COMPETITION FOR BUMBLEBEE POLLINATORS
IN ROCKY MOUNTAIN PLANT COMMUNITIES[1]

JOHN M. PLEASANTS[2]
*Department of Biology, University of California at Los Angeles,
Los Angeles, California 90024 USA*

Abstract. Meadow plant communities at four sites in the Colorado Rocky Mountains were studied to evaluate the influence of competition for bumblebee pollinators. The niche relationships among plant species were characterized by overlap with respect to species of bumblebee visitors and times of flowering. Species in each community could be divided into two to three guilds based upon the identity of the species' major bumblebee visitor. Only the members of a guild would potentially be in competition with one another for pollinators. The competition hypothesis is that guild members have segregated blooming periods which would minimize competition. The null hypothesis is that blooming periods are dispersed randomly through time. The competition hypothesis was tested by comparing the actual temporal spacing pattern for a guild with random patterns generated by computer simulation. For 10 out of 11 guilds the sequence of blooming periods was more regular than expected (either at the statistically significant level [five cases] or near it [five cases]).

I also examined the relationships among guild members using another measure of the competitive effect of one species on another which is more accurate than temporal overlap. This variable, called competitive load, includes information on the overlap, abundance, and floral attractiveness of competitors. It is an indicator of the number of visits a species loses to competitors. In general species were found to lose approximately half the number of visits they could potentially receive during the time they were in flower. All species received approximately the same number of visits despite large differences in floral abundance. Thus the pool of available pollinator visits appears to be rather evenly divided among the species in a community. This regularity in resource partitioning is further inferential evidence of competition for pollinators. Rare species avoid the potentially heavy loss of visitors to more abundant competitors by having flowers which are more attractive to pollinators. Attractiveness appears to be a function of the nectar production rate of a species' flowers. There are some exceptions to these generalizations. Species which can also reproduce vegetatively are less attractive, and lose more visits that expected.

The competitive effect that one species experiences because of the presence of another may be the result of a loss of pollinator visits (exploitation) and/or a disruption of conspecific pollen flow (interference). Species may reduce the interference component of competition by spatial isolation. For the one guild that had a random flowering sequence with broad overlap among species, spatial isolation and competition between guild members were positively correlated. Temporal divergence and differential attractiveness are seen to be primarily a means of avoiding exploitation competition.

Key words: bumblebees; competition; competitive load; exploitation; floral attractiveness; interference; pollinators; temporal segregation.

INTRODUCTION

One major question in community ecology is whether communities are organized or structured, i.e., whether there are patterns to the numbers of species present, species abundances, and the niche relationships among species. A related question concerns the type of species interactions or environmental conditions that act as organizing principles (Paine 1966, Mac Arthur 1972, Cody 1974, Schoener 1974, Connell 1975). In this study I examine meadow plant communities at four sites in the Rocky Mountains to determine if competition for resources plays an important role in determining plant community structure. Although plants may be competing for a number of

resources, such as water, nutrients, and space, I chose to focus on one resource, pollinator visitation.

Interspecific competition for pollinators may come about in two ways. When two plant species are visited by the same pollinator the number of visits one receives is reduced because of the visits that go to the other. When visits are a limiting resource this may result in exploitation competition. In addition, plants may experience interference competition. When pollinators move repeatedly between individuals of the two species during a foraging bout, the pollen flow between conspecifics may be interfered with. This will occur if pollen is removed from a pollinator's body when the pollinator visits a heterospecific or if stigmatic surfaces become clogged with heterospecific pollen (Waser 1978*b*). Field studies dealing with competition for pollinators include Gentry 1974, Heithaus 1974, Heinrich 1975, 1976*b, c,* Reader 1975, Stiles 1977, Waser 1978*a,* and Zimmerman 1979.

One of the strongest statements to emerge from the-

oretical treatments of competition is that there should be a limit to the similarity of resource use by coexisting species (Mac Arthur and Levins 1967, May 1973, Roughgarden 1974). The prediction is not simply that differences among species should exist but that there should be an overdispersion of niches in niche space, i.e., resource partitioning. For species that use resources which can be arranged along a continuum, this translates into a regular arrangment of species along that continuum (Cody 1968, Hespenheide 1971, Brown 1972, Shoener 1974).

I investigated the pattern of niche space partitioning among the plant species in the study communities. There are two major resource dimensions associated with pollinator visits and along which separation might occur. The first is the pollinator dimension. I examined the extent to which plants differ from one another by having different pollinator visitors. A second dimension is time. Plants that share pollinators may experience reduced competition if they flower at different times during the season. For species which have large pollinator overlap we would expect a regular temporal segregation of blooming periods. Several previous studies have indicated the occurrence of a regular sequence of flowering among species visited by a single major class of pollinators (Gentry 1974, Heithaus 1974, Feinsinger 1976, Heinrich 1976c, Stiles 1977). However, these studies have provided little or no statistical verification of a regular spacing pattern. Instead they have relied on visual inspection of flowering sequences to confirm the regularity. In this paper I provide a rigorous examination of spacing of blooming periods. I also examine the competitive status of each species in the community by measuring its ability to attract pollinator visits and by assessing the competitive load on it from other species.

METHODS

Study sites

This study was conducted in mountain meadow plant communities. Four sites in the Gunnison Basin of Colorado (Barrell 1969) were chosen. The three lower elevation sites are near the town of Crested Butte and the highest is at Cumberland Pass near Tincup. Site 1 (2590 m elevation) is a 0.6-ha opening in the aspen woods (*Populus tremuloides*); Site 2 (2743 m) is ≈2 ha, surrounded by aspens; Site 3 (3048 m) is a 0.6-ha meadow bordered by Engelmann spruce (*Picea engelmannii*); and Site 4 (3657 m) is 2 ha of alpine tundra. Site 3 consists of two distinct parts, hereafter called front meadow (FM) and back meadow (BM).

I collected data on plants and pollinators from late June to mid-August in 1973, 1974, and 1975. The length of the study period was sufficient to include the main portion of the flowering season. The most extensive data, collected in 1975, are discussed below.

Plants

All plant species visited primarily by bees were considered in this study but not those visited primarily by flies or hummingbirds. Extremely rare species, or those not growing in the meadow proper, were not included. All plants were examined to determine if they required pollinator visits to set fruit. Prior to flowering I placed insect exclosures around individual plants of each species. These plants were then checked for fruit-set at the end of the season. For a few species some flowers were also self-pollinated to test for self-compatibility. The fruit-set of a number of species under field conditions was also measured. Enlargement of ovarian tissue was assumed to indicate fruit-set. I also excavated the root systems of many of the species to determine the extent of vegetative reproduction.

A flowering phenology for each species was determined by counting the number of open flowers in 5–10 permanent 9.3-m² quadrats at 5-d intervals. For species not present in these quadrats I tagged 20 representative individuals and counted the number of open flowers every 5 d. For members of the Asteraceae I counted the number of flower heads with open florets. These data were used to construct flowering curves which were then standardized so that each had 100 area units under the curve. The height of a curve thus gives the proportion of the total flowers open on a given day.

I also measured the floral abundance of each species by counting flowers in 0.56-m² quadrats, five paces apart, along transect lines positioned to cover as much of the meadow as possible. Two abundance censuses were made, one in the early season for early-blooming species and one later in the season for later blooming species. At each site ≈40 quadrats were sampled in the early census and 100 in the later one. For each species I counted the number of individual plants, flowering stalks, flowering heads, or clusters of flowers, whichever was more feasible. Then for each species, 20 of these counting units were examined and the average number of flowers (old, open, and buds) per unit recorded. The number of counting units per square metre was multiplied by the number of actual or potential flowers per unit to give the total floral production of a species. Since individual flowers stay open for several days and continue to secrete nectar and produce pollen, floral production should be multiplied by flower longevity. I marked individual flower buds with different colors of embroidery thread and recorded the amount of time from flower opening to senescence. For composites, longevity was measured for entire flower heads rather than for florets. The measure of species abundance I use below is equal to the total number of flowers per square metre times the average flower longevity and is expressed as flower-days.

I also measured the corolla depths of all species, from the point of entry to the flower (determined by observing pollinator behavior) to the base of the flower where the nectar was located. For four of the species corolla depth measurements were obtained from Inouye (1976).

Flower visitors

I estimated the frequency of visitation by different pollinators to each plant species by censusing insect activity at flowers every 5 d. During each census two observers walked parallel courses over a fixed route designed to provide representative coverage of the entire meadow. The species of pollinator and the identity of the flower it was visiting were recorded. Pollinators appeared to be undisturbed by our presence. Censuses lasted 30–120 min, depending on the time required to record all the bees seen. Censuses at all sites were conducted between 1000 and 1200. When censuses were conducted at other times in the day (Pleasants 1977 and J. Pleasants, *personal observation*), a few species showed diurnal differences in visitation frequency but in most cases it was the number of bees seen and not the kind of bee that changed. For the summers of 1974 and 1975, >4000 pollinator visits to flowers were recorded.

I used several different methods to identify each major group of pollinators. Bumblebees (*Bombus* spp.), which were the major pollinator group, could usually be identified to species by their distinctive abdominal and thoracic color patterns. Individuals that could not be identified while on flowers were collected with a net and placed in an observation jar for more careful inspection. I also recorded the bumblebee's caste (queen, worker, or male) and the type of resource it was collecting (pollen, nectar, or both). Pollen collecting was judged by the presence of a corbicular pollen load. A bee without a pollen load was assumed to be collecting nectar only. Bees which were probing flowers for nectar but also had a pollen load were considered to be collecting both resources.

For solitary bees I collected several specimens of every type that I could distinguish by field inspection. Solitary bees encountered during a census were compared to this reference collection. I felt that more extensive collection would seriously affect population sizes. This method may have resulted in some species misidentification but the error is probably not serious due to the relatively minor importance of solitary bees as pollinators. For syrphid and muscoid flies common groups were identified by their color pattern but in the analysis these groups are referred to as "syrphid fly" or "muscoid fly." No attempt was made to quantify the extent of visitation by hummingbirds although I did note which species received frequent visits.

I have made what I think is the reasonable assumption that flower visitors are, in fact, pollinators. For most of the plants visited by bumblebees these bees are their only visitors and the plants cannot set seed in their absence.

RESULTS

Separation into guilds

Forty plant species, most of which are herbaceous perennials, were included in this study. Insect exclosure experiments showed that virtually all of these species required pollinators for seed-set (Pleasants 1977). A few species, which will be discussed below, are capable of reproducing vegetatively.

Two pieces of evidence indicate that pollinators are a limiting resource for the plants in this study. The first, which is somewhat equivocal, concerns the fruit-set of untreated plants. Of 21 species I examined, an average of 50% of the flowers produced by plants set fruit (range: 0.5%–90%, Pleasants 1977). Other factors besides pollination success could account for these low figures. There are indications that energy or nutrient limitation can affect inflorescence characteristics (Willson and Price 1977, Herbert 1979). The maximum possible fruit-set may not be 100%. A second piece of evidence is more compelling. Zimmerman (1979) has found that for one species included in this study, *Polemonium foliosissimum*, the seed-set per flower of individual plants is significantly positively correlated with the number of visits per flower they receive. In addition, the average number of visits per flower for plants in general decreased during the latter part of the species' blooming period and there was a corresponding drop in average seed-set.

As mentioned previously, competition for pollinators may occur if species share pollinators and overlap in blooming time. I first examine the extent to which species differ in the identity of their pollinator visitors. Bumblebees are the most common visitors (>70% of all visitors observed). Because of their more rapid foraging speed (approximately twice as many flowers visited per unit time as solitary bees, Pleasants 1977) bumblebees actually account for an even greater proportion of flower visits. Figs. 1–4 show the proportion of different visitor species observed on each plant species. One conspicuous pattern at each site is that there are a number of plants which have the same bumblebee species as their principal visitor. This suggests that the species at each site can be divided into several guilds based on the identity of their principal bumblebee visitor. Species in the same guild would potentially be in competition for pollinators whereas species from different guilds would not. Thus, there does appear to be some segregation of plant species along the pollinator dimension. Whether this segregation is the result of competition for pollinators is difficult to determine. One question that can be answered is whether species that belong to the same guild are segregated along the second important di-
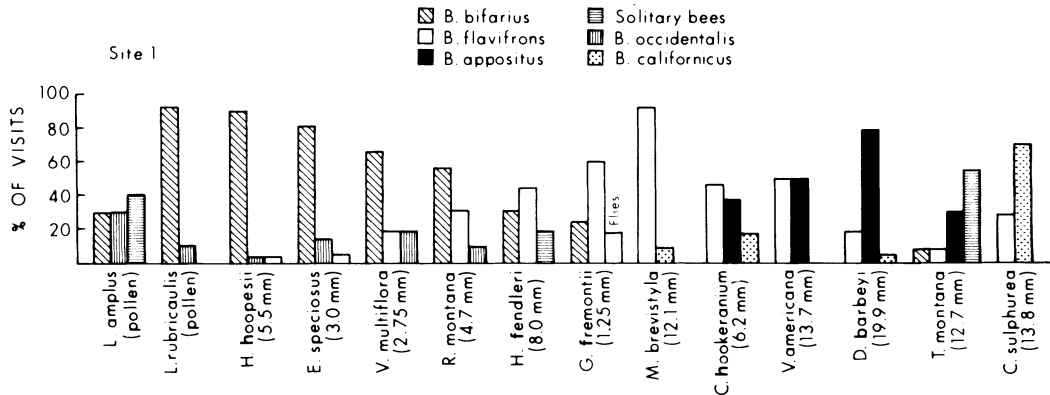
FIG. 1. Frequency distribution of visitors to each plant species at Site 1. Corolla depths are in parentheses below species name (see Table 3 for full names). Species visited primarily by queens: *T. montana*; species visited 10–25% by queens: *V. americana* and *H. fendleri*.

mension, time. The expectation from competition theory, which can be compared with the observed pattern, is that the flowering times of guild members are regularly dispersed throughout the summer season.

To examine the question of spacing of blooming periods I first had to establish a criterion for inclusion in a guild. From Figs. 1–4 it can be seen that very few species receive all of their visits from a single bumblebee and some species are visited by two "principal" visitors. I decided that all species which received 50% or more of their visits from a particular bumblebee would belong to the same guild. Many species in Figs. 1–4 are visited almost exclusively by one bumblebee species and can be easily assigned to the guild named for that bumblebee. Some of the species satisfying the 50% criterion are also visited to a relatively large extent by a second major bumblebee species. Such species are borderline members of a second guild and could be in moderate competition with members

of that second guild. To be on the conservative side these species were assigned to both guilds. The criterion for inclusion in a second guild was that the second bumblebee species must account for at least 30% of the visits to the species. In several cases species were assigned to a second guild when only 15–20% of their visits were from the second bumblebee species. This was done with species which were judged to have a large potential competitive effect on members of second guild (see *Competitive load*).

Guilds are clearly not sharply delimited entities but guild classification does appear to reflect natural differences among species. A number of authors have pointed out a correspondence between a bumblebee's proboscis length and the corolla depth of the flower it visits (Brian 1957, Macior 1974, Heinrich 1976*b*, Inouye 1976). The corolla depth of the flowers of each species is indicated in Figs. 1–4. The proboscis length of different bee visitors and the average corolla depth
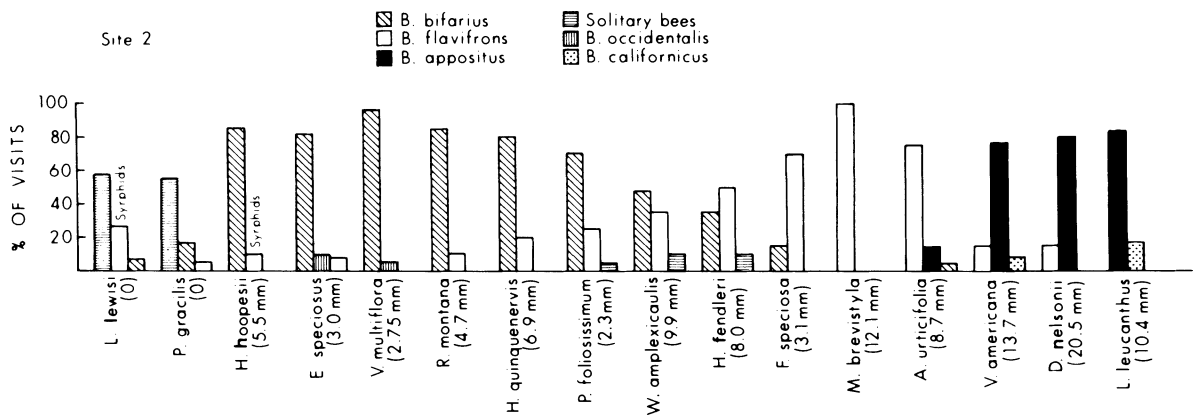

FIG. 2. Frequency distribution of visitors to each plant species at Site 2. Corolla depths are in parentheses below species name. Species visited primarily by queens: *D. nelsonii*; species visited 10–25% by queens: *V. americana, H. fendleri,* and *W. amplexicaulis*. Species also visited to a moderate extent by hummingbirds: *D. nelsonii* and *A. urticifolia*.
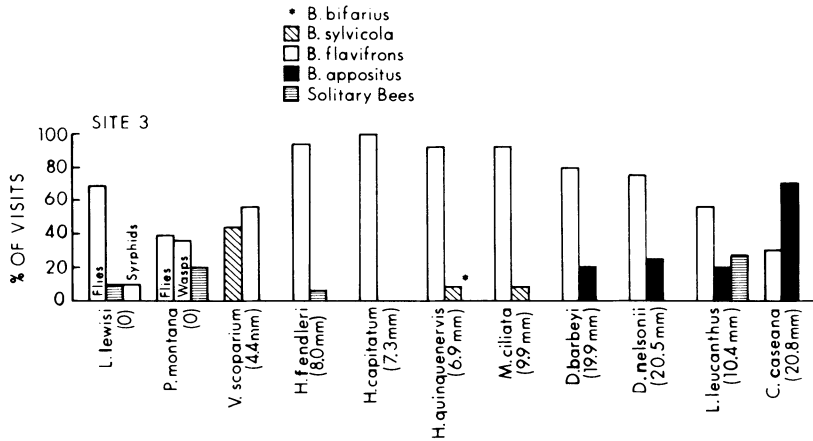
FIG. 3. Frequency distribution of visitors to each plant species at Site 3. Corolla depths are in parentheses below species name. Species visited primarily by queens: *D. nelsonii* and *C. caseana*. Species visited to a moderate extent by humming-birds: *D. nelsonii*, *D. barbeyi*, and *C. caseana*.

of the flowers they visit are shown in Table 1. The average corolla depth corresponds closely with worker proboscis length. Included in the group of species visited by each bumblebee are ones visited primarily by queens and others visited exclusively by workers. Bumblebee queens have longer tongues and might be expected to visit flowers with longer corollas. Lumping the castes together obscures this relationship, but I have done this for all species and the primary purpose of Table 1 is to compare the relative differences among the flowers in each guild. Because queens forage only in the early part of the season, most of the plants visited by a particular species are visited by the worker caste.

Temporal segregation

The flowering phenologies for each guild are shown in Figs. 5–8. If competition for pollinators is important the blooming periods for members of the

same guild should be regularly dispersed through time. The null hypothesis is that blooming periods have a random dispersion pattern. To characterize the dispersion pattern for each guild I measured the overlap between flowering curves for all pairs of guild members. Divergence of blooming periods to avoid competition should minimize the average temporal overlap between species. Randomly positioned species, on the other hand, should result in a greater average temporal overlap. To determine the expected average overlap under the null hypothesis I used computer simulations to generate a random assemblage of blooming periods. Fifty simulations were run for each guild using the following procedure. The start of the blooming period for each guild member was determined by randomly selecting a day during the summer season. If this day fell so late in the season that the blooming period of the species would extend beyond the season's end point
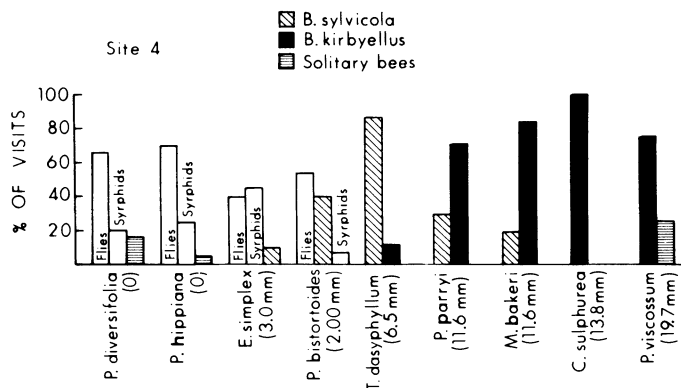

FIG. 4. Frequency distribution of visitors to each plant species at Site 4. Corolla depths are in parentheses below species name. Species visited primarily by queens: *P. viscossum*; species visited 10–25% by queens: *T. dasyphyllum*, *M. brevistyla*, and *C. sulphurea*.

TABLE 1. List of bee species, proboscis lengths, and average corolla depths of flowers in that guild.

Bee species	Mean proboscis length* (mm)		Mean corolla depth of species visited† (mm)
	Queen	Workers	
Bombus bifarius	8.38	5.75	5.38
B. occidentalis	8.29	5.71	5.57
B. sylvicola	8.50	5.79	6.13
B. flavifrons	10.23	7.81	9.80
B. appositus	12.81	10.48	14.11
B. kirbyellus	12.11	9.36	14.18
B. californicus	12.26	10.01	13.75
B. nevadensis	11.81	10.13	8.90
Psithyrus sp.	8.18		5.68
Apis mellifera		6.00	5.70

* Data from Macior (1974).
† Most species visited by workers.

then another date was chosen. For each guild, the length of the summer season consisted of all the days from the date when the earliest blooming guild member actually began flowering to when the latest bloomer finished flowering. The shape of each species' flowering curve was retained in these simulations. After positioning the flowering curves of all guild members, temporal overlap between all species pairs was calculated using the Schoener (1970) formula for niche overlap, $1 - \frac{1}{2} \sum_{k=1}^{n} |p_{ik} - p_{jk}|$, where p_{ik} and p_{jk} are the proportion of the flowers of species i and species j open on the kth day and n is the total number of days in the season. An average pairwise temporal overlap was then computed for the simulation run. After completing 50 simulation runs a grand mean temporal overlap and the variance over all runs was computed. The average pairwise temporal overlap for the actual dispersion pattern of guild members was compared with this grand mean using a t test which compares a single observation with a large sample.

The results of the comparison between observed and expected overlap values for each guild are shown in Table 2. For 10 out of the 11 guilds the average temporal overlap is less than that obtained from simulated random dispersion patterns. The reduction in overlap for these 10 guilds is statistically significant in five cases and near the significance level in the others.

DISCUSSION

In general the results above indicate that, for species visited by the same pollinator, competition is sufficiently strong to have produced divergence in blooming periods. This is in agreement with the conclusions of a number of studies (Mosquin 1971, Frankie et al. 1974, Gentry 1974, Heithaus 1974, Pojar 1974, Reader

1974, Heinrich 1976b,c, Stiles 1977), but stands in contrast to several others (Schemske et al. 1978, Parrish and Bazzaz 1979, B. Rathcke, personal communication). However, in most of the studies indicating a regular sequence, with a few exceptions (Gentry 1974, Reader 1974), the flowering periods are characterized only by the dates of initiation and cessation of blooming with a general indication of the dates of peak bloom. More importantly, in none of these studies was a rigorous attempt made to analyze statistically the flowering sequence with regard to the null hypothesis of random blooming times. A preliminary attempt was made by Heithaus (1974) and by Poole and Rathcke (1979, reanalysis of Stiles' 1977 data). Both of these used only information on the dates of peak bloom and neither involved simulations. As a result they do not have the resolution of the procedure I employ (using the statistical technique developed by Poole and Rathcke 1979 only one of the guilds in my study had a significantly regular flowering sequence).

I also used an alternative simulation method which is computationally easier and gave comparable results to those in Table 2. It uses information only on the length of the blooming period. A random dispersion pattern was simulated as before. The season was then subdivided into 2-d intervals and the number of species in flower in each interval was recorded. Results from each simulation run were cast in a frequency histogram showing the number of intervals in the following classes: 0 species in flower, 1 species, 2 species, etc. The competition hypothesis predicts that approximately the same number of species should be in bloom at any time. Thus, the frequency histogram should consist of a concentration of entries in one or two classes producing a distribution with low variance. A random flowering sequence should result in a frequency distribution with entries spread over more classes and thus a larger variance. A Mann-Whitney U test was used to compare the variance from the actual frequency distribution with the set of variances from the frequency distributions resulting from the simulation runs.

Competitive load

Despite the general conclusion that flowering sequences are nonrandom, an inspection of Figs. 5–8 shows that the pattern of species replacement through time is not always very regular. One possible explanation for this might be that the way in which competition is measured is not entirely appropriate. In the analysis above I assumed that the strength of competition between two guild members was proportional to the extent to which their blooming periods overlapped. Thus the competition hypothesis was that overlap between temporal neighbors should be minimized. However, to determine accurately the detrimental effect of one species on another, and hence the strength of selection for competitive displacement,
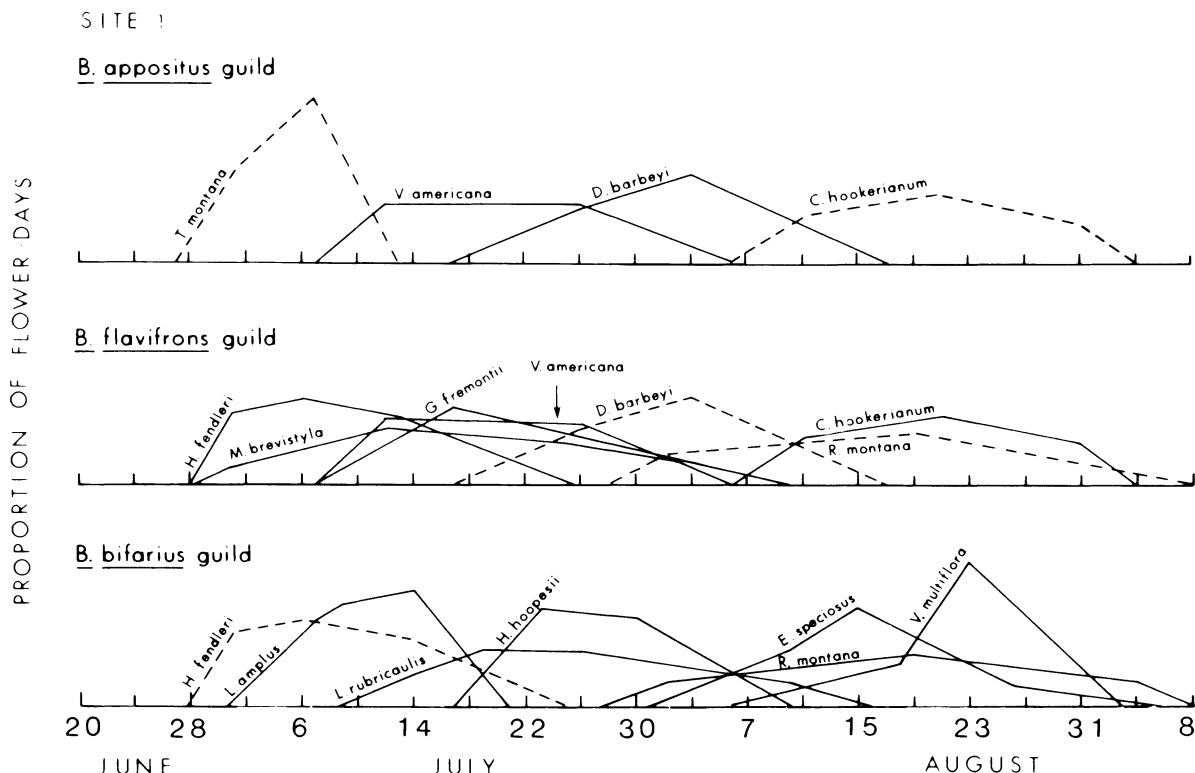
SITE 1

FIG. 5. Flowering phenologies for guilds at Site 1. Flowering curves in solid lines indicate that the species received
>50% of visits from that bumblebee; dashed lines indicate 30–50% of visits, or only 15–20% of visits but found to be an
important potential competitor; the latter species is *D. barbeyi* (*B. flavifrons* guild). The height of each curve indicates the
percentage of the season's total flower number which was open on that day.

one must know more than the overlap between them.
The extent to which a competitor depresses the pop-
ulation growth of a species is a function of the quantity
of that species' resources the competitor consumes.
This is equal to the probability that the competitor
uses a species' resources (niche overlap) times the
population size of the competitor. In the Lotka-Vol-
terra equation for population growth, $dN_i/dt =$
$r_iN_i(K_i - N_i - \Sigma\alpha_{ij}N_j)/K_i$, the term $\Sigma\alpha_{ij}N_j$ denotes the
cumulative negative effect of all interspecific competi-
tors on species i. This term I call competitive load. The
term α_{ij} is taken to be equivalent to the overlap of
species j on species i.

The importance of competitive load has not always
been appreciated in studies of community competitive
interactions, although it is implicit in the concept of
diffuse competition (Mac Arthur 1972). For example,
to infer that two species are seriously affecting each
other because they have a 90% overlap in resource
use ($\alpha = .90$) would be improper without considering
their abundances. If one species is much rarer than
the other then the competitive load on the common
species (the reduction in resources it experiences be-
cause of the presence of the rare species) will be small,
whereas the load on the rare species will be large. By
accounting for asymmetries in competition between

species pairs, and by including the cumulative nega-
tive effect of all competitors, competitive load gives
a more accurate assessment of the competitive status
of a species in a community. The competition hypoth-
esis can thus be restated as: blooming periods should
diverge such that competitive load is minimized.

I examined the magnitude of the competitive load
experienced by plants at the four study sites. The α_{ij}
in the term $\alpha_{ij}N_j$ is equal to the probability of species
i and species j using the same pollinator at the same
time, i.e., pollinator overlap times temporal overlap.
For pollinator overlap I used the value 1.0 for guild
members, 0 for nonmembers, and 0.5 for borderline
guild members. Temporal overlap values were ob-
tained from Figs. 5–8. To determine the abundance
component of competitive load, N_j, some weighting
factors were required. In general, an individual of a
competitor species may not consume an amount of
resource per unit time equal to that of an individual of
a subject species. For animal species this might be due
to differences in body size. Abundances should there-
fore be weighted by the per capita consumption rate
to reflect accurately the amount of resource con-
sumed. In this study the measure of species abundance
is the total number of flowers open over time. The
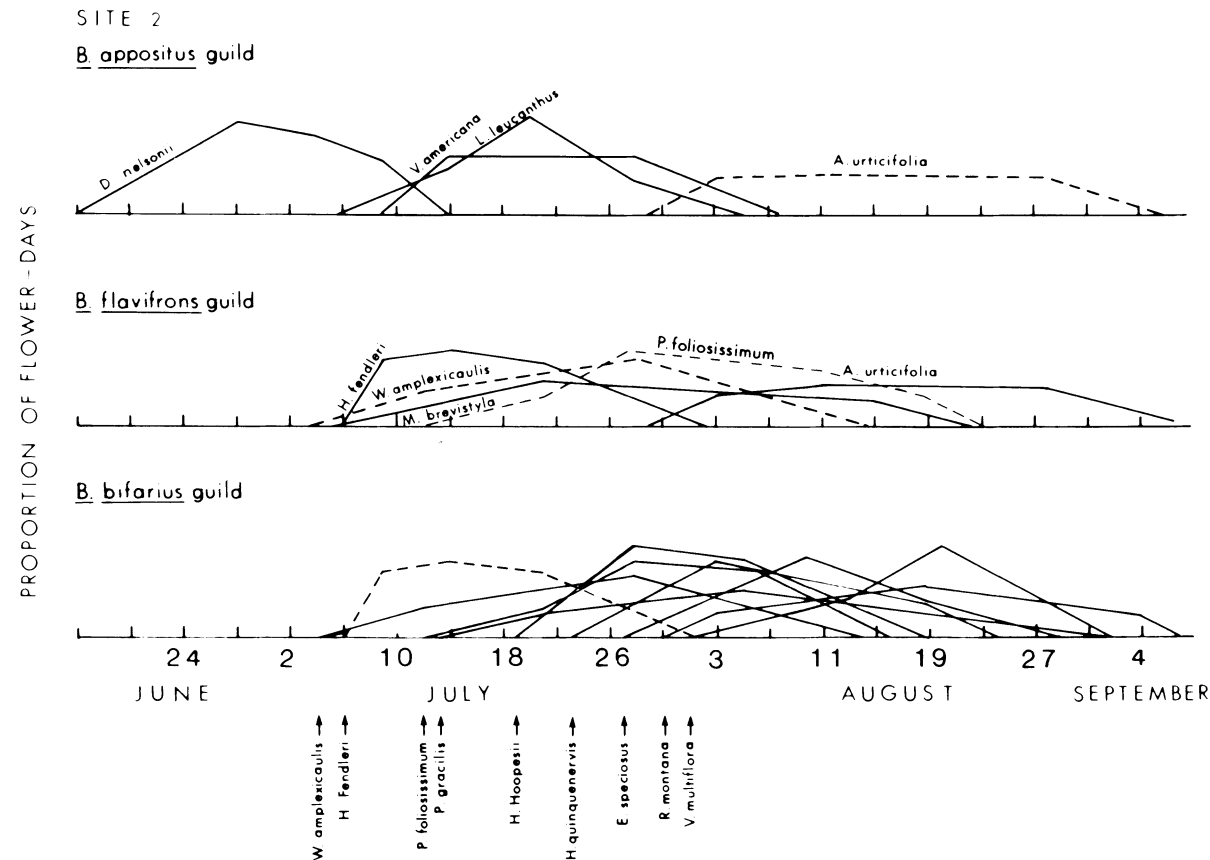"individual" is the flower. Per capita consumption

FIG. 6. Flowering phenologies for guilds at Site 2. Flowering curves in solid lines indicate that the species received >50% of visits from that bumblebee; dashed lines indicate 30–50% of visits, or only 15–20% of visits but found to be important potential competitors; these latter species are: *A. urticifolia* (*B. appositus* guild), *P. foliosissimum* (*B. flavifrons* guild). *Frasera speciosa* not included because it is a sporadic bloomer. The height of each curve indicates the percentage of the season's total flower number which was open on that day.

rate then reflects the ability of flowers to monopolize pollinator visitation time. This is a function of the attractiveness of a flower to pollinators and the amount of time it takes a pollinator to visit it and go to the next. A species whose flowers attract more visits (on a per-flower basis) has a greater per capita ability to draw away visits from another species. Also flowers that take longer to visit have a greater capacity to monopolize pollinators' visitation time. As an index of attractiveness I use the number of visitors seen on a species during a census period, divided by the density of its open flowers at that time. The attractiveness value for a species is an average from three to four censuses made during its blooming period. Attractiveness changed little over this time and only a few species showed diurnal changes in attractiveness (Pleasants 1977 and J. Pleasants, *personal observation*). Total competitive load on species i is therefore given by:

$$\sum \alpha_{ij} N_j \left(\frac{\text{attractiveness, sp } j}{\text{attractiveness, sp } i} \right) \left(\frac{\text{time per visit, sp } j}{\text{time per visit, sp } i} \right),$$

(1)

where N_j is the abundance of competitor j (number of flower-days) and the last two terms indicate the per capita consumption rate of species j relative to species i.

In this context competitive load is an index of the number of pollinator visits a subject species loses to competitors. To see this, consider the pool of visits that are available to a subject species during the time it is in flower. We wish to know how these visits are apportioned between the subject species and its competitors. The number of flowers of the subject species present during this period is N_i, the species' abundance, and the total number of flowers of competitors also present is $\Sigma \alpha_{ij} N_j$, where α_{ij} is equal to the proportion of species j's flowers that are open during species i's blooming period. Without including information on attractiveness, we would expect the number of visits to species i to be proportional to N_i and those to competitors to be proportional to $\Sigma \alpha_{ij} N_j$. When abundance is weighted by attractiveness, the actual ability of flowers to draw visits is reflected. Since this weighting factor was expressed relative to the subject
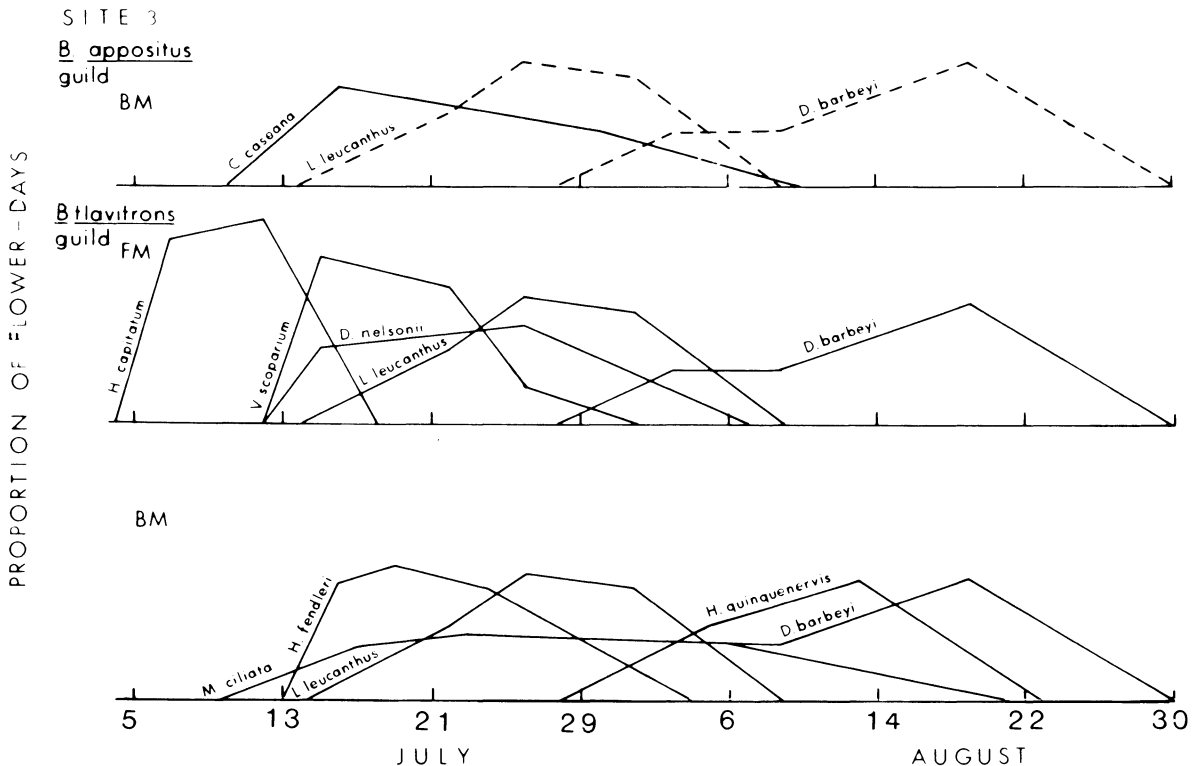
FIG. 7. Flowering phenologies for guilds at Site 3. FM = front meadow, BM = back meadow. Flowering curves in solid lines indicate that the species received >50% of visits from that bumblebee; dashed lines indicate 30–50% of visits, or only 15–20% of visits but found to be important potential competitors; these latter species are: *L. leucanthus* (*B. appositus* guild [BM]), *D. barbeyi* (*B. appositus* guild [BM]). The height of each curve indicates the percentage of the season's total flower number which was open on that day.

species this means that the number of visits the subject receives is still proportional to N_i while those received by competitors is proportional to competitive load (expression 1). It should be noted that a species' competitive load and its abundance are only proportional and not equal to the number of visits lost and gained. Since the proportionality constant may be different for different species, cross-species comparisons are not possible. What I examine below is the number of visits lost relative to the number gained for each species.

The competitive load and abundance for each species are shown in Table 3 and the two are plotted against one another in Fig. 9. There is a significant positive correlation between number of visits lost (competitive load) and number gained (abundance) ($r = .65$, $P < .001$). In general, one is approximately equal to the other which means that for each species the number of pollinator visits potentially available to it during the time it is in flower is roughly equally divided between itself and its competitors. The fact that all species show this pattern, with some exceptions discussed below, indicates that these communities are structured.

It is also of interest to know something about the absolute number of visits each species receives. This can be obtained by multiplying the attractiveness value for each species (the average number of visits per flower) by its abundance (the number of flowers). There is a strong negative correlation between these two variables (Fig. 10, $r = -.817$ $P < .001$); rare species receive more visits per flower than common species. Other authors (Beattie et al. 1973, Heinrich 1976a) also note the presence of rare but highly attractive species in certain plant communities. There also appears to be, in general, a one-to-one correspondence between attractiveness and abundance (Fig. 10, slope = -0.828) indicating that abundance multiplied by attractiveness equals a constant. This leads to the remarkable conclusion that all species receive approximately the same number of visits. Coupled with the observation from above that species lose as many visits as they receive, this means that all species are very similar with regard to the number of visits gained and lost. Thus the resource of pollinator visits has been evenly partitioned among species. This supports the competition hypothesis.

The greater attractiveness of rare species appears to be an adaptation to compensate for an otherwise poor competitive situation. Theoretical (Levin and Anderson 1970, Straw 1972) and field studies on the

SITE 4

B. kirbyellus guild
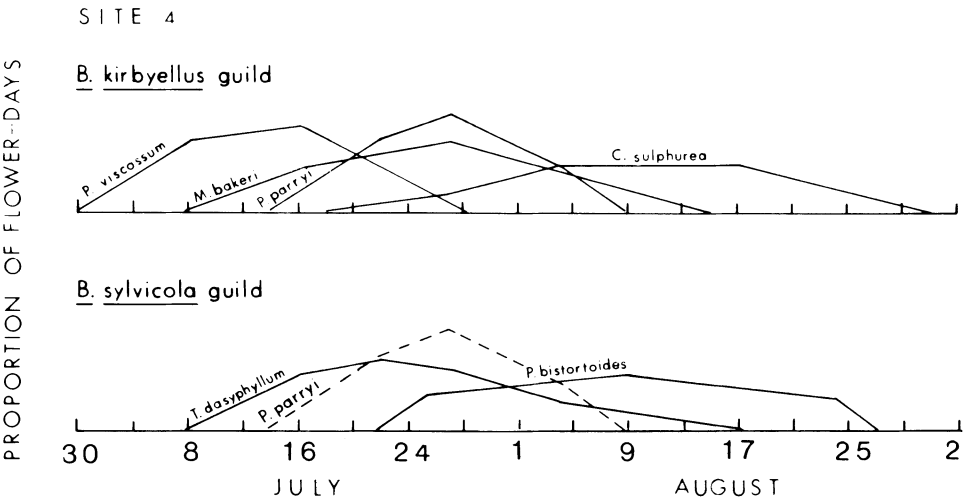

B. sylvicola guild

FIG. 8. Flowering phenologies for guilds at Site 4. Flowering curves in solid lines indicate that the species received >50% of visits from that bumblebee; dashed line indicates 30–50% of visits. The height of each curve indicates the percentage of the season's total flower number which was open on that day.

fate of rare morphs in a population (Levin 1972) indicate that when the attractiveness of morphs or species is equal the rare one is at a pollination disadvantage. If rare species in my study were any less attractive, the partitioning of pollinator visits would favor competitors, perhaps leading to competitive exclusion. The greater attractiveness of rare species does not appear to be related to floral properties such as color, shape, or odor (J. Pleasants, *personal observation*). Instead, it appears to be a consequence of their higher reward value to pollinators. For 11 species I have examined to date, their relative attractiveness is closely predicted by the nectar sugar production rate of their flowers (Pleasants 1977 and J. Pleasants, *personal observation*; also see Heinrich 1976*a*, *b*).

There are some exceptions to the general trends evident in Figs. 9 and 10. There are some species with a much greater load and much lower attractiveness relative to abundance than the average. Many of these species reproduce vegetatively as well as by seeds. Species with some degree of vegetative reproduction are the three species in the genus *Mertensia* (Pelton 1961), *Lathyrus leucanthus* (found at Sites 2 and 3 [FM], 3 [BM]), *Vicia americana* (found at Sites 1 and 2), and *Vaccinium scoparium*. The importance of pollination as a means of reproduction and thus the importance of competition for pollinators is reduced for such species. There are also several species that have a much lower competitive load than the average. All of these species are specialists of one sort or another. Members of this group include two species which are the earliest to flower at the sites where they are found (*Thermopsis montana*, Site 1 and *Delphinium nelsonii*, Site 2). Pollinator abundances are lowest at the be-

ginning of the season (Pleasants 1977) so these species are not as well off as their small loss of visits to competitors would suggest. They occupy an average position in Fig. 10. Three species also included in this group are the only ones which are visited exclusively for pollen and produce no nectar (*Lupinus amplus*, *Lupinus rubricaulis*, and *Potentilla gracilis*). Lastly this set includes the two dominant species in separate guilds at Site 4 (*Trifolium dasyphyllum* and *Castilleja sulphurea*).

TABLE 2. Comparison of actual and simulated random temporal dispersion patterns (*t* test).

| | Average temporal overlap | | Probability of *t* statistic |
Guild	Actual	Simulation	
Site 1			
Bombus appositus	.126	.359	$P < .05$
B. flavifrons	.328	.503	$P < .05$
B. bifarius	.229	.354	$P < .01$
Site 2			
B. appositus	.211	.359	$P = .12$
B. flavifrons	.454	.609	$P = .06$
B. bifarius	.483	.459	$P = .60$
Site 3			
B. appositus (BM)*	.337	.555	$P = .07$
B. flavifrons (FM)*	.249	.366	$P = .13$
B. flavifrons (BM)	.385	.546	$P < .05$
Site 4			
B. kirbyellus	.362	.522	$P = .07$
B. sylvicola	.369	.701	$P < .005$

* BM = back meadow, FM = front meadow.

TABLE 3. List of species at each site and their competitive load, abundance, and attractiveness.

Species*	Family†	Competitive load	Abundance‡	Attractiveness§
Site 1				
Lupinus amplus	(2)	130.2	161.2	0.35
Lupinus rubricaulis	(2)	81.0	630.0	0.24
Helenium hoopesii	(1)	11.5	16.9	12.39
Erigeron speciosus	(1)	1446.0	223.6	.53
Viguera multiflora	(1)	104.8	136.6	4.11
Rudbeckia montana	(1)	7.6	8.4	41.43
Hydrophyllum fendleri	(5)	27.4	44.0	1.34
Geranium fremontii	(12)	28.2	10.2	5.50
Mertensia brevistyla	(4)	1433.2	105.0	0.11
Circium hookeranium	(1)	13.9	3.4	17.86
Vicia americana	(2)	77.9	12.8	3.93
Delphinium barbeyi	(7)	100.2	100.4	1.57
Thermopsis montana	(2)	14.5	181.9	0.35
Castilleja sulphurea	(8)	85.6	69.4	0.91
Site 2				
Pontentilla gracilis	(3)	59.7	178.0	2.28
Helenium hoopesii	(1)	182.0	39.2	2.49
Erigeron speciosus	(1)	1868.4	141.7	0.46
Viguera multiflora	(1)	274.0	112.1	1.45
Rudbeckia montana	(1)	13.4	10.1	14.52
Helianthella quinquenervis	(1)	41.4	38.0	6.63
Polemonium foliosissimum	(6)	1210.0	400.1	0.50
Wyethia amplexicaulis	(1)	19.1	9.9	13.50
Hydrophyllum fendleri	(5)	6.4	2.4	23.10
Agastache urticifolia	(9)	862.2	1992.0	0.18
Vicia americana	(2)	21.9	39.4	1.17
Delphinium nelsonii	(7)	45.5	161.7	0.26
Lathyrus leucanthus	(2)	258.2	104.7	0.18
Site 3 FM‖				
Vaccinium scoparium	(15)	602.7	279.0	0.15
Hydrophyllum capitatum	(5)	9.8	8.1	2.76
Delphinium barbeyi	(7)	32.9	42.2	1.15
Delphinium nelsonii	(7)	53.1	84.3	1.23
Lathyrus leucanthus	(2)	343.2	75.3	0.53
Site 3 BM‖				
Hydrophyllum fendleri	(5)	21.9	28.4	1.98
Helianthella quinquenervis	(1)	39.7	32.0	2.84
Mertensia ciliata	(4)	589.0	125.0	0.81
Delphinium barbeyi	(7)	240.0	273.4	1.00
Lathyrus leucanthus	(7)	37.6	6.9	3.15
Corydalis caseana	(11)	247.7	320.0	0.41
Site 4				
Polygonum bistortoides	(10)	43.1	8.8	1.53
Trifolium dasyphyllum	(2)	15.0	387.5	0.46
Pedicularis parryi	(8)	176.8	35.2	0.42
Mertensia bakeri	(4)	1100.2	190.3	0.20
Castilleja sulphurea	(8)	43.1	510.6	0.45
Polemonium viscossum	(6)	7.8	7.8	3.21

* Additional species found at sites but not members of a bumblebee guild (see Figs. 1–4): Site 2—*Linum lewisi* (13), Site 3—*Linum lewisi* (13), *Pseudocymopterus montanus* (14), Site 4—*Potentilla diversifolia* (3), *Potentilla hippiana* (3), *Erigeron simplex* (1).

† Code for families: (1) Asteraceae, (2) Fabaceae, (3) Rosaceae, (4) Boraginaceae, (5) Hydrophyllaceae, (6) Polemoniaceae, (7) Ranunculaceae, (8) Scrophulariaceae, (9) Lamiaceae, (10) Polygonaceae, (11) Fumariaceae, (12) Geraniaceae, (13) Linaceae, (14) Apiaceae, (15) Ericaceae.

‡ Number of flower-days per m^2 (number of flowerhead-days for composites).

§ Attractiveness index = number of bees seen on a species during a 30-min census period divided by number of open flowers per m^2, averaged over a number of census periods.
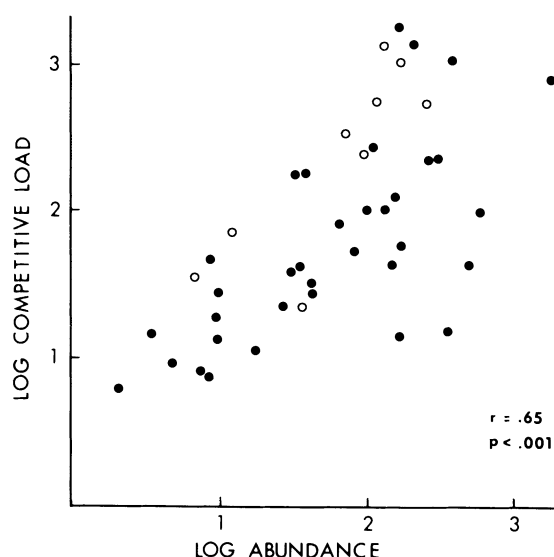
‖ FM = front meadow; BM = back meadow.

FIG. 9. Relationship between abundance (AB) and competitive load (CL). Abundance in this context is an index of the number of visits a species receives and competitive load is a comparable index of the number of visits it loses to competitors. Equation of regression line through points: log $CL = 0.681 + 0.685 \log AB$ or $CL = 4.79 AB^{0.685}$. Open circles indicate species with vegetative reproduction. (Some points are the same species at different sites, see text.)
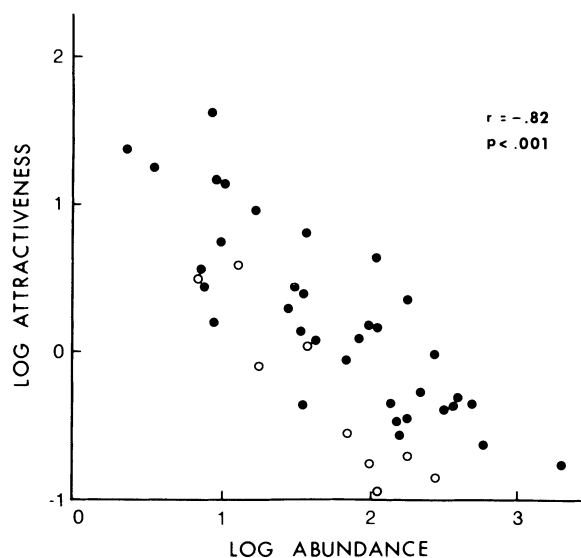
FIG. 10. Relationship between abundance (AB) and attractiveness (AT). Attractiveness is an index of the number of visits a flower receives per day. Abundance in this context is simply the number of flowers produced by a species during its blooming period. Open circles indicate species with vegetative reproduction. Equation of regression line: log $AT = 1.86 - .828 \log AB$ or $AT = 72.4 AB^{-.828}$.

Other coexistence mechanisms

Besides divergence in blooming time or increasing attractiveness, there may be other ways to reduce the impact of competitors. It has been suggested that in situations where the interference component of competition for pollinators is strong, which would be the case when a number of species was in bloom simultaneously, coexistence can occur if species grow in different microhabitats (Bobislud and Neuhaus 1971, Pleasants 1977, Waser 1978 and 1979). This is because the frequency of interspecific visitation is reduced when species have a spatial refugium. As long as they receive enough pollinator visits to maintain themselves in this refugium, species are less likely to be driven to extinction by another (see Waser 1978b for theoretical explanation). This would be particularly true of long-lived perennials. In my study most of the members of guilds are sufficiently segregated temporally that interspecific visitation would already be at a low level. The *Bombus bifarius* guild at Site 2, however, exhibits large temporal overlaps among its nine members and also failed to show a regular dispersion of blooming periods. In addition, six out of the nine species are composites and thus have similar floral morphologies. For these species, interference is potentially important so I examined the extent of spatial isolation among them. Data on presence or absence of a species in the >100 quadrat samples made at this site were used to measure the spatial overlap between species. Three of the nine species in the guild have conspicuous characteristics that make interference unlikely. *Hydrophyllum fendleri* blooms much earlier than the others; *Wyethia amplexicaulis* grows in dense monospecific stands; *Potentilla gracilis* is visited to the exclusion of others while bees forage on it for pollen (Pleasants 1977). For each of the remaining six species I ranked its five competitors according to the proportion of quadrats containing the subject species which also contained a particular competitor. I then ranked these same five competitors with regard to their contribution to the subject species' competitive load (potential for interference). A contingency table was constructed which compared the rank value of competitors for spatial overlap and competitive load. Rank combinations for the competitors of each species were tallied in this table. There is a significant negative association between spatial overlap and competitive load ($\chi^2 = 6.53$ $P < .001$). The conclusion is that species tend to be more spatially isolated from their stronger competitors. Hurlbert (1970) found a relationship somewhat similar to this. He observed that for 10 species of co-occurring *Solidago* there was a significant tendency for species with high overlap in their blooming period to have low spatial overlap. His explanation for this pattern was that it promotes reproductive isolation. This is equivalent to reducing cross-species pollination, i.e., reducing interference.

Assessing whether the competitive displacement patterns illustrated in Figs. 5–10 are the result of ex-

ploitation or interference competition, or both, is a difficult task. The two are not mutually exclusive. The regularity of the displacement patterns indicates that interspecific competition is important or at least was important in the past. Thus we can presume that the amount of conspecific pollen a stigma receives is (or was) less than required for maximum seed-set. The question then is to what extent this deficiency results from not receiving enough visits as opposed to not receiving enough conspecific pollen on those visits. The importance of the interference component depends on the frequency with which pollinator visits are preceded by visits to heterospecifics. I followed 111 bumblebees as they foraged on a variety of species. These observations were made when other potential forage species were in bloom: Each foraging sequence consisted of visits to 20–40 flowers and at least five different inflorescences. Seventy-six percent of these sequences were composed of visits to a single species. Those involving more than one species often consisted of runs of visits to one species and then another. Corbicular pollen loads also provide some information on the number of species visited during a foraging bout. Of 68 loads I examined, 66% contained pollen from essentially one species (trace amounts of pollen from other species were sometimes found). This is similar to the percentage found by Macior (1974) for pollen loads from bumblebees on the Colorado Front Range.

The low frequency of interspecific visitation could simply reflect the spatial isolation or clumping of potentially interfering species, or it could be due to constancy on the part of the bees (Free 1963, 1970). Sixty-five percent of the species pairs involving members of the same guild had sufficient spatial isolation to make interspecific visitation unlikely (Pleasants 1977). Fifteen percent of the species pairs had very different floral morphologies which could facilitate constancy by allowing bees to distinguish between them or promote constancy by making it inefficient for bees to switch from one to the other (Heinrich 1975, 1979). An additional 9% of species pairs involved a species visited strictly for pollen and one visited only for nectar. Interspecific foraging is uncommon in such cases (Free 1970; J. Pleasants, *personal observation*). For only 11% of species pairs there was no discernible characteristic that would make interference unlikely. Of course, differences in plants' microhabitat preference or floral morphology could have evolved to reduce interference, which may by why it is at low levels currently. It should be noted, however, that such mechanisms would not reduce exploitation competition.

While these data are not adequate to assess fully the importance of interference, they do suggest that the majority of visits any flower receives has been immediately preceded by one or more visits to conspecifics (also see Heinrich 1976a, 1979). Thus if a defi-

ciency in conspecific pollen on stigmatic surfaces does exist, it is more probably the result of competitors taking away visits rather than interfering with pollen flow. The importance of exploitation competition, and an indication that it is a current phenomenon, are demonstrated by the observation that within a population of *Polemonium foliosissimum* at Site 2 some plants are able to attract more visits per flower and these plants are found to have a higher seed-set (Zimmerman 1979). Such intraspecific competitive effects can only result from exploitation because interference with pollen flow does not exist on the intraspecific level. While interference can be important (Levin and Berube 1972, Waser 1978a) it is probably at a low level in most cases because of factors other than temporal divergence. The patterns of segregation of blooming periods and differential attractiveness shown in this study are probably a means of avoiding exploitation competition.

LITERATURE CITED

Barrell, J. 1969. Flora of the Gunnison Basin. Natural Land Institute, Rockford, Illinois, USA.

Beattie, A. J., D. E. Breedlove, and P. R. Ehrlich. 1973. The ecology of the pollinators and predators of *Frasera speciosa*. Ecology **54**:81–91.

Bobislud, L. B., and R. J. Neuhaus. 1975. Pollinator constancy and survival of the rare species. Oecologia **21**:263–272.

Brian, A. D. 1957. Differences in the flowers visited by four species of bumblebees and their causes. Journal of Animal Ecology **26**:71–98.

Brown, J. H. 1975. Geographical ecology of desert rodents. Pages 315–341 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts USA.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. American Naturalist **102**:107–137.

———. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey, USA.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities. Pages 460–490 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecological Monographs. **46**:257–291.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Com-

parative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology **62**:881–913.

Free, J. B. 1963. The flower constancy of honeybees. Journal of Animal Ecology **32**:119–131.

———. 1970. The flower constancy of bumblebees. Journal of Animal Ecology **39**:395–402.

Gentry, A. H. 1974. Flowering phenology and diversity in tropical Bignoniaceae. Biotropica **6**(1):64–68.

Heinrich, B. 1975. Bee flowers: a hypothesis on flower variety and blooming times. Evolution **29**:325–334.

———. 1976*a*. The foraging specializations of individual bumblebees. Ecological Monographs **46**:105–128.

———. 1976*b*. Resource partitioning among eusocial insects: bumblebees. Ecology **57**:874–889.

———. 1976*c*. Flowering phenologies: bog, woodland, and disturbed habitats. Ecology **57**:890–899.

———. 1979. "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. Ecology **60**:245–255.

Heithaus, E. R. 1974. The role of plant-pollinator interactions in determining community structure. Annals of the Missouri Botanical Garden **61**:675–691.

Herbert, S. J. 1979. Density studies on Lupins. II. Components of seed yield. Annals of Botany **43**:65–73.

Hespenheide, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyranidae. Ibis **113**:59–72.

Hurlbert, S. H. 1970. Flower number, flowering time, and reproductive isolation among ten species of *Solidago* (Compositae). Bulletin of the Torrey Botanical Club **97**:189–193.

Inouye, D. 1976. Resource partitioning and community structure: a study of bumblebees in the Colorado Rocky Mountains. Dissertation. University of North Carolina, Chapel Hill, North Carolina, USA.

Levin, D. A. 1972. Low frequency disadvantage in the exploitation of pollinators by corolla variants in *Phlox*. American Naturalist **106**:453–460.

Levin, D. A., and W. W. Anderson. 1970. Competition for pollinators between simultaneously flowering species. American Naturalist **104**:455–467.

Levin, D. A., and D. Berube. 1972. *Phlox* and *Colias*: the efficiency of a pollination system. Evolution **26**:242–250.

Mac Arthur, R. H. 1972. Geographical ecology. Harper and Row, New York, New York, USA.

Mac Arthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist **101**:377–385.

Macior, L. W. 1974. Pollination ecology of the Front Range of the Colorado Rocky Mountains. Melanderia **15**.

May, R. M. 1973. Stability and complexity in model eco-

systems. Princeton University Press, Princeton, New Jersey, USA.

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

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

Parrish, J. A. D., and F. A. Bazzaz. 1979. Difference in pollination niche relationships in early and late successional plant communities. Ecology **60**:597–610.

Pelton, J. 1961. An investigation of the ecology of *Mertensia ciliata* in Colorado. Ecology **42**:38–52.

Pleasants, J. M. 1977. Competition in plant-pollinator systems: an analysis of meadow communities in the Colorado Rocky Mountains. Dissertation. University of California, Los Angeles, California, USA.

Pojar, J. 1974. Reproductive dynamics of four plant communities of southwestern British Columbia. Canadian Journal of Botany **52**:1819–1834.

Poole, R. W., and B. J. Rathcke. 1979. Regularity, randomness, and aggregation in flowering phenologies. Science **203**:470–471.

Reader, R. J. 1975. Competitive relationships of bog ericads for major insect pollinators. Canadial Journal of Botany **53**:1300–1305.

Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. Theoretical Population Biology **5**:163–186.

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

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology **51**:408–418.

———. 1974. Resource partitioning in ecological communities. Science **185**:27–39.

Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. Science **198**: 1177–1178.

Straw, K. M. 1972. A Markov model for pollinator constancy and competition. American Naturalist **106**:597–620.

Waser, N. M. 1978*a*. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. Ecology **59**:934–944.

———. 1978*b*. Interspecific pollen transfer and competition between co-occurring plant species. Oecologia **36**:223–236.

Willson, M. F., and P. Price. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). Evolution **31**:495–511.

Zimmerman, M. J. 1979. An analysis of the reproductive strategies of *Polemonium* in Colorado. Dissertation. Washington University, St. Louis, Missouri, USA.