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RESOURCE PARTITIONING IN BUMBLEBEES: EXPERIMENTAL STUDIES OF FORAGING BEHAVIOR¹

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Abstract. A system comprising 2 species of bumblebees (*Bombus appositus* and *Bombus flavifrons*) and 2 species of flowers (*Delphinium barbeyi* and *Aconitum columbianum*) in Gothic, Colorado, USA, was manipulated to determine whether resource utilization by each bumblebee species was influenced by the presence of the other species of bumblebee. Each bumblebee species concentrated its foraging efforts on a different flower species, apparently choosing the species whose corolla tube length matched its proboscis length most closely. When each bumblebee species was temporarily removed from its preferred flower species, the remaining bumblebee species increased visitation to the other, previously less-utilized, flower species. The remaining bumblebees visited more flowers per stay in the patch, suggesting that they were finding greater amounts of nectar in the absence of other bumblebee species.

These removal experiments demonstrated that the bumblebees were sampling flowers frequently enough and were flexible enough in their foraging behavior to respond rapidly to short-term changes in nectar availability. In another area, where its preferred flower species and the other bumblebee species were absent, *B. flavifrons* foraged actively on the flower species it rarely used in Gothic. This observation and the experiments demonstrate that resource utilization by a bumblebee species is influenced by the presence of other species and suggest that the phenomenon of competitive release can be observed in bumblebees. In this system, interspecific exploitation competition appears to be the primary mechanism involved in resource partitioning.

Key Words: *Aconitum*; *Bombus* spp.; bumblebees; Colorado Rocky Mountains; competition; competitive release; *Delphinium*; foraging behavior; *Insecta*; nectar; niche shift; resource partitioning.

INTRODUCTION

The premise that the organization of animal communities is determined in large part by competition underlies much of current ecological theory (e.g., MacArthur 1972, Werner and Hall 1976). It is possible to implicate competition indirectly, through a study of resource partitioning based on morphological differences between coexisting species (Schoener 1974). Thus, from the observation that coexisting bumblebee species differ in mean proboscis length by a constant factor of 1.2 to 1.4 (Inouye 1976), one may infer that bumblebees compete for nectar resources (Hutchinson 1957, MacArthur 1972, May 1974). Nevertheless, it is not possible to demonstrate unequivocally in this way that competition is occurring. Manipulative experiments that perturb the system away from equilibrium allow one to test the hypothesis that the foraging behavior of a species of bumblebee is determined in part by the presence of other bumblebee species.

Bumblebees and the flowers they visit for pollen and nectar comprise a system particularly well suited for experimental investigations (e.g., Morse 1977). The foraging behavior of bumblebees is diurnal and easily observed and quantified. Although the technique has apparently not been attempted previously with bumblebees, it is relatively easy to manipulate densities of bees on flowers. The experiments described here involved temporary removal of 2 bee species. If bum-

blebees are indeed competing for food resources, there should be observable changes in foraging behavior (i.e., a niche shift) on the part of the remaining species during a removal experiment.

MATERIALS AND METHODS

During the summers of 1974 and 1975, *Delphinium barbeyi*, *Aconitum columbianum* (both Ranunculaceae) and 2 species of bumblebees were used to investigate the effects of the removal of 1 bumblebee species on the foraging behavior of the remaining species. The 2 plant species overlap in habitat and time of flowering. I chose a study site where the 2 plants grow together in an area $\approx 15 \times 20$ metres in the town-site of Gothic (elevation 2886 metres), Gunnison County, Colorado, USA (site of the Rocky Mountain Biological Laboratory), along the junction of a low, wet area and a drier hillside. *Aconitum* was also found in the wet area, interspersed with *Salix* shrubs, while *Delphinium* occurred farther up the hillside.

Both the larkspur (*Delphinium*) and monkshood (*Aconitum*) are visited almost exclusively by bumblebee workers. Both species flower in mid-season, before males appear, and after most queens have ceased foraging. *Delphinium barbeyi* is visited primarily by workers of long proboscis length (*Bombus appositus* in Gothic) while *Aconitum columbianum* is visited primarily by workers of a species of intermediate proboscis length, *Bombus flavifrons* (Inouye 1976). The corolla tube length of *Delphinium barbeyi* ($\bar{x} = 13.96$ mm, $SD = 1.19$, $N = 31$) is correspondingly longer

¹ Manuscript received 6 May 1977; accepted 10 December 1977.

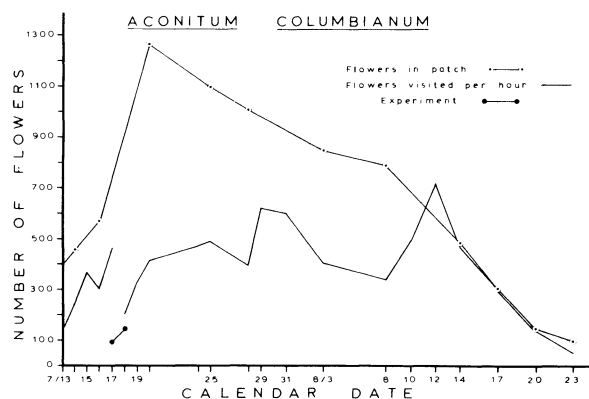


FIG. 1. The availability and utilization of flowers of *Aconitum columbianum* in the experimental patch in Gothic, Colorado, 1974. Total visitation dropped significantly on 17 and 18 July, when *Bombus flavifrons* was removed. The drop in utilization on 28 July was due to inclement weather.

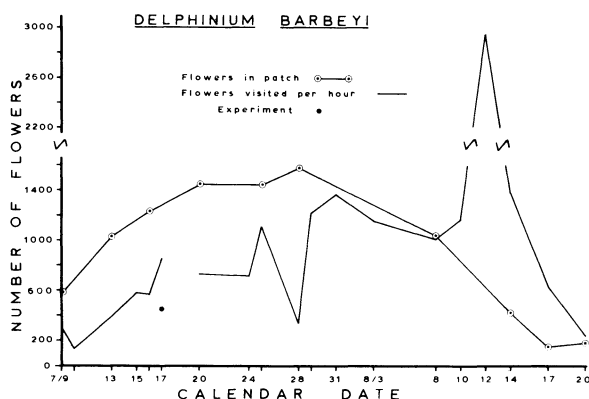


FIG. 2. The availability and utilization of flowers of *Delphinium barbeyi* in the experimental patch in Gothic, Colorado, 1974. Total visitation dropped on 17 July, when *Bombus flavifrons* was removed from *Aconitum columbianum*. The drop in utilization on 28 July was due to inclement weather.

than that of *Aconitum columbianum* ($\bar{x} = 8.44$ mm, $SD = 0.60$, $N = 66$). Both species of flowers are subject to nectar robbing by *Bombus occidentalis*, which bites holes in the corolla tubes over the nectar chambers. Bumblebee foraging activity and flower densities were censused during pre- and post-experimental control periods as well as during the experimental period. The total number of flowers available in the patch was estimated using data from the census of flower densities (Figs. 1 and 2).

At the beginning of the experimental period, foragers of one bee species were caught as they were encountered and placed individually in plastic vials. Bees were caught by carefully placing the net over the flower or the entire inflorescence on which a bee was foraging and allowing the bee to fly up into the end of the net. This procedure did not disturb other bees in the vicinity. The vials were stored temporarily in the shade and then periodically transferred inside to a cool, dark location until the termination of the experiment, when they were released. In 1974, the bees were released at the end of each day. In 1975, the bees were not released until the end of the 2nd day. Before being released, some bees were marked with numbered, colored plastic tags.

Different census methods were used in 1974 and 1975. The 2 methods yielded compatible results, so that data from the 2 yr can be compared. In 1974, I observed bees visiting *Delphinium* for a total of 16.5 h during 15 periods usually 0.5 or 1.0 h in length, and *Aconitum* for 28 periods totalling 23.5 h. I alternated observations between the 2 species of flowers, and recorded the number of flowers visited on each flower stalk while a bee remained within the designated patch of flowers, as well as the total amount of time spent in the patch and the amount of time spent in flight between flower stalks. This enabled me to calculate the amount of time spent on flowers, as well as a mean

time per flower. "Time per flower" still includes a minimal amount of time spent in flight (the time spent flying between flowers on a single flower stalk). If 2 or more bees were observed on flowers in the patch at the same time, 1 bee was observed as described while the total amount of time spent by each of the other bees was recorded. I later estimated the number of flowers visited by the other bees (total time – mean % time in flight, \div mean time per flower). An index of the intensity of visitation of the flowers available was created by dividing the total number of bees observed during a census period by the number of hours of observation during that period.

In 1975, I recorded only the number of bees on each flower species, permitting a more rapid sampling of the study area than was possible in 1974. During 10-min periods I censused the bees foraging on 1 flower species by walking from 1 end of the patch to the other. This avoided duplicate sightings of individual bees. (Approximately 40% of the sightings of marked bees per hour of observation in 1974 were of bees seen previously during that hour of observation). Comparison of numbers of flowers and of times per flower indicated no significant difference between years.

During the experimental period in 1974, all observed individuals (all workers) of *Bombus flavifrons* were removed from *Aconitum* as they were encountered. A total of 28 bees was captured in 2.75 h on 17 July 1974. They were all released at the end of the day. On 18 July, a total of 48 bees was captured in 5 h. Three bees died before the end of the experiment, when again all bees were released.

Two separate experiments were carried out in 1975. The first was a removal experiment similar to the 1 conducted in 1974, in which all *Bombus flavifrons* workers were removed from *Aconitum* as they were encountered. The second was the reciprocal experiment in which *B. appositus* was removed from *Del-*

phinium. The first experiment was carried out on 4 and 5 August. The difference in calendar date compared to 1974 is due in part to the fact that the flowering phenology in 1975 was ≈ 7 –10 days behind that of 1974. On 4 August, 62 *B. flavifrons* were captured in 125 min, and 24 more bees were captured in 80 min on 5 August. All captured bees were held until the end of the second experimental day. Of the 86 bees captured, 24 (28%) died before being released. The second experiment was conducted on 11 and 12 August, when all *B. appositus* seen foraging on *Delphinium* were captured. On 11 August 48 bees were captured during 100 min of observations; another 7 bees were captured in 50 min on 12 August. Five of the total of 55 bees (9%) died before the bees were released at the end of the 2nd experimental day.

In 1975, *Delphinium barbeyi* was also observed along portions of an elevational transect following a foot-trail (the Washington Gulch trail) in Gunnison National Forest, 3.25 kilometres from Gothic. *Aconitum columbianum* is quite rare along the transect, in contrast to the abundance of *Delphinium*.

RESULTS 1974

When both bee species are present, they exhibit different preferences for the flower species, which are reflected in visitation rates. During control periods, *Aconitum columbianum* was visited by *B. flavifrons* with a frequency of 32.1 bees/h, compared to 4.2 bees/h for *B. appositus*. For *Delphinium barbeyi*, the corresponding figures are 30.2 bees/h for *B. appositus* and 0.7 bees/h for *B. flavifrons*. An explanation for these preferences is suggested by the rates at which the 2 species forage on these flowers. *Bombus flavifrons* forages more rapidly on *Aconitum* than does *B. appositus* (*B. flavifrons* $\bar{x} = 4.1$ s, SD = 1.4 s, $N = 328$; *B. appositus* $\bar{x} = 6.1$ s, SD = 2.8 s, $N = 60$). In turn, *B. appositus* forages more rapidly on *Delphinium* (*B. appositus* $\bar{x} = 2.0$ s, SD = 0.9 s, $N = 390$; *B. flavifrons* $\bar{x} = 2.9$ s, SD = 1.2 s, $N = 92$).

The removal of *B. flavifrons* as they were encountered on *Aconitum* significantly reduced the overall visitation rate per *Aconitum* flower per hour (to 0.15 visits/flower/h) compared to both pre- and postexperimental control periods (Table 1; Fig. 1). The number of *B. flavifrons* observed per hour never dropped to 0, presumably because individuals from adjacent areas were moving into the study area during the course of the experiment, or because new foragers were arriving from the colonies affected by the continuing capture of workers.

The foraging behavior of *B. appositus* on *Aconitum* (the nonpreferred flower) changed in several respects during the removal of *B. flavifrons* (Table 1). The mean number of *B. appositus* recorded per hour of observation increased during the experimental period, but the difference is not statistically significant. With 1 exception, the number of *B. appositus* seen per hour

TABLE 1. *Bombus appositus* foraging on *Aconitum columbianum*, Gothic, Colorado, 1974

Parameter	\bar{x} (SD)	N	p*
Preexperiment control (7/13–7/17)			
Flowers visited/flower stalk	2.16 (1.50)	113	.01
Flowers visited/stay in patch	10.24 (7.07)	25	.01
Bees seen/hour	5.00 (5.57)	5	NS
Visits/flower/hour (both bee species)	.55 (.14)	5	.001
Time/flower	5.76 (1.43)	20	NS
Experimental Period (7/17–7/18)			
Flowers visited/flower stalk	2.71 (1.97)	259	
Flowers visited/stay in patch	17.44 (15.94)	50	
Bees seen/hour	5.82 (2.73)	2	
Visits/flower/hour (<i>B. appositus</i> only)	.15 (.02)	2	
Time/flower	5.78 (1.47)	36	
Postexperimental Control (7/19–8/23)			
Flowers visited/flower stalk	1.90 (1.00)	181	.001
Flowers visited/stay in patch	10.24 (9.57)	43	.02
Bees seen/hour	4.33 (3.79)	15	NS
Visits/flower/hour (both bee species)	.66 (.33)	15	.001
Time/per flower	5.66 (2.96)	10	NS

* p indicates the level of significance of the difference between experimental and control values (t-test).

increased during both experimental days (from 3/h to 9/h on the first day and 5/h to 9/h on the second). During the experimental periods, *B. appositus* foragers visited significantly more flowers per flower stalk and more flowers per stay in the patch, than during control periods (Table 1; Figs. 3 and 4). The curves for *B. appositus* in Figs. 3 and 4 are very similar to those for *B. flavifrons* observed at a variety of naturally occurring densities (Figs. 5 and 6). The mean number of flowers available on each flower stalk during the study was ≈ 7 ($\bar{x} = 7.1$, SD = 3.4, $N = 81$ on 16 July; $\bar{x} = 6.9$, SD = 3.5, $N = 184$ on 20 July).

During the first experimental day, when *B. flavifrons* was removed from *Aconitum*, the number of *B. appositus* on *Delphinium* (the preferred flower) was significantly reduced (from 30.2 bees observed/h to 18.0 bees/h, $p < .05$, t-test). This difference probably reflects the increased visitation by individual *B. appositus* foragers to *Aconitum*. Visitation to *Delphinium* was not recorded on the second experimental day.

RESULTS 1975

Only the parameter of *B. appositus* seen per hour did not change significantly during the 1974 experiment. The lack of a significant difference could have been due to the release of all captured *B. flavifrons* workers at the end of each day. Therefore, in 1975 I

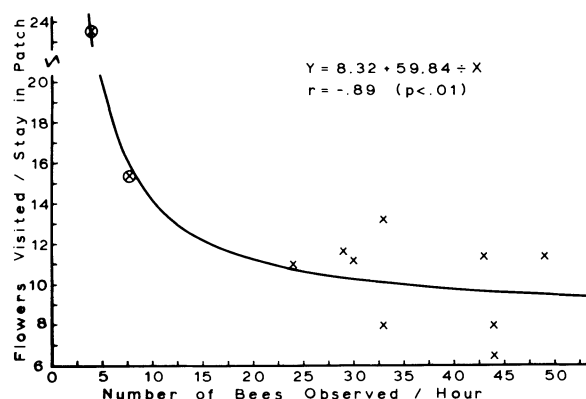


FIG. 3. The relationship between total visitation to *Aconitum columbianum* flowers in the experimental patch and the numbers of flowers visited per individual of *Bombus appositus* before leaving the patch. The circled points indicate the 2 experimental periods. Gothic, Colorado, 1974.

retained all bees captured during the 2 experimental days until the end of the 2nd day. I also conducted the reciprocal experiment, capturing foragers of *B. appositus* feeding on *Delphinium* in order to see if *B. flavifrons* would increase utilization of the unpreferred flower, *Aconitum*.

In both experiments, removal of foragers of a species from the preferred flower significantly reduced visitation to the flower by that bee species (Table 2). Visitation to the preferred flower is actually lower than indicated by the mean number of bees observed, because those bees were removed as soon as they were observed. As in 1974, the number of bees of the species being removed did not drop to 0. In both experiments, the remaining bee species increased foraging activity on the less-preferred flower, as indicated by the mean number of bees observed, compared to preexperiment control periods. The difference between experimental and postexperimental control values is significant for the first experiment, but not for the second. This can probably be attributed to the rapid decline in flower availability after the second experiment.

During both experiments, particularly on the 2nd days, very small individuals of the species being removed were observed on flowers in the patch. Evidently the smaller individuals in the colonies concerned, which usually assume the duties of "house bees" and do not forage, were abandoning these duties in the face of food shortages and were assuming the duties of foragers. Such a switch in the behavior of individual bees has been observed in other studies of individual colonies (Richards 1946, Brian 1952, Free 1955, Miyamoto 1959).

Both *B. flavifrons* and *B. appositus* were observed on flowers along the Washington Gulch trail in 1975, but *B. flavifrons* was much more common (76% of all bees seen, compared to 4% for *B. appositus*). In these

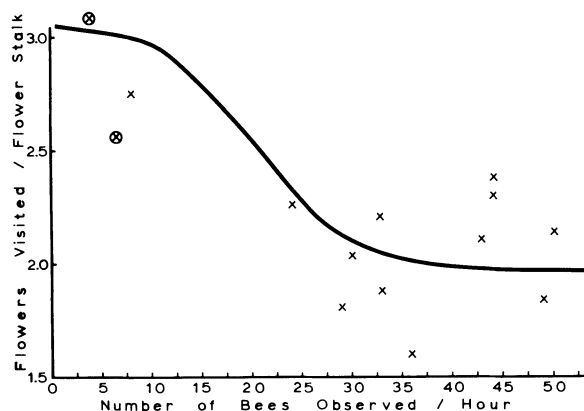


FIG. 4. The relationship between total visitation to *Aconitum columbianum* flowers in the experimental patch and the number of flowers visited per flower stalk by individuals of *Bombus appositus*. The circled points indicate the 2 experimental periods. Gothic, Colorado, 1974. The line was fitted by eye.

circumstances, where *Delphinium* was present and *Aconitum* almost absent, *B. flavifrons* foraged heavily on *Delphinium* (227 observations compared to 32 for *B. appositus*).

DISCUSSION

When both bee species were present, each showed a marked preference for 1 of the 2 flower species. The preferences appear to be correlated with the ease with which the bee species can forage on the flowers, as has been suggested previously for other bees (Hobbs et al. 1961). Despite these preferences, however, results of the experiments show that bumblebees are flexible enough in their foraging behavior to respond rapidly to short-term changes in the pattern of visitation in 2 flower species. The experiments demonstrated that, for each species, the observed pattern of resource utilization was determined in part by the presence of the other species. The shifts in foraging behavior provide an experimental confirmation of the conclusion based on morphological studies, that there is interspecific competition for nectar resources in bumblebees (Inouye 1976).

The phenomenon of competitive release, in which an organism expands its pattern of resource utilization in the presence of reduced competition, is an appropriate description of the results of the experiments. This interpretation is also supported by the observations made on the Washington Gulch trail, where *B. flavifrons* foraged on *Delphinium* in the absence of *B. appositus*. This phenomenon has previously been investigated primarily in birds and lizards, through comparison of island populations with mainland or other island populations (e.g., Diamond 1970, Morse 1971, Lister 1976).

Standing crops of nectar were not censused because the procedure is very time consuming and involves

TABLE 2. Results of 1975 removal experiments

Bee species		Control	Expt. I	Control	Expt. II	Control
On <i>Aconitum columbianum</i>						
<i>Bombus flavifrons</i>	N (a)	5	14	17	13	9
	Bees	57	61	128	89	50
	\bar{x}	11.40***	4.36***	7.53	6.85	5.56
	SD	1.67	2.34	1.84	2.34	2.55
<i>Bomus appositus</i>	N	5	14	17	13	9
	Bees	1	21	3	3	10
	\bar{x}	.20*	1.50**	.18	.23**	1.11
	SD	.45	1.29	.53	.44	.60
On <i>Delphinium barbeyi</i>						
<i>Bombus appositus</i>	N	5	14	17	13	10
	Bees	61	172	167	49	115
	\bar{x}	12.20	12.29	9.72***	3.77***	3.92
<i>Bombus flavifrons</i>	N	5	14	17	13	10
	Bees	21	27	72	84	63
	\bar{x}	4.20***	1.93***	4.24*	6.46	6.30
	SD	.45	1.07	1.71	2.44	2.87
<i>Bombus californicus</i>	N	5	14	17	13	10
	Bees	1	3	12	26	36
	\bar{x}	.20	.21	.71	2.00	3.60
	SD	.45	.58	.77	1.35	2.01

Bombus flavifrons was removed from *Aconitum* during Experiment I and *B. appositus* was removed from *Delphinium* during Experiment II.

First control period = 4 August.

First experiment = 4 and 5 August.

Second control period = 6, 8, 9, 10, and 11 August.

Second experiment = 11 and 12 August.

^a N = Number of 10-min observation periods.

Asterisks indicate significant differences between mean number of bees in consecutive control and experimental periods.

* Difference significant at $p < .02$, t -test.

** Difference significant at $p < .01$, t -test.

*** Difference significant at $p < .001$, t -test.

destructive sampling. However, the observed changes suggest that flowers are more attractive to the remaining bees when the primary foragers on that flower are removed. There is no evidence that bumblebee foragers mark flowers as they visit them, and it seems reasonable to assume that the increased visitation was a response to increased amounts of nectar present when the density of foragers decreased. Similarly, Free (1965) found that bumblebees and honeybees visited more florets on red clover heads if they had been bagged previously to exclude bees than if they had been continuously exposed.

Increased utilization of flowers was detected in both the number of flowers visited per flower stalk and the number of flowers or flower stalks visited before the bees left the patch. Smith (1974a, b) and Pyke (1978) have proposed similar models of foraging behavior which are appropriate to consideration of the patterns of movement of individual bees in flower patches. Pyke (1978) suggested that bees finding little or no nectar would tend to fly farther between stops to visit flowers and turn less between stops. Bees finding a significant amount of nectar in flowers would tend to fly shorter distances between stops and turn more frequently. Pyke (1978) collected data from bumblebees

in the Gothic area to substantiate these aspects of his model. Bees sampling a patch of flowers will visit increasing numbers of flowers in the patch as the amount of nectar available in flowers increases.

Flexibility in foraging behavior has also been noted in other organisms. Ribbands (1949) observed foraging honeybees (*Apis mellifera*) and concluded that foraging behavior involves continuous exercise of choice by a bee, for the best portions of any alternative food sources. Brian (1952), Manning (1956) and Heinrich (1976a, b) have also emphasized flexibility in the foraging behavior of bumblebees. The length of a bumblebee worker's life often surpasses the flowering period of a single flower species, requiring flexibility in foraging behavior. Flexibility has also been noted in food searching behavior of titmice in patchy environments (Smith and Sweatman 1974) and underlies the phenomenon of switching described for predatory fish (Murdoch et al. 1975). Disproportionate allocation of feeding behavior to the more abundant "prey", whether it be flowers or fish food, should be adaptive because it is more efficient.

Interference competition (Miller 1969) was never observed during the study, and I have never observed aggressive interactions between bumblebee species in

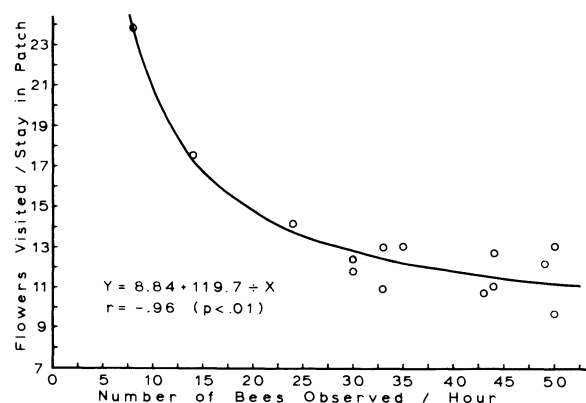


FIG. 5. The relationship between total visitation to *Aconitum columbianum* flowers in the experimental patch and the mean number of flowers visited per individual of *Bombus flavifrons* before leaving the patch. Gothic, Colorado, 1974.

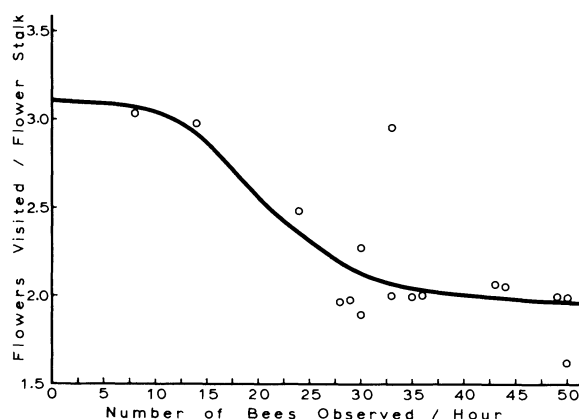


FIG. 6. The relationship between total visitation to *Aconitum columbianum* flowers in the experimental patch and the mean number of flowers visited per flower stalk by individuals of *Bombus flavifrons*. Gothic, Colorado, 1974. The line was fitted by eye.

the East River Valley. Competition for nectar probably occurs through direct depletion of resources. Thus, the exclusion of *B. flavifrons* from *Delphinium* is probably a consequence of the longer proboscis of *B. appositus*. In the absence of *B. appositus* nectar should accumulate in corolla tubes of *Delphinium* to a level that makes the flowers more attractive to *B. flavifrons*. Such an increase in nectar availability probably underlies the change in behavior of *B. flavifrons* foraging at different densities on *Aconitum* (Figs. 5, 6). The mean amount of time per flower required for *B. appositus* workers foraging on *Aconitum* is 3× that required on *Delphinium*. When foragers of *B. flavifrons* are continually removing nectar, *Aconitum* may not be an attractive resource in terms of cost-benefit ratios. In the absence of other bees, however, *B. appositus* foragers should find it much more rewarding to visit *Aconitum* flowers (Figs. 3, 4).

Interference competition has been described for bumblebees in other studies. Brian (1957) found that, on artificial flowers, 1 bumblebee species was "definitely aggressive toward other species." This aggressiveness was effective against 1 other species, but had little effect on another. Brian (1957) observed a very low level of interaction on natural flowers, but these did reinforce the conclusions drawn from experiments with artificial flowers. Morse (1977) has observed shifts in foraging location on the part of 1 bumblebee species in the presence of a second, and (D. H. Morse, *personal communication*) has observed aggressive interactions between species of bumblebees in Maine on a rich pollen source (*Rosa carolina*) and on artificial feeders.

There is no obvious explanation for the different types of competition observed in bumblebees studied by Brian (1957) and Morse (1977) and those I studied. Case and Gilpin (1974) suggested that, in a situation in which an individual must compete for common re-

sources, it can either increase its exploitation efficiency or somehow interfere with its competitors. They summarized evidence suggesting that species frequently evolve toward interference. If there is more competition for food resources at the lower elevations where Brian (1957) and Morse (1977) worked, there may have been greater selective pressure for the evolution of mechanisms for interference competition. Although there is no basis for comparison of levels of competition between the studies, the results of my study imply the action of competition between bumblebees in montane environments.

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LITERATURE CITED

- Brian, A. D. 1952. Division of labour and foraging in *Bombus agrorum* Fabricius. *Journal of Animal Ecology* 21:223-240.
- . 1957. Differences in the flowers visited by four species of bumblebees and their causes. *Journal of Animal Ecology* 26:71-98.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Science (USA)* 71:3073-3077.
- Diamond, J. M. 1970. Ecological consequences of island colonization by southwest Pacific birds I: Types of niche shifts. *Proceedings of the National Academy of Science (USA)* 67:529-536.
- Free, J. B. 1955. The division of labour within bumblebee colonies. *Insectes Sociaux* 2:195-212.

- . 1965. The ability of bumblebees and honeybees to pollinate red clover. *Journal of Applied Ecology* 2:289–294.
- Heinrich, B. 1976a. Resource partitioning among some eusocial insects: bumblebees. *Ecology* 57:874–889.
- . 1976b. The foraging specializations of individual bumblebees. *Ecological Monographs* 46:105–128.
- Hobbs, G. A., W. O. Nummi, and J. F. Virostek. 1961. Food-gathering behavior of honey, bumble and leaf-cutter bees (Hymenoptera:Apoidea) in Alberta. *Canadian Entomologist* 93:409–419.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Inouye, D. W. 1976. Resource partitioning and community structure: a study of bumblebees in the Colorado Rocky Mountains. Doctoral dissertation, University of North Carolina, Chapel Hill, North Carolina, USA.
- Lister, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards I: Ecological consequences of reduced competition. *Evolution* 30:659–676.
- MacArthur, R. H. 1972. *Geographic ecology*. Harper and Row, New York, New York, USA.
- Manning, A. 1956. Some aspects of the foraging behaviour of bumble-bees. *Behaviour* 9:164–201.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Miller, R. S. 1969. Competition and species diversity. *Brookhaven Symposia in Biology* 22:63–70.
- Miyamoto, S. 1959. On the nest of *Bombus diversus* which collapsed before completion. *Akitsu* 8:85–90.
- Morse, D. H. 1971. The foraging of warblers isolated on small islands. *Ecology* 52:216–228.
- . 1977. Resource partitioning in bumble bees: the role of behavioral factors. *Science* 197:678–680.
- Murdoch, W. W., S. Avery, and M. E. B. Smith. 1975. Switching in predatory fish. *Ecology* 56:1094–1105.
- Pyke, G. H. 1978. *in press*. Optimal foraging in bumblebees: patterns of movements between inflorescences. *Theoretical Population Biology*.
- Ribbands, C. R. 1949. The foraging method of individual honey bees. *Journal of Animal Ecology* 18:47–66.
- Richards, O. W. 1946. Observations on *Bombus agrorum*. *Proceedings of the Royal Entomological Society of London Series A* 21:66–71.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Smith, J. N. M. 1974a. The food search behavior of two European thrushes. I. Description and analysis of search paths. *Behaviour* 48:276–302.
- . 1974b. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. *Behaviour* 49:1–61.
- , and H. P. A. Sweatman. 1974. Food-searching behaviour of titmice in patchy environments. *Ecology* 55:1216–1232.
- Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. *Science* 191:404–406.