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LOCAL GEOGRAPHIC DISTRIBUTIONS OF BUMBLEBEES NEAR CRESTED BUTTE, COLORADO: COMPETITION AND COMMUNITY STRUCTURE¹

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Abstract. It was hypothesized that the local geographic distributions of bumblebees near Crested Butte, Colorado and the community patterns exhibited by these bumblebees are the products of competition for plants. To evaluate this hypothesis several transects were established and at regular intervals throughout a summer growing season, data were collected along each transect on how many bumblebees of each species and caste were visiting the various plant species. The distributions and abundances of the plant species involved were recorded qualitatively.

Seven species of bumblebees accounted for 97% of all bumblebees observed and in this paper attention is restricted to these species. Five other species were observed in very low numbers. Each bumblebee species had a different distributional pattern.

The seven bumblebee species form four groups in terms of both their proboscis lengths and the corolla lengths of the plants they preferentially visit. Long-, medium-, and short-tongued groups were most often observed foraging at flowers with long, medium, and short corollas, respectively. Furthermore proboscis lengths of bumblebees tended to be very similar within each group but quite dissimilar between groups. The fourth group consisted of a single short-tongued species which has well-developed mandibles which enable it to rob nectar from many plants with long corollas. It also feeds legitimately on short-corolla flowers. Some anomalies in the above groupings are mentioned and discussed.

When the data on bumblebees and plant distributions are combined with data on flower preferences, a pattern consistent with the competition hypothesis emerges. Within each proboscis-length group, bumblebee species tend to replace one another altitudinally in a manner consistent with the hypothesis. The nectar-robbing species is most abundant in areas where a plant that is usually visited by hummingbirds is most common. Other species of bumblebees are unable to gain access to the nectar of this plant.

In any uniform well-isolated area, similar floristically to the present study area, only three or four species of bumblebees appear to be able to coexist. Furthermore, a bumblebee community in such an area will apparently consist of a short-, a medium-, and a long-tongued species and in some cases a short-tongued nectar-robber. These patterns are also consistent with the competition hypothesis, as similarity in proboscis length reflects similarity in diet and the intensity of competition should, for these bumblebees, be closely related to diet similarity.

It is possible that the observed distributional patterns could also be explained on the basis of different distributions of suitable nest sites for each bumblebee species or different responses to local variations in climatic conditions. Neither alternative seems able, however, to explain the observed patterns.

Key words: *bumblebees; community structure; competition; corolla length; distribution; flower preference; nectar-robber; plants; proboscis length.*

INTRODUCTION

The aim of the present study was to consider two closely related aspects of the ecology of bumblebees, namely the distribution on a local scale (i.e., within one valley) of several species of bumblebees and also various properties of the bumblebee communities, such as the number and kinds of various coexisting species. In this paper I present data on the local distributions of several bumblebee species, their utilizations of the various plant species, and patterns of community structure.

At both the onset of the study and at present, competition between bumblebees for nectar seemed to be

the factor most likely to determine the local distributions of the species and also the number and kinds of coexisting species. Excluding the results of the present study, there are several lines of evidence for the existence of competition between bumblebees for nectar in the present study area. First, in the present study area, bumblebees spend most of their foraging time collecting nectar and typically collect pollen only incidentally through its adherence to their bodies (G. Pyke, *personal observation*). Second, the average nectar volumes per flower are considerably below what they would be in the absence of bumblebees (G. Pyke, *personal observation*). Third, the bumblebees tend to forage in ways that maximize their net rate of energy intake (Pyke 1978a, b, 1979, 1980). This is expected since the growth, survival, and reproduction of a bumblebee colony are likely to depend on the colony's rate of energy gain (Pyke 1979). Fourth, when

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bumblebees of one species are removed from a patch of flowers they are replaced by members of another species (Inouye 1978). Thus bumblebees limit the availability of nectar energy to other bumblebees and consequently limit the fitness of other bumblebees. In other words, bumblebees appear to compete with one another. Heinrich (1976a, b) also argues that in his study areas in Maine there is strong competition between bumblebees for nectar. As shown below, in the present study area the distributions of the various bumblebee species and the patterns of their community structure are consistent with the hypothesis that these distributions and community patterns are the products of competition for nectar.

METHODS

This study was carried out in the vicinity of the Rocky Mountain Biological Laboratory, Crested Butte, Colorado. The sites encompassed an elevational range from the town of Crested Butte at 2730 m to the tops of two mountains ≈ 16 km north of Crested Butte, each with maximum elevation of ≈ 3730 m. To study the local distributions of bumblebees a total of 36 sites was established. These sites were at regular intervals along three transects and also at one location between two of the transects. These transects and the various sites were situated as follows:

- (1) Gothic Transect: This transect consisted of 21 sites along the road from Crested Butte, Colorado (elevation 2730 m) to Schofield Pass (3240 m). The elevations of the sites above 2860 m are shown on Figs. 1 and 4.
- (2) Washington Gulch Transect: This transect consisted of a foot trail from the Gothic Campground (2940 m) on the Crested Butte-Schofield Pass Road, to Washington Gulch (3440 m). The elevations of the eight sites are shown in Figs. 2 and 5.
- (3) Schofield Transect: This transect consisted of a regular but unmarked route from Schofield Park (3180 m), which lies just north of Schofield Pass along the road to Marble, to the summit (3760 m) of Bellevue Mountain which rises at the eastern edge of the park. This mountain is the nearest mountain to the north of Mount Bellevue. The elevations of the six sites are shown on Figs. 3 and 6.
- (4) Emerald Lake Site: This site was located at the southern end of Emerald Lake which is just south of Schofield Pass on the Crested Butte-Schofield Pass Road. The elevation of this site was 3180 m.

In areas where a transect was not very steep a site was defined as being everything within 50 m of a chosen center. In steep areas, however, a site was everything between certain elevational limits and within 25 m of a regular foot route along the transect. With the exception of that part of the Gothic Transect below

3150 m and the Emerald Lake site, all sites were reached by foot.

From 22 June to 8 September 1974 I and either one or two assistants visited each site about once every 8 d. During each visit to a site the following data were recorded:

- (1) Identity of each plant species in flower within the site.
- (2) Qualitative notes on the flowering stage and abundance of each plant species.
- (3) Identity of bumblebees feeding on different plant species. Sampling at a site was usually continued until at least 20 bumblebees had been examined from each plant species. In almost all instances, a bumblebee was released unharmed after identification and only in rare cases of uncertainty were bumblebees killed for later examination. Hence our observations probably had a negligible effect on the abundances of the bumblebees. Voucher specimens of the bumblebees were retained.
- (4) The amount of time spent by the group at each site. This was recorded in the hope of being able to present the bumblebee abundance in terms of bees per person-hour.
- (5) The number of cuckoo-bumblebees (genus *Psithyrus*) observed feeding on each plant species. These data were recorded because the cuckoo-bumblebees closely resemble and are very closely related to the bumblebees, upon which they are nest parasites.

Bumblebees differ between species and between castes in terms of the length of their proboscis (i.e., mentum plus prementum). Data on the average proboscis lengths were obtained for queens and workers from Macior (1974) and for males from Inouye (1976, 1980).

The flowers of different plant species differ in terms of effective corolla length (i.e., the distance between where a bumblebee is able to position its head during nectar-feeding and the location of the nectar). Data on effective corolla lengths were obtained for most species from Inouye (1976, 1980). Other plant species were measured during the present study.

RESULTS AND DISCUSSION

Composition of bumblebee fauna and areas in which bumblebees are successful

A total of 12 bumblebee species was found during the summer. The number of queens, workers, and males of each of these species examined during the summer are presented in Table 1. The species are listed in order of decreasing overall abundance. The first seven species account for 95% of all bumblebees examined and >99% of all males examined. In other words, the other five species were rare overall and were virtually completely unsuccessful in terms of re-

TABLE 1. Numbers of queens, workers, and males of bumblebee species examined during the study.

Bumblebee species	Number of queens	Number of workers	Number of males	Total	Percent of total
<i>Bombus flavifrons</i>	627	2745	1278	4650	35.4
<i>B. kirbyellus</i>	361	756	681	1798	13.7
<i>B. sylvicola</i>	131	895	635	1661	12.6
<i>B. bifarius</i>	48	1167	296	1511	11.5
<i>B. appositus</i>	193	881	261	1335	10.2
<i>B. frigidus</i>	41	706	523	1270	9.7
<i>B. occidentalis</i>	17	394	91	502	3.8
<i>B. californicus</i>	43	108	1	152	1.2
<i>B. nevadensis</i>	66	27	4	97	0.7
<i>B. mixtus</i>	35	45	0	80	0.6
<i>B. rufocinctus</i>	12	42	9	63	0.5
<i>B. centralis</i>	0	17	0	17	0.1
All species	1574	7783	3779	13 136	

production. Consequently, the remainder of this paper will deal solely with the first seven species listed in Table 1.

Although the lowest transect (i.e., Gothic Transect) began at 2730 m, it was found that below 2860 m all the bumblebees apparently failed to reproduce. Be-

tween these two elevations on the transect were several kilometres of dry terrain dominated by sagebrush and, despite the fact that 93 queens and 517 workers were found there, only 39 males were found during the course of the summer. Because of this the following results and discussion will concentrate on those sites at or above 2860 m. The apparent failure of bumblebees below this elevation will be discussed later.

Distributions of bumblebees above 2860 m along the Gothic Transect

As mentioned above, the amounts of time spent by our group at each site were recorded so that the abundances of the various species of bumblebees could be determined and presented in terms of bees per person-hour. However, it was found that there was a great deal of variation between members of our group in bumblebee-catching ability and there was also much variation in the composition of the group. Furthermore, the extreme patchiness of the plant species meant that different members of the group tended to concentrate on different plant species. Hence I have chosen to present the data not in terms of bees per person-hour but instead as the percentage that each bumblebee species makes of the total number of bum-

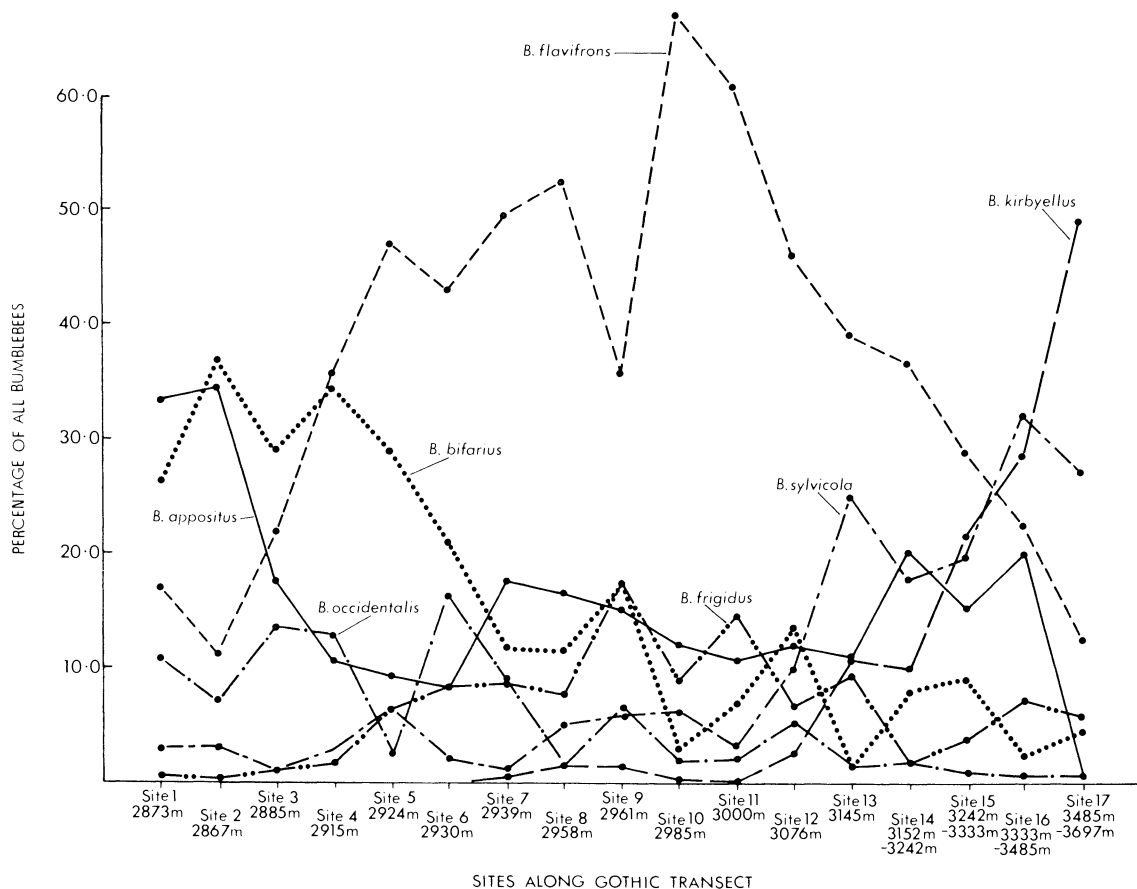


FIG. 1. Relative abundances of all bumblebee species along the Gothic Transect.

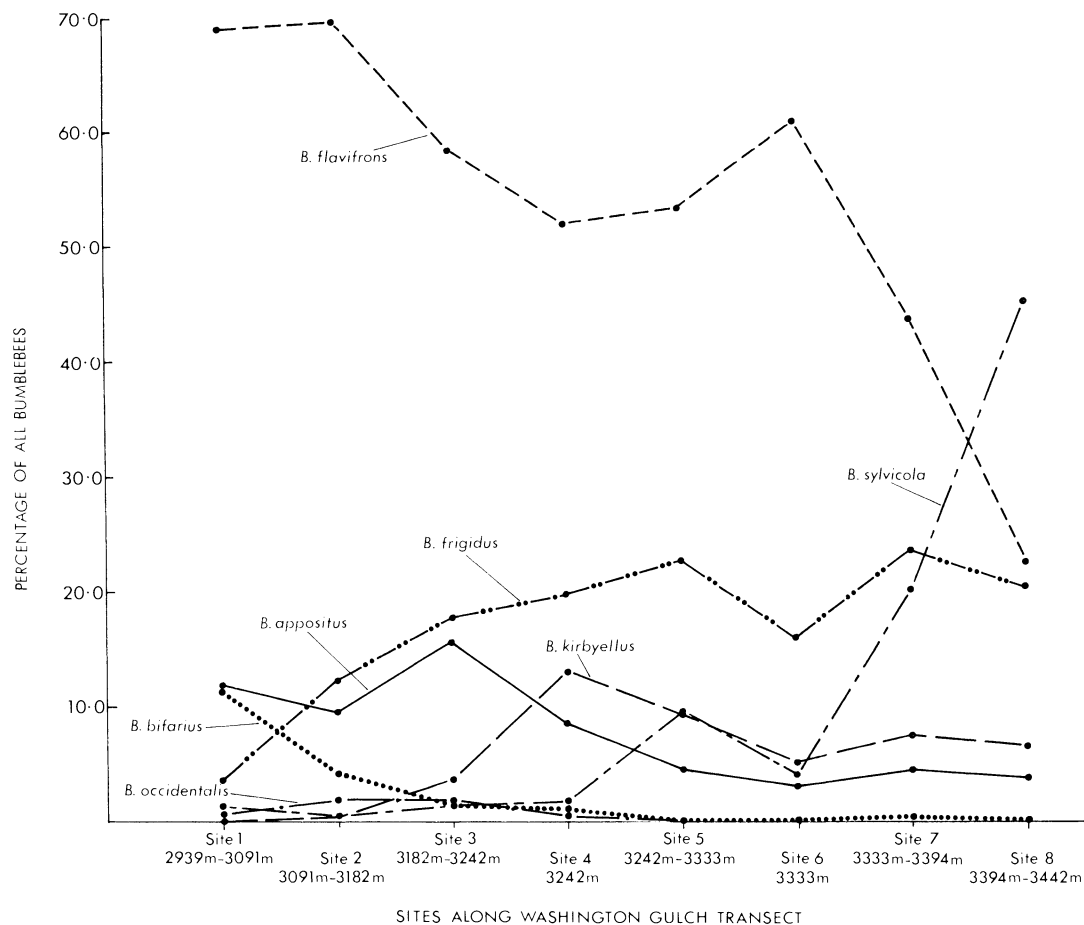


FIG. 2. Relative abundances of all bumblebee species along the Washington Gulch Transect.

blebees examined at each site. During the course of the summer the total bumblebee abundances appeared to be similar at each site and so these percentages are probably reasonable approximations of the relative abundances of the bumblebee species throughout the summer.

Fig. 1 shows the percentage of all bumblebees summed over all plant species made up by each of various bumblebee species for each site along the Gothic transect. This particular transect rises slowly at first and then quite steeply at the end, so neither distance nor elevation is an appropriate scale for the entire transect. Because of this, the sites are spaced equally along the abscissa with the elevation given below the abscissa. For many sites the percentages do not quite sum to one due to the presence of small numbers of the omitted species. Figs. 2 and 3 present the same data for the Washington Gulch and the Schofield Transects, respectively, and data for the Emerald Lake site are also shown in Fig. 3. Since the steepness of these transects fluctuated the sites are spaced equally along the abscissa with the elevation or elevational range of each site given below the abscissa.

From these figures it is seen that, as expected, each bumblebee species has its own unique distribution, and that there are considerable differences among the species.

Utilization of plant species by the bumblebees

In order to obtain an approximation of the extent to which the various plant species in the study area were utilized by bumblebees and the extent to which different bumblebee species utilized different plant species, the total numbers of each bumblebee species examined on each plant species were calculated for the entire study area. These data are presented in Table 2.

From this table it can be seen that the bumblebees can be divided into four groups based on their utilization of the plants. The first group consists of *Bombus appositus* and *B. kirbyellus*. These two species both were most often caught on *Delphinium barbeyi* and also overlap in their utilization of *Gentiana calycosa* and *G. thermalis*. They are not identical, however, for *B. appositus* favors *Aconitum columbianum* while *B. kirbyellus* favors *Castilleja sulphurea* and

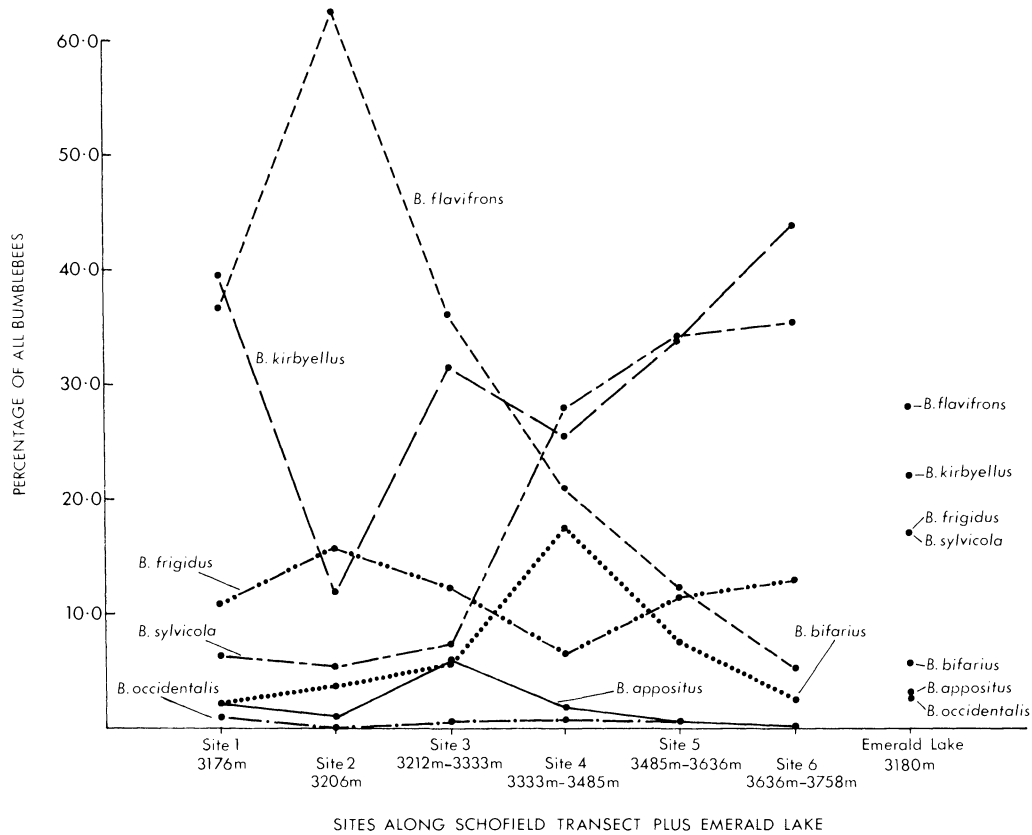


FIG. 3. Relative abundances of all bumblebee species along the Schofield Transect and at the Emerald Lake site.

Mertensia ciliata. These last three plant species occur throughout the distributions of both species of bumblebee. *Delphinium nelsoni* and *Vicia americana* appear to be favored by *B. appositus*, but they rarely occur within the distribution of *B. kirbyellus*.

A second category consists solely of *B. flavifrons*. This bumblebee was caught in large numbers on a very wide variety of plants and it has considerable overlap in utilization of plants with the bees of the first and also with those in the next two groups.

The third group consists of *B. bifarius*, *B. sylvicola*, and *B. frigidus*. These bumblebees all favored such plants as *Helianthella quinquenervis*, *Helonium hoopesii*, and *Viguiera multiflora* and there was also much overlap between at least two of the three on *Senecio triangularis*, *Senecio crassulus*, *Senecio bigelovii*, *Mertensia ciliata*, and *Epilobium angustifolium*.

The final group consists of *B. occidentalis*. This bumblebee is put in a separate group mostly because of its habit of nectar-robbing such plants as *Ipomopsis aggregata*, *Delphinium barbeyi*, and *Aconitum columbianum*. In other years it has also been seen in reasonable numbers nectar-robbing *Aquilegia caerulea* (G. Pyke, personal observation; D. Inouye, personal communication; R. Miller, personal communication). It also is unique in that it feeds on such plants

as *Ligusticum porteri* and *Heracleum lanatum*, on which other bumblebee species are almost never seen in the study area. Otherwise it was found in reasonable numbers on *Epilobium angustifolium* and in low numbers on a wide variety of plants.

These four groups of bumblebees tend to form three distinct groupings with respect to proboscis length. This is shown in Table 2 which gives the proboscis length of each bumblebee species. From the first group of bumblebees through to the third group there tends to be a steady decrease in proboscis length and furthermore, there appears to be a tendency for the first three groups to be spaced apart on the proboscis-length axis. This spacing phenomenon has also been discussed by Inouye (1976, 1980) and will be considered in more detail in a later section of this paper. The third and fourth groups have very similar proboscis lengths but differ in terms of mandible morphology. *B. occidentalis* has larger, stronger mandibles than the bumblebees of the third group and is apparently adapted to nectar-robbing flowers (Inouye 1976, 1980).

The plants favored by the first three groups of bumblebees are found to form natural groups with regard to the corolla lengths of each plant species. This may also be seen from examination of Table 2 which gives the corolla length for as many as possible of the plants

TABLE 2. Numbers of each bumblebee species observed on each plant plus proboscis lengths for each caste of each bumblebee species and corolla length for each plant species. The plant species are arranged in order of decreasing corolla length.

Plant species	Corolla length (mm)	Bumblebee species and proboscis lengths (mm) of each caste						
		Group 1		Group 2	Group 3		Group 4	
		<i>B. appositus</i>	<i>B. kirbyellus</i>	<i>B. flavifrons</i>	<i>B. sylvicola</i>	<i>B. bifarius</i>	<i>B. frigidus</i>	<i>B. occidentalis</i>
		♀ 12.8 ♀ 10.5 ♂ 11.4	♀ 12.1 ♀ 9.4 ♂ 12.5	♀ 10.2 ♀ 7.3 ♂ 9.0	♀ 8.5 ♀ 5.8 ♂ 7.4	♀ 8.4 ♀ 5.8 ♂ 6.6	♀ 7.3 ♀ 5.7 ♂ 7.0	♀ 8.3 ♀ 5.7 ♂ 7.2
<i>Ipomopsis aggregata</i>	27.2							9
<i>Delphinium nelsoni</i>	18.6	52		36			1	
<i>Pedicularis bracteosa</i>	15.0		13	4		1		
<i>Delphinium barbeyi</i>	14.0	828	1294	859			11	34
<i>Lonicera involucrata</i>	13.0			28				
<i>Vicia americana</i>	12.4	30		22			1	8
<i>Castilleja sulphurea</i>	12.3	2	127	17				
<i>Gentiana calycosa</i>	11.6	112	68	11	1			1
<i>G. thermalis</i>	10.9	23	127	8			4	6
<i>Mertensia ciliata</i>	9.9		120	430	75	12	132	6
<i>Lathyrus leucanthus</i>	8.8	14		9		5		7
<i>Aconitum columbianum</i>	8.4	208	4	589		23	3	50
<i>Hydrophyllum fendleri</i>	8.1			92	21		6	
<i>H. capitatum</i>	7.3			10				
<i>Haplopappus croceus</i>	6.3	3		2	4	74		17
<i>Cirsium</i> sp.	6.2	34	4	72	1	5		1
<i>Helianthella quinquenervis</i>	5.9		3	529	239	279	89	8
<i>Senecio serra</i>	5.8			109	13	33	19	6
<i>Aster engelmannii</i>	5.4	6		52	7	22	1	5
<i>Senecio bigelovii</i>	5.2	2		237	31	219	72	27
<i>S. aplectens</i>	5.1		3	25	52	2	12	
<i>S. crassulus</i>	4.9	2	6	61	283	28	114	2
<i>S. fremonti</i>	4.7			22	54	25	38	
<i>S. triangularis</i>	4.5			242	113	31	282	2
<i>S. atractus</i>	4.3			2	40	34	11	16
<i>Helenium hoopesii</i>	4.0	10		175	350	159	157	9
<i>Hymenoxys grandiflora</i>	3.9			16	16		1	
<i>Viguiera multiflora</i>	3.6	2		93	68	139	52	9
<i>Frasera speciosa</i>	3.1	14	6	16	24	130	11	9
<i>Haplopappus parryi</i>	2.7	1	1	16	22	46	21	12
<i>Epilobium angustifolium</i>	2	8		534	22	77	76	72
<i>Phacelia leucophylla</i>	0	5	11	182	64	44	15	3
<i>Heracleum lanatum</i>	0				1			14
<i>Ligusticum porteri</i>	0							27

utilized by bumblebees. From these data it is evident that for the first three bumblebee groups there is a correlation between the proboscis length of each bumblebee species and the corolla lengths of the plant species it favors. The long-tongued bumblebees (i.e., bumblebees with long proboscises), *B. appositus* and *B. kirbyellus*, favor *Delphinium barbeyi*, which has a long corolla. The short-tongued *B. bifarius* and *B. sylvicola* favor various composite species and *Epilobium angustifolium*, all of which have fairly short corollas, and the medium-tongued *B. flavifrons* feeds on the entire range of corolla lengths. The short-tongued *B. occidentalis*, which forms the fourth group, feeds legitimately on the plants with short corollas and robs nectar from the plants with long corollas.

This correlation between the proboscis length of a bumblebee and the corolla length of the plant species it favors has been previously noted by several authors (Brian 1957, Hobbs et al. 1961, Hobbs 1962, Medler

and Carney 1963, Heinrich 1976a, b, Inouye 1976, 1978, 1980). However, the correlation in the present study area is not at all perfect and leaves several things unexplained (see also Heinrich 1976a). The following are some examples:

(1) *Aconitum columbianum* is favored by *B. appositus* and *B. flavifrons*. However, *B. kirbyellus*, which has a proboscis length intermediate between those of the former two species, almost totally ignored this plant (Table 2) despite the fact that at the lowermost part of the Schofield Transect both the bee and the plant were abundant and a total of 44 bumblebees of other species was caught on the plant at this site.

(2) *Castilleja sulphurea* is fed upon extensively by *B. kirbyellus* but is ignored by both the shorter tongued *B. flavifrons* and the slightly longer tongued *B. appositus*. The plant and all three bee species overlap extensively.

(3) *Lonicera involucrata*, which has a long corolla

(13.0 mm), is fed upon exclusively by *B. flavifrons* and is ignored by all other bees.

A possible explanation for the above anomalies is that plants having the same corolla length may not be nutritionally equivalent; different bumblebee species may have different nutritional requirements, and the combination of these two factors results in a certain amount of bee selectivity independent of corolla length. There is now abundant evidence that the nectars of different plant species are not chemically identical (e.g., Fahn 1949, Baker and Baker 1973, 1975, Watt et al. 1974, Baker, 1975), nor are their pollens (e.g., Todd and Bretherick 1942, Standifer 1966b). There is also some evidence that the differences among plants in these regards are important nutritionally to bees and other animals (e.g., Doull 1966, Standifer 1966a, Hagedorn and Burger 1968, Gilbert 1972). It is also possible that the density of a particular bumblebee species feeding on a particular plant species in a particular location reflects the density of other bumblebee species feeding on the plant and the availability of alternative nectar sources. The densities of bumblebees and plants could easily change from one location to another in such a way that any proboscis length-corolla length correlation breaks down.

With the exception of anomalies similar to the above, the correlations between bumblebee proboscis lengths and flower corolla lengths are quite good. So far, however, these correlations have not been well explained. One possibility is that the net rate of energy intake to a bumblebee while it is feeding on a particular plant species is a function of the average nectar volume per flower, the proboscis length of the bumblebee, and the corolla length of the plant (Holm 1966, Heinrich 1976a,b, Inouye 1976, 1980). This is a reasonable possibility since most bumblebee feeding appears to be for nectar (G. Pyke, *personal observation*; Heinrich 1976b) and it could operate as follows: The plants with the longest corollas tend to produce the greatest nectar volumes (Inouye 1976, Baker 1977; G. Pyke, *personal observations*) and hence, all other things being equal, bumblebees should favor these plants. However, for the plants with long corollas, the rate at which the nectar can be obtained is likely to decrease as the proboscis length of the bumblebee decreases since a long proboscis can reach farther into the nectar than a short proboscis. Also, for the plants with short corollas, the rate is likely to increase as proboscis length decreases since the flowers on many of these plants are very close together (i.e., composite flower heads) and the longer the proboscis the more unwieldy it might be (Inouye 1976, 1980). Hence, the long-tongued bumblebees could have a higher net rate of energy gain than the short-tongued bumblebees on the plants with long corollas, and vice versa for the plants with short corollas. By the same argument the medium-tongued bumblebees may well do better than other bees on the plants with medium corollas.

The data that are presently available on the relationships between rate of flower visitation, bumblebee proboscis length, and flower corolla length do not provide complete support for the above thesis. Inouye (1976, 1980) found for the long-corolla plant *Delphinium barbeyi* (14.0 mm) that, as expected, the average time spent per flower is a decreasing function of bumblebee proboscis length (i.e., longer tongued bumblebees visit flowers at a higher rate than shorter tongued bumblebees). However, for *Helianthella quinquerervis* (5.9 mm) and *Frasera speciosa* (3.1 mm), which both have corolla lengths at the short end of the spectrum, he found that the average time spent per flower reached a maximum for bumblebees with a particular proboscis length and was lower for bumblebees with both shorter and longer proboscises. This is exactly the antithesis of what would be expected from the argument in the preceding paragraph. For *Aconitum columbianum*, which has a medium-length corolla (i.e., 8.4 mm), Inouye (1978) found that the average time per flower was lower for a medium-tongued bumblebee than for a long-tongued bumblebee. Heinrich (1976a) found that, on very short-corolla flowers, the short tongued bumblebees visited flowers at a higher rate than the longer tongued bumblebees. I have observed that for *Agastache urticifolia*, which has a medium-length corolla (i.e., 10.0 mm) a medium-tongued bumblebee visited flowers at a higher rate than either short- or long-tongued bumblebees. The last three observations are all consistent with the above argument. More data are required to settle the issue.

Distributions of plants utilized by the bumblebees

Before proceeding to consider the distributions of the bumblebees in more detail, it is necessary to present data on the distributions of the plants utilized by all the bumblebees. Since only qualitative notes were made of the abundances of each plant species, it is not possible to give accurate quantitative descriptions of the abundances of all the plants. Furthermore, the extreme patchiness of almost all the plant species would have made quantitative measurements of their abundances almost impossible and certainly prohibitive in terms of time. However, it is possible to gain a good idea of the distributions of the plants by tabulating for each site the total number of bumblebees and cuckoo-bumblebees (*Psithyrus* spp.) (independent of species) caught on the various plant species. This is done in Table 3. In many cases no bees were observed to visit some of the plants at a site although the plants were present and were sometimes even abundant. In such cases the letter 'P' (for present) is recorded in Table 3.

The distribution of B. appositus and B. kirbyellus

Since the bumblebees form groupings in terms of their proboscis lengths and the plants upon which they

TABLE 3. Numbers of bees observed on each plant species at each site or presence (P) if no bees observed.

	<i>Aquilegia caerulea</i>	<i>Ipomopsis aggregata</i>	<i>Delphinium nelsoni</i>	<i>Delphinium barbeyi</i>	<i>Gentiana calycosa</i>	<i>Gentiana thermalis</i>	<i>Lonicera involucrata</i>	<i>Vicia americana</i>	<i>Castilleja sulphurea</i>	<i>Mertensia ciliata</i>	<i>Lathyrus leucanthus</i>	<i>Aconitum columbianum</i>	<i>Hydrophyllum fendleri</i>	<i>Hydrophyllum capitatum</i>	<i>Haplopappus croceus</i>	<i>Cirsium</i> sp.
Gothic Transect																
Site 1		P	6	32	2	20		2	2		2	123			1	1
2	P	P	1	140				P	2	19	P	53	5	P	75	1
3	3	P		128	P	P	P	P	3	P	15	116		P	28	3
4	P	P		8	9			P	P	1		28		P		
5	2	P		9	9	P	P	4	P	3		24	P	P		
6		P		34	3	4	P	P	2	19	1	95		P		12
7	P	P	21	44	6	P		P	P	28	P	24	P	P		P
8	P	P	26	90	10		2	6	1	150	5	110	P	P		P
9		P	10	44	5	2		2	P	18	5		2	P		6
10		P	1	95	14	11		9	P	46	5	34	52	P		3
11		P	13	79		P		4	P	35	9	30	16	P		6
12	P	P		135	7	1	P	3	P	16	1	P	45	P		8
13	2	P		43	7	P	P	3	8	50	P	2	42	P		
14	1	P		115	8	P		4	1	6	1	3	P	P		34
15	P	P		177		P		2	13	15	P		P	P		1
16	P	P		210		P	2	P	9	36	P		2			P
17	4			236			1		7	17						
Washington Gulch Transect																
Site 1	P	P		60	P		P	3		P	P		P			7
2	P	P		71		2		2	P	12	P	16		P		7
3	P	P		112	21	P	P	P	P	5	P	11	P	P		9
4	P			60	P	1	P		1	52		4				
5	P			73	1				2	7		1				
6				1	5				5	28						
7	P	P		88	2	P		P	2	13	P	13		P		
8	P	P		25	2				2	4						
Schofield Transect																
Site 1	P			113	15	16	P	P	15	122		34		P		
2	P			86	P		P		P	46		P		P		
3	P			59	14	1	2		14	7		1		P		
4	P			112	23	4			23	7		3		11		1
5	P			85	21	P			21	8				P		7
6	P			122	15	12			15	23						P
Emerald Lake																
	P	P		209	15		P		P	100				P		10

feed, the distributions of these bumblebees will be considered separately for each group. The first group, it will be recalled, consists of *B. appositus* and *B. kirbyellus* and the distributions of these two species can be seen most clearly from graphs which show for each site the proportion of bees in the group which is made up by each species separately. Figs. 4, 5, and 6 show these graphs for the Gothic, the Washington Gulch, and the Schofield Transects, respectively. From these figures it can be seen that, although there is some overlap, the two species tend to have disjunct distributions, with *B. kirbyellus* replacing *B. appositus* at the higher elevations. This observation and the additional one that these two bumblebee species overlap extensively in the plants upon which they feed are

consistent with the hypothesis that there is competition for plants between the bumblebees and that this competition limits the distributions of the two species and hence their coexistence. I shall discuss this hypothesis below.

Gothic Transect.—From Fig. 4 it is seen that the region of overlap along the Gothic Transect in the distributions of *B. appositus* and *B. kirbyellus* is mostly between ≈ 3120 and 3290 m. Within this region the plants fed upon extensively by either or both of these two bees were *Castilleja sulphurea*, *Mertensia ciliata*, *Delphinium barbeyi*, *Cirsium* sp., and *Gentiana calycosa* (see Tables 2 and 3). With the exception of *Gentiana calycosa*, which did not flower until towards the end of the summer (i.e., after about 8 August),

TABLE 3. Continued.

<i>Helianthella quinquenervis</i>	<i>Senecio serpa</i>	<i>Aster engelmannii</i>	<i>Senecio bigelovii</i>	<i>Senecio triangularis</i>	<i>Senecio atratus</i>	<i>Senecio fremontii</i>	<i>Senecio amplexens</i>	<i>Senecio crassulus</i>	<i>Helentium hoopesii</i>	<i>Hymenoxys grandiflora</i>	<i>Viguiera multiflora</i>	<i>Frasera speciosa</i>	<i>Haplopappus parryi</i>	<i>Epilobium angustifolium</i>	<i>Phacelia leucophylla</i>	<i>Heracleum lanatum</i>	<i>Ligusticum porteri</i>
1			23						P			55	P				1
45	2		3								28	8	P			5	P
53	1		75	1					P		17	28	9	51		2	15
30	P		47						1		53		12	125		P	1
52			68	14				2	14		2		49	54		P	P
37	P		107	P					1				5	1		1	2
57	45		31	8					4		4	5	33	8		P	4
85			56	P				2	23		P	11	13	P		P	P
87			89						7		P	P	10	24		P	1
31	5	P	48	32					P		97		3	P		P	P
28	24	P	45	17				P	1		49			165		P	P
37	61	2		P					14		96	1		167		P	P
74	6	6						1	5		11	1	12	21	15	P	P
95	8	37	P	P		21		5	51		77		6	47	27	5	P
51	2	2	1	15		31		65	19		3	1		42	57	P	1
101		P		63		49	26	75	65			2	2	1	68	P	1
23		P		50		6	27	53	P	P		10	1		90		P
26	32	24	P	4				P	P		12		P	19		P	P
38	45	9		33				P	P		1			1		P	P
36	35	21	4	31				10	52		37			4		P	P
39				8				P	11		1						P
4				76			6	13	16			2	6			P	P
28				P				19	6								P
31	P			35				42	82				3			P	P
24	1	P						65	103				2				P
P	P			34				8	21				3	P		P	P
3	61		P	78				P	102		P	P		P		P	P
9	37	1	P	13				P	83		1	7				P	P
31		1	P	21			3	14	321			P	1				P
30	2		P	P			P	50	194	P		7		8			P
18			9			16	20	80	57	23				1			P
2	P			132	140	65	30	75	72				3	118	85	P	P

these plant species had very similar periods of bloom and of use by the bumblebees. Table 4 presents a summary of foraging observations of *B. appositus* and *B. kirbyellus* between 3120 and 3290 m along the Gothic Transect. This table shows that for most of the summer *B. appositus* fed almost exclusively on *Delphinium barbeyi* while *B. kirbyellus* fed upon both this and also *Castilleja sulphurea* and *Mertensia ciliata*. Both species fed late in the summer upon *Gentiana calycosa* but neither did so to any great extent. Thus *B. appositus* suffers complete overlap with *B. kirbyellus* in terms of plant utilization while *B. kirbyellus* shares only some of its plants with *B. appositus*. If there is competition between these species this should result in the elimination of *B. appositus* from the area.

Such elimination would probably take place were it not for the fact that dispersal of queens will each year bring *B. appositus* into the region from lower elevations where it is quite successful. Hence, in areas that have comparable elevation and plant composition, but that are likely to have low rates of immigration by *B. appositus* from the areas where it is successful, there should be, under the competition hypothesis, very few *B. appositus* and many *B. kirbyellus*. There are several examples where this appears to be true.

(1) At the lowermost part of the Schofield Transect, which is isolated by ≈ 4 km from the area in which *B. appositus* is successful, of which the last third is heavily wooded, there is abundant flowering by *Castilleja sulphurea*, *Mertensia ciliata*, *Delphinium barbeyi*, and

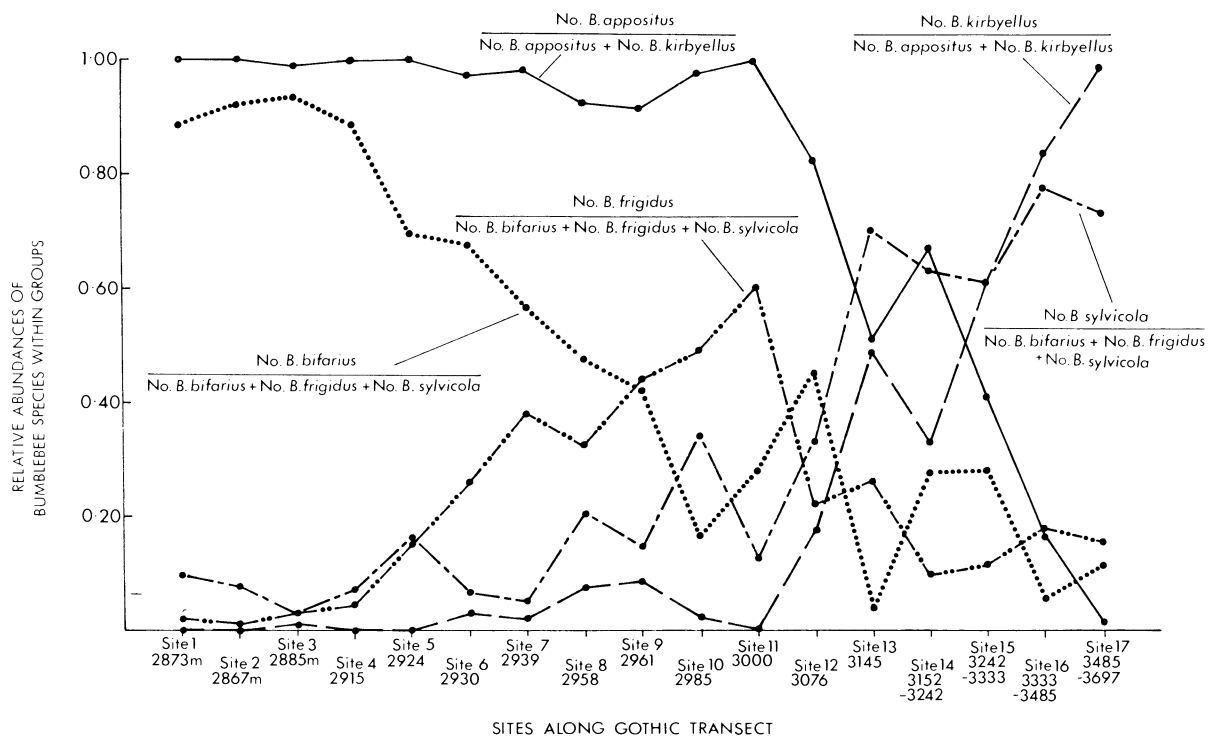


FIG. 4. Relative abundances of bumblebee species within groups along the Gothic Transect.

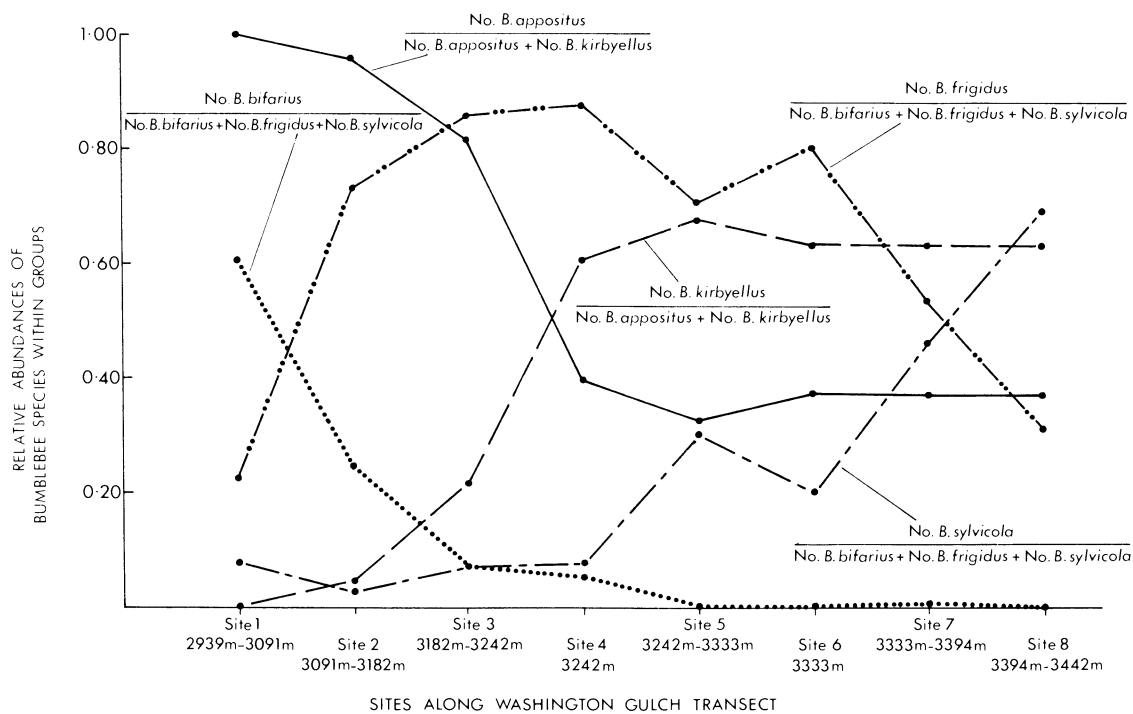


FIG. 5. Relative abundances of bumblebee species within groups along the Washington Gulch Transect.

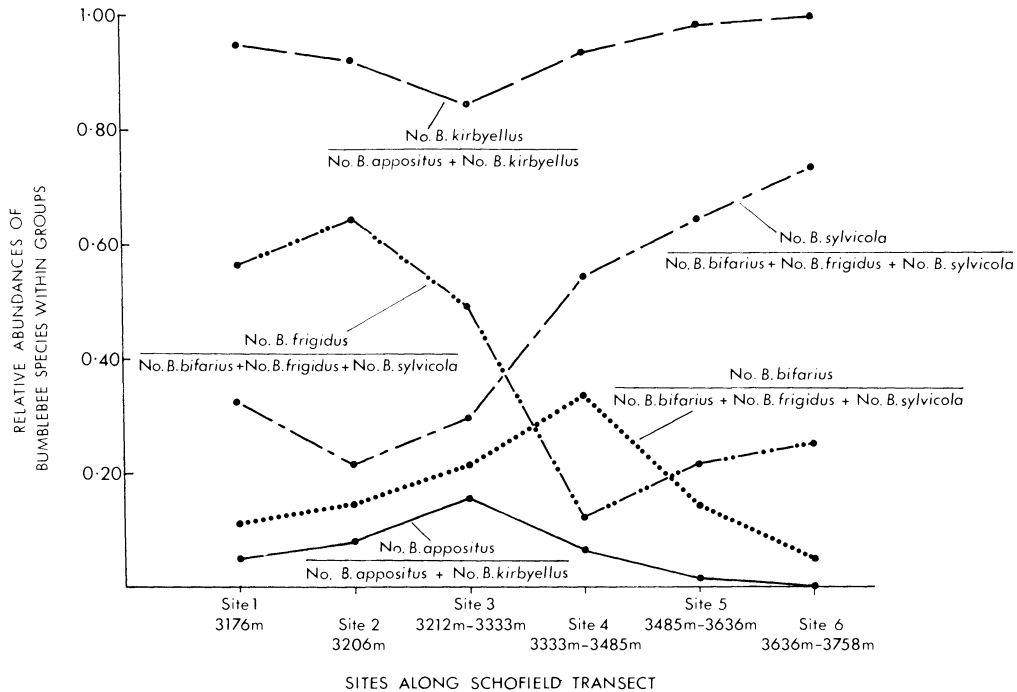


FIG. 6. Relative abundances of bumblebee species within groups along the Schofield transect.

Aconitum columbianum, and scattered flowers of *Gentiana calycosa*. As mentioned before, the *Aconitum* is favored by *B. appositus* but not *B. kirbyellus*. At this location it was visited heavily and exclusively by *B. flavifrons*. As expected only 11 *B. appositus*, representing 1.9% of all bumblebees, were captured at this site during the summer.

(2) Along the remaining upper part of the Schofield Transect there is abundant flowering by *Castilleja sulphurea*, *Mertensia ciliata*, and *Delphinium barbeyi*, scattered flowers of *Gentiana calycosa*, and a few flowers of *Aconitum columbianum*. As expected, only 27 *B. appositus*, representing 1.9% of all bumblebees, were captured along this transect during the summer.

(3) Along the Gothic Transect from 3120 to 3420 m, the plant community changes rather little, with abundant flowering throughout this range by *Castilleja sulphurea*, *Mertensia ciliata*, *Delphinium barbeyi*, *Lath-*

yrus leucanthus, and *Vicia americana*, and scattered flowers of *Gentiana calycosa*. The greater the height on this transect the greater is the distance from the area where *B. appositus* is successful and as expected the rarer this bee becomes relative to *B. kirbyellus* (see Fig. 6).

The upper limit along the Gothic Transect to the distribution of *B. appositus* is thus consistent with the hypothesis of competition with *B. kirbyellus*. I shall now consider the lower limit of the distribution of *B. kirbyellus*.

At elevations below 3120 m there is abundant flowering by *Mertensia ciliata* and *Delphinium barbeyi* and occasional patches of *Castilleja sulphurea*. It seems likely therefore that *B. kirbyellus* would be successful and abundant in these areas in the absence of *B. appositus*. However, the plant community below 3120 m is different from that above 3120 m in several important respects. First, *Castilleja sulphurea* is much less abundant below 3120 m than above that elevation. Second, *Aconitum columbianum* is very abundant below 3120 m along the Gothic Transect and rare above 3120 m. This plant, as mentioned above, is favored by *B. appositus* but not at all by *B. kirbyellus*. Third, below 3120 m there is fairly abundant flowering by *Delphinium nelsoni*. This plant has quite a long corolla (Table 1) and hence it is likely that *B. appositus*, the longest-tongued bumblebee, would be the most efficient at extracting nectar from *D. nelsoni* flowers. The plant also has very little if any overlap with the dis-

TABLE 4. Summary of foraging observations of *B. appositus* and *B. kirbyellus* between 3120 and 3290 m along the Gothic Transect.

Plant species	Number of bees observed	
	<i>B. appositus</i>	<i>B. kirbyellus</i>
<i>Castilleja sulphurea</i>	0	17
<i>Mertensia ciliata</i>	0	25
<i>Delphinium barbeyi</i>	147	105
<i>Gentiana calycosa</i>	10	5

tribution of *B. kirbyellus* and so it is likely that *B. kirbyellus* does not favor this plant just as it does not favor *Aconitum columbianum*. This possibility is supported somewhat by the observation that not one *B. kirbyellus* was caught on *Delphinium nelsoni* in areas where there were at least a few *B. kirbyellus*. Hence, below 3120 m, there is a marked shift in the plant community in favor of *B. appositus* and to the detriment of *B. kirbyellus*. The replacement of *B. kirbyellus* by *B. appositus* at the lower elevation is therefore consistent with the competition hypothesis.

At this point it is worthwhile to consider the possible competitive effect that *B. flavifrons* has on *B. appositus* and *B. kirbyellus*. In the absence of *B. flavifrons* at the lower elevations *B. kirbyellus* could feed on *Mertensia ciliata*, *Delphinium barbeyi*, and to some extent *C. sulphurea* during most of the summer, while *B. appositus* could feed on *Aconitum columbianum* and *Delphinium barbeyi*. Such a situation should allow coexistence of both *B. appositus* and *B. kirbyellus*. However, at these lower elevations *B. flavifrons* is extremely abundant and it tends to dominate the *Mertensia ciliata* and the *Aconitum columbianum*. It is possible therefore that the combined competitive effect of *B. appositus* and *B. flavifrons* creates a lower limit to the distribution of *B. kirbyellus*. So competition provides an explanation for both the lower limit of the distribution of *B. kirbyellus* and the upper limit of the distribution of *B. appositus* along the principal transect.

Washington Gulch Transect.—This transect provides data that agree well with those obtained for the Gothic Transect. Throughout the elevational range of the transect there is fairly abundant flowering by *Mertensia ciliata*, *Delphinium barbeyi*, *Lathyrus leucanthus*, and *Vicia americana*, and scattered flowers of *Aconitum columbianum*. Above 3230 m *Castilleja sulphurea* is abundant while below that elevation it is quite rare; just as for the Gothic Transect *B. kirbyellus* steadily replaces *B. appositus* above 3230 m, a trend which supports the competition hypothesis. It also appears that the rarity of *Castilleja sulphurea* below 3230 m may be sufficient to result in outcompetition of *B. kirbyellus* below that elevation. Once again the limits to the distributions are consistent with the competition hypothesis.

Distribution of *B. flavifrons*

As mentioned above, *B. flavifrons* was the most abundant bee at most sites. This is not at all surprising considering that it appears to favor a very wide variety of plants (see Table 2). However, it does not appear to treat all plants equally and this provides a clue to understanding its distribution. The plants favored by this medium-tongued bumblebee tend to be such medium corolla length plants as *Mertensia ciliata*, *Aconitum columbianum*, and *Helianthella quinquenervis*.

Although the bee was also frequently caught on *Delphinium barbeyi* and *Epilobium angustifolium*, the former of these two plants was sometimes relatively ignored by this bumblebee (e.g., at Site 8 on the Gothic Transect 94 *B. flavifrons* were caught on *Aconitum columbianum* and 45 on *Helianthella quinquenervis*, while only 19 were caught on *Delphinium barbeyi*) and *E. angustifolium* was very spotty in its distribution and flowered late in the summer when little else was available (see Table 3). *B. flavifrons* would also, under the competition hypothesis, have experienced considerable competition from *B. appositus* or *B. kirbyellus* on *Delphinium barbeyi* depending on the site. These observations suggest that the local distribution of *B. flavifrons* might be determined at least in part by the local abundances of the plants which have medium-length corollas.

Another factor likely under the competition hypothesis to influence strongly the local abundances of *B. flavifrons* is competition from other species of bumblebees. *B. flavifrons* is in the unique position of potentially competing with both the long-tongued bees for *Delphinium barbeyi* and *Aconitum columbianum* and the short-tongued bees for such plants as *Helianthella quinquenervis*, *Mertensia ciliata*, and *Epilobium angustifolium*. It would be predicted therefore that, as the abundances of the medium corolla length plants decrease relative to those of plants with long and short corollas, the abundances of *B. flavifrons* would decrease relative to other bumblebees. This prediction is given some support by the following data obtained in the present study:

(1) Above ≈ 3030 m along the Gothic Transect *Aconitum columbianum* is uncommon to rare, whereas below this elevation it is abundant. The other plants fed upon extensively by *B. flavifrons* appear to change little in abundance through all but the lowest part of this transect. In other words, above 3030 m *B. flavifrons* has one fewer of its favored plants than below 3030 m. Furthermore, the plant that drops out has a medium-length corolla and may as a result represent a major loss to this species of bumblebee. Hence it would be predicted that the relative abundance of *B. flavifrons* should be less above 3030 m than below that elevation. This is indeed the case (Fig. 2).

(2) Exactly the same situation occurs along the Washington Gulch Transect with *Aconitum columbianum* dropping out above 3330 m and *B. flavifrons* becoming, as expected, relatively much less abundant above that elevation (Fig. 2).

(3) At the lower end of the Gothic Transect a similar phenomenon occurs. This time it is *Mertensia ciliata* that essentially disappears and it does so at an elevation of 2890 m. Also, at sites near this elevation both *Aconitum columbianum* and *Helianthella quinquenervis* appeared to be less abundant than at higher elevations. It is thus consistent with the competition hypothesis that *B. flavifrons* is relatively less abundant

at the lower end of the Gothic Transect than at somewhat higher elevations.

Distribution of B. bifarius, B. sylvicola, and B. frigidus

These three bumblebee species, as mentioned above, form a group by virtue of their similarly short proboscises and their favoring of plants with short- and medium-length corollas. They should therefore under the competition hypothesis compete most heavily amongst themselves and with the medium-tongued *B. flavifrons*.

The distribution of each of these species is best seen by plotting for each site the ratios of the numbers of each species taken separately to the sum of all the numbers of all three species. This has been done in Figs. 4, 5, and 6 for the three transects. From these figures the following additional observations may be made on the distributions of these species:

(1) Along the Gothic Transect there is a tendency toward a succession of the three species, with *B. bifarius* and *B. sylvicola* at the lowest and highest elevations, respectively, and with *B. frigidus* at intermediate elevations. *B. frigidus* reaches its peak in relative abundance at ≈ 3000 m.

(2) Along the Washington Gulch Transect there is the same succession of these three species with *B. frigidus* reaching its peak in relative abundance at ≈ 3240 m. *B. frigidus* is relatively more abundant along this transect than along the previous one.

(3) Along the Schofield Transect there does appear to be a succession of species but the order is different from that in the other two transects. In this case *B. frigidus* and *B. sylvicola* are the most abundant of the three species at the lower and upper ends of the transect, respectively, while *B. bifarius*, though it is never the most abundant species, reaches its peak in relative abundance between 3330 and 3480 m.

These three species appear, as mentioned above, to have very similar preferences for the various plant species (Table 1). So, if their respective distributions are related to differences from one site to another in the plant community, there should be at least some small difference in the preferences these bumblebees have for the different plants. Such differences are not easy to detect but the data presently available do suggest some likely possibilities.

It is possible to obtain an indication of which plants are favored by a bumblebee species by examining closely the utilization of the plant species which flower in areas where the bumblebee species is very successful. These data are presented below for each of the three species.

(1) *B. frigidus*: This species reached its greatest relative abundance between 3180 and 3330 m along the Washington Gulch and Schofield Transects. A summary of the foraging observations of this bum-

TABLE 5. Summary of feeding observations of *B. frigidus* in regions where it has relatively high abundance.

Plant species	Number of <i>B. frigidus</i> observed	
	Washington Gulch Transect between 3180 and 3330 m	Schofield Transect between 3180 and 3330 m
<i>Mertensia ciliata</i>	33	25
<i>Senecio triangularis</i>	66	54
<i>Helenium hoopesii</i>	15	26
<i>Senecio crassulus</i>	14	2
<i>Helianthella quinquenervis</i>	7	0
Other plants	12	10

blebee species in these two regions is presented in Table 5. With the exception of the first two plant species in this table there was much overlap in the flowering times of the plant species. There was almost no overlap, however, between the flowering of *Mertensia ciliata* early in the season and the later flowering of *Senecio triangularis*. Thus Table 5 suggests that *B. frigidus* favors *Mertensia ciliata* for the first part of the season and *Senecio triangularis* for the second part. *B. frigidus* is also apparently willing to accept *Helenium hoopesii* as a food source.

(2) *B. sylvicola*: This species reaches its greatest relative abundances at the uppermost ends of the three transects. Within these regions *B. sylvicola* feeds on *Mertensia ciliata* early in the season and later appears to prefer *Senecio crassulus* over other plants (Table 6). It also forages extensively on *Helianthella quinquenervis* and/or *Helenium hoopesii* depending on the availability of these two plant species (Tables 3 and 6).

(3) *B. bifarius*: This species reaches its greatest relative abundance below 2960 m along the Gothic Transect and between 3330 and 3480 m along the Schofield Transect. Within these two regions *B. bifarius* appears to prefer to forage on *Helenium hoopesii* though it will also readily accept *Helianthella quinquenervis* and/or *Senecio bigelovii* (Tables 3 and 7). Early in the season *B. bifarius*, like the other two species, feeds on *Mertensia ciliata* (Table 7).

The above analysis indicates that each of the three bumblebee species appears to prefer a different plant species, *Senecio triangularis* for *B. frigidus*, *Senecio crassulus* for *B. sylvicola*, and *Helenium hoopesii* for *B. bifarius*.

Since all three bumblebee species will readily accept a similar array of plants, it is likely that, at least in the absence of the other species, they could each be successful at almost any of the study sites. At all but the

TABLE 6. Summary of feeding observations of *B. sylvicola* in regions where it has relatively high abundance.

Plant species	Number of <i>B. sylvicola</i> observed		
	Gothic Transect above 3150 m	Washington Gulch Transect above 3330 m	Schofield Transect above 3480 m
<i>Mertensia ciliata</i>	25	5	1
<i>Senecio crassulus</i>	105	46	88
<i>Helianthus quinquenervis</i>	136	11	10
<i>Helenium hoopesii</i>	37	56	82
<i>Senecio triangularis</i>	57	8	0
<i>Phacelia leucophylla</i>	47	0	0
<i>Senecio fremontii</i>	38	0	0
<i>S. amplexans</i>	36	0	9
<i>Lupinus</i> sp.	26	0	0
<i>Viguiera multiflora</i>	20	0	0
<i>Hydrophyllum fendleri</i>	12	0	0
<i>Epilobium angustifolium</i>	6	0	0
<i>Haplopappus parryi</i>	5	3	1
<i>Hymenoxys grandiflora</i>	0	0	22
Other plants	28	15	0

lowest sites *Mertensia ciliata* could provide an early food source for each of the species. Also at every study site there were, in the later part of the summer, at least two abundant plant species that were somewhere extensively used by each of the three bumblebee species.

Another indication of flower preference comes from a comparison of the numbers of the three bumblebee species observed foraging on particular plant species with the overall relative abundances of the three bumblebee species. These relative abundances can be estimated from the total numbers of bumblebee species observed throughout the summer in each location. If, for example, two bumblebee species are equally abundant in an area but one species predominates on a particular plant species, then that bumblebee species must have a greater preference for the plant than the other bumblebee species. In general, the same must be true whenever the relative occurrence of a bumblebee species on a particular plant species is greater than its overall relative abundance.

Table 8 presents a summary of the numbers of *B. frigidus*, *B. sylvicola*, and *B. bifarius* observed foraging in various locations on *Senecio triangularis*, *Senecio crassulus*, and *Helenium hoopesii*. Also presented are the total numbers of each bumblebee species observed on all plant species over the course of the summer for each location. The locations in Table 8 were chosen for detailed analysis solely because they give clear results. Other sites were not included in this presentation either because the results were identical or because they were ambiguous. No sites gave results which conflicted with the results of the analysis.

TABLE 7. Summary of feeding observations of *B. bifarius* in regions where it has relatively high abundance.

Plant species	Number of <i>B. bifarius</i> observed	
	Gothic Transect below 2960 m	Schofield Transect between 3330 and 3480 m
<i>Mertensia ciliata</i>	11	1
<i>Fraseria speciosa</i>	44	0
<i>Helenium hoopesii</i>	22	59
<i>Helianthella quinquenervis</i>	172	2
<i>Senecio bigelovii</i>	175	0
<i>Viguiera multiflora</i>	56	0
<i>Haplopappus parryi</i>	44	0
<i>H. croceus</i>	60	0
<i>Epilobium angustifolium</i>	50	0
<i>Erigeron</i> sp.	28	0
<i>Senecio triangularis</i>	0	9
<i>S. crassulus</i>	1	3
Other plants	82	0

Several conclusions about foraging preferences can be drawn from Table 8. These are summarized in Table 9. Each of the three plant species is most preferred by a different bumblebee species: *Senecio triangularis* by *B. frigidus*, *Senecio crassulus* by *B. sylvicola*, and *Helenium hoopesii* by *B. bifarius*. I shall assume that these preferences reflect the qualities of the plants in terms of the fitness of the bumblebees. In other words I shall assume that the bumblebees are tending to forage optimally (Pyke et al. 1977).

The three bumblebee species appear to differ in foraging only by the most preferred plant species for each bumblebee species (Table 9). Otherwise they are very similar (Table 2). Consequently, in the absence of competition, the relative abundances of the three bumblebee species should be increasing functions of the relative abundances of the three most preferred plant species. This appears to be approximately true for *B. frigidus* and for *B. sylvicola* (see Figs. 4, 5, and 6 and Table 3). The relative abundance of *B. bifarius* is, however, not at all well correlated with the relative abundance of *Helenium hoopesii*. Instead this species is relatively most abundant where *Helenium hoopesii* and sometimes *Helianthella quinquenervis* are abundant and where *Senecio triangularis* and *S. crassulus* are rare or absent (see Figs. 4, 5, and 6, and Table 3). This suggests that, in areas where there is one or more of the most preferred plants of *B. frigidus* or *B. sylvicola*, *B. bifarius* suffers reduced numbers through competition with one or both of the other two bumblebee species.

Examination of areas in which *Senecio triangularis* and *S. crassulus* are both abundant suggests that there is also competition between *B. frigidus* and *B. sylvicola*. Along the Washington Gulch Transect between 3180 and 3260 m both *Senecio triangularis* and *S.*

TABLE 8. Numbers of *B. frigidus*, *B. sylvicola*, and *B. bifarius* observed foraging in various locations on *Senecio triangularis*, *S. crassulus*, *Helenium hoopesii*, and on all plant species combined.

Location	Plant species	Number of bumblebees observed		
		<i>B. frigidus</i>	<i>B. sylvicola</i>	<i>B. bifarius</i>
Emerald Lake (3180 m)	<i>Senecio triangularis</i>	27	4	0
	<i>S. crassulus</i>	8	21	0
	<i>Helenium hoopesii</i>	14	20	4
	All plants	147	148	53
Schofield Transect (3330–3480 m)	<i>Senecio crassulus</i>	4	10	3
	All plants	33	146	91
Schofield Transect (3480–3640 m)	<i>Senecio crassulus</i>	3	33	3
	All plants	44	133	29
Gothic Transect (2970–3030 m)	<i>Senecio triangularis</i>	17	0	0
	All plants	112	42	47
Washington Gulch Transect (3090–3180 m)	<i>Senecio triangularis</i>	19	0	1
	All plants	27	1	9
Gothic Transect (Sites 8 and 9)	<i>Helenium hoopesii</i>	7	6	24
	All plants	96	46	118
Schofield Transect (3330–3480 m)	<i>Senecio triangularis</i>	2	6	9
	All plants	33	146	91

crassulus occurred although the former species appeared to be about four times as abundant as the latter (see Table 3). In this region, however, *B. frigidus* was relatively much more abundant than *B. sylvicola* (95 vs. 8 for all castes, 48 vs. 2 for males). On the other hand, along the Gothic Transect above 3330 m the same two plant species were common with *S. crassulus* slightly more abundant than *S. triangularis* (see Table 2). In this region *B. sylvicola* was about five times as abundant as *B. frigidus* (see Fig. 4). These two observations suggest that competition occurs between *B. frigidus* and *B. sylvicola* and that the outcome of this competition depends on the relative abundances of the most preferred plant species of the two bumblebee species. If one of the most preferred plant species is more abundant than the other the associated bumblebee species appears to outcompete the other bumblebee species. The result of this competition in the present situation is never, however, the complete

absence of one species, as there are always nearby areas in which any particular bumblebee species is quite successful and from which it can easily disperse.

In summary, the present analysis suggests that there is competition for food between *B. frigidus*, *B. sylvicola*, and *B. bifarius*. *B. bifarius* apparently outcompetes the other species only where its most preferred plant species occurs and the most preferred plant species of *B. frigidus* and *B. sylvicola* do not occur. If the preferred plant species of *B. frigidus* and *B. sylvicola* both occur then the bumblebee species associated with the more abundant of the two plant species appears to outcompete the other bumblebee species.

The distribution of *B. occidentalis*

This bumblebee species, as mentioned above, is similar to the previous three species in having a short tongue, but differs from them in possessing the habit of nectar-robbing a variety of plants, some of which are not visited at all by the other bumblebee species, but are usually visited by hummingbirds and moths (i.e., *Ipomopsis aggregata* and *Aquilegia caerulea*). It also feeds on *Heracleum lanatum* and *Ligusticum porteri*, plants that are most often visited by flies and were almost never seen to be visited by any of the other bumblebee species (see Table 2). Table 2 also indicates that this bumblebee species visits a very wide variety of plants visited by the other bumblebee species and that it shows no strong preferences for one plant over another. Hence this bumblebee is the most catholic of all in terms of its utilization of the various plant species and as a result it should suffer heavy competition from all the other bumblebee species.

TABLE 9. Summary of preference orderings of *B. frigidus*, *B. sylvicola*, and *B. bifarius* for *Senecio triangularis*, *S. crassulus*, and *Helenium hoopesii*.

Plant species	Preferences
<i>Senecio triangularis</i>	<i>B. frigidus</i> > <i>B. sylvicola</i>
	<i>B. frigidus</i> > <i>B. bifarius</i>
	<i>B. bifarius</i> > <i>B. sylvicola</i>
	∴ <i>B. frigidus</i> > <i>B. bifarius</i>
	> <i>B. sylvicola</i>
<i>S. crassulus</i>	<i>B. sylvicola</i> > <i>B. frigidus</i>
	<i>B. sylvicola</i> > <i>B. bifarius</i>
<i>Helenium hoopesii</i>	<i>B. frigidus</i> ≈ <i>B. sylvicola</i>
	<i>B. bifarius</i> > [<i>B. frigidus</i> and <i>B. sylvicola</i>]

Since *B. occidentalis* utilizes the widest array of plant species and has the unique habit of nectar-robbing, a reasonable hypothesis would be that it would have a virtually uniform distribution. This is clearly not the case as this species was virtually absent everywhere except the lowermost part of the Gothic Transect (see Figs. 1, 2, and 3). However, since this bumblebee species does utilize some plant species that are not utilized at all by the other species (i.e., *Ipomopsis aggregata*, *Aquilegia caerulea*, *Heracleum lanatum*, *Ligusticum porteri*), another hypothesis would be that the distribution of this species would be fairly well correlated with the distributions of one or more of these particular plant species. It is likely that it would be outcompeted in areas where such plants are not reasonably abundant.

Consideration of the Schofield Transect shows that the distribution of *B. occidentalis* is poorly correlated with the distributions of *Aquilegia caerulea*, *Ligusticum porteri*, and *Heracleum lanatum*. The first two plants were abundant throughout the transect while the last plant was abundant below 3330 m. Despite the presence of all these plants only 11 *B. occidentalis*, representing 0.5% of all bumblebees, were caught along the transect. Furthermore, only two males of *B. occidentalis* were caught along this transect, another indication of essential exclusion of this species from the entire transect. However, there was absolutely no *Ipomopsis aggregata* along this transect and this suggests that the presence of this plant species might be essential for the success of *B. occidentalis*.

The relative abundances of *B. occidentalis* do, in fact, appear to be quite well correlated with the local abundances of *Ipomopsis aggregata*. This plant attains its greatest abundance in the lowest part of the Gothic Transect and occurs in much lower abundances along the rest of the Gothic Transect up to an elevation of 3485 m. The abundance of this plant is great enough in the lowest part of the Gothic Transect that it forms in this region the basis for territories of Broad-tailed Hummingbirds (*Selasphorus platycercus*). It does not form the basis for such territories at higher elevations, presumably due to its lower abundance. The relative abundance of *B. occidentalis* is thus greatest where the greatest abundances of *Ipomopsis aggregata* occur and decreases as the abundance of *Ipomopsis aggregata* decreases.

The success of *B. occidentalis* in the presence of abundant *Ipomopsis aggregata* is perhaps not too surprising. This plant produces an average of $\approx 3\text{--}7\ \mu\text{L}$ nectar/d (Watt et al. 1974, Waser 1977) and has standing crops of $\approx 2\text{--}3\ \mu\text{L}$ nectar/flower (G. Pyke 1978c and *personal observation*), much more than any of the "bumblebee plants" amongst which the most copious producers are *Delphinium barbeyi*, *D. nelsoni*, and *Aconitum columbianum*. These flowers all produce a maximum of 3 or 4 μL nectar/d depending on the age of the flower (Pyke 1978b), with average daily pro-

ductions per flower between 0.5 and 2 μL (Watt et al. 1974). Standing crops for these species seldom exceed 1 μL (G. Pyke, *personal observation*). The nectar-robbing habit of *B. occidentalis* thus enables it to utilize an abundant nectar source that is unattainable by the other bumblebee species and which exceeds the supplies of nectar available in other plants. Whether or not such plants as *Heracleum lanatum* and *Ligusticum porteri* are also necessary for the success of *B. occidentalis* is not clear at this point because these plants were also reasonably abundant in the areas where *B. occidentalis* was most successful. However, the apparently catholic tastes of this bumblebee species would suggest that it would be successful in any area where *Ipomopsis aggregata* is abundant and there are some other plants for the bee to feed upon.

In summary, the distribution of *B. occidentalis* appears to be determined by the distribution of *Ipomopsis aggregata*. The bee is at its most abundant where *Ipomopsis* is abundant and is probably outcompeted by the other bumblebee species in areas where this plant is not abundant or is absent.

Bumblebee community structure

The above discussions of the distributions of the various bumblebee species suggest that, in any uniform well-isolated area similar floristically to the study area, only three or four species of bumblebees can coexist and that these species will consist of a short-, a medium-, and a long-tongued species and in some cases a short-tongued nectar-robbler. In a parallel study Inouye (1976, 1980) reached basically the same conclusion. Presumably any two non-nectar-robbing bumblebee species having very similar tongue lengths will be unable to coexist because of competition for plants. In the present study area the short-tongued bumblebee should be either *B. bifarius*, *B. frigidus*, or *B. sylvicola* depending on the relative abundances of the various short-corolla plants in the area and the long-tongued bumblebee should be either *B. appositus* or *B. kirbyellus*, depending on the relative abundances of the long-corolla plants. Throughout the present study area the medium-tongued *B. flavifrons* is as ubiquitous as the medium-corolla plants while the nectar-robbler *B. occidentalis* is successful only in areas where it has an abundant and exclusive source of nectar in the form of the "hummingbird plant" *Ipomopsis aggregata*.

The above discussions also suggest that, if areas where different bumblebee species with similar tongue lengths are successful are not well isolated, these areas will be found to contain two or more bumblebee species from the one tongue length group. This will occur even though one species would outcompete the others if the areas were isolated. Because of this phenomenon studies of single locations without reference to nearby locations may be very misleading in terms of community structure, and transect studies like the

present are probably essential to developing an understanding of the distribution and abundances of any fairly mobile organism.

The apparent coexistence of two or more species of non-nectar-robbing bumblebees, only if the lengths of their proboscises are sufficiently different, suggests two ways that the bumblebee community should change with changes in the plant community. First, there should be a correlation between the diversity of corolla lengths and the bumblebee diversity. Second, in areas where plants belonging to a particular corolla-length category are rare or absent bumblebees belonging to the corresponding proboscis-length category should be unable to coexist with the other bumblebee species in the area. Both of these predictions arise essentially from the idea that a bumblebee will do best on plants which have corolla lengths corresponding to the length of the bumblebee's proboscis, will tend to outcompete other bumblebees on these plants, and will tend to be outcompeted by other bumblebees on other plants. More recent data support both these predictions (G. Pyke, *personal observation*).

Although there appears to be considerable pattern to the bumblebee communities in the present study area in the array of tongue lengths permissible in a community of coexisting bumblebees, there is much difference from one location to another in the identities of the species forming the communities. To predict the actual identities of the species in a community it is necessary to know the identities and abundances of all the plants in the particular community. The present study suggests that with such a knowledge of the plant community in a location and a knowledge of plant preferences as revealed by a study like the present, it should be possible to predict the identities of the bumblebee species that form the bumblebee community. To test this prediction a study has now been carried out in which the distributions of bumblebee species were considered over both a local scale (several transects in Utah) and over a fairly large scale (most of Utah and Arizona). The data from this later study support the prediction (G. Pyke, *personal observation*).

Alternative explanations of bumblebee distributions

There are two alternative explanations of the distributions of the various bumblebee species that seem worthy of discussion. First, it is possible that each bumblebee species may be primarily adapted to nesting in different kinds of soil or in different kinds of cavities and that the distribution of each species is determined by the distribution of suitable nest sites, perhaps modified by competition for limited nest sites. The plant preferences, it might be argued, could represent secondary adaptations to the plants that happen to occur in areas suitable for nesting and there might not be any competition for plants at all.

The best evidence against this explanation is the

close agreement between predictions based on competition for plants and on the distribution of the plants and the observed distributions of the various bumblebee species. Additional evidence is provided by the lack of any apparent geological changes in the present study area which correlate with changes in the bumblebee community and by the fact that areas of very different geological history may have the same species of bumblebees, presumably as a result of having similar plant communities (G. Pyke, *personal observation*). Furthermore, it is difficult to imagine how the disjunct distribution of *B. bifarius* could be due to a disjunct distribution of suitable nest sites.

At this point it should be mentioned that the existence of competition for nest sites between bumblebees has been postulated previously (e.g., Plath 1934, Free and Butler 1959, Richards 1975). The only quantitative data, however, which have been put forward in support of this postulate are those of Richards (1975). He found that $\approx 10\%$ of nests established in artificial nest boxes were invaded and experienced attempted usurpations. However, most of these occurred at least 30 d after the nests had all been established. This suggests that there is some failure rate amongst nests and that, after having her nest fail, a queen bumblebee has a better chance of ultimate success if she attempts to take over a nest which is already established than if she starts a new nest. The lack of attempted usurpations at the time of nest establishment suggests, furthermore, that there is little if any competition for nest sites *per se*. The results of the present study suggest that there is competition for plants rather than for nest sites.

A second alternative explanation is that the distributions of the various bumblebee species are determined by adaptations to different climatological conditions. The best evidence against this explanation is the occurrence of different assemblages of bumblebees in areas which are close to one another, are of similar elevation, and appear to have similar climatic conditions. The present study provides several examples of this phenomenon: *B. appositus*, for example, occurred along the Gothic Transect and made up $\approx 10\%$ of the bees caught between 3150 and 3500 m (see Fig. 1). At the Emerald Lake site which was only ≈ 1 km from the Gothic Transect and which was somewhat lower in elevation, this species was, however, virtually absent for most of the summer and appeared only in low numbers toward the end of the summer (see Fig. 3). Similarly this species was virtually absent along the Schofield Transect except for around 3300 m where it was found in low numbers toward the end of the summer. As mentioned above, the Schofield transect and the upper part of the Gothic transect were on nearby mountains and covered similar elevational ranges. They were both in the south-facing slopes of the mountains and appeared to have similar climatic conditions. A second example is provided by the disjunct

distribution of *B. bifarius*. It was found in reasonable numbers throughout the summer at ≈ 3400 m along the Schofield transect (see Fig. 3), but was virtually absent at lower elevations on the same transect and throughout most of the Washington Gulch transect which covers elevations similar to the Schofield transect. It was abundant along the lower part of the Gothic transect and declined gradually in numbers along this transect with increasing elevation. The same distributional pattern occurred in the next summer (D. Inouye, *personal communication*). A rather peculiar climatic pattern would have to be invoked to explain this distributional pattern of *B. bifarius*. The climatic conditions appeared, however, to be very similar throughout. Other examples of patterns that are difficult to explain on the basis of climate were found in the present study and in a subsequent study in Utah and Arizona (G. Pyke, *personal observation*).

*Area in which bumblebees appear
to be unsuccessful*

As mentioned previously, no bumblebee species were apparently able to reproduce along the Gothic Transect below 2860 m. The most likely explanation for this phenomenon is that there is a minimum length to the flowering season for successful reproduction by bumblebees and the season in this area was shorter than this minimum. Several studies now suggest that for bumblebees in general, ≈ 4 wk are required from the time of egg laying to the emergence of the first workers (Hasselrot 1960, Hobbs 1965a, b, 1966a, b, Alford 1975). If the food collected by these first workers is used to produce reproductives rather than more workers, about another 4 wk should be required until the reproductives emerge. To these times must be added the times required to locate and establish a nest site and to build the first cells with food. The whole life cycle would seem to require at least 9 or 10 wk and hence should dictate a minimum flowering season of at least 9 or 10 wk in length. Data from the present study suggest that bumblebees are in fact only successful where the flowering season is >9 or 10 wk. The length of the flowering season in those parts of the study area where bumblebees were successful varied upwards from ≈ 11 wk. In the area where the bumblebees appeared to be unsuccessful, however, the length of the flowering season was at all sites <9 wk. More recent data on the distributions of bumblebees in Utah are consistent with such a minimum flowering season (G. Pyke, *personal observation*).

The presence of bumblebees at all in the areas where they appear to be unsuccessful is probably due to dispersal of fertilized queens both at the end of one summer and at the beginning of the next. Since these areas are at most only a few kilometres from areas where bumblebees are successful such dispersal into these areas seems very likely.

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