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Behavior of Bumble Bee Pollinators of *Aralia hispida* Vent. (Araliaceae)

James D. Thomson*, Wayne P. Maddison**, and R.C. Plowright
Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1 Canada

Summary. The andromonoecious plant *Aralia hispida* has a complicated blooming schedule involving alternations between male and female phases. Nectar and pollen are released gradually through the day. Plants vary considerably in number of flowers per umbel and number of umbels per plant. The major pollinators, bumble bees, show several characteristic behaviors in response to the plant's presentation.

1. Foraging bees preferentially visit umbels that bear large numbers of open, male-phase flowers. They also prefer shoots with large numbers of umbels.

2. If bees have received high nectar rewards at one umbel, they are more likely to visit a neighboring umbel rather than leaving the area. On drained umbels, bees probe more empty flowers before rejecting the umbel if they have been rewarded just previously.

3. Individual bees restrict their foraging to limited areas. Within these areas, they concentrate their visits on certain shoots which they tend to visit in repeatable sequences, or "traplines". It is inappropriate to consider these bees as "searching".

4. We discuss some of the implications of these data for two areas of current theoretical interest: plant reproductive strategies and optimal foraging.

Introduction

This is the fourth paper in a series treating the reproductive biology of the plant genus *Aralia* (Araliaceae). *Aralia nudicaulis* L., which is dioecious, has been treated by Barrett and Helenurm (1981), Barrett and Thomson (1982), and Bawa et al. (1982). Thomson and Barrett (1981) have described the floral biology of *Aralia hispida* Vent., which is andromonoecious. In this paper we outline some aspects of pollinator behavior, particularly what animals visit the flowers, how effective they are as transporters of pollen, how they react to variations in plant size and quality, and how they respond to the spatial distribution of plants. The pollination ecology of *Aralia hispida* has some peculiar features resulting from complex patterns of sexuality in the plants and from repetitive visitation patterns of the pollinators. As we discuss below, these features complicate the application of optimal foraging theory to the animals.

Floral biology of Aralia hispida

The flowering schedule is quite complex (for more details see Thomson and Barrett 1981). *Aralia hispida* is a rhizomatous perennial, common in disturbed sites with poor, sandy soils in northeastern North America. Plants (genets) in our sites usually comprise a small number (1 to 10) of flowering ramets. Ramets are andromonoecious, i.e., bear male-only flowers and hermaphrodite flowers. Flowering begins with a single, primary umbel usually bearing 10–40 flower buds. During about 4–7 days, the flowers open and function as males. Flowers in the male phase bear five small greenish petals and five whitish-green anthers. Within an umbel, flowers open and anthers dehisce at various times of day. During the male phase the five styles remain short and tightly appressed, and nectar is usually visible at their base. Many insects visit the flowers for nectar, which is easily accessible. Nectar quantities are so small that we do not have reliable data on secretion rates or concentrations under field conditions, although nectar seems to be produced in a continuous trickle during the period of anther dehiscence. Nectar removal promotes secretion. Most flowers complete their male function in one day. Then nectar secretion ceases and the petals and anthers are shed. Hermaphrodite flowers may remain in this inactive state for several days while other flowers in the umbel open and function as males. Only after all flowers have finished their male, polliniferous phase do the hermaphrodites become receptive as females. Stigmatic receptivity is indicated by the divergence of the five styles and by a renewed nectar secretion. All hermaphrodite flowers in an umbel usually become female within two days: thus "female opening" is more highly synchronized than male opening.

After the primary umbel has passed through the above cycle, all the secondary umbels pass through it in unison, and after them the tertiaries. A few very small ramets have no secondary umbels, but most have four or more. Only larger ramets have tertiary umbels. There is usually some overlap between the end of stigmatic receptivity of one umbel order and the first anther dehiscence of the next order; thus some geitonogamous selfing may occur if the pollination rate is so low that outcrossing has not occurred before the overlap period.

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* Present address: Ecology and Evolution Department, State University of New York, Stony Brook, NY 11794, USA
** Present address: Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA

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Methods and Materials

Study sites

We conducted field work near Doaktown, in Northumberland Co., central New Brunswick, Canada, in 1979 and 1980. We recorded data primarily at two similar sites, described in greater detail by Thomson and Barrett (1981) as the Logging Road and Clearing sites. Both were recently cleared patches in highly disturbed spruce-fir forest. There was considerable bare ground at each site. The sparse vegetation consisted mostly of *Aralia hispida*, bracken fern (*Pteridium*), and raspberries (*Rubus* sp.). The surrounding areas made up a mosaic of habitats in various stages of recovery from logging. Various entomophilous weeds bloomed near the sites, but attracted fewer flower-visiting insects than the *A. hispida*/*Rubus* stands. *Rubus* finishes blooming during the *A. hispida* bloom, leaving the latter as the sole floral resource in the most open areas.

Identity and Effectiveness of Visitors

At various times during 1979, we collected all insects feeding on *Aralia* flowers, with the exception of bumble bees, which were often being observed for other purposes. In 1980, we made a small collection of all visitors including bumble bees, to determine the proportion of bumble bees in the visitor fauna.

In 1980, we timed by stopwatch the foraging rates of the major classes of visitors at the Clearing site. We observed a visitor for no longer than 20 umbel visits; in practice, most runs were much shorter. We recorded the number of flowers probed at each umbel. Time spent flying between umbels was usually negligible compared to time spent on umbels, so we did not attempt to record them separately, instead simply timing the entire run. Pooling all observations for a pollinator type, we divided the total number of umbels visited by the total time to provide an index of foraging speed.

Pollen Carryover by Field-Foraging Bumble Bees

To determine the extent of pollen transport by bumble bees, we followed the procedures of Thomson and Plowright (1980), with minor modifications. We emasculated umbels in bud, then held them in vases indoors until all hermaphrodite flowers had become stigmatically receptive. We then trimmed all umbels to a standard size of 20 flowers. In the field we offered series of these umbels to naturally foraging *Bombus* cf. *vagans* workers that had previously been feeding at male-phase umbels with dehiscent anthers. To standardize the umbels and ensure feeding, we added ~0.3 µl of 30% sucrose solution to each flower. In 1980, we obtained four runs (sets of four or more consecutively visited umbels). We prepared microscope slides of the entire stylar apparatus of each flower, using Beattie's (1971a) basic fuchsin-glycerin jelly technique, and counted the number of pollen grains deposited. We did not attempt to record the order in which individual flowers were visited within an umbel. Some flowers received two probes, as commonly happens when an umbel is highly rewarding. The bees had to fly a short distance between successive umbels.

Field Choice Experiments

We used Thomson's (1981) "mobile boquet" technique to determine visitors' responses to variations in inflorescence size and quality. The general procedure was to place two umbels, about 8 cm apart, in small vials of water attached to the end of a 75 cm aluminum rod. We offered the bouquet to field-foraging insects in such a manner that the two test umbels were equidistant from the insect. If the insect flew to the bouquet, we recorded the umbel chosen and the number of flowers probed. If it subsequently flew to the second umbel, we recorded the number of flowers probed there as well. We replaced the umbels at about 15 min intervals, alternating the positions of the sexual phases. We made the following comparisons:

a) Size Preference: Number of Flowers Varied, Diameter Held Constant. In 1980, we picked male-phase, matched secondary umbels and removed flower pedicels to yield one large umbel with 12 open flowers and one small one with 6 flowers. We thinned in such a way that the remaining open flowers were equally spaced and the overall diameters of the umbels remained equal. The numbers chosen are well within the normal range of open flowers on primary and secondary umbels. We tested various visitor types for these flower-number comparisons; for the experiments which follow, we tested only bumble bees.

b) Size Preference: Diameter Varied, Flower Number Constant. Here the large and small umbels both had 13 open flowers but were approximately 3 and 2 cm in diameter, respectively. These sizes represent extremes of the naturally occurring variation.

c) Sexual Preference. We selected male-phase and female-phase umbels of equal diameter and trimmed them as necessary to present 8 open flowers on each. In 1979 we tested bees shortly after the middle of the *Aralia* bloom (24 July), while in 1980 the tests were done very late (2 August).

d) Variation in Nectar. During the middle of the 1980 bloom, we prepared matched male-phase umbels with 12 flowers. One was enriched after each visit to it, by placing ~0.5 µl of 30% sucrose solution in each flower. We applied the solution with a squeeze bottle equipped with a finely-drawn glass tip, judging the volume applied by the diameter of the droplet; thus the volume applied was not precisely constant. We drained the other umbel initially by adsorbing nectar to filter paper wicks and did not replenish the nectar during the course of the experiment.

Bumble Bee Movement Patterns

In 1979 and 1980 we recorded the movements of individually marked bumble bees as they foraged in stands where we had individually marked ramets of *A. hispida*. A selected subset of the data are presented here.

We marked bees by dusting them with Radiant® fluorescent powders (1979) or by applying a spot of white Liquid Paper® typewriting correction fluid to the interalar area and then applying as many as three differently colored stripes to the dried spot with fine felt-tipped pens (1980). With practice, the Liquid Paper/felt-tip marks could be applied through the mesh of an insect net while the bee was restrained in a fold. We avoided narcotizing the bees because it may affect behavior (Ribbands 1950; Austin 1955; Pomeroy and Plowright 1979) and minimized handling to reduce the tendency of disturbed bees to leave the habitat (Pesenko 1972).

Table 1

a) Insect visitors recorded on *Aralia hispida* in New Brunswick, 1979

Coleoptera

- Mordellidae
  - *Mordella* sp.
- Scarabeidae
  - *Trichiotinus assimilis* (Kby.)
- Cerambycidae
  - *Cosmosalia chrysocoma* (Kby.)
  - *Gnathacmaeops pratensis* (Laich.)

Hymenoptera

- Apidae
  - *Bombus terricola* Kby.
  - *B. vagans* Sm.
  - *B. sandersoni* Fkln.
  - *B. ternarius* Say
  - *B. perplexus* Cress.
  - *B. borealis* Kby.
  - *B. fervidus* Fabr.
  - *B. rufocinctus* Cress.
  - *Psithyrus* sp.
- Colletidae
  - *Hylaeus basalis* Sm.
  - *H. modestus* Say
  - *H. gaigei* Ckll.
  - *H. ellipiticus* (Kby.)
- Halictidae
  - *Halictus rubicundus* (Christ.)
  - *Dialictus* spp.
  - *Evylaeus quebecensis* (Cwfd.)
  - *Sphecodes* spp.
- Anthophoridae
  - *Holopasites caliopsidis* (Lins.)
  - *Nomada lepida* Cress.
  - *N. sayi* Rbtsn.
- Megachilidae
  - *Megachile relativa* Cress.
  - *Coelioxys rufitarsus* Sm.
  - *Hoplitis cylindrica* Cress.
  - *Heriades variolosa* Cress.
  - *Stelis tabiata* (Prov.)
- Andrenidae
  - *Andrena (Andrena) thaspii* Graen.
  - *A.* (Larandrena) *w-scripta.* Vier.
  - *A.* (Taeniandrena) *wilkella* (Kby.)
- Sphecidae
  - *Oxybelus* sp.
  - *Ammophila* sp.
- Eumenidae
  - *Euodynerus* spp.
  - *Ancistrocerus* spp.
  - *Eumenes* sp.
- Vespidae
  - *Vespula arenaria* Fabr.
  - *V. arctica* Rohmer
- Crabronidae
  - *Crabro* sp.
- Chrysididae
  - *Hedychrum* sp.
- Mellinidae
  - *Lestica* sp.

Diptera

- Syrphidae
  - *Sphegina rufiventris* Lw.
  - *Mallota bautias* Walk.
  - *Parasyrphus* sp.
  - *Temnostoma vespiformis* L.
- Sarcophagidae
  - *Sarcophaga nearctica* Park.
  - *Wohlfahrtia vigil* (Walk.)

Taxon	A. Foraging speed (umbels/min) (n umbels, n bees)	B. Estimated no. grains carried[a]	C. Relative abundance (Fraction of total)	Relative pollination potential (ABC/ΣABC)
b) Estimates of relative pollination effectiveness of insect visitors				
Bees				
Bombus spp. (Apidae)	9.28 (241,22)	2,800	0.193	0.702
Halictidae	4.22 (78,12)	915	0.070	0.038
Andrenidae	6.23 (80,5)	915	0.053	0.042
Wasps				
large	[b]	790	0.070	0.102[b]
medium	7.51 (154,18)	790	0.053	
small	5.33 (72,8)	790	0.070	0.041
Flies				
large	6.37 (67,6)	570	0.053	0.027
medium	5.42 (69,7)	159	0.316	0.038
small	4.27 (45,6)	159	0.105	0.010
Beetles				
large	3.07 (9,2)	[c]	0.018	–

[a] Grain numbers are very crude estimates derived from O'Brien (1980), who gave frequency distributions of grains. We have used the class marks of her distributions, except for her category "$>$1000 grains", for which we have used 1500 grains, probably an underestimate. She gives data for *Apis* but not *Bombus*; we have estimated *Bombus* loads as 2 × her *Apis* loads to reflect greater surface area

[b] Since no foraging speeds were available for large wasps, we have assumed them equal to medium wasps and lumped the two wasp types in the last column

[c] No estimates available, but beetles are probably neglible pollinators by virtue of their rarity

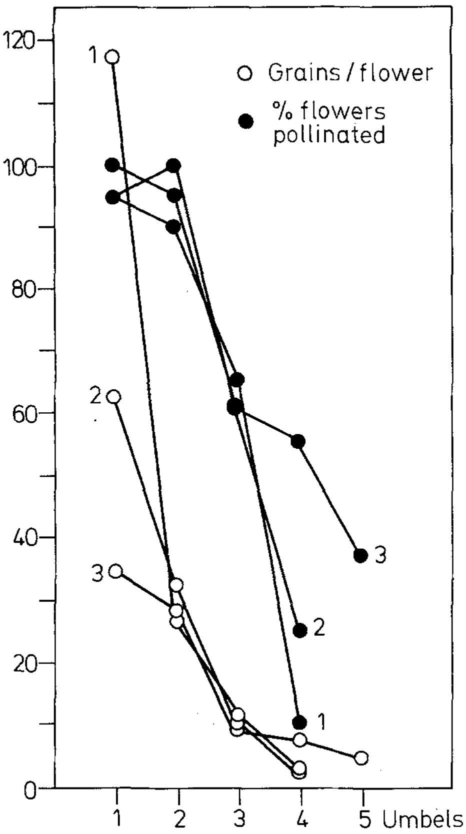


Fig. 1. Extent of pollen transport by *Bombus* workers visiting a series of female-phase umbels of *Aralia hispida* after coming from a male-phase umbel. Umbels had 20 flowers. Grains were counted on all flowers. There are three runs, labelled 1–3 in the figure. The curves for "% flowers pollinated" show the percentage of flowers that had five or more grains deposited. This cutoff value is used because each flower has five ovules, but is arbitrary in the sense that there is no experimental work to suggest that five grains will actually yield complete seed set

At the Logging Road site, we labelled all 77 *A. hispida* ramets in a 9 × 10 m area with numbered string tags, and mapped the population. On the mornings of 25 and 26 July 1979 we recorded the number and sexual phase of potentially rewarding umbels on each ramet.

We observed foraging *Bombus* cf. *vagans* workers and males on the afternoon of 25 July and the morning and afternoon of 26 July. An observer stood within the stand and looked for marked bees, recording their transitions from ramet to ramet within the patch. Usually bees were first seen inside the stand. When two marked bees were present simultaneously, the observer followed the one for which fewer data had been recorded. We repeated this procedure for a 10 × 15 m area near the Clearing site in July 1980.

Results

Flower Visitors

Table 1 lists those insect visitors to *Aralia hispida* that we considered potentially effective pollinators. Because the flowers are small and open, and because anthers and stigmas are borne in similar positions, almost any regular visitor is a potential pollinator, although we excluded ants, phytophagous Hemiptera, and various tiny insects from consideration. Bumble bees appear to be the most important pollinators.

Pollen Carryover

Pollen transport by *Bombus* cf. *vagans* workers is displayed in Fig. 1. Deposition of grains on flowers is highly variable, and series of adjacent flowers (which usually are visited sequentially) may receive drastically different numbers of grains, e.g., the sequence 9, 5, 83, 0, 11. Although some grains may travel far, carryover at the umbel level is not extensive; most of the pollen placed on stigmas is deposited on the first two umbels visited. By the third umbel, only 60% of the flowers are receiving 5 or more grains, the extreme theoretical minimum for complete seed set. Because we had enriched the flowers, the bees visited more flowers on these umbels than they typically do when foraging in the field (see below), which could result in low estimates of pollen carryover between umbels due to abnormally high deposition within umbels. However, we feel that the most important source of pollen loss is probably grooming by the bees while flying between umbels, and that the deposition of grains on stigmas is a relatively minor source of grain loss from the bee (Thomson and Plowright 1980). If carryover were computed in terms of flowers rather than umbels, it would seem much more extensive.

Table 2. Choice experiments. Field-foraging insects were presented with a large umbel (12 flowers, denoted by L) and a small umbel (6 flowers, denoted by S). Umbels were taken from the same inflorescence to ensure similarity. Diameters were the same. Flower number was adjusted surgically

Visitor taxon	Visit sequences				Fraction of initial moves to S	Fraction of total moves to S	Fraction of double visits
	only S	only L	S→L	L→S			
Bombus spp.	7	27	4	8	0.239**	0.328**	0.261
Solitary bees, mostly Halictidae	20	29	7	8	0.435	0.443	0.234
Large (*Vespula* spp.) and medium wasps	7	21	4	6	0.289**	0.354*	0.263
Small wasps	12	16	4	4	0.444	0.455	0.222
Large flies	8	11	2	4	0.417	0.452	0.240
Medium flies	10	16	3	0	0.448	0.406	0.103
Small flies	15	23	3	5	0.391	0.426	0.174

** and * denote departures from equal visit frequencies at $p<0.01$ and $p<0.05$ respectively, by χ^2 test

Table 3. Choice experiments. Foraging bees (*Bombus* spp.) were presented with a large-diameter (3 cm, denoted by L) and a small diameter (2 cm, denoted by S) umbel. Each umbel bore 13 flowers. No significant differences between S and L visit frequencies were found

Visit sequences				Fraction of initial moves to S	Fraction of total moves to S	Fraction of double visits
only S	only L	S→L	L→S			
21	29	20	28	0.452	0.473	0.490

Table 4. Choice experiments. Foraging bumble bees (*Bombus* spp) were presented with a male-phase and a female-phase umbel of equal diameter and flower number. Values in table are total visits for 1979 and 1980. The 1979 and 1980 values are given separately in parentheses. Bees coming from male-phase umbels prefer male-phase umbels (1979 data, $\chi^2 = 7.71$, 1980, $\chi^2 = 13.24$, both 1 d.f., both $p < 0.01$). Bees coming from female-phase umbels showed no preference in 1979 ($\chi^2 = 0.03$, ns) but preferred male-phase umbels in 1980 (exact probability < 0.05)

Sex-phase of umbel the bee came from in the field	Sex-phase of the umbel chosen on the bouquet	
	♂	♀
♂	46 (30,16)	13 (12,1)
♀	22 (16,6)	15 (15,0)

Pollinator Choice Experiments – Umbel Size

Pollinators showed preference for umbels with more flowers when umbel diameters were held constant (Table 2). The Hymenoptera as a whole were more discriminating than the Diptera and, within each order, larger species were more discriminating than small. Of the categories in Table 2, bumble bees were the most highly discriminating, making less than 25% of initial visits to the smaller umbel. The large (*Vespula*) and medium wasps are lumped in Table 2, although if the medium wasps are considered alone, they are slightly more discriminating than *Bombus* (22%); the difference is insignificant. The bumble bees and the larger wasps were also more thorough than other visitors, having the highest proportion of tests in which they visited both umbels.

When flower number was held constant and umbel diameter varied, *Bombus* were much less discriminating (Table 3). Thus it seems that they respond more strongly to flower quantity.

Pollinator Sexual Preference

We performed this test in 1979 and 1980 and the results differed (Table 4). In 1979, *Bombus* that had been foraging on a male-phase inflorescence before moving to the bouquet were significantly more likely to move to the male-phase umbel in the bouquet, while those coming from female-phase umbels showed no significant preference on the bouquet. In 1980, incoming bees showed significant preference for male-phase umbels regardless of their immediate previous choice. The difference may be due to different sex ratios prevailing in the population. We took the 1980 data late in the season (2 August, in contrast to 24 July in 1979), when most ramets were in their tertiary umbel phase and very few umbels had substantial numbers of female-phase flowers (see Thomson and Barrett 1981). During the 1979 testing, the sex-phases were more equally represented in the population.

Table 5. Bumble bee visits to a bouquet of paired umbels, one of which was continually enriched with 30% sucrose solution, while the other was kept drained

Umbel type bee landed on initially	Did bee subsequently visit the other umbel?	
	Yes	No
Drained	1	30
Enriched	19	1

Significance tests

a) Do bees make initial choices randomly?
$\chi^2 = 2.37$, 1 d.f., ns
b) Are initial visit type and subsequent visit independent?
2 × 2 contingency $\chi^2 = 43.0$, 1 d.f., $p \ll 0.001$

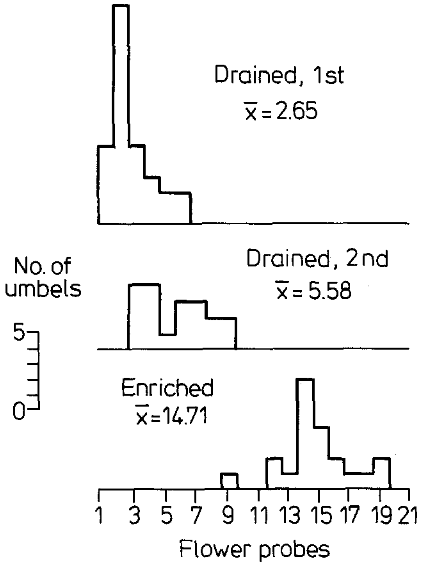


Fig. 2. Frequency distributions of the number of times *Bombus* workers probed flowers when visiting paired umbels of *Aralia hispida* with 12 flowers each. The "enriched" umbel was replenished with nectar after each visit; the "drained" umbel was not. The heading "drained, 1st" indicates visits in which the bee visited the drained umbel without previously visiting the enriched one, while "drained, 2nd" indicates visits to the drained umbel immediately following visits to the enriched one. The distributions all have significantly different locations by Mann-Whitney U-tests

Pollinator Response to Enrichment

Moves by *Bombus* to the bouquet showed no significant preference for the sucrose-enriched umbel (Table 5a). Thus there is apparently no remote discrimination based on nectar appearance (see Thorp et al. 1975; Kevan 1976), although the droplets of sucrose solution were apparent to us. Bees that encountered the enriched umbel first almost

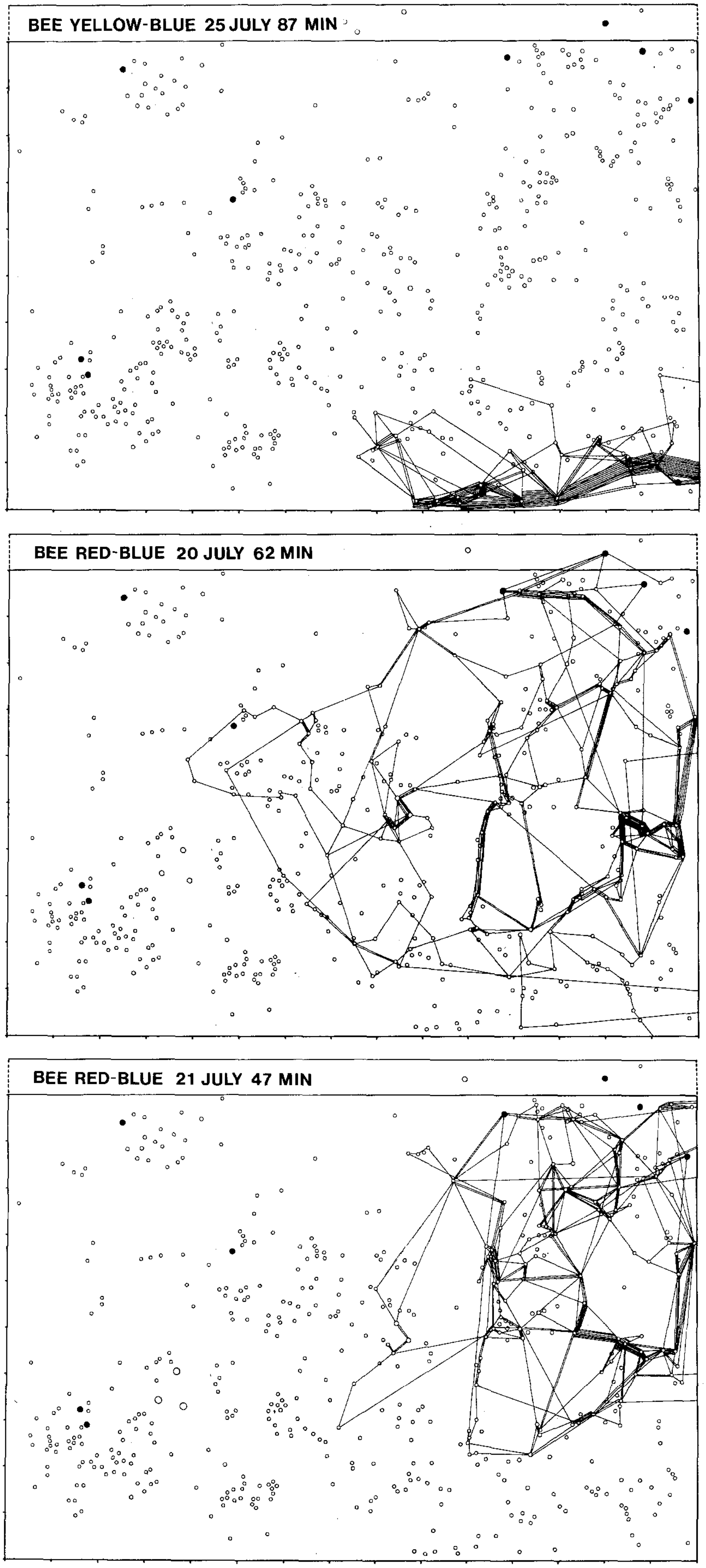
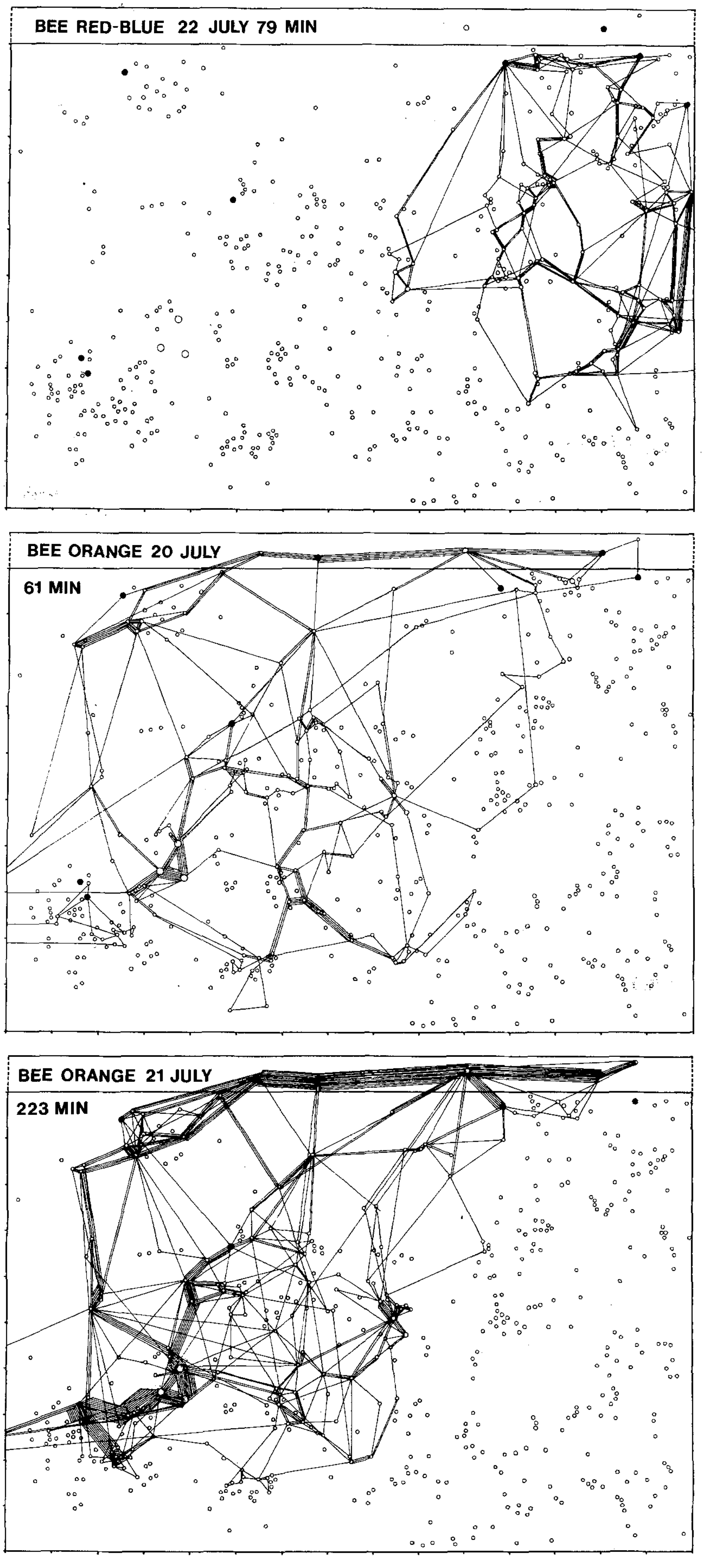


Fig. 3a–f. Maps of interplant flights by *Bombus* cf. *vagans* workers within a 10 × 15 meter grid of marked *Aralia hispida* plants. Small open circles represent *Aralia* ramets. Larger open circles indicate tight clumps of several ramets where it would have been impractical to draw all the connecting flights. Black circles represent *Rubus* sp. shrubs. The adjunct strip at the top of the graph was added to provide additional information about the flights of bee Orange (e–f). This area was not mapped precisely, and the symbols for both *Aralia* and *Rubus* represent the approximate locations of patches of flowering shoots, not single individuals. Although flight



directions are not shown, the paths flown most often tend to be flown in one direction. Data were recorded between 0800 and 1800 h. Each map shows several different foraging trips. The marked bees were observed only part of the time they foraged in the mapped block. The total time under observation and the date are given on the graphs. Thus Figs. b–d depict the flight of bee Red-Blue on July 20–22. The essential similarity of succeeding days' patterns is evident. Apparent deletions of plants from traplines could usually be attributed to cessation of flowering or a shift from male to female phase

Table 6. Plants visited by individual bees in 1979 (see text)

Ramets are classified into several types: ♂ = at least one male-phase umbel with apparently rewarding flowers; ♀ = at least one female-phase umbel with apparently rewarding flowers; interphase = both sexes apparently rewarding simultaneously; flowering = all of the above categories summed; non flowering = umbels with no flowers rewarding; unknown = not labeled and flowering status not ascertained; *Rubus* sp. = shrubs of *Rubus* sp., in flower. Contingency χ^2 values are given for two tests: (a) visitation is independent of sex-phase (♂ vs. ♀); (b) visitation is independent of reward (flowering vs. non flowering). In general, both hypotheses are rejected. Bees prefer flowering and male-phase ramets. Two of three bees made regular visits to *Rubus*.

	Blue male				Pink male				Orange worker	
	25 July		26 July		25 July		26 July		26 July	
	visited	not	visited	not	visited	not	visited	not	visited	not
♂	20	9	16	5	16	13	15	6	12	9
♀	8	9	7	16	8	9	8	15	4	19
interphase	2	3	0	0	4	1	0	0	0	0
flowering	30	21	23	21	28	23	23	21	16	28
non-flowering	2	19	2	25	0	21	1	26	2	25
unknown	1	3	3	2	0	5	1	4	1	4
Rubus	0	4	3	1	2	2	1	3	0	4
χ^2(a)	2.2		9.2**		0.3		5.9*		7.5**	
χ^2(b)	14.6**		14.8**		18.9**		17.6**		7.4**	

Overall χ^2(a) = 14.9*; χ^2(b) = 48.2**

invariably moved to the drained umbel, but bees that visited the drained umbel first usually left without sampling the enriched one (Table 5b). Frequency distributions of flower visits are given in Fig. 2. When bees encountered the drained umbel first, they usually probed two flowers before departing. On the enriched umbel they usually probed all 12 flowers once and some twice, working systematically around the umbel. The modal number of flower probes was 14. Bees that encountered the drained umbel second always probed more than two flowers ($\bar{x} = 5.58$). Bees probed significantly more flowers on drained umbels encountered second than on drained umbels encountered first (Mann-Whitney U-test, $p < 0.01$ (Sokal and Rohlf 1969)).

Foraging Patterns of Marked Bees

A large proportion of the bees marked in 1980 were seen regularly in the 10 × 15 m grid, and several seemed to do all their foraging there. We have selected three *Bombus* cf. *vagans* workers from the several for which we have many observations, for illustrative purposes. Summary maps of their interramet flights are given in Fig. 3a–f. Each map shows several different foraging trips during the day. All bees did some pollen collecting in addition to foraging for nectar, but corbicular loads were never large. It appears that each bee tended to visit subsets of the available ramet in fairly specific and repeatable sequences, or "traplines", a useful term apparently introduced by D. Janzen (see Heinrich 1979a, p. 177). For instance, bee Yellow-blue followed a particular back-and-forth path with surprising regularity on 25 July 1980 (Fig. 3a). The patterns are less clearcut in the other bees, but the flights are clearly nonrandom and all the bees display some tendency to trapline. It is particularly interesting that the traplines included both *Aralia* and *Rubus* flowers. Also noteworthy is the similarity of the patterns flown on successive days. It appears that one day's trapline is developed from the previous day's. Some of the changes between the days coincided with changes in the status of the plants. This was especially apparent with respect to the *Rubus* plants, which were sporadically flowering by this time. Males and other species of *Bombus* behaved similarly.

In Table 6 we summarize numbers of visits to different categories of ramets for the 1979 data (two males and one worker bee). It is clear that the bees generally visit rewarding rather than unrewarding ramets, preferentially visit ramets with large numbers of rewarding umbels, and visit male-phase more often than female-phase ramets. Thus traplines seem to reflect some of the same preferences shown by bees in experimental choices.

Discussion

Importance of Pollinators

Table 1 implies that bumble bees are the most important pollinators of *Aralia hispida* at our study sites. This conclusion unfortunately depends in part on extrapolation from O'Brien's (1980) data on relative pollen-carrying abilities of bees and flies. We plan to test the validity of this extrapolation by directly examining pollen deposition by field-foraging insects on test umbels with clean stigmas. Until these tests are complete, we will assume that bumble bees are performing most of the pollinations. This conclusion is consistent with other reports on the pollen-carrying abilities of bumble bees and other visitors (Beattie 1971b; Beattie et al. 1973), but requires confirmation.

The uniformly high fruit set in these populations suggests that female fecundity is not pollinator-limited at these sites (Thomson and Barrett 1981); however, the sites were chosen for their high densities of flowers and insects.

Consequences for Aralia hispida of the observed pollinator behavior

a) Umbel-Type Preference. The preference of bees for male-phase umbels recalls observations in other plants where female flowers mimic male flowers, apparently to compensate for lower intrinsic attractiveness (Baker 1976; Bawa 1980). While the presence of pollen in male-phase flowers may partially explain this preference in *A. hispida*, male bees (which do not collect pollen) still preferred male-phase flowers. Bees and other visitors also showed preference for umbels with larger numbers of flowers, which has also been observed elsewhere (Willson and Rathcke 1974; Willson and Price 1977; Schemske 1980). Taken together, these preferences may constitute a selection pressure favoring a sexual difference in the opening schedules of flowers: the male openings of hermaphrodite flowers in an umbel usually span 4–5 days, while the later female openings of the same flowers are compressed into 1 or 2 days. The greater synchrony of the female phase increases the effective umbel size, and may represent a numerical compensation for the lesser individual attractiveness of female-phase flowers (Thomson and Barrett 1981). A similar explanation has been proposed for the longer flowering period of male inflorescences in the dioecious *Aralia nudicaulis* (Barrett and Thomson 1981). David Lloyd and Jocelyn Yates (pers. comm.) report parallel data on the duration of male and female phases of flowers of *Wahlenbergia albomarginata*.

b) Traplining foraging. The protracted bloom of ramets (up to 33 days) and the gradual release of pollen and nectar through the day make traplining more likely. What are the consequences of traplining for the plant? Although the visitation rate of a plant is probably increased by installation on a trapline, its mate diversity may be decreased. Compared to randomly directional foraging, traplining will produce more elongated pollen shadows (e.g., be Yellow-Blue, Fig. 3a). Such a shadow will reduce some pollen wastage caused by intraclonal flights. Elongated shadows will reduce the spatial variation in population sex ratio "experienced" by a plant (see Thomson and Barrett 1981) and should reduce the frequency of complete male failure. Because traplining bees drop unrewarding ramets and because unreceptive ramets are unrewarding, traplining will reduce wastage of pollen delivered to unreceptive ramets.

Bees repeat their traplines frequently: Yellow-Blue visited a particular ramet once for every 4.8 min of observation. Nectar secretion is probably not great enough for this revisitation rate to pay a direct profit. Indirectly, rapid revisitation will keep ramets drained and therefore less likely to be appropriated by other bees. Bees can assess the nectar status of their traplined ramets with minimal effort because of their efficient sampling techniques (Table 5, Fig. 2). Pollen, also important for bees, becomes available frequently but temporarily and at unpredictable locations as anthers dehisce. Davies and Houston (1981) have shown that regularly patrolling a feeding area is an efficient way to harvest such food.

Optimal Foraging

Pyke (1979) has suggested that bumble bee workers conform especially well to the assumptions of optimal foraging models, and several workers have adopted them (or honey bees) as study organisms for investigating the methods by which animals obtain food (Pyke 1974, 1978a, 1978b, 1979; Hartling and Plowright 1979; Pleasants and Zimmerman 1979; Heinrich 1976, 1979a, b, c; Heinrich et al. 1977; Thomson 1981; Waddington 1979b, 1980; Waddington and Heinrich 1979; Waddington and Holden 1979; Zimmerman 1979). Most of these authors have addressed either movement patterns between inflorescences, which they have treated as "search behavior", or flower species choices, which at least Heinrich (1976, 1979a, b; Oster and Heinrich 1976) has treated as a process involving sampling of "minor" species to stay abreast of changing relative values of different forage species. While these processes are probably components of bee foraging on many kinds of plants, most bee movement within *Aralia hispida* stands is not best described as searching, and the regular visits to *Rubus* are not best described as sampling. In both cases, the bee's actions are part of a largely repetitive process of harvesting rewards from a set of plants with which the bee is clearly familiar. Searching is a relatively small component.

To treat the sampling point first, not only did the bees visiting *Rubus* usually make their visits to *Rubus* at the same points in their traplines, they predictably flew into the *Robus* foliage at these points on days when no flowers were produced. The *Rubus* bloom was sharply waning at this time.

Concerning traplining, it has long been known that bumble bees and honey bees often maintain small, individual foraging areas (Müller 1882; Giltay 1904; Bonnier 1906 (cited by Manning 1956); Ribbands 1949; Singh 1950). Darwin (1876) and Ribbands (1949) both stress that honey bees have accurate memories of the locations of specific plants. However, although Heinrich (1976, 1979b) described individually marked bumble bees following similar foraging paths over time, relatively little has been said about this in the recent bumble bee literature. Especially neglected is Manning's (1956) clear demonstration of traplining. R.A. Johnson (pers. comm.) has observed *Bombus vagans* traplining on *Agastache foeniculum* their behavior is very similar to that found on *Aralia hispida*.

An ignorant bee's optimal search path through a stand of flowers will presumably not be the same as a harvesting path that has been developed and modified through time according to rewards received at certain flowers. Thus tests of optimal search models with data from field bees should include determinations of whether the bees are searching or not. This will usually require individual marking of bees and of plants.

Individual recognition of bees may also yield better data on the relationship between the reward received at a plant and subsequent movements to other plants. Pyke (1974, 1978a) proposed that bees should turn more and fly shorter distances after leaving richer inflorescences. These behaviors would keep the bees in local concentrations of rich inflorescences. Several authors (e.g., Heinrich 1979c; Pleasants and Zimmerman 1979; Waddington 1980; Zimmerman 1979) have elaborated on this "restricted area foraging" hypothesis, providing general support for it in various field and laboratory investigations with bumble bees and honey bees. Because it is hard to estimate the amount of reward (usually nectar) in flowers without removing it, some field studies have used pollinator residence time as an estimate of an inflorescence's richness. While there is certainly a good correlation between nectar volume or concentration and residence time in some flowers (Thomson and Plowright 1980; but see Heinrich 1979c), there is also great individual variation in residence time among bees. Our marked bees tended to forage much more slowly as they aged, and they also made fewer long flights. Thus, observed correlations – across individuals – between visitation time and subsequent flight may not indicate correlations within individuals. This problem does not compromise studies using artificial flowers with known amounts of nectar (Waddington 1979b, 1980), or those manipulating nectar levels in the field on a gross scale (Heinrich 1979c), nor does it affect our enriched-umbel choice experiment described above. That experiment verified a small-scale manifestation of restricted-area foraging by showing that the bees almost always use the reward found in one umbel of a pair to predict the reward in the second. It also showed that the bees react in "disbelief" when this prediction is wrong, because they probe significantly more flowers before abandoning a drained umbel if they have just been rewarded (Fig. 2). Gill and Wolf (1977) and Heinrich (1979c) report analogous modification of foraging based on the richness of recent rewards, in sunbirds and bees respectively.

Conclusion

Bumble bees are important pollinators of *Aralia hispida*. Experienced individuals forage in ways that show they possess considerable familiarity with the locations of different ramets (traplining). They also show keen discrimination among umbels of different size and quality. One major goal for further research is to determine the way in which traplines develop and the roles played by plant size and sex-phase in trapline ontogeny. Because the bees trapline, some predictions of optimal search theory should not apply to them, although those predictions may hold for the same bees when they are working other crops. Because several characteristics of *Aralia hispida* seem to promote traplining, it is of considerable interest what consequences such foraging has for the plants. We have identified some possible hypotheses and believe several of them can be tested by manipulative experiments in the field.

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