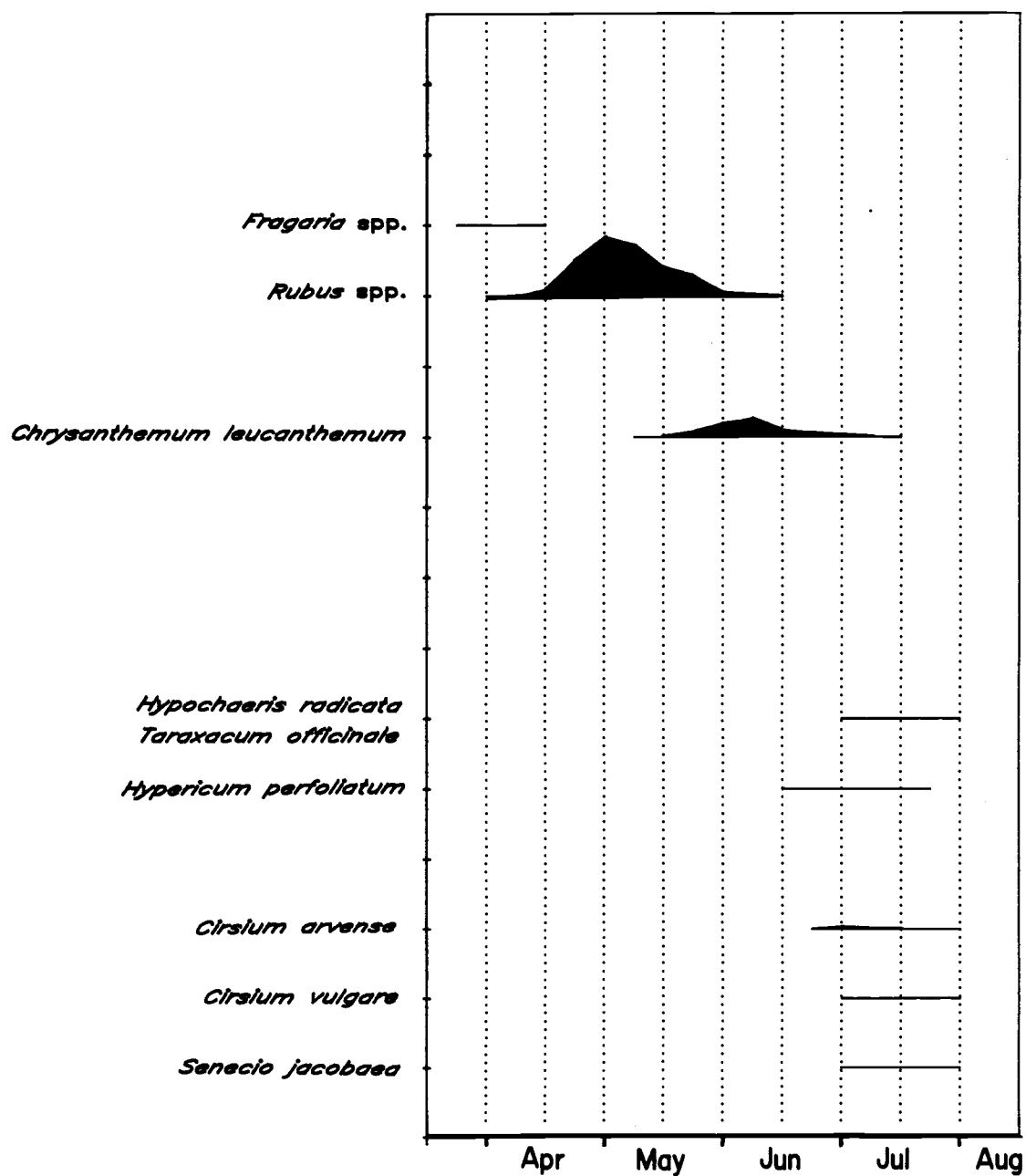
Figure 2. Phenologies of common flower species at site 1
(herb stage). Thickness of line indicates
relative abundance. Data from quadrats sample
in 1984.
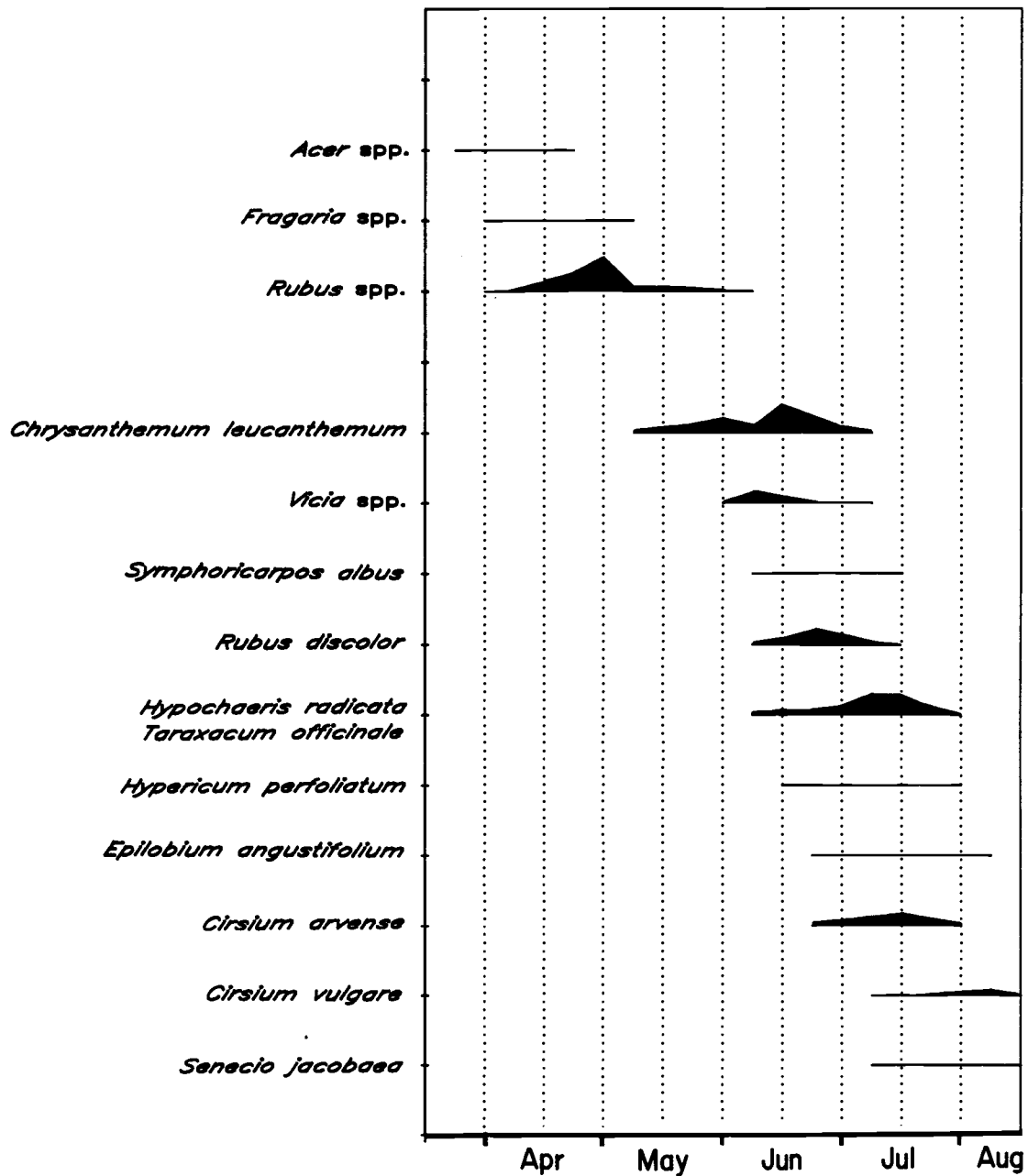
Figure 3. Phenologies of common flower species at site 2
(herb-shrub stage). Thickness of line indicates
relative abundance. Data from quadrats sample
in 1984.
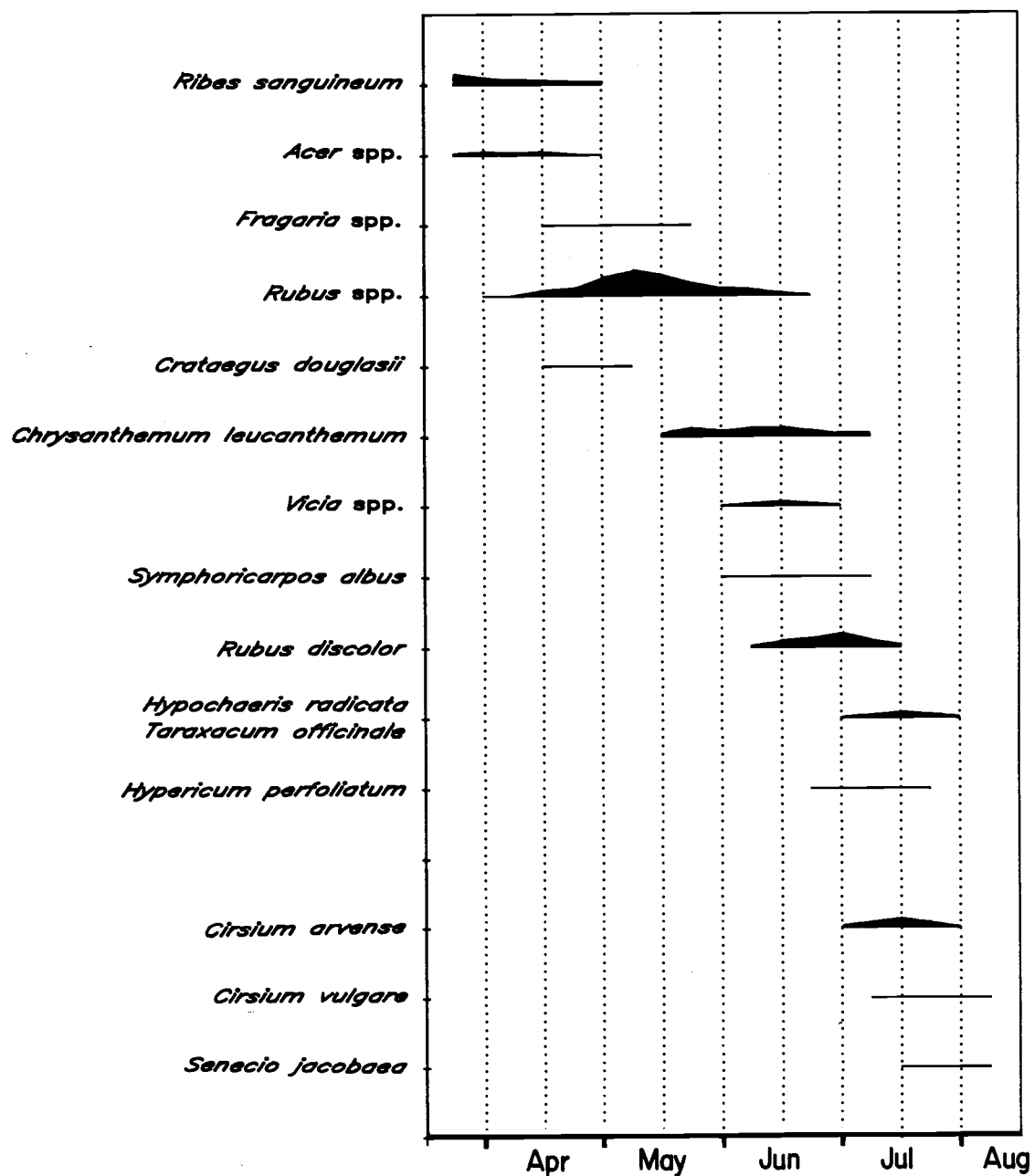
Figure 4. Phenologies of common flower species at site 3
(shrub stage). Thickness of line indicates
relative abundance. Data from quadrats sample
in 1984.

thistle (*Cirsium arvense*), and common thistle (*C. vulgare*). Flowering season in the early stages of clear-cut regeneration ended with the flowering of tansy ragwort (*Senecio jacobaea* L.), which begins blooming in July.

Species composition and relative abundance of floral taxa were different among three study sites as shown in Figures 2, 3, and 4. At site 1, which was classified as the herb stage of the early successional patterns, flowering species were *Fragaria* spp., *C. leucanthemum*, *H. radicata*, *T. officinale*, *H. perfoliatum*, *C. arvense*, *C. vulgare*, and *S. jacobaea*. Both *H. radicata* and *T. officinale* were labeled together in the figure because they are similar in general appearance, and it is not practical to separate them in the field. Native species of residual shrubs also were found. These were trailing blackberry (*R. ursinus*) and black raspberry (*R. leucodermis*), collectively labeled as *Rubus* spp. in the figure. This successional stage is dominated mainly by flowers of *Rubus* spp. and *C. leucanthemum*, and will eventually be covered by an increasing number of shrubs and by the expanding Douglas-fir (*Pseudotsuga menziesii*), which were planted following clear-cutting.

At site 2 (herb-shrub stage), flower species similar to those in site 1 were found, with an increasing abundance of some species such as *H. radicata*, *T. officinale*, *C. arvense*, and *C. vulgare* (Figure 3). Five more taxa of common floral resources appeared: *Acer* spp.,

Vicia spp., *S. albus*, *R. discolor*, and *E. angustifolium*.
The dominant flower species in site 2 were *Rubus* spp., *C.
leucanthemum*, *Vicia* spp., *R. discolor*, *H. radicata*, *T.
officinale*, *C. arvense*, and *C. vulgare*. Flowers of woody
plant species, such as *R. sanguineum*, *Acer* spp., and *C.
douglasii*, were common in the spring at site 3 (shrub
stage). At this stage (14 year old clear-cut), cultivated
Douglas-fir overtopped the herbaceous species growing
inside the clear-cut. Most of the flowering herbs and
shrubs were in abundance along the roadsides surrounding
the study site. The dominant floral resources at this
site were *R. sanguineum*, *Acer* spp., *Rubus* spp., *C.
leucanthemum*, *Vicia* spp., *R. discolor*, *H. radicata*, *T.
officinale*, and *C. arvense*.

The general trends in resource availability for
pollinators over the season are shown in Figure 5. They
are similar between site 2 and site 3 with three flowering
peaks, compared to one enormous peak at site 1 in the
spring. At site 1, the number of flowers increased
rapidly and reached its peak in early May, and then
declined to the end of the season in late July. The
flowering peak was obtained mainly from the native
blackberry (*Rubus* spp.) as indicated by the abundance area
in Figure 2. *Rubus* spp. were also abundant in site 2
(Figure 3) and site 3 (Figure 4), and contributed to an
early peak in both communities (Figure 5). The early
summer peaks of site 2 and site 3, as shown in Figure 5,
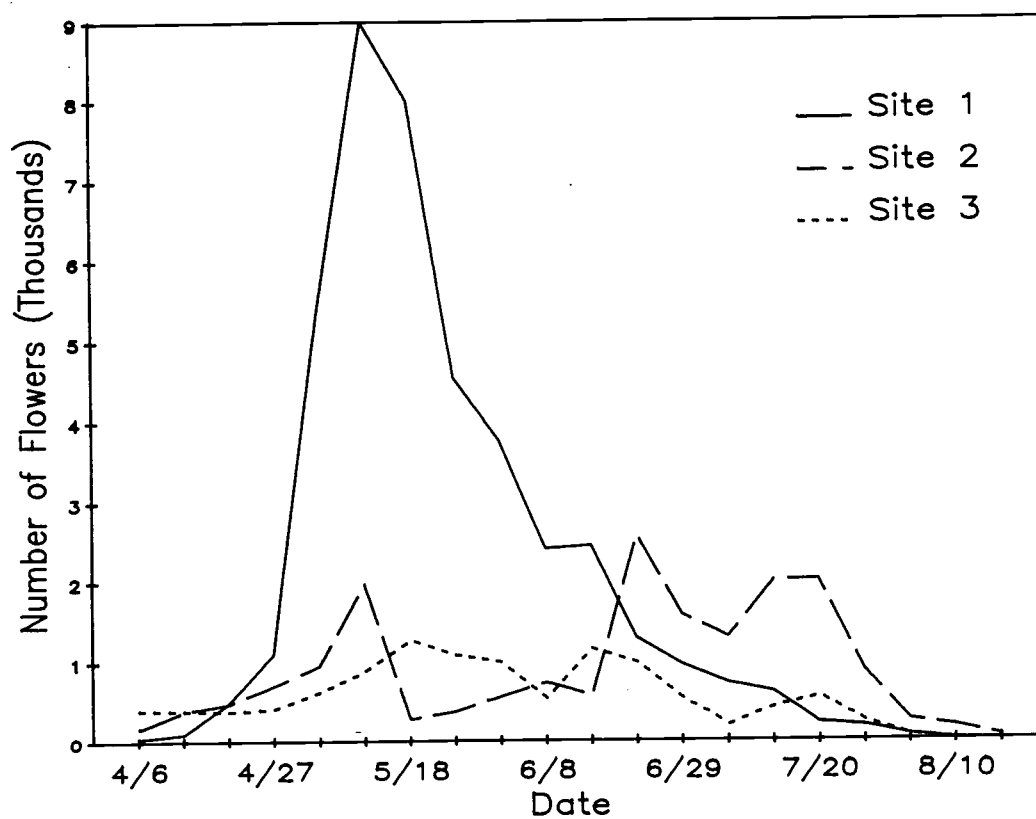
Figure 5. Relative abundance of floral resource (number of
flower in 100 square meters) in three study
sites. Data from quadrat samples in 1984.

were due to the blooming of *C. leucanthemum* and *Vicia* spp. The late summer peaks were obtained from flowers of *H. radicata*, *T. officinale*, and *C. arvense*. The flowering season of both site 2 and site 3 ended in August, and were longer than that of site 1.

Similarity of floral resources

Similarity of floral resources in the clear-cuts over the season has been quantified by considering two types of coefficients of similarity (CS & CN). A coefficient of similarity is a measure of the extent to which two habitats have species or individuals in common. The formulas for calculating CS and CN are obtained from Southwood (1978).

$$CS = 2j/(a + b),$$

where   a = number of species in habitat A

b = number of species in habitat B

j = number of species common to both habitats.

$$CN = 2jN/(aN + bN),$$

where   aN = total individuals sampled in habitat A

bN = total individuals sampled in habitat B

jN = sum of the lesser values for the species

common to both habitats.

Both coefficients were calculated for every 2-week period over the 1984 season among the three study sites. Their

values are shown in Table 1. Number of flower species was used as an estimate of abundance for calculating CN. The coefficient CS indicates the similarity in blooming species between the two compared sites. For example, in early June (6/8), site 1 and site 2 had ca. 85% (CS=.8571) of their species in common, while two weeks later the similarlity of species dropped down to 15% (CS=.1538). Both site 1 and site 2 were rather similar in species composition from the beginning of the season through the summer with CS values ranging from .6667 - .8571. The difference between CS and CN is that CN also includes the abundance of each species as a function of compositional similarity. Slightly more than half of the CS values in Table 1 had more than 50% similarity (i.e. 15 out of 27 cases), compared to 4 out of the total 27 cases obtained from the coefficient CN. This indicates that abundance was an important component of similarity among the study sites or, in other words, the relative abundance of each flower species was different from site to site.

Similarity is greater between the adjacent stages of early successional patterns, as indicated by the mean similarity coefficient values at the end of Table 1. The mean values of CS of site 1 & site 2 (.6345) and site 2 & site 3 (.5106) were larger than the value of site 1 & site 3 (.4820). A similar agreement is found also for the coefficient CN. Both mean values obtained from comparisons between the adjacent stages (.4221 and .3313)

Table 1. Coefficients of similarity (CS & CN) of resource
          availability over the season among three study
          sites (1, 2, and 3) in 1984.

Date	CS = 2j/(a+b)			CN = 2jN/(aN+bN)		
	1 & 2	1 & 3	2 & 3	1 & 2	1 & 3	2 & 3
4/13	.8000	.3333	.5714	.4286	.0124	.0608
4/27	.8000	.5000	.6667	.7661	.2199	.3143
5/11	.6667	.5714	.5714	.3578	.1642	.5559
5/25	.8000	.6667	.5714	.1382	.3017	.3292
6/8	.8571	.4444	.5000	.4657	.2345	.3221
6/22	.1538	.3636	.4286	.6364	.3076	.3693
7/6	.5000	.4286	.5556	.4610	.2920	.2603
7/20	.5333	.3636	.2857	.1583	.3868	.4042
8/3	.6000	.6667	.4444	.3869	.8070	.3654
Mean	.6345	.4820	.5106	.4221	.3029	.3313
Sum(>.50)	7	3	5	2	1	1

were larger than the value from the non-adjacent stages (.3029).

Pollinator fauna

Common flower-visitors or pollinators in the clear-cuts were bees, flies, pollen-feeding beetles, and hummingbirds. Of all flower visitors found in this study (96 species), 83.34% (80 species) were bees, 14.58% (14 species) were flies (Diptera), and 2.08% were cerambycid beetles (1 species) and hummingbirds (1 species) (Figure 6). Species of flower-visiting insects and their floral resources in this study are presented in the Appendix.

The estimated number of bee species and genera in the clear-cuts and in the Pacific Northwest are given in Table 2. Fifteen out of 65 Pacific Northwest genera were observed during the course of this study. The total number of bee species found in the clear-cuts (80 species) is 13.5% of that described for the Pacific Northwest (594 species, Stephen et al. 1969). Of the 80 species, 43 were solitary, 28 were social or semi-social, and 9 were parasitic. Among the northwestern species of bees, it was estimated by Stephen et al. (1969) that 80% are solitary, 10% are either social or semi-social, and the remaining 10% are parasitic. The observed proportion (43 : 28 : 9) of the three life styles of bees in the clear-cuts was significantly different from the expected value (64 : 8 :
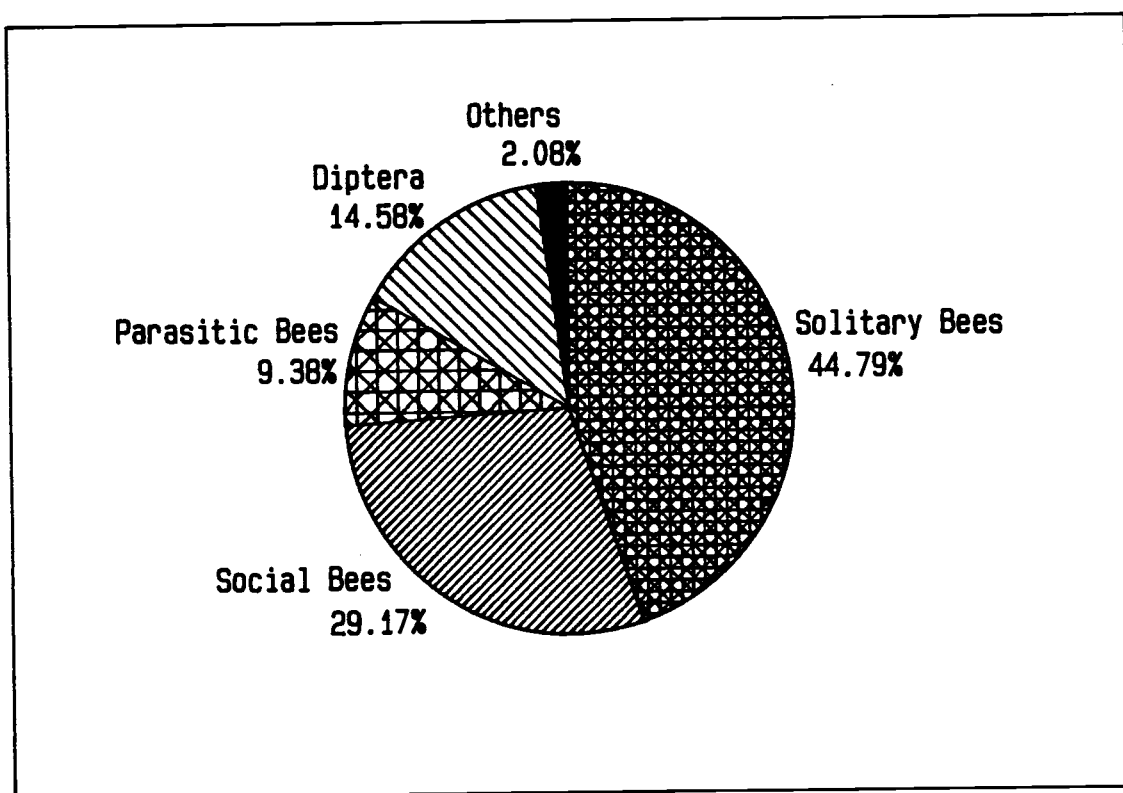
Figure 6. Proportion of flower visitors in the study sites. Full circle represents the total of 96 species.

Table 2. Estimated number of species of bee genera in the study sites, with reference to the number of species in the Pacific Northwest (PNW)[1].

Genus	Life style	Species		as % of PNW species
		PNW	This study	
Agapostemon	Solitary	5	1	20.0
Andrena	Solitary	200	22	11.0
Apis[2]	Social	1	1	100.0
Bombus	Social	27	10	37.4
Ceratina	Solitary	5	2	40.0
Halictus[3]	Social[4]	50	19	38.0
Hylaeus	Solitary	20	1	5.0
Megachile	Solitary	40	3	7.5
Melissodes	Solitary	40	1	2.5
Nomada	Parasitic	90	5	5.6
Osmia	Solitary	75	9	12.0
Panurginus	Solitary	7	1	14.3
Psithyrus	Parasitic	4	2	50.0
Sphecodes	Parasitic	20	2	10.0
Synhalonia	Solitary	10	1	10.0
Totals		594	80	

[1]Data from Stephen et al. (1969).
[2]Introduced species.
[3]*Halictus* + *Lasioglossum* + *Evylaeus* + *Dialictus*.
[4]include communal species (see Roberts 1973).

8) of the Pacific Northwest (goodness of fit test; chi-square = 57.02, df = 2, P <.001, Sokal and Rohlf 1981).

The increased number of social taxa suggests an availability of nesting sites and floral resources for these bees. The social bees, specifically social halictines (*Halictus*, *Lasioglossum*, *Evylaeus*, and *Dialictus*) and bumble bees (*Bombus*), generally have colony life cycles longer than the blooming of any individual plant species. These bees start their colony cycles with overwintered females in the spring and have their first generation of workers emerge in late spring or in early summer. Because of the lengthy periods of their colony cycles, the social bees must rely on more than a single flower species. In this study, the blooming sequence, beginning with the native species of blackberry (*R. ursinus* and *R. leucodermis*) in the spring followed by the introduced species (*R. discolor*) in the summer as well as members of Cichorieae (*H. radicata* and *T. officinale*), was synchronized well with the cycles of these social bees.

The 80 species of bees found in this study are in six families; Colletidae, Andrenidae, Halictidae, Megachilidae, Anthophoridae, and Apidae (see Appendix). The most primitive family of living bees, Colletidae, is represented by one species in this study, *Hylaeus* (*Paraprosopis*) *wootoni* (Cockerell).

The family Andrenidae is represented by two genera, *Andrena* and *Panurginus*. The common species of *Andrena* in

the study sites are *A.(Andrena)* *hemileuca* Viereck, *A.(Euandrena)* *nigrocaerulea* Cockerell, *A.(Melandrena)* *nivalis* Smith, *A.(Opandrena)* *cressonii infasciata* Lanham, and *A.(Trachandrena)* *amphibola* (Viereck). These bees are all polylectic, i.e. non-specific in pollen gathering (Krombein et al. 1979), and frequently were associated with flowers of *Rubus* spp. in the clear-cuts.

The family Halictidae is represented in this study by genera in the subfamily Halictinae. These include *Agapostemon, Halictus, Lasioglossum, Evylaeus,* and *Dialictus.* Two species of parasitic halictines in the genus *Sphecodes* were found; the larger species, *S. arvensiformis* Cockerell, is a parasite of *Halictus (H.) farinosus* Smith

Halictus, Lasioglossum, Evylaeus, and *Dialictus* were collectively labeled as *Halictus* by Stephen et al. (1969). Two genera, *Halictus* and *Lasioglossum (Lasioglossum +* *Evylaeus + Dialictus)* were recognized by Michener (1974). These social halictines are treated here as four separate genera, unless otherwise specified. The common social halictines in the study sites are *H.(H.) farinosus, H.(H.) ligatus* Say, *H.(Seladonia) confusus arapahonum* Cockerell, and *Lasioglossum olympiae* (Cockerell).

The family Megachilidae is represented by the genera *Osmia* and *Megachile.* Members of *Osmia,* especially *O.(Monilosmia) atrocyanea atrocyanea* Cockerell and

O.(Osmia) lignaria propinqua Cresson, are commonly found in the study sites.

The family Anthophoridae is represented by a parasitic genus *Nomada*, and by members of the solitary bee genera *Melissodes, Synhalonia,* and *Ceratina.* The most common species observed in this study was *Ceratina (Zadontomerus) acantha* Provancher.

The family Apidae is represented by two genera, *Bombus* and *Apis.* The common species of bumble bees found in the study sites are *Bombus (Pyrobombus) mixtus* Cressen, and *B.(Fervidobombus) californicus* Smith. The single occurring species of the genus *Apis, A. mellifera,* was the dominant flower visitor in this study.

The 14 species of flies (Order Diptera) found in the study sites are in two families, Bombyliidae and Syrphidae. One species of Bombyliidae, *Bombylius major* L., was found. Of the 13 species of syrphid flies, *Eristalis tenax* L. and *Scaeva pyrastri* (L.) were the most abundant dipterous pollinators. Three species of syrphids, *Criorhina nigripes* (Williston), *C. tricolor* Coquillett, and *Eristalis bardus* (Say), exhibit Batesian mimicry of bumble bees. Mimetic relationships are quite common in many temperate habitats as pointed out by Waldbauer and LaBerge (1985). Both *C. nigripes* and *C. discolor* resemble *B.(P.) mixtus,* while *E. bardus* is a bumblebee mimic of *B.(Subterraneobombus) appositus* Cresson.

<u>Foraging Activity</u>

Seasonal activity

Foraging activity levels of pollinators closely follow resource availability over the season (Figure 7). Both factors are positively correlated as indicated by the correlation coefficients (r- values). The r-values for site 1, site 2, and site 3 are 0.99, 0.68, and 0.75, respectively; each coefficient is significantly different from zero with P <.01, n=20 (Neter et al. 1983). Foraging activity levels are the sum of the activity levels of *Apis*, *Bombus*, *Halictus* (*Halictus* + *Lasioglossum* + *Evylaeus* + *Dialictus*), *Andrena*, other bees, and flies (Diptera). The activity levels of these insects were subjected to correlation analysis with resource availability. The results, as presented in values of simple correlation coefficient, are shown in Table 3. Foraging levels of five common forager taxa, i.e. *Apis*, *Bombus*, *Halictus*, *Andrena*, and Diptera are also plotted against resource availability in Figure 8.

At site 1 (herb stage), the population levels of most forager taxa are highly correlated with food sources (number of flowers), except those of *Bombus* and of certain other bees (Table 3). The r-values between the number of these forager taxa (*Apis*, *Halictus*, *Andrena*, and Diptera) and the number of flowers are greater than .94 (Table 3). The two most abundant taxa contributing to an enormous

Figure 7. Relationships between resource availability
levels (number of flowers in 100 square meters)
and flower-visitors (number of foragers seen in
1 hour and 40 minutes) in three study sites;
i.e. site 1 (top chart), site 2 (middle chart),
and site 3 (bottom chart). Correlation
coefficient (r) between the two factors is
presented in a box. Data from quadrat samples
in 1984.
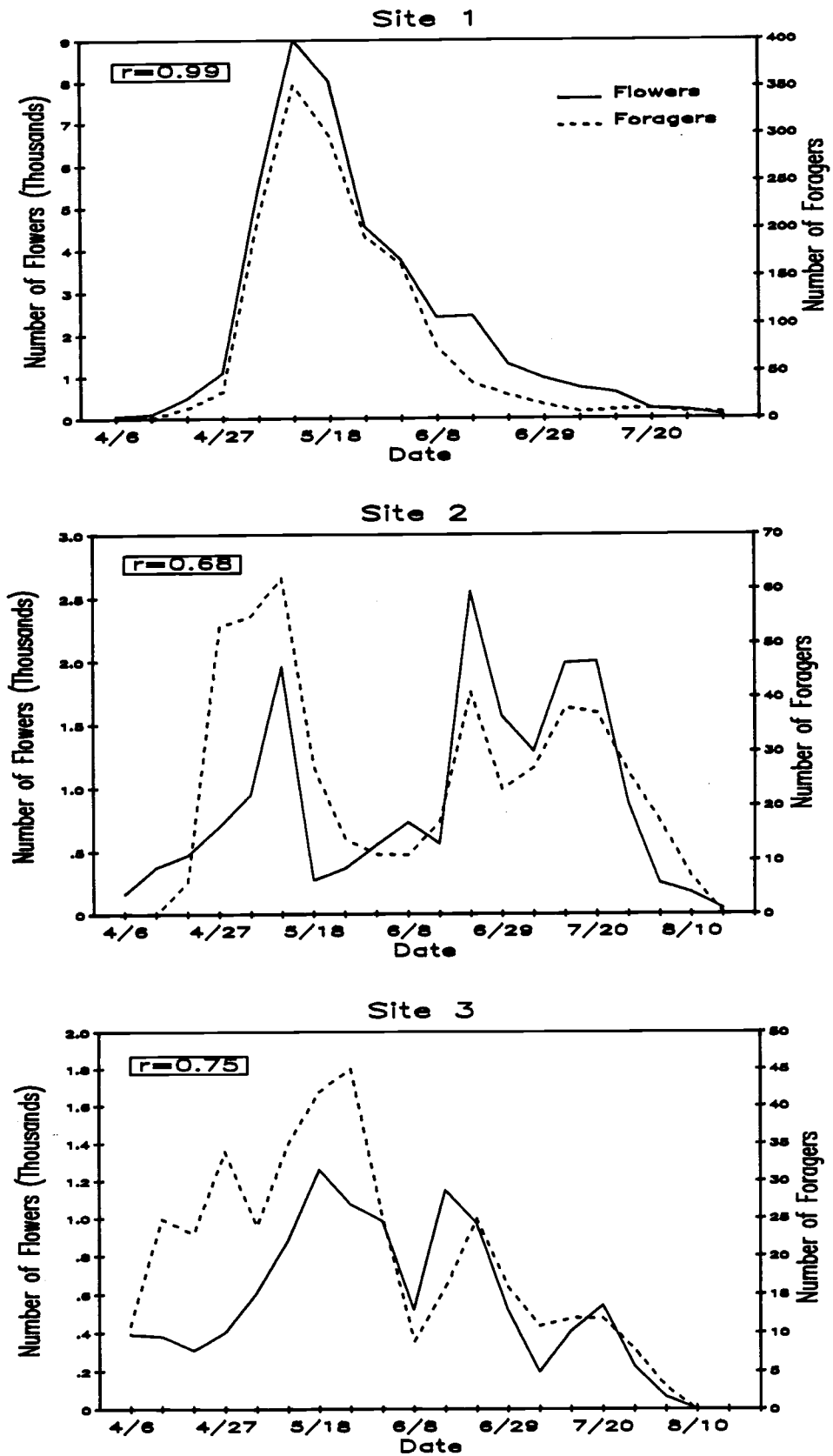
Figure 7.

Table 3. Correlation coefficients among the number of
flowers (Fl), total insects (In), total bees
(Be), *Apis* (Ap), *Bombus* (Bo), *Halictus* (Ha),
Andrena (An), other bees (Ot), and Diptera (Di)
in the study sites. Data from quadrat samples
in 1984.

Site 1

	Fl	In	Be	Ap	Bo	Ha	An	Ot
In	.989							
Be	.985	.999						
Ap	.979	.996	.998					
Bo	-.153[N]	-.125[N]	-.124[N]	-.133[N]				
Ha	.958	.934	.921	.903	-.142[N]			
An	.949	.957	.947	.938	-.007[N]	.947		
Ot	.211[N]	.249[N]	.269[N]	.264[N]	-.289[N]	.088[N]	.017[N]	
Di	.987	.992	.985	.978	-.126[N]	.955	.971	.193[N]

Site 2

	Fl	In	Be	Ap	Bo	Ha	An	Ot
In	.681							
Be	.703	.995						
Ap	.763	.917	.906					
Bo	.583	.506	.542	.452				
Ha	.539	.715	.741	.516	.406[N]			
An	.021[N]	.696	.667	.479	-.024[N]	.525		
Ot	.638	.694	.735	.526	.399[N]	.639	.359[N]	
Di	.261[N]	.589	.511	.643	.029[N]	.181[N]	.527	.010[N]

Site 3

	Fl	In	Be	Ap	Bo	Ha	An	Ot
In	.751							
Be	.777	.978						
Ap	.802	.844	.913					
Bo	-.168[N]	-.148[N]	-.121[N]	-.110[N]				
Ha	.632	.695	.713	.798	-.102[N]			
An	.215[N]	.678	.604	.411[N]	-.159[N]	.400[N]		
Ot	.437[N]	.544	.534	.281[N]	-.380[N]	-.046[N]	.160[N]	
Di	.481	.780	.634	.406[N]	-.220[N]	.422[N]	.675	.451

[N] Non-significant different from zero, P>.05, n=20.

Figure 8. Foraging activity levels (number of foragers seen in 1 hour and 40 minutes) of five common insect taxa (*Apis, Bombus, Halictus, Andrena,* and Diptera) in three study sites; i.e. site 1 (top chart), site 2 (middle chart), and site 3 (bottom chart). Data from quadrat samples in 1984.

Site 1

Apis
Bombus
Halictus
Andrena
Diptera
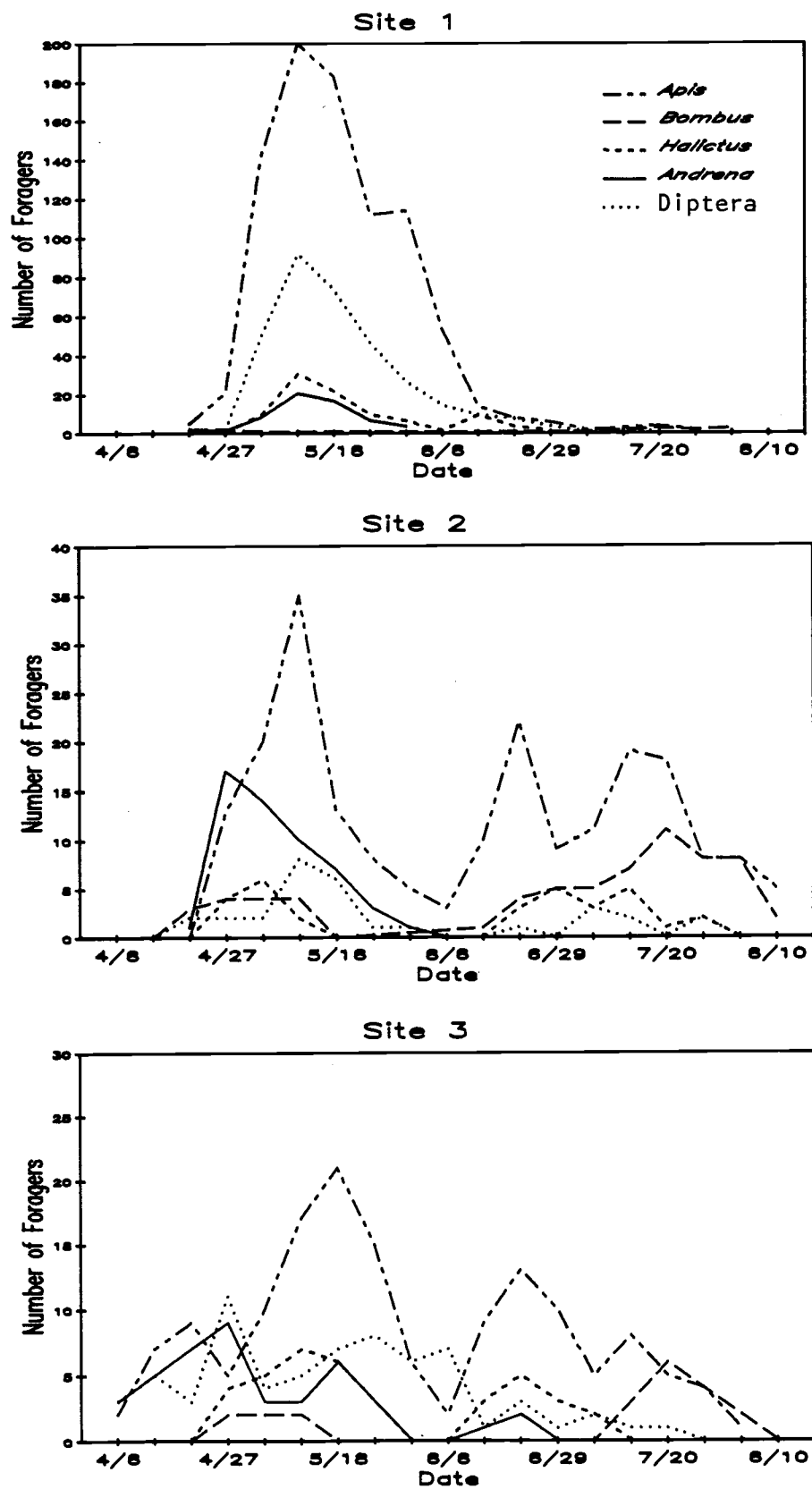
Site 2

Site 3

Figure 8.

peak in the spring at site 1, are *Apis*, and Diptera (Figure 8). At both site 2 (herb-shrub stage) and site 3 (shrub stage), the population levels of *Apis* are highly correlated with the number of flowers (Table 3: site 2, r=.763; site 3, r=.802). *Apis* are also abundant at both site 2 and site 3 as illustrated in Figure 8. Diptera and *Andrena* are the second most abundant forager taxa in the clear-cuts. Dipterous adults are more common in the spring than *Andrena* at site 1, and their foraging activity levels fluctuated throughout the season in other study sites (Figure 8). Species of *Andrena* are commonly found in the spring, and only at site 3 are their activities prolonged into early summer as shown in Figure 8. They are found collecting pollen from thimbleberry (*Rubus parviflorus* Nutt.), which is a pollen source during late spring and early summer at site 3. Females of the primitively social *Halictus* emerge from overwintering sites, begin their life-cycle in the spring, and continue to forage into the summer with their worker castes (Stephen et al. 1969, Nye 1980). These two rhythms of activity are well represented in the clear-cuts as shown by the two peaks of seasonal activity of *Halictus* in Figure 8.

Foraging levels of another primitively social group, *Bombus*, are similar to those of *Halictus* at clear-cut site 2 and site 3 (Figure 8). *Bombus* populations are relatively low compared to other forager taxa,

particularly at site 1 (Figure 8), despite the richness of floral resources (Figure 5). Their foraging levels are not correlated with resource availability as indicated in Table 3 ($r = -.153$; not significantly different from zero, $P > .05$). It is possible that the preferred foraging areas of bumble bees are not in the clear-cuts, but rather at sites close to water, in which bumble bees often are abundant (Heinrich 1979). Such ideal foraging sites for bumble bees are found in abundance along the creeks throughout McDonald and Dunn Forests (Figure 1). Another reason for the low *Bombus* populations may be the competitive interactions with other flower foragers. *Bombus* may prefer not to forage at flower patches already occupied by other foragers, as indicated by the lack of correlation between the number of *Bombus* and the number of other flower foragers at site 1 (Table 3).

Daily activity

Only the day-time activity (diurnal) of flower-foragers was investigated in this study. Night-time activity (nocturnal) as well as marginal activities, such as matinal and crepuscular, of pollinators were not examined. These later activities are common in warmer regions such as in the southwestern United States (Linsley 1978).

Effects of relative humidity, air temperature, number of flowers, and nectar production, on daily activity of

flower foragers were investigated. The activity levels of
flower foragers were measured as the number of such
foragers seen in 5-10 minutes. These were done with *Ribes
sanguineum* in early spring, with *Rubus ursinus* in mid-
spring, and with *Rubus discolor* in the summer. Multiple
regression of forager activity levels on relative humidity
(RH), temperature (TC), number of flowers (FW), and nectar
production (NP) was performed in order to examine which
effect is significantly involved in the variation observed
in forager activity. The independent variables (RH, TC,
FW, and NP) included in the regression equation were
judged by the method of stepwise selection in a regression
subprogram of the SPSS computer package (Anonymous 1986).
The summary of multiple regression analyses is presented
in Table 4. With *R. sanguineum*, there is a regression of
foraging activity (number of foragers) on temperature
(TC). Temperature accounts for 29.68% (R^2 = .2968) of the
variation in the number of foragers observed on *R.
sanguineum*. Foraging activity increases as temperature
increases, as indicated by the positive value of the
regression coefficient (.374). With *R. ursinus*, there is
a multiple regression of forager activity on number of
flowers (FW), temperature (TC), and relative humidity
(RH). All three factors account for 72.88% (overall R^2 =
.7288) of the variation in the number of foragers observed
on *R. ursinus*. Relative humidity (RH) has an inverse
relationship with foraging activity as indicated by the

Table 4. Regression report on the effects of relative humidity (RH), temperature (TC), number of flowers (FW), and nectar production (NP) on number of foragers observed on three plant species: *Ribes sanguineum* (n=28), *Rubus ursinus* (n=30), and *Rubus discolor* (n=30).

Plant species	Variables Included[1]	Regression coefficient	Simple R-squared	Overall F	R-squared
Ribes sanguineum	TC	.374*	.2968	10.97*	.2968
Rubus ursinus	FW	.020*	.5907	23.29*	.7288
	TC	5.479*	.2347		
	RH	-2.884*	.0185		
Rubus discolor	FW	.045*	.5512	35.88*	.7266
	NP	21.867*	.1813		

[1]stepwise selection in regression subprogram of SPSS.
*significant different at $P < .05$; test for regression coefficient = 0.

negative value in Table 4 (-2.884). This means that foraging activity increases as relative humidity decreases. Number of flowers (FW) and daily nectar production (NP) explain 55.12% and 18.13% of the variation in the number of foragers seen on *R. discolor*, respectively. When both factors are included in the regression equation, they account for 72.66% of the variation in forager activity. The number of foragers increases with increase in nectar production and number of flowers (Table 4). Another environmental factor, i.e. wind speed, was generally under 8 kilometers per hour in the study sites. At this level it seems to have only a minor effect on foraging activity. For *A. mellifera*, the wind-speed threshold is 11 kilometers per hour (Eisikowitch 1978), which is above the maximum wind speed in the study sites.

Larger bees, such as bumble bees, which can regulate their own body temperature, start flying at 7-9 degrees Celsius in early spring. The early-spring bees such as *Andrena*, honey bees (*A. mellifera*), and pollen-feeding flies and beetles, start their flying activities at 11-13 degrees Celsius and often restrict themselves to the sunlit flower patches. Temperature effects are noticeable in cool weather (Kevan and Baker 1983), especially in early spring in the study sites as indicated by the regression analysis on *R. sanguineum*. The only factor

that accounts for the variation in foraging activity is air temperature (Table 4).

In early May, pollinator flying activity in the clear-cuts begins at 14-16 degrees Celsius. Extrinsic factors still influence flower-visiting insects during this period. Air temperature often stays lower than the threshold level of flight. Both rain and near continual cloudiness over the day, which are quite common in early May, generally obstruct pollinator activity. The result of multiple regression analysis on *R. ursinus* (Table 4) specifically illustrates the effects of these environmental factors. Pollinator foraging activity during this period is governed by the number of flowers available, air temperature, and finally relative humidity.

Daily secretion of floral nectar is one of the best estimators of resource availability for pollination studies (Zimmerman and Pleasants 1982). It should be a good indicator of foraging activity when the effects of physical factors such as temperature and relative humidity are not so severe, as appeared during the summer in the study sites. The foraging activity study on *R. discolor* clearly illustrates this point. Nectar production, as well as number of *R. discolor* flowers, account for most of the variation in the number of foragers (Table 4).

Resource Partitioning

Temporal partitioning

The pollinator taxa in the clear-cuts may be grouped into four categories based on seasonal activity and life histories. These are (1) spring native pollinators, (2) summer native pollinators, (3) parasitic bees, and (4) the introduced honey bee (*A. mellifera*). The beginning of summer was judged from the blooming of *R. discolor* in the study sites.

Spring native pollinators are comprised of solitary bees in the genera *Andrena*, *Ceratina*, *Osmia*, and *Synhalonia*; of emerging females of primitively social bees in the genera *Bombus*, *Dialictus*, *Evylaeus*, *Halictus*, and *Lasioglossum*; and of pollen-feeding flies and beetles. These bees, as well as syrphid flies, are commonly found on native shrubs (*R. ursinus* and *R. leucodermis*). Pollen-feeding flies and beetles are also common in the spring, especially on flowers of woody plant species such as *A. macrophylllum*, and *C. douglasii*.

Summer native pollinators include solitary bees of the genera *Hylaeus*, *Megachile*, *Panurginus*, and *Melissodes*. First-generation workers of the primitively social genera also emerge at this time. The majority of these bees are foraging for pollen and nectar from flowers of *R. discolor*. Flies are also found in the summer, and often

associate with flowers of *C. leucanthemum*, *H. radicata*, and *T. officinale*.

Genera of the parasitic group found in the study sites are *Nomada*, *Sphecodes*, and *Psithyrus*, which are social parasites of *Andrena*, *Halictus*, and *Bombus*, respectively. Both *Nomada* and *Sphecodes*, which are univoltine, forage for their own needs on the same flower species as their hosts. Males and females of *Psithyrus* are common on the flowers of late summer-blooming species, especially those of *C. arvense*.

Honey bees are commonly found throughout the season. Their seasonal trends follow resource availability as indicated by the correlation coefficients in Table 3. The population levels of *A. mellifera* were much higher than other foragers over the season (Figure 8), and may have depressed the foraging populations of certain native bee taxa.

Intrinsic features of forager life cycles seem to offer the most direct explanation of the differences in foraging times, or seasonal partitioning. Species of holarctic *Andrena* are typically abundant in the spring (Michener 1974), and often forage on spring forest flowers (Schemske et al. 1978). The fertilized females of multivoltine social bees, such as *Bombus*, *Halictus*, *Lasioglossum*, and *Evylaeus*, emerge from overwintering sites in the spring, begin their colony cycles, and produce offspring or workers which are common in the

summer (Stephen et al. 1969). Two closely related genera, *Synhalonia* and *Melissodes*, of the tribe Eucerini, subfamily Anthophorinae, may be easily separated from each other by using differences in seasonal occurrence (Stephen et al. 1969). *Melissodes*, the most common eucerine genus in the Pacific Northwest in both numbers and species, is found flying in the summer, whereas the second most abundant eucerine, *Synhalonia*, is common in the spring. This could have been the result of competitive interactions in the past. Large colony size, longevity, polyphagy, and the ability to recruit additional foragers to favorable resource sites, allow the honey bees to utilize the most productive period of the flowering season. The foraging phenology in the clear-cuts is more likely to result from innate or intrinsic factors rather than local or extrinsic factors.

In the spring, floral resource partitioning by divergence in diel flight periods appears between *Apis* and *Bombus*. Observations made on *R. ursinus* and *R. leucodermis* at site 1 (herb stage) indicated that *Bombus* forages early in the morning at lower temperature (13.5 degrees Celsius) than does *Apis*, which is common at higher ambient temperatures (16 degrees Celsius) (Figure 9). There were ca. 5.47 individuals of *Bombus* seen in 5 minutes on 100 *Rubus* flowers at 13.5 degrees Celsius, compared to 2.47 individuals at 16 degrees Celsius. The mean difference of 3 individuals (5.47 - 2.47) is
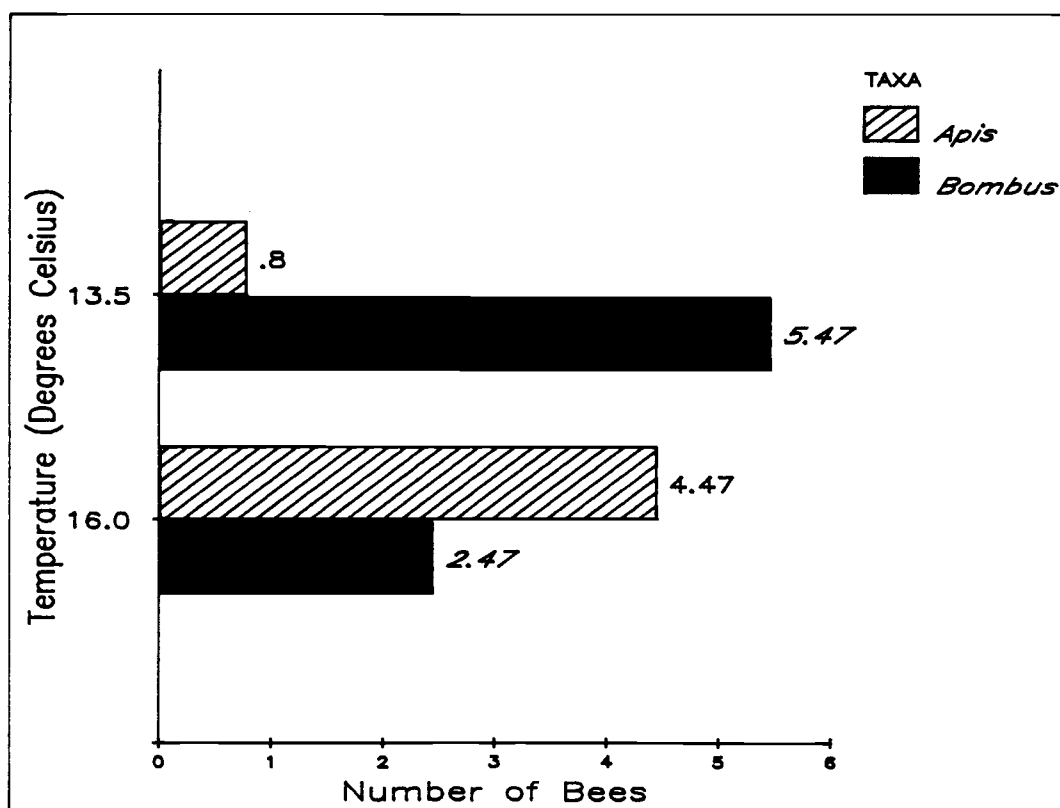
Figure 9. Comparison of visitation rates (number of bees
in 5 minutes) of *Apis* versus *Bombus* at two
levels of ambient temperature (13.5 and 16.0
degrees Celsius) on *Rubus* spp. at site 1, in
1985.

statistically significant (t=3.32, P=.003, df=30, Sokal and Rohlf 1981). The mean difference of 3.67 individuals between visitation rates of *Apis* at 13.5 degrees Celsius (.8 individuals) and at 16 degrees Celsius (4.47 individuals), also is statistically significant (t=6.63, P <.001, df=30).

In the summer, differences in diel flight times among pollinators were investigated using *R. discolor*. An R x C test of independence using G-test (Sokal and Rohlf 1981) was used to examine whether or not the foraging activity of a particular bee taxon is dependent on time. The results are shown in Table 5. Visitation rates of *Apis* and *Bombus* on *R. discolor* are dependent on time of day at site 3 (shrub stage), but not at site 2 (herb-shrub stage), as indicated by the significance of the G-value (Table 5). In other words, the significance of G-values at site 3 suggests that the proportions of *Apis* versus *Bombus* on flowers of *R. discolor* change over the day (Figure 10), indicating daily partitioning of food sources. The indication of interdependency between visitation of *Apis*, *Bombus*, and other bees on *R. discolor* at site 2 (Table 5) is subjected to further examination for other types of resource partitioning in the following sections.

Table 5. Interactions between visitation rates of
different bee taxa and time of day.
Significance determined by G-statistic, R x C
contingency tables (Sokal and Rohlf 1981).

Site	Plant	Date	Interaction		G (N)
			Bee taxon	Time of day	
2	*Rubus discolor*	6/18/85	*Apis*[1] *Bombus* Others	0900-1000 1000-1100 1100-1200 1300-1400 1500-1600	15.43 (424)
		6/26/85	*Apis*[1] *Bombus* Others	1200-1300 1400-1500 1500-1600	5.54 (415)
		6/11/86	*Apis*[1] Others	0800-1000 1000-1100 1100-1200 1500-1600 1600-1700 1700-1800	3.78 (293)
3	*Rubus discolor*	7/8/85	*Apis*[1] *Bombus*	0900-1000 1100-1200 1300-1400 1400-1500 1500-1600	10.34* (370)
		7/12/85	*Apis*[1] *Bombus*	0900-1000 1100-1200 1300-1400 1400-1500 1500-1600 1600-1700	17.54** (551)
		7/18/85	*Apis*[1] *Bombus*	0900-1000 1000-1100 1200-1300 1300-1400 1500-1600	10.01* (318)

[1] feral and cordovan honey bees.
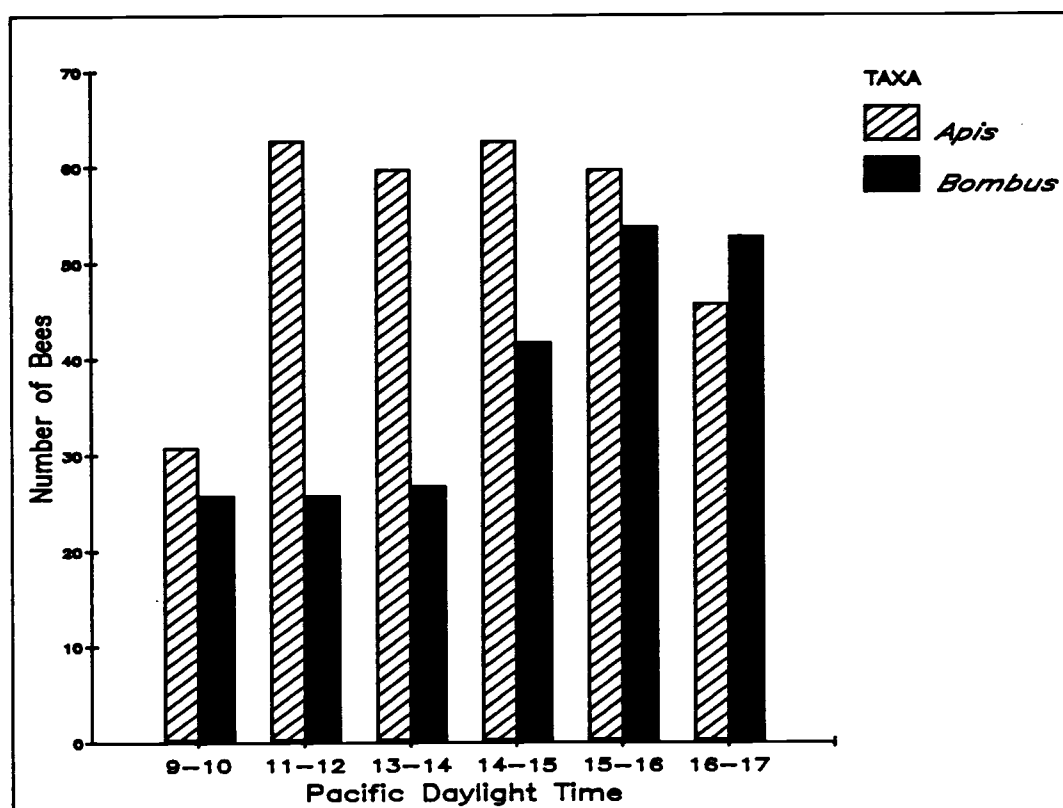* $P < .05$.
** $P < .01$.

Figure 10. Daily activity (number of bees on 150 flowers
in 15 minutes) of *Apis*, and *Bombus* on *Rubus
discolor*. Data from July 12, 1985 at site 3.

Spatial partitioning

Spatial partitioning based on different sizes of flower patches or clusters was examined using *R. ursinus* in the spring, and *R. discolor* in the summer. Sizes were determined by the numbers of flowers. Both *Rubus* species were used because they have a more defined flower patch or cluster, compared to other plant species such as *C. leucanthemum*, *H. radicata*, *T. officinale*, and *C. arvense*. These plants are randomly distributed over the study site, except for *C. arvense* which grows in a lineate pattern. There is an interaction in the form of spatial partitioning among forager taxa due to patch size of *R. ursinus* in the spring (Table 6; significance of the G-statistic). However, there might not be enough evidence to conclude that forager taxa are partitioning food sources from flowers of *R. discolor* at site 2 according to patch size (Table 6; one out of three cases having P-value <.05). The number of *Apis* markedly increases with the increase in patch size of *R. ursinus*, unlike other bees which exhibit no discernible patterns (Figure 11). Visitation of dipterous insects (flies) diminishes when patches are larger.

Partitioning of flower species and flower preferences

Partitioning of flower species among pollinators in the clear-cuts was examined during the summer at site 2 (herb-shrub stage) and site 3 (shrub stage). At site 1

Table 6. Interactions between visitation rates of
         different bee taxa and patch sizes.
         Significance determined by G-statistic, R x C
         contingency tables (Sokal and Rohlf 1981).

Site	Plant	Date	Interaction		G (N)
			Bee taxon	Patch size	
1	*Rubus ursinus*	5/12/84	*Apis*	500	21.23**
			Flies	1000	(344)
			Others	1500	
2	*Rubus discolor*	6/20/85	*Apis*[1]	125	3.80
			Bombus	350	(234)
			Others	500	
		6/26/85	*Apis*[1]	100	10.74*
			Others	500	(436)
				1000	
				2000	
		6/11/86	*Apis*[1]	300	0.18
			Others	1200	(293)
				5000	

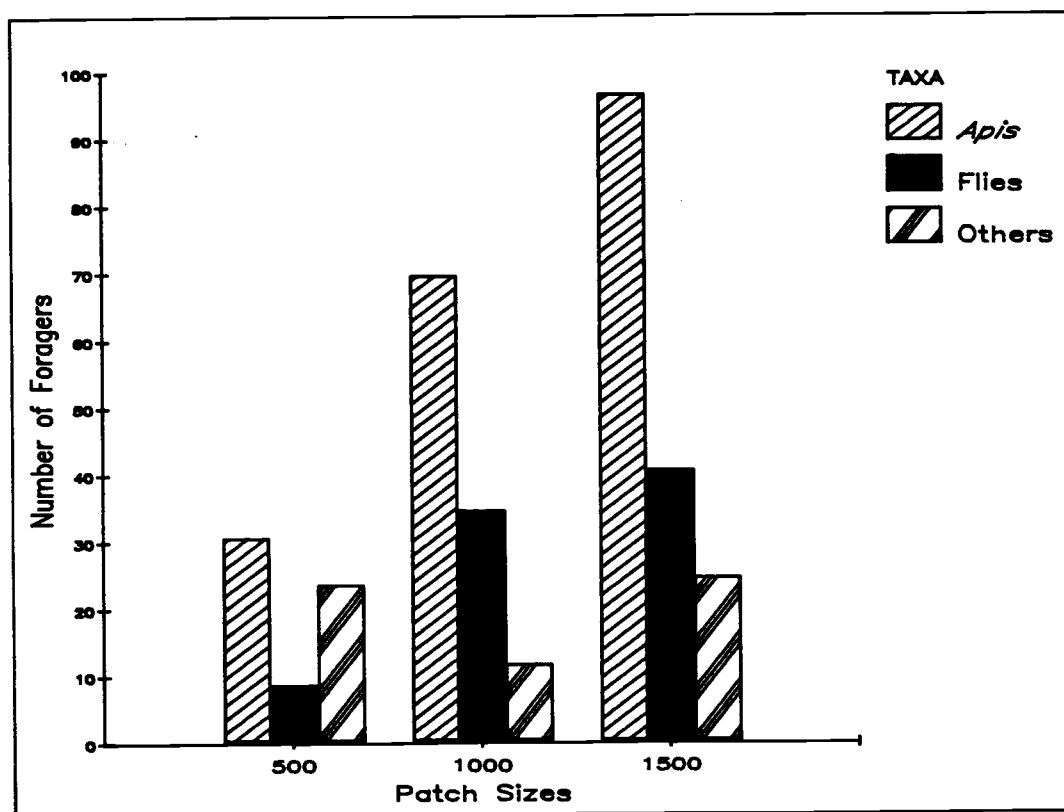[1] feral and cordovan honey bees.
* P <.05.
** P <.01.

Figure 11. Visitation rates (number of foragers seen in 30
minutes) of *Apis*, Diptera (flies), and other
bees (others) on *Rubus ursinus*. Data from May
12, 1984 at site 1.

(herb stage), floral resources are scarce during the summer, and thus it is not suitable for the study. The study was not done in the spring because of the domination of a single plant species, *R. ursinus*, in the study sites.

Results of G-statistic in Table 7 show that there was evidence for resource partitioning, due to flower species, between *Apis* and other bees during the summer of 1985 at site 2, and during late summer of the same year at site 3. During both periods, supplemental cordovan *A. mellifera* were introduced into the study sites. The results are based on flower visitation data, regardless of the purpose of the visits, i.e. nectar and/or pollen foraging. The strong indication of the dependency of *Apis* versus other bees on different plant species during the summer of 1985 at site 2 (Table 7) explains why there is no evidence of temporal and spatial partitioning in the previous sections. The bees were concentrating on different floral resources instead of competing on the same flower clusters at the same periods of time.

Data on plant species, their flower-visitors, and the types of resources used by these visitors in the study sites are shown in the Appendix. *A. mellifera* utilized almost every plant species in this study (25 out of 33). Bumble bees (*Bombus*), when considered at the generic level, were able to utilize some plant species that had not been visited by other foragers because of structural limitation of the flowers such as corolla length. Larger

Table 7. Differences in visitation rates of *Apis* versus
other bees on different plant species.
Significance determined by G-statistic, R x 2
contingency tables (Sokal and Rohlf 1981).

Site	Season	Plant species	G (N)
2	1985, early summer[1]	*R.ursinus, R.leucodermis, R.laciniatus, R.discolor, H.radicata + T.officinale, V.cracca*	26.20** (183)
	late summer[1]	*R.discolor, V.cracca, S.albus, H.perfoliatum, H.radicata + T.officinale, T.repens, C.arvense*	81.38** (510)
3	1984, early summer	*R.ursinus, R.parviflorus, R.discolor*	1.84 (63)
	1985, early summer	*R.discolor, C.arvense*	2.09 (414)
	late summer[1]	*R.discolor, C.arvense*	87.42** (848)

[1] with cordovan honey bees.
** P <.01.

bees, having longer tongues, generally foraged for nectar from long-corolla flowers; contrarily bees with shorter tongues visited short-corolla flowers (Brian 1957, Hobbs 1962, Heinrich 1979). Workers of *Bombus* (*Subterraneobombus*) *appositus* and *B.* (*Fervidobombus*) *californicus*, which have proboscis lengths ca. 10.5 and 7.5 milimeters, respectively (Pyke 1982), were able to utilize nectar from long-corolla flowers such as vetch (*V. cracca*) and teasel (*Dipsacus sylvestris* Huds.). *V. cracca* have corolla lengths of 6.1-6.4 milimeters (Morse 1978), and bloom in late spring-early summer. *A. mellifera* has a tongue length of ca. 6.0 millimeters (Heinrich 1976) and is physically unable to probe for nectar from the florets of *V. cracca*. However, *A. mellifera* fed on *V. cracca* by nectar-robbing from the holes at the base of the floret. These holes had been produced by the small workers of *B. californicus*.

The majority of the solitary bees in the genus *Andrena* are common on flowers of *Rubus* spp. Some species of *Andrena* show greater degrees of specificity. *Andrena* (*Scaphandrena*) *plana* Viereck is found exclusively collecting pollen and nectar from *T. repens* in the study site. Other solitary bees that are pollen specific (oligolectic) include *Synhalonia edwardsii* (Cresson) on *V. cracca*, and *Melissodes* (*Heliomelissodes*) *rivalis* Cresson on *C. vulgare*.

Members of the primitively social bees in the genera *Halictus* and *Lasioglossum* are polyphagous. They frequently forage on the same floral resources as *A. mellifera*. Certain species, such as *Halictus (Halictus) ligatus*, visit only a few plant species, i.e. *H. radicata* and *C. leucanthemum*. *C. leucanthemum*, which is one of the dominant flower species during late spring-early summer, has been used by only a few foragers in both numbers and taxa (see Appendix for forager taxa), relative to the abundance of the plant. This may be evidence that floral resources are unlimited in the summer.

The question of native bees being more common on native plant species than on introduced species was not addressed in this study. Comparison is impossible in the spring because there are no blooming introduced plant species at that time. The abundance of the introduced flowering plants in both numbers and species during the summer, would prejudice such an hypothesis.

Competition from Apis mellifera

Studies of competition and community structure emphasize that two or more species utilizing the same limiting food source will partition it in order to avoid competition (MacArthur and Levin 1967, Brown and Lieberman 1973, Pulliam 1975, Rosenzweig 1977). Are food resources a limiting factor in the study sites? Results from the summer of 1985 at site 2 (herb-shrub stage) and site 3 (shrub stage), as well as other evidence, suggest that forage resources are unlimited in the summer. Graphic presentation of the number of bees at site 2 (Figure 12) and site 3 (Figure 13) on R. discolor indicates that supplemental A. mellifera (cordovan) do not affect visitation rates of other bee species. This is supported by the result of a 6 x 3 contingency table (six observation periods from 6/18-7/1 in Figure 12 vs. Apis, Bombus, and other bees) which is non-significant using the G-statistic = 10.25, N=343, P >.05, df=10 (Sokal and Rohlf 1981). This means that the proportions of Apis: Bombus: other bees on R. discolor are independent of the observation period or, in other words, there are no interactions between pollinator taxa and observation period. Many studies, such as those of Roubik 1978, 1980, Schaffer et al. 1979, 1983, and Ginsberg 1983, illustrate that A. mellifera often is able to numerically dominate native bees at the most productive sources of nectar and

Figure 12. Visitation rates (number of bees seen on 100 flowers in 5 minutes) on *Rubus discolor* at site 2, in 1985. (IN)=cordovan *Apis* moved in, (OUT)=cordovan *Apis* moved out.
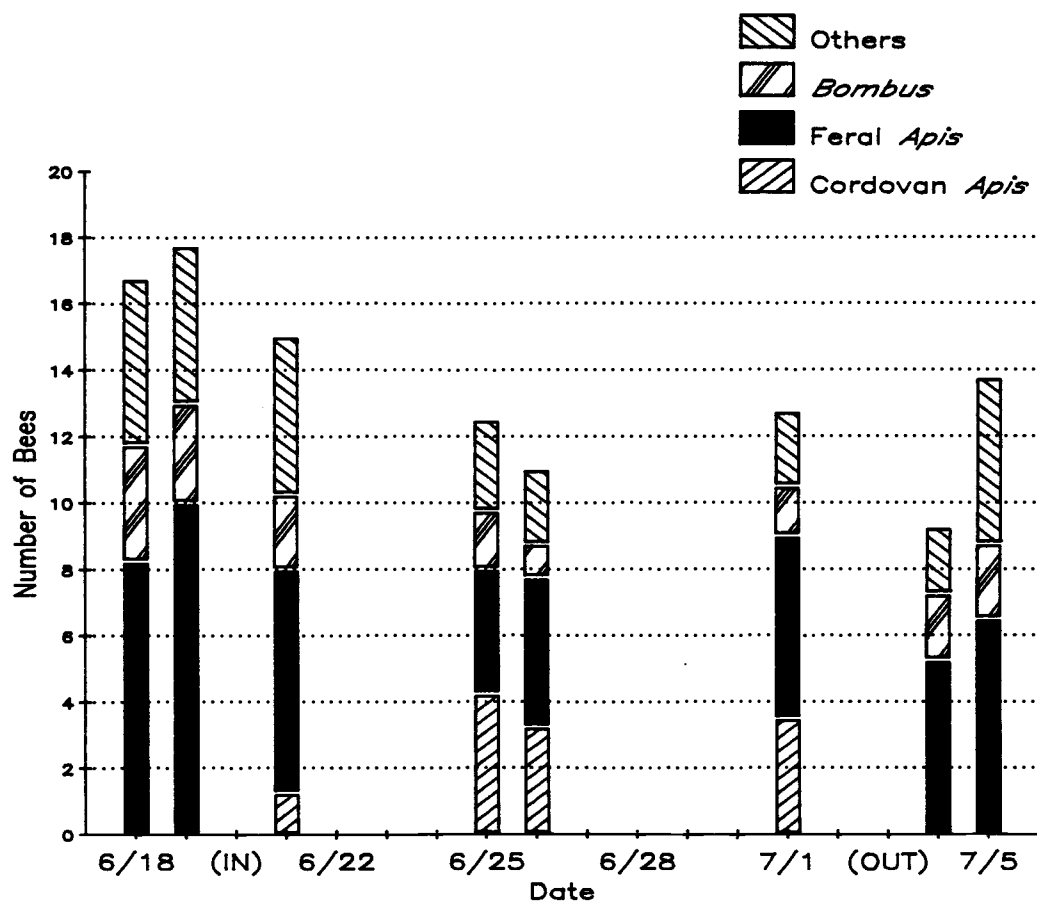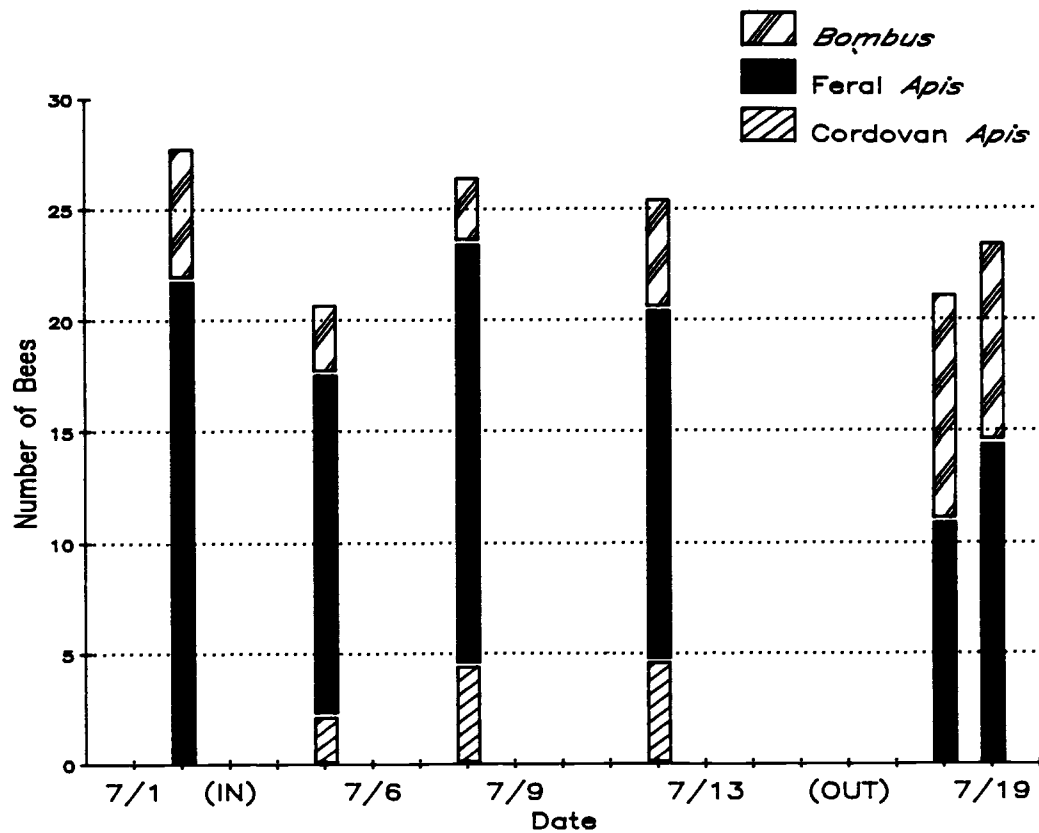
Figure 13. Visitation rates (number of bees seen on 50 flowers in 5 minutes) on *Rubus discolor* at site 3, in 1985. (IN)=cordovan *Apis* moved in, (OUT)=cordovan *Apis* moved out.

pollen, with the consequence that the native species tend to be restricted to less favorable sites and species of flowers. If floral resources are limiting, we would be able to see changes in the proportion of the bees during the *Apis* supplementation periods. Further evidence to support the inference that floral resources are non-limiting is the observation that the flowers of certain plant species, such as *C. leucanthemum, H. radicata*, and *T. officinale*, were not visited by many pollinators in terms of either numbers or species during the course of this study. These plant species are considered to be important pollen and/or nectar resources in other pollination systems (Free 1968, Ginsberg 1985).

Similar agreement concerning non-limiting resources also is seen at site 3 during the summer of 1985. Significance of the G-statistic (G=7.29, N=604, P >.05, df=3) was not demonstrated from the test of independence of a 4 x 2 contingency table (four observation periods from 7/1-7/13 in Figure 13 vs. *Apis*, and *Bombus*). The supplemental cordovan *Apis* actually replaced some proportion of the feral *Apis* (Figure 12, and 13), but the combination of cordovan and feral *Apis* did not displace the native pollinator taxa.

Supplementation and removal of the cordovan *A. mellifera* did not affect the population of other flower foragers on *R. discolor* at site 2. The result of the 8 x 3 contingency table (eight observation periods from 6/18-

7/5 in Figure 12 vs. *Apis*, *Bombus*, and other bees) is non-significant with the G-statistic = 14.61, N=435, P >.05, df=12 (Table 8). There is no interaction among the number of bees (*Apis*, *Bombus*, and other bees) during the eight observation periods. The percentage of *Apis*:*Bombus*:other bees in any observation period is ca. 58:16:26 (Table 8). Supplementation and removal of the cordovan *A. mellifera* did influence native foragers at site 3. A highly significant G-statistic was obtained from a 6 x 2 contingency table in Table 8 (G=72.71, N=872, P <.01, df=5). The percentage of *Apis* remained constant at the 80's level during the first four observation periods, but dropped down to 52% when the cordovan hives were removed, and then increased to 62% during the last observation period (Table 8). Contrarily, the percentage of *Bombus* significantly increased to 48% from ca. 20% when the hives were removed, followed by a reduction to 38%. This would have been an indication of competitive release due to removal of the supplemental *Apis*.

I was unable to experimentally prove that floral resources are limited in the spring at the study sites. However, from empirical evidence, it is suggested that there is a limiting food source in early spring. First, only few floral species, *R. ursinus* and *R. leucoderrmis*, dominate the study sites in the spring (Figure 2, 3, and 4). Secondly, results from foraging activity studies indicate that abiotic factors (temperature and relative

Table 8. Visitation frequencies of bees during the supplementation by cordovan *Apis mellifera* in the summer of 1985. Significance determined by G-statistic, R x C contingency tables (Sokal and Rohlf 1981).

Site 2

Date	Visitation frequency			Total	Percent			G (N)
	Apis[1]	*Bombus*	Others		*Apis*[1]	*Bombus*	Others	
6/18	33	14	20	67	49	21	30	14.61
6/19 (hives in)	40	12	19	71	56	17	27	(435)
6/21	32	9	19	60	53	15	32	
6/25	32	7	11	50	64	14	22	
6/26	31	4	9	44	70	9	21	
7/1 (hives out)	36	6	9	51	70	12	18	
7/4	21	8	8	37	56	22	22	
7/5	26	9	20	55	47	17	36	
Percent average					58	16	26	

Site 3

Date	Visitation frequency		Total	Percent		G (N)
	Apis[1]	*Bombus*		*Apis*[1]	*Bombus*	
7/2 (hives in)	131	36	167	78	22	72.71**
7/5	106	19	125	85	15	(872)
7/8	141	18	159	89	11	
7/12 (hives out)	123	30	153	80	20	
7/18	66	61	127	52	48	
7/19	87	54	141	62	38	
Percent average				75	25	

[1] feral or feral and cordovan *Apis* when applicable.
** P <.01.

humidity), as well as floral densities, determine the foraging patterns of pollinators (Table 4). Finally, both rain and continual cloudiness over many days, which are quite common in early spring, generally restrict forager activity. Floral resources are limited in the sense that they are available for a relatively short period of time for any given day because of the uncertainty of the environment, as well as a lack of floral species diversity.

The results of the exclusion of *A. mellifera* from flower patches of *R. leucodermis* in the spring of 1986 at site 1 (herb stage), indicate that there is an observable difference in visitation of *Bombus* between the exclusion treatment and the control treatment. The mean difference of 2.9 (11.9 - 9.0) is statistically significant with the t-statistic = 3.37, P <.01, df=11, paired observations (Snedecor and Cochran 1967) (Table 9). Species of *Bombus* observed in this experiment are workers of *B.(Pyrobombus) mixtus*, and *B.(P.) melanopygus* Nylander and emergent overwintered queens of *B.(B.) terricola occidentalis* Greene, *B.(Fervidobombus) californicus*, *B.(P.) vosnesenskii* Radoszkowski, *B.(Separatobombus) griseocollis* (Degeer), and *B.(Bombias) nevadensis nevadensis* Cresson. The reduction in numbers of *A. mellifera* from flower patches provided an opportunity for *Bombus* foraging to increase. The increase in visitations of ca. 3 individuals of *Bombus* per hour has been observed per

Table 9. Comparisons of visitation rates (number per hour) of bumble bees (*Bombus*) between the exclusion of *Apis mellifera* versus the control treatment. Significance determined by t-test, paired observations (Snedecor and Cochran 1967).

Observation	Treatment		
	Exclude(E)	Control(C)	E - C
1	19	11	8
2	14	12	2
3	22	19	3
4	6	4	2
5	16	10	6
6	17	11	6
7	4	4	0
8	4	6	-2
9	8	9	-1
10	11	8	3
11	15	10	5
12	7	4	3
Mean	11.9	9	2.9

Standard error of difference (E - C) = .866
t-statistic = 3.37
P-value < .01
degree of freedom = 11

flower patch where *A. mellifera* were excluded, compared to the normal situation. On the basis of these results, competition from *A. mellifera* on native foragers is indicated.

SUMMARY AND CONCLUSIONS

Thirty-three entomophilous plant species were primary forage sources for pollinator taxa in the early stages of secondary succession, or clear-cut regeneration, in the McDonald and Paul Dunn Forests. Among these species, members of the genus *Rubus*, i.e. *R. ursinus*, *R. leucodermis*, and *R. discolor*, are the major floral resources for pollinators. Flowers of herbaceous species and residual shrubs dominate in the early years after clear-cutting. This herb stage gives way to an herb-shrub dominated period with many introduced plant species. Woody plants become increasingly important in the shrub-dominated period. Flowers of native plant species are common in the spring, while the introduced species are abundant in the summer.

Similarity of floral composition is greatest between the adjacent stages of the early successional patterns. The general trends in resource availability are similar between the herb-shrub and the shrub stages (sites 2 and 3) with three flowering peaks (spring, early-summer, and late-summer) occurring in both, as compared to one enormous peak in the spring at the herb stage (site 1). The spring, early-summer, and late-summer flowering peaks are due primarily to *R. ursinus* and *R. leucodermis*, *C. leucanthemum* and *R. discolor*, and *Cirsium* spp., respectively.

Eighty of the 96 species of pollinators found during the course of this study were bees (Hymenoptera: Apoidea). Among the three major life styles of the bees recognized in this study (solitary, social or semi-social, and parasitic), the social species are best represented. Common native bee genera are *Andrena*, *Bombus*, *Halictus*, *Lasioglossum*, and *Osmia*. The honey bee (*A. mellifera*) is the most dominant flower visitor.

Insect pollinators in the clear-cut habitat partition floral resources by foraging at different times of the season or at different times of the day (temporal partitioning), by utilizing different sizes of flower patches (spatial partitioning), or by concentrating on different flower species. Seasonal occurrence of the bees is generally controlled by intrinsic or innate features, which may have resulted from competitive pressures in the past. Differences in diel flight periods among pollinator taxa in early spring are strongly influenced by the ambient temperature. For example, bumble bees (*Bombus* spp.) are more abundant on *Rubus* at lower ambient temperature than honey bees, which are common at higher temperatures. In the summer, daily pollinator activity is largely determined by resource availability.

Spatial partitioning among pollinators, as indicated by the uses of different sizes of flower patches, is evident in early spring on *R. ursinus*. With increasing floral diversity in the summer, pollinator taxa

concentrate more on different flower species than on competing on the same flower clusters at the same periods of time.

The honey bee (*A. mellifera*), which is the dominant flower-visitor, was found foraging on almost every flower species in the study sites. Honey bees are especially concentrated on abundant floral resources throughout the flowering season. Their population levels closely follow resource availability, and may depress foraging populations of certain wild bee taxa, especially *Bombus*.

The ecological impact of *A. mellifera* on native bee species in terms of competition for floral resources is noticeable in early spring and late summer. The exclusion of *A. mellifera* from flower patches of *R. leucodermis* in the spring increased the visitation rates of the wild bees (*Bombus* spp.), which implies competition for food between the two taxa. A competitive release on flower visitation by *Bombus* was demonstrated when *Apis* populations were suppressed during late summer.

BIBLIOGRAPHY

Anonymous. 1986. SPSS[X] User's Guide (2nd ed.). SPSS Inc., Chicogo, Illinois. 988 pp.

Baker, H.G., and P.D. Hurd. 1968. Intrafloral ecology. Ann. Rev. Entomol. 13: 385-414.

Bouseman, J.K., and W.E. LaBerge. 1979. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IX. Subgenus *Melandrena*. Trans. Amer. Ent. Soc. 104: 275-389.

Brian, A.D. 1957. Differences in the flowers visited by four species of bumblebees and their causes. J. Anim. Ecol 26: 71-98.

Brown, J.H., and G.A. Lieberman. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology 54: 788-797.

Crepet, W.L. 1984. Ancient flowers for the faithful. Nat. Hist. 93: 39-45.

Donovan, B.J. 1977. A revision of North American bees of the subgenus *Cnemidandrena* (Hymenoptera: Andrenidae). Univ. Calif. Pubs. Ent. 81: 1-107.

Dyrness, C.T. 1965. The effect of logging and slash burning on understory vegetation in the H.J. Andrews Experiment Forest. USDA Forest Service Research Note PNW-31. Pacific Northwest Forest and Range Experiment Station, Portland. 13 pp.

Dyrness, C.T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54: 57-69.

Eickwort, G.C., and H.S. Ginsberg. 1980. Foraging and mating behavior in Apoidea. Ann. Rev. Entomol. 25: 421-446.

Eisikowitch, D. 1978. Insect visiting of two subspecies of *Nigella arvensis* under adverse seaside conditions. In: The Pollination of Flowers by Insects, A.J. Richards (ed.), pp. 125-132. Linnean Society Symposium Series No. 6. Academic Press, New York.

Faegri, K., and L. van der Pijl. 1978. The Principles of Pollination Ecology (3rd ed.). Pergamon Press, New York. 244 pp.

Frankie, G.W., and R. Coville. 1979. An experimental study of the foraging behavior of selected solitary bee species in the Costa Rican dry forest. J. Kansas Entomol. Soc. 52: 591-602.

Frankie, G.W., P.A. Opler, and K.S. Bawa. 1976. Foraging behavior of solitary bees: implications for outcrossing of a Neotropical forest tree species. J. Ecol. 64: 1049-1057.

Franklin, J.F., and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Pacific Northwest Forest and Range Experiment Station, Portland. 417 pp.

Free, J.B. 1968. Dandelion as a competitor to fruit trees for bee visits. J. App. Ecol. 5: 169-178.

Free, J.B. 1970. Insect Pollination of Crops. Academic Press, New York. 544 pp.

Frisch, K. von. 1967. The Dance Language and Orientation of Bees. Harvard University Press, Cambridge, Massachusettes. 566 pp.

Gary, N.E. 1975. Activities and behavior of honey bees. In: The Hive and the Honeybee, Dadant and Sons (eds.), pp. 185-264. Dadant and Sons, Hamilton, Illinois.

Gary, N.E., P.C. Witherell, and K. Lorenzen. 1978. A comparison of the foraging activities of common Italian and "Hy-Queen" honey bees. Environ. Entomol. 7: 228-232.

Ginsberg, H.S. 1983. Foraging ecology of bees in an old field. Ecology 64: 165-175.

Ginsberg, H.S. 1985. Foraging movements of *Halictus ligatus* (Hymenoptera: Halictidae) and *Ceratina calcarata* (Hymenoptera: Anthophoridae) on *Chrysanthemum leucanthemum* and *Erigeron annuus* (Asteraceae). J. Kansas Ent. Soc. 58: 19-26.

Graenicher, S. 1930. Bee-fauna and vegetation of Miami, Florida. Ann. Entomol. Soc. Amer. 23: 153-174.

Hall, J.K., and P.B. Alaback. 1982. Preliminary checklist of the vascular flora of McDonald and Paul Dunn State Forests. Special Publication 3. Forest Research Laboratory, Oregon State Univ., Corvallis. 42 pp.

Heinrich, B. 1976a. The foraging specializations of individual bumblebees. Ecol. Monogr. 46: 105-128.

Heinrich, B. 1976b. Resource partitioning among some eusocial insects: bumblebees. Ecology 57: 874-889.

Heinrich, B. 1979. Bumblebee Economics. Harvard University Press, Cambridge, Massachusetts. 245 pp.

Heinrich, B. 1983. Insect foraging energetics. In: Handbook of Experimental Pollination Biology, C.E. Jones and R.J. Little (eds.), pp. 187-214. Van Nostrand Reinhold Company Inc., New York.

Heinrich, B., and P.H. Raven. 1972. Energetics and pollination ecology. Science 176: 579-602.

Heithaus, E.R. 1974. The role of plant-pollinator interactions in determining community structure. Ann. Missouri Bot. Gard. 61: 675-691.

Heithaus, E.R. 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. Ecology 60: 190-202.

Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle. 730 pp.

Hobbs, G.A. 1962. Further studies on the food-gathering behavior of bumblebees (Hymenoptera: Apidae). Can. Ent. 94: 538-541.

Hodges, C.M. 1981. Optimal foraging in bumblebees: Hunting by expectation. Anim. Behav. 29: 1166-1171.

Ikudome, S. 1978. A wild bee survey in Kochi Plain (Kochi Pref.) Shikoku, Japan (Hymenoptera, Apoidea). Kontyu 46: 512-536.

Inouye, D.W. 1977. Species structure of bumblebee communities in North America and Europe. In: The Role of Arthropods in Forest Ecosystem, W. J. Mattson (ed.), pp. 35-40. Springer-Verlag, New York.

Inouye, D.W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. Ecology 59: 672-678.

Janzen, D.H. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science 171: 203-205.

Johnson, L.K., and S.P. Hubbell. 1974. Aggression and competition among stingless bees: field studies. Ecology 55: 120-127.

Johnson, L.K., and S.P. Hubbell. 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. Ecology 56: 1398-1406.

Juday, G.P. 1976. The location, composition, and structure of old-growth forests of the Oregon Coast Range. Ph.D. thesis, Department of Botany and Plant Pathology, Oregon State Univ., Corvallis. 187 pp.

Kevan, P.G. 1972. Insect pollination of High Arctic flowers. J. Ecol. 60: 831-867.

Kevan, P.G., and H.G. Baker. 1983. Insects as flower visitors and pollinators. Ann. Rev. Entomol. 28: 407-453.

Knezevich, C.A. 1975. Soil survey of Benton Co., Oregon. U.S. Department of Agriculture, Soil Conservation Service, in cooperation with Oregon Agricultural Experiment Station. Oregon State University, Corvallis. 119 pp.

Krombein, K.V., P.D. Hurd, D.R. Smith, B.D. Burks, and others. 1979. Catalog of Hymenoptera in America North of Mexico. Vol. 2. Apocrita (Aculeata). Smithsonian Institution Press, Washington, D.C. 2209 pp.

LaBerge, W.E. 1977. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part VIII. Subgenus *Thysandrena, Dasyandrena, Psammandrena, Rhacandrena, Euandrena, Oxyandrena*. Trans. Amer. Ent. Soc. 103: 1-143.

LaBerge, W.E. 1980. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part X. Subgenus *Andrena*. Trans. Amer. Ent. Soc. 106: 395-525.

Laverty, T.M., and R.C. Plowright. 1985. Competition between hummingbirds and bumble bees for nectar in flower of *Impatiens biflora*. Oecologia 66: 25-32.

Linsley, E.G. 1958. The ecology of solitary bees. Hilgradia 27: 543-599.

Linsley, E.G. 1978. Temporal patterns of flower visitation by solitary bees, with particular reference to the southwestern United States. J. Kansas Entomol. Soc. 51: 531-546.

Linsley, E.G., and M.A. Cazier. 1970. Some competitive relationships among matinal and late afternoon foraging activities of caupolicanine bees in southeastern Arizona. J. Kansas Entomol. Soc. 43: 251-261.

Linsley, E.G., and J.W. MacSwain. 1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. Univ. California Publ. Entomol. 16: 1-33.

MacArthur, R.H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Amer. Nat. 101: 377-385.

Macior, L.W. 1978. Pollination ecology of vernal angiosperms. Oikos 30: 452-460.

Michener, C.D. 1974. The Social Behavior of the Bees. A Comparative Study. Harvard Univ. Press, Cambridge, Massachusetts. 404 pp.

Michener, C.D. 1979. Biogeography of the bees. Ann. Missouri Bot. Gard. 66: 277-347.

Michener, C.D., and L. Greenberg. 1980. Ctenoplectidae and the origin of long-tongued bees. Zool. J. Linn. Soc. 69: 183-203.

Moldenke, A.R. 1975. Niche specialization and species diversity along a California transect. Oecologia 21: 219-242.

Moldenke, A.R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305-361.

Moldenke, A.R., and P.G. Lincoln. 1979. Pollination ecology in montane Colorado: a community analysis. Phytologia 42: 349-379.

Morris, W.G. 1958. Influence of slash burning on regeneration, other plant cover, and fire hazard in the Douglas-fir region. Pacific Northwest Forest and Range Experiment Station Research Paper 29. Pacific Northwest Forest and Range Experiment Station, Portland. 49 pp.

Morse, D.H. 1977. Resource partitioning in bumblebees: the role of behavioral factors. Science 197: 678-680.

Morse, D.H. 1978. Size-related foraging differences of bumble bee workers. Ecol. Ent. 3: 189-192.

Mosquin, T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22: 398-402.

Neter, J., W. Wasserman, and M.H. Kutner. 1983. Applied Linear Regression Models. Richard D. Irwin, Inc., Illinois. 547 pp.

Nye, W.P. 1980. Notes on the biology of *Halictus* (*Halictus*) *farinosus* Smith (Hymenoptera: Halictidae). Agricultural Research Results, Western Series, No. 11. Science and Education Administration, U.S. Department of Agriculture. 29 pp.

Pearson, J.F.W. 1933. Studies on the ecological relations of bees in the Chicago region. Ecol. Monogr. 3: 375-441.

Peer, D.F. 1956. Multiple mating of queen honey bees. J. Econ. Ent. 49: 741-743.

Plowright, R.C., B.A. Pendrel, and I.A. McLaren. 1978. The impact of aerial fenitrothion spraying upon the population biology of bumble bees (*Bombus* Latr.: Hymenoptera) in south-western New Brunswick. Can. Entomol. 110: 1145-1156

Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. Can. J. Bot. 52: 1819-1834.

Proctor, M.C.G. 1978. Insect pollination syndromes in an evolutionary and ecosystematic context. In: The Pollination of Flowers by Insects, A.J. Richards (ed.), pp. 105-116. Linnean Society Symposium Series No. 6. Academic Press, New York.

Proctor, M., and P. Yeo. 1973. The Pollination of Flowers. Taplinger Publishing Co., New York. 418 pp.

Pulliam, R.H. 1975. Coexistence of sparrows: a test of community theory. Science 189: 474-476.

Pyke, G.H. 1978a. Optimal foraging movement patterns of bumblebees between inflorescences. Theor. Pop. Biol. 13: 72-98.

Pyke, G.H. 1978b. Optimal foraging in bumblebees and coevolution with their plants. Oecologia 36: 281-293.

Pyke, G.H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and comunity structure. Ecology 63: 555-573.

Roberts, R.B. 1973. Bees of Northwestern America: *Halictus* (Hymenoptera: Halictidae). Oregon Agric. Expt. Sta. Tech. Bull. 126. Oregon State Univ., Corvallis. 23 pp.

Robertson, C. 1925. Heterotropic bees. Ecology 6: 412-436.

Rosenzweig, M.L. 1977. Coexistence and diversity in heteromyid rodents. In: Evolutionary Ecology, B. Stonehouse and C.M. Perrins (eds.), pp. 89-100. MacMillan, London.

Roubik, D.W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. Science 201: 1030-1032.

Roubik, D.W. 1980. Foraging behavior of competing Africanized honeybees and stingless bees. Ecology 61: 836-845.

Sakagami, S.F., and H. Fukuda. 1973. Wild bee survey at the campus of Hokkaido University. J. Fac. Sci., Hokkaido Univ., Ser. UI, Zool. 19: 190-250.

Schaffer, W.M., D.B. Jensen, D.E. Hobbs, J. Gurevitch, J.R. Todd, and V.M. Schaffer. 1979. Competition, foraging energetics and the cost of sociality in three species of bees. Ecology 60: 976-987.

Schaffer, W.M., D.W. Zeh, S.L. Buchmann, S. Kleinhans, V.M. Schaffer, and J. Autrim. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. Ecology 64: 564-577.

Schemske, D.W., M.F. Wilson, M.N. Melampy, L.J. Miller, L. Verner, K.M. Schemske, and L.B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59: 351-366.

Scullen, H.A., and G.A. Vansell. 1942. Nectar and Pollen Plants of Oregon. Oregon State Coll. Sta. Bull. 412. Oregon State Univ., Corvallis. 63 pp.

Seeley, T.D. 1985. Honeybee Ecology. A Study of Adaptation in Social Life. Princeton University Press, Princeton, New Jersey. 201 pp.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical Methods (6th ed.). Iowa State Univ. Press, Ames, Iowa. 593 pp.

Sokal, R.R, and F.J. Rohlf. 1981. Biometry (2nd ed.). W.H. Freeman and Co., San Francisco. 859 pp.

Southwood, T.R.E. 1978. Ecological Method with Particular Reference to the Study of Insect Populations. Chapman and Hall, London. 524 pp.

Steen, H.K. 1966. Vegetation following slash fires in one western Oregon locality. Northwest Sci. 40: 113-120.

Stephen, W.P., G.E. Bohart, and P.F. Torchio. 1969. The Biology and External Morphology of Bees: with a Synopsis of the Genera of Northwestern America. Agric. Expt. Sta., Oregon State Univ., Corvallis. 140 pp.

Taber, S. 1954. The frequency of multiple mating of queen honey bees. J. Econ. Ent. 47: 995-998.

Tepedino, V.J., and N.L. Stanton. 1982. Estimating floral resources and flower visitors in studies of pollinator-plant communities. Oikos 38: 384-386.

Thomson, J.D. 1983. Component analysis of community-level interactions in pollination systems. In: Handbook of Experimental Pollination Biology, C.E.Jones and R.J. Little (eds.), pp. 451-460. Van Nostrand Reinhold Company Inc., New York.

Thorp, R.W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann. Missouri Bot. Gard. 66: 788-812.

Thorp, R.W., and J.R. Estes. 1975. Intrafloral behavior of bees on flowers of *Cassia fasciculata*. J. Kansas Entomol. Soc. 48: 175-184.

Visscher, P.K., and T.D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63: 1790-1801.

Waddington, K.D. 1983. Foraging behavior of pollinators. In: Pollination Biology, L. Real (ed.), pp. 213-239. Academic Press, New York.

Waldbauer, G.P., and W.E. LaBerge. 1985. Phenological relationships of wasps, bumblebees, their mimics and insectivorous birds in northern Michigan. Ecol. Ent. 10: 99-110.

Whitham, T.G. 1977. Coevolution of foraging in *Bombus* and nectar dispensing in *Chilopsis*: a last dreg theory. Science 197: 593-595.

Wille, A., and E. Orozco. 1970. The life cycle and behavior of the social bee *Lasioglossum* (*Dialictus*) *umbripenne*. Rev. Biol. Trop. 17: 199-245.

Williams, C. 1975. Bringing honey to the land of milk and beekeeping in the Oregon Territory. The Amer. West 12: 32-37.

Zimmerman, M., and J.M. Pleasants. 1982. Competition among pollinators: quantification of available resources. Oikos 38: 381-383.

APPENDIX

APPENDIX

Insect Pollinators

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)

ORDER HYMENOPTERA

Family Colletidae

Insect species	Study site	Month	Plant species[1]
Hylaeus (*Paraprosopis*) *wootoni* (Cockerell)	2	Jul-Aug	CA(NP)

Family Andrenidae

Insect species	Study site	Month	Plant species[1]
Andrena (*Andrena*) *hemileuca* Viereck	1,2,3	Apr-May	RS(N),RU(NP), RE(NP),CD(N)
Andrena (*Andrena*) *saccata* Viereck	1	May	RE(NP)
Andrena (*Cremnandrena*) *anisochlora* Cockerell	2	Apr-May	RU(NP)
Andrena (*Euandrena*) *auricoma* Smith	2,3	Apr-Jun	RU(NP),RD(NP)
Andrena (*Euandrena*) *caerulea* Smith	3	Apr	CD(N)
Andrena (*Euandrena*) *chlorura* Cockerell	2	May	FV(P)
Andrena (*Euandrena*) *nigrihirta* (Ashmead)	3	Apr	RU(N)
Andrena (*Euandrena*) *nigrocaerulea* Cockerell	1,2,3	Apr-Jun	RU(NP),CD(N),CL(P)
Andrena (*Melandrena*) *nivalis* Smith	1,2,3	Apr-May	RS(N),RU(NP), RE(NP),SA(N)
Andrena (*Micrandrena*) *illinoiensis* Robertson	1	Apr	RU(NP)
Andrena (*Opandrena*) *cressonii infasciata* Lanham	1,3	Apr-Jun	RS(N),RU(NP),CL(P)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Andrena (*Plastandrena*) *crataegi* Robertson	3	Apr	CD(N)
Andrena (*Plastandrena*) *prunorum prunorum* Cockerell	2	Apr	RU(NP)
Andrena (*Scaphandrena*) *plana* Viereck	2	Jun	TR(NP)
Andrena (*Simandrena*) *angustitarsata* Viereck	1	May	RU(NP)
Andrena (*Trachandrena*) *amphibola* (Viereck)	1,2	May-Jun	RU(NP),CL(P),RD(NP)
Andrena (*Trachandrena*) *forbesii* Robertson	2	May	RU(NP)
Andrena (*Trachandrena*) *miranda* Smith	2	May	RU(NP)
Andrena (*Trachandrena*) *salicifloris* Cockerell	2	Apr-May	RU(NP)
Andrena (*Thysandrena*) *candida* Smith	3	May	CD(N)
Andrena (*Thysandrena*) *w-scripta* Viereck	3	Jun	RP(P)
Andrena (*Tylandrena*) *perplexa* Smith	3	May	CD(N)
Panurginus atriceps (Cresson)	1,2,3	Apr-Jun	RU(NP),CL(NP)

Family Halictidae

Agapostemon virescens (Fabricius)	1	May	RU(NP)
Halictus (*Halictus*) *farinosus* Smith	1,2	Apr-May	RU(NP),RE(NP),CL(P)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Halictus (*Halictus*) *ligatus* Say	2	May-Jul	CL(P),HR(NP),TO(NP)
Halictus (*Halictus*) *rubicundus* (Christ)	1,2	Apr-Jun	RU(NP),CL(P)
Halictus (*Seladonia*) *confusus arapahonum* Cockerell	1,2,3	Apr-Jun	RU(NP),CD(N),RD(NP)
Halictus (*Seladonia*) *tripartitus* Cockerell	2	Jun	RD(NP)
Lasioglossum olympiae (Cockerell)	2	Apr-Jul	RU(NP),SV(N),CL(P), RD(NP),HP(P)
Lasioglossum pacificum (Cockerell)	2	Jun	RD(NP)
Lasioglossum titusi (Crawford)	2	Apr	RU(NP)
Lasioglossum trizonatum (Cresson)	2	Jul	HR(NP),TO(NP)
Lasioglossum zonulum (Smith)	2	Jul	HP(P)
Evylaeus allonotus (Cockerell)	2,3	Apr	AM(N),RU(NP)
Evylaeus argemonis (Cockerell)	2,3	Apr	AM(N),RU(NP)
Evylaeus cooleyi (Crawford)	2,3	Apr-Jul	CD(N),CA(NP)
Evylaeus cordleyi (Crawford)	2	Jun	RD(NP)
Evylaeus macoupinensis (Robertson)	1,2	Apr-May	RU(NP)
Evylaeus niger (Viereck)	2	May-Jul	CU(N)
Evylaeus robustus (Crawford)	3	Apr	AM(N)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Dialictus obscurus (Robertson)	2	May	FC(P)
Dialictus zephyrus (Smith)	2	Apr-May	FC(P),FV(P)
Sphecodes arvensiformis Cockerell	1,2	Apr-May	RU(N)
Sphecodes hesperellus Cockerell	2	Apr	RU(N)

Family Megachilidae

Osmia (Chenosmia) dolerosa Sandhouse	2	Jun	RD(N),TR(NP)
Osmia (Chenosmia) kincaidii Cockerell	1	Apr	RU(NP)
Osmia (Chenosmia) nanula Cockerell	2,3	Jun	VC(NP),RD(NP)
Osmia (Chenosmia) pusilla Cresson	1	May	RU(NP)
Osmia (Chenosmia) trevoris Cockerell	2	Jul	VC(NP),RD(NP)
Osmia (Chenosmia) tristella tristella Cockerell	2	Jun	TR(NP)
Osmia (Monilosmia) albolateralis albolateralis Cockerell	2	May	SV(N)
Osmia (Monilosmia) atrocyanea atrocyanea Cockerell	1,2	May-Jun	RU(N),VC(NP)
Osmia (Osmia) lignaria propinqua Cresson	2,3	Apr-Jun	RS(N),RU(NP), RA(N),RD(NP)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Megachile (*Litomegachile*) *brevis brevis* Say	2	Jul	HR(NP),TO(NP),EA(N)
Megachile (*Sayapis*) *fidelis* Cresson	1	Jul	TO(NP)
Megachile (*Xanthosarus*) *perihirta* Cockerell	1	Jul	CV(NP)

Family Anthophoridae

Nomada species 1	2	Apr-May	RU(N)
Nomada species 2	2	Apr	RU(N)
Nomada species 3	3	May	CD(N)
Nomada species 4	1	May	RU(N)
Nomada species 5	2	May	RU(N)
Melissodes (*Heliomelissodes*) *rivalis* Cresson	1,2	Jul-Aug	CV(NP)
Synhalonia edwardsii (Cresson)	2	Apr-Jun	RU(N),VC(NP)
Ceratina (*Zadontomerus*) *acantha* Provancher	1,2	Apr-Jun	RU(NP),RD(NP)
Ceratina (*Zadontomerus*) *micheneri* Daly	2	Apr	RU(NP)

Family Apidae

Bombus (*Bombus*) *terricola occidentalis* Greene	1	May	RE(N)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Bombus (Bombias) nevadensis nevadensis Cresson	1	May	RE(N)
Bombus (Separatobombus) griseocollis (Degeer)	1	Apr-Jun	RU(N),RE(N),CV(N)
Bombus (Pyrobombus) flavifrons dimidiatus Ashmead	1,2,3	Apr-Jul	RU(N),RE(N),LH(N)
Bombus (Pyrobombus) melanopygus Nylander	1,2	Apr-May	RU(N),RE(N)
Bombus (Pyrobombus) mixtus Cresson	1,2,3	Apr-Jul	RU(N),RE(N),SA(N), RD(N),CA(N)
Bombus (Pyrobombus) sitkensis Nylander	2,3	Apr-Jul	RS(N),RU(N),LH(N)
Bombus (Pyrobombus) vosnesenskii Radoszkowski	1,3	Apr-Jul	RS(N),RE(N),VS(N), CA(N)
Bombus (Subterraneobombus) appositus Cresson	2	Apr-Aug	RU(N),VC(N),CA(N), DS(N)
Bombus (Fervidobombus) californicus Smith	1,2,3	Apr-Aug	RU(N),RE(N),IT(N), VS(N),VC(N),RA(N), RD(NP),HR(NP), TO(NP),LH(N),CC(N), PV(N),HP(P),EA(N), CA(N),CV(N),DS(N), SJ(N)
Psithyrus fernaldae Franklin	3	Jul	CA(N)
Psithyrus insularis (Smith)	3	Jul	CA(N)

Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Apis mellifera L.	1,2,3	Apr- Aug	RS(N),AC(N),AM(N), FC(P),FV(P),RU(NP), RE(NP),CD(N),RP(P), CL(P),RH(N),VC(N), SA(N),HD(N),RA(N), RD(NP),HR(NP), TO(NP),TD(N),TR(N), HP(P),EA(NP), CA(NP),CV(NP), SJ(NP)

ORDER DIPTERA

Family Bombyliidae

Bombylius major L.	2,3	Apr	RS(N),RU(N),VC(N)

Family Syrphidae

Carposcaris coerulescens (Williston)	1	May	RU(P)
Criorhina grandis Lovett	2	Jun	CL(NP)
Criorhina nigripes (Williston)	3	Apr	RS(NP)
Criorhina tricolor Coquillett	3	May	CD(NP)
Eristalis bardus (Say)	3	Apr	RS(NP)
Eristalis tenax L.	1,2	May- Jun	FC(P),RU(NP), CL(NP)
Mesograpta boscii (Macquart)	3	Apr	RU(NP)
Metasyrphus americanus (Wiedemann)	1	May	RU(NP)
Pocota bomboides Hunter	2	Apr	FC(NP)

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Insect species	Study site	Month	Plant species[1] (N=nectar, P=pollen)
Scaeva pyrastri (L.)	1,2	May- Jun	RU(NP),CL(NP)
Sphaerophoria cylindrica (Say)	2	May	FC(NP),FV(NP)
Syritta pipiens (L.)	3	Apr	FC(NP)
Toxomerus occidentalis Curran	2	May	FC(NP)

ORDER COLEOPTERA

Family Cerambycidae

Cerambycid species 1	3	Apr	AM(NP),CD(NP)

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[1]AC = *Acer circinatum* Pursh (Aceraceae)
AM = *Acer macrophyllum* Pursh (Aceraceae)
CC = *Centaurea cyanus* L. (Compositae)
CU = *Centaurium umbellatum* Gilib. (Gentianaceae)
CL = *Chrysanthemum leucanthemum* L. (Compositae)
CA = *Cirsium arvense* (L.) Scop. (Compositae)
CV = *Cirsium vulgare* (Savi) Tenore (Compositae)
CD = *Crataegus douglasii* Lindl. (Rosaceae)
DS = *Dipsacus sylvestris* Huds. (Dipsacaceae)
EA = *Epilobium angustifolium* L. (Onagraceae)
FC = *Fragaria vesca* L. (Rosaceae)
FV = *Fragaria virginiana* Duchesne (Rosaceae)
HD = *Holodiscus discolor* (Pursh) Maxim. (Rosaceae)
HP = *Hypericum perfoliatum* L. (Hypericaceae)
HR = *Hypochaeris radicata* L. (Compositae)
IT = *Iris tenex* Dougl. (Iridaceae)
LH = *Lonicera hispidula* (Lindl.) Dougl. (Caprifoliaceae)
PV = *Prunella vulgaris* L. (Lamiaceae)
RH = *Rhus diversiloba* T. & G. (Anacardiaceae)
RS = *Ribes sanguineum* Pursh (Grossulariaceae)
RD = *Rubus discolor* Weihe & Nees (Rosaceae)
RA = *Rubus laciniatus* Willd. (Rosaceae)
RE = *Rubus leucodermis* Dougl. (Rosaceae)
RP = *Rubus parviflorus* Nutt. (Rosaceae)
RU = *Rubus ursinus* Cham. & Schlecht (Rosaceae)
SJ = *Senecio jacobaea* L. (Compositae)
SV = *Sidalcea virgata* Howell (Malvaceae)

SA = *Symphoricarpos albus* (L.) Blake (Caprifoliaceae)
TO = *Taraxacum officinale* Weber (Compositae)
TD = *Trifolium dubium* Sibth. (Leguminosae)
TR = *Trifolium repens* L. (Leguminosae)
VC = *Vicia cracca* L. (Leguminosae)
VS = *Vicia sativa* L. (Leguminosae)