Effects of variation in inflorescence size and floral rewards on the visitation rates of traplining pollinators of *Aralia hispida*

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Summary

In field experiments with *Aralia hispida* inflorescences, the following variables were manipulated: number of umbels per inflorescence, number of flowers per umbel, and amounts of pollen and nectar per flower. Visitation rates by bumble bees, the principal pollinators, were then observed. In the reward-variation experiments, bees appeared to learn the positions of nectar-rich shoots, and visited them significantly more often than nectar-poor shoots. They did not respond to similar variation in pollen production. The nectar preferences developed slowly after the treatments were imposed, and bees continued to favor sites that had been occupied by nectar-rich shoots even after the treatments were discontinued. Visitation rate was approximately proportional to flower number, making it unlikely that increases in inflorescence size produced a disproportionate gain in male reproductive success (a necessary condition in certain models for the evolution of dioecy). For a fixed number of flowers per inflorescence, bees preferred inflorescences with more umbels. In pairwise choice tests of male-phase and female-phase umbels of various sizes, bees preferred male-phase umbels and larger umbels; the preference for male-phase umbels is stronger in bees that had previously fed on male-phase umbels.

Keywords: *Aralia hispida*; *Bombus*; inflorescence size; nectar; pollen; selective foraging; trapline; choice experiments; dioecy; pollination; pollinator visitation rate.

Introduction

Evolutionary ecologists frequently invoke interplant variation in pollinator service as a selective force in shaping plant reproductive systems. Variation in plant qualities may affect visitation rates; visitation rates in turn affect fitness through variation in pollen donation and receipt. The plant qualities most likely to have such effects are those that determine foraging profitability for the pollinators, principally (1) the number of flowers and (2) the amount of reward (pollen, nectar, resin, oil, etc.) per flower. The relationship between flower number and visitation rate has received much attention (e.g., Willson and Price, 1977; Schaffer and Schaffer, 1979; Schemske 1980; review by Bertin, 1987), but relatively little experimental work under natural conditions. The relationship between reward per flower and visitation rate has received much less attention; for example, nectar has generally been considered to influence how long a pollinator stays, or what it does upon leaving, but not the probability of visiting. This assumption is obviously dubious if the pollinators selectively revisit plants (as in trapline foraging) or if they can assess rewards remotely (Thorpe *et al.*, 1975; Heinrich, 1979b). Here, I report coordinated manipulative studies of the effects of nectar amount, pollen amount, and flower number variation on the visitation rates of bumble bees to *Aralia hispida* Vent. (Araliaceae) in the field.

Because visitation rate is a key variable in so many evolutionary scenarios, the results have very diffuse implications. To focus the discussion, I present the flower-number results primarily in terms of sex allocation models for the evolution of dioecy from the hermaphrodite or cosexual condition (e.g., Charlesworth and Charlesworth, 1981; Charnov, 1982; Lloyd, 1984). I especially consider one hypothesis (due principally to Bawa and Beach, 1981; also Willson, 1979; Bawa, 1980; Beach, 1981) that depends on the functional relationship between male reproductive success and investment. Essentially, I use visitation rate to index male reproductive success, and flower number to index investment. If pollinating visits to cosexual plants are an accelerating function of flower number, Bawa and Beach argue that female sterility genes could spread because a reallocation of resources from female to male function would permit increased flower production, hence greater net reproductive success. After male plants become frequent, male sterility genes could secondarily spread, with females driving out the remaining hermaphrodites. Thus the hypothesis proposes a pathway from cosexuality to androdioecy to dioecy. In my study area, bumble bees are the primary pollinators of both cosexual (*A. hispida*) and dioecious (*A. nudicaulis*) species of *Aralia*; thus it is reasonable to ask whether the bees show selective foraging behavior consistent with the hypothesis (Thomson and Barrett, 1981a,b; Cruden and Hermann-Parker, 1977; Lloyd, 1982).

There are no similar pre-existing hypotheses explicitly concerned with reward variation, so I concentrate discussion of those results on the complications that they pose for the application of simple investment models.

Materials and methods

Large rhizomatous clones of *Aralia hispida* grow abundantly in disturbed sites in northeastern North America. At flowering, each shoot alternately offers male-phase and female-phase flowers, as up to three orders of umbels pass through successive, synchronized waves of protandry (Thomson and Barrett, 1981a). An umbel typically presents 5–15 open flowers at a time, but this varies greatly, as does the number of secondary and tertiary umbels per shoot. All shoots have a single primary umbel. Male-phase flowers present pollen and nectar; female-phase flowers present only nectar, and also shed their petals. Because the sexual phases are, to some extent, synchronized within clones, a stand of flowering *A. hispida* presents to its pollinators a shifting mosaic of patches containing different amounts and types of food.

Although many species of insects visit the flowers, the major pollinators are bumble bee workers (Thomson *et al.*, 1982), which collect nectar and pollen. At our sites, the most abundant are *Bombus ternarius* Say, *B. vagans* Smith, *B. sandersoni* Franklin, and *B. terricola* Kirby. *Bombus vagans* and *B. sandersoni* are difficult to distinguish and must be lumped as '*B. cf. vagans*' for field observations. *Bombus ternarius* and *B. cf. vagans* respond to the shifting mosaic of floral resources by establishing 'traplines' of specific favored shoots that they revisit in a fairly predictable sequence at frequent (~10 min) intervals. Traplines change through time, presumably as a result of changes in relative plant quality. In the following experiments, seven to nine observers recorded the behavior of bees at variously arranged and modified combinations of *Aralia hispida* umbels. We worked in large stands near Wesley and Northfield, Maine, where bees are abundant on *A. hispida*. Except as noted, all data were collected from 19–23 July 1984.

Paired-umbel sex choice experiments

Several assistants and I simultaneously presented freely foraging bees with a male-phase and a female-phase umbel. The ratios of the female-phase umbel size (measured as number of flowers on anthesis) to the male-phase umbel size ranged from 39:1 to 1.5:1. We tested a series of sex ratios for each of two umbel size treatments: in large umbel treatments there were 40 flowers on the two umbels combined; in small umbel treatments there were 20 flowers in total.

Umbels were placed in short lengths of Tygon tubing attached to one end of a 0.5 m rod. The tubes held the umbels at a realistic separation distance and angle, and were sealed at the lower end and filled with water to keep the umbels fresh. The observers used uniform criteria for choosing the umbels, which were replaced by fresh ones at 15 min intervals.

We located bumble bees foraging on *Aralia hispida* and presented the stick to each bee so that the paired umbels were equidistant from it. If the bee flew to one of the umbels, we recorded the species of the bee, the sex-phase of the umbel upon which it had been feeding prior to making its choice, and the sex-phase of the umbel that it chose. We avoided knowingly resampling the same bee by moving about. To avoid unfilled data categories in the analysis, we made special efforts to record data on bees coming from female-phase umbels; therefore, the data overrepresent the 'from female' category.

Unlike those above, a second set of experiments measured cumulative visits to umbels that remained fixed in one place, so that selective revisiting could be realistically assessed. These 'array' experiments simulated variation at two spatial scales, the single shoot and the small clone.

All array experiments involved 8 permanent stations located at 5–15 m spacing along the periphery of a dense stand of *Aralia hispida*. At each station we set up four 'artificial inflorescences' at the corners of a 0.5 m square. Each inflorescence was a 0.5 m green bamboo rod stuck in the ground with four Tygon umbel holders at the top. Bees visited without obvious hesitation and foraged normally. Observers sat at the fixed stations, changing stations at 15 min intervals to equalize observation time at each station and to spread any observer bias over all treatments. We recorded the bee species, the time of the visit, the sequence of inflorescences visited, and the number of flowers probed on each umbel. All umbels were replaced with fresh ones at 2–3 h intervals, which prevented wilting and preserved apparently normal rates of anther dehiscence. The cut umbels continued to secrete nectar, but the rate of this secretion was not measured.

Variation in inflorescence size experiment, 19 July 1984, 1030–1730. All stations had the same four inflorescences (from male-phase secondary umbels): 1 umbel with 4 flowers; 3 umbels with 4 flowers each; 1 umbel with 12 flowers each; 3 umbels with 12 flowers each.

Variation in inflorescence quality experiment, 20 July, 1130–1530; 21 July, 0930–1245. All stations were uniform, and each inflorescence at each station had 2 male-phase secondary umbels with 8 flowers each. We varied pollen supply by emasculation and nectar supply by adding 1 μl of 35% sucrose solution to each flower at intervals. I denote intact anthers as $+P$, emasculation as $-P$, nectar addition as $+N$, and no nectar addition as $-N$. Each station had 4 inflorescences: $+P+N$; $+P-N$; $-P+N$; and, $-P-N$. On 20 July the nectar additions were 45–60 min apart; on 21 July, 30 min (for better conformity with earlier work).

Variation in station quality, 21 July, 1300–1700; 22 July 0930–1245. We varied pollen and nectar supplies as above, but all inflorescences within a station were uniform and stations differed from each other. For each of the treatments ($+P+N$, $+P-N$, $-P+N$, $-P-N$) there were 2 replicate stations. This experiment immediately followed the inflorescence quality experiment. At 1100 on 22 July we replaced all inflorescences at all stations with uniform, female-phase secondary umbels with 8 flowers each.

Results

Paired-umbel sex choice experiments

Visits made by 'interviewed' bees can be summarized as a contingency table with four dimensions (Table 1: 1 – absolute umbel size (a total of either 20 or 40 flowers on the two umbels

Table 1.   Choices of paired male-phase and female-phase umbels of *Aralia hispida* by foraging *Bombus* workers. The data are arranged as a 2 × 2 × 2 × 5 contingency table (see text). The ratios in parentheses under the relative umbel size categories give the number of flowers on the male umbel: the number of flowers on the female umbel. The entries in the table are the observed number of visits to an umbel type. The design created structural zeroes, denoted by 's.z.' in the body of the table.

1	2	3	4				
Absolute umbel size	Sex moved from	Sex moved to	Relative umbel size (fraction male)				
			0.025 —	0.05 (1:19)	0.10 (2:18)	0.20 (4:16)	0.40 (8:12)
Small (20 fls total)	Male	Male	s.z.	33	39	54	36
		Female	s.z.	18	28	20	17
	Female	Male	s.z.	12	5	11	14
		Female	s.z.	16	11	9	15
			0.025 (1:39)	0.05 (2:38)	0.10 (4:36)	0.20 (8:32)	0.40 —
Large (40 fls total)	Male	Male	3	49	31	37	s.z.
		Female	14	37	17	11	s.z.
	Female	Male	4	10	9	14	s.z.
		Female	9	27	23	19	s.z.

combined); 2 – sex of umbel a bee came from; 3 – sex of umbel a bee moved to; and, 4 – size of male umbel relative to female umbel (2.5%, 5%, 10%, 20%, and 40%)). This table was analysed by specifying a series of log-linear models (Fienberg, 1980) to determine the significant interactions among these variables. The number of visits assigned to different categories of three of the variables (1, 2, and 4) were determined by the observers and were therefore fixed by the experimental design. To ensure that the expected values for these variables remain fixed, the [1,2,4] interaction was included in all log-linear models examined. With this design constraint, the most parsimonious model that still fits the data ($G = 9.3$, 12 d.f., $p > 0.05$) included three interactions ([1,2,4], [2,3], and [3,4]), which indicates that the sex of umbel a bee went to [3] was independently affected by the sex of the umbel it came from ([2,3]) and the relative size of the male test umbel [3,4]). The combined absolute size of the test umbels did not apparently influence bee behavior.

The biological interpretation of these data is clarified in Fig. 1, where data from large and small absolute size categories are pooled (because these categories have been shown to be statistically homogeneous). Clearly, bees feeding on female-phase umbels in the field are more willing to choose a female-phase umbel in a choice test. To a bee coming from a male-phase umbel, a female-phase umbel must be about 20 times larger than its paired male-phase umbel to achieve an equal visitation rate. Bees coming from females give nearly equal attention to females that are only 1.25 times larger than paired males, and in fact, such bees did not show a male preference under any of the experimental treatments (Fig. 1).

Array experiments

Variation in inflorescence size experiments. Table 2 summarizes the numbers of inflorescence visits and the numbers of flower probes. Although all stations provided the same floral offerings,
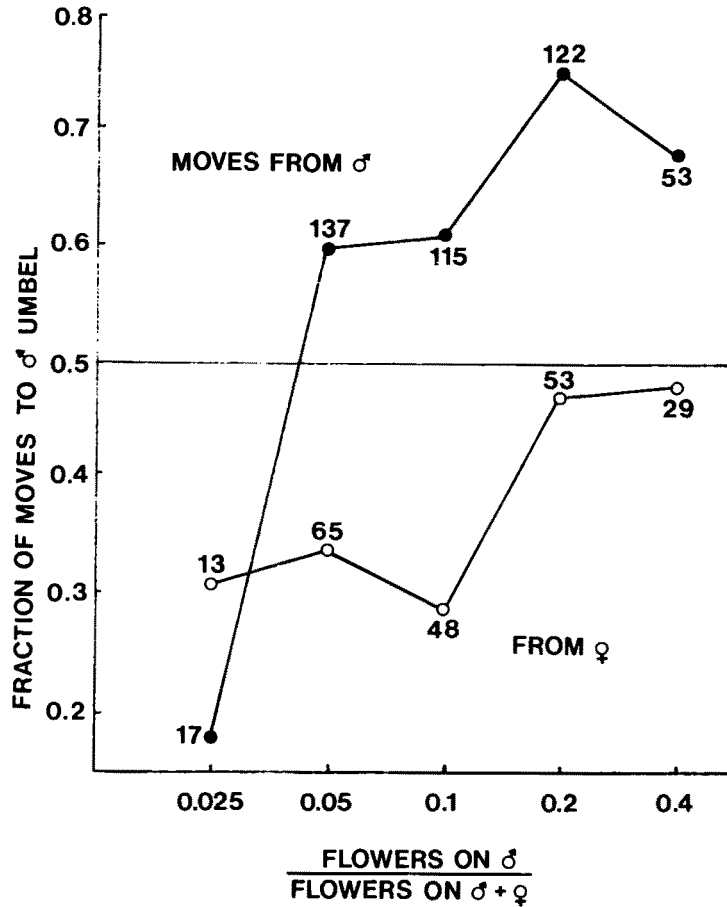
Figure 1. Summary of experiments in which bees chose between male-phase and female-phase umbels of different size. Data from large and small umbel treatments are combined; see text. The numbers near each point represent the number of flower choices contributing to the observed fraction.

Table 2. Variation in inflorescence size experiment; visits by *Bombus* workers to the four inflorescence types. The first two lines give the total visits, pooled across stations; on the last two lines, these are reexpressed on a per-flower basis.

	Inflorescence type (number of umbels × flowers per umbel)			
	1×4	1×12	3×4	3×12
Inflorescence visits	33	45	70	111
Flower visits	76	160	254	890
Inflorescence visits per flower	8.25	3.75	5.83	3.08
Flower visits per flower	19.0	13.3	21.2	24.7

Bombus visitation rates varied considerably among stations, ranging from 21 to 57 station visits. This variation will be discussed below because it affects the interpretation of the station quality experiments, but it is not critical to the within-station choices analysed in Table 2.

Inflorescence visits increased with both umbel number and umbel size (Table 2, Fig. 2). For 4 of the 8 stations, the observed distribution of visits departed significantly ($p < 0.05$) from a uniform expectation. There was no significant heterogeneity among stations in this respect (Heterogeneity $G = 14.1$, 21 d.f., ns), and the deviation from uniformity is highly significant for the pooled data ($G = 51.6$, 3 d.f.). Within the two types of inflorescence with 12 flowers, there were significantly more visits to the three 4-flowered umbels than to the single 12-flowered umbel. Essentially the same patterns hold for flower visits to the four types of inflorescence, but these cannot be tested statistically because flower visits within an umbel are not independent events.

If, however, visits are re-expressed on a per-flower basis to yield a 'success vs investment' relation, different patterns emerge (Table 2). Inflorescence visits per flower generally decline with increasing flower numbers, whereas flower visits per flower do not show any consistent trend. These data do not permit a direct test of linearity *per se*, although one can test for direct proportionality of inflorescence visits to flower numbers (pooling the 1 × 12 and 3 × 4 data). The relation is not proportional ($G = 29.0$, 2 d.f., $p < 0.001$), with the four and twelve-flowered inflorescences receiving more visits than expected and the 36-flowered inflorescence fewer. Again, flower visits cannot be so tested.

Table 3.   Pooled inflorescence visits for the first and second days of the 'inflorescence quality' experiment (20–21 July).

Date	Inflorescence treatment				Total	G(3 d.f.)
	+P+N	+P−N	−P−N	−P+N		
20 July	119	107	90	115	431	4.72 ns
21 July	216	168	174	226	784	13.1 **
Total	335	275	264	341	1215	15.7 **

Data pooled by pollen or nectar only

	+P		−P			G(1 d.f.)
	610		605			0.02 ns
	+N		−N			
	676		539			15.5 **

Variation in inflorescence quality experiment. On 20 July (when the nectar restocking rate for the '+N' treatments was low), the total numbers of inflorescence visits were not statistically distinguishable from a uniform distribution (Table 3). Late in the day, however, the +P+N and −P+N treatments appeared to be accumulating visits more rapidly than the +P−N and −P−N treatments. The distribution of visits for the continuation of this experiment on 21 July differed significantly from uniformity, the primary differentiation being between the '+N' and '−N' treatments (Table 3). Pollen quantity had no effect. Nectar additions also greatly increased the numbers of flowers visited.

Table 4. Frequency of *Bombus* visits to different pollen (+P, −P) and nectar (+N, −N, see methods) treatments during the station quality experiment. Dates and treatments: a. 21 July AM. Pre-experimental control – stations uniform; b. 21 July PM. Experimental treatments applied; c. 22 July AM. Experimental treatments continued; d. Total experimental (b + c); e. 22 July PM. Post-experimental control – stations uniform.

Date and treat-ment	Station (treatment)							
	1 (+P+N)	2 (+P−N)	3 (−P−N)	4 (−P+N)	5 (+P+N)	6 (+P−N)	7 (−P−N)	8 (−P+N)
a	30	31	44	52	50	38	46	29
b	45	46	56	74	84	42	48	52
c	18	9	26	31	36	12	12	25
d	63	55	82	105	120	54	60	77
e	11	10	15	25	30	14	8	20

Pooled data: treatment

	(+P+N)	(+P−N)	(−P−N)	(−P+N)
a	80	69	90	81
b	129	88	104	126
c	54	21	38	56
d	183	109	142	182
e	41	24	23	45

Variation in station quality experiments. Because the stations differed in their attractiveness even when they were stocked with uniformly rewarding umbels, the appropriate test of whether station treatment affects visits to stations is not one against a uniform distribution but a comparison against the observed pre-experimental distribution, via a 2 × N contingency table. I use data from the morning of 21 July (when all stations were uniform) as the baseline control for the experimental data from the afternoon of 21 July and the morning of 22 July.

The most obvious comparison is for total station visits before the experiment vs during the experiment (i.e., comparison of lines a and d in Table 4) across the 8 stations. There is no significant departure from independence, whether or not the 2 replicate stations are pooled for each treatment (e.g., for unpooled data, $G = 10.3$, 7 d.f., $p > 0.05$). As in the inflorescence quality experiments, however, significant treatment effects developed with time. If the data for the second half of the afternoon of 21 July are compared to the pre-experimental controls, there is a significant effect ($G = 15.1$, 7 d.f., $p < 0.05$); if the data from 22 July are included, the difference becomes highly significant ($G = 21.5$, 7 d.f., $p < 0.005$). After uniform female-phase umbels were restored to all stations (the afternoon of 22 July) bees continued to prefer the previously favored stations (comparison of lines a and e, Table 4; for unpooled data, $G = 13.2$, 7 d.f., which is insignificant but suggestive; for pooled data, $G = 8.8$, 3 d.f., $p < 0.05$).

As in the inflorescence quality experiment, nectar addition appears to control the distribution of visits. Overall, the nectar-enriched stations received more visits than predicted by the pre-experimental controls, and non-enriched stations received fewer visits (Table 4, lines a and d, pooled data). Casting these data into a three-way contingency table [(+N vs −N) × (+P vs −P) × (pre-experiment vs. experiment)] reveals a significant interaction between nectar treatment and experimental period with pollen treatment held constant ($G = 6.8$, 2 d.f., $p < 0.05$), but no such interaction for pollen treatment ($G = 0.01$, 2 d.f.). Again, pollen quantity was unimportant.

Discussion

Bumble bee pollinators of *Aralia hispida* do respond to variation in both inflorescence structure and reward levels in ways that result in different visitation rates to different plants. In the case of inflorescence structure, the bees' preferences are instantaneous and appear in pairwise choice tests. Reward-level preferences, in contrast, do not appear in pairwise choice tests (Thomson *et al.*, 1982), but develop with time, presumably as individual bees return preferentially to more rewarding plants. Reward-level effects remain poorly appreciated. Such preferences need not be universal – they seem to require special pollinator behaviors and special patterns of reward presentation by the plants – but they should be considered in further explorations of the factors controlling visitation rates. Below, I try to show how explicit recognition of the spatial and temporal nature of pollinator responses to plant variation can clarify the translation of those responses into selection pressures on plant form.

Tradeoffs of inflorescence size and sex: the importance of context

Sex-choice experiments. Figure 1 plays the bees' preference for larger umbels against their preference for male-phase umbels in a 'behavioral titration' (Moermond and Denslow, 1983), locating equivalence points at which the greater size of a female umbel compensates for its sexual disadvantage. That the equivalence points are quite different for bees coming from male-phase and female-phase umbels suggests a conservative tendency for bees to continue visiting the sex-phase just encountered.

Several considerations affect the interpretation of this conservatism. The natural distribution of *Aralia hispida* flowers is highly patchy with respect to sexual phase. Thus a bee that visited, say, a female-phase umbel in the field just prior to moving to the experimental bouquet had probably been visiting numerous females for some time before being tested. If bees in the field showed individual sex-phase preferences, most of the female-preferring individuals would tend to be found in patches dominated by female-phase flowers. Therefore, most of the visits to the bouquet from female-phase flowers would be recorded in these areas. Because of these spatial effects, the associations of variables that were detected by log-linear model fitting must be interpreted cautiously. They do not necessarily measure the behavior one would expect from a randomly chosen bee that could somehow, regardless of foraging history and spatial context, be compelled to visit a male- or a female-phase umbel, and then be given the choice test.

The functional relationship of visitation to inflorescence size

Charnov (1982), Charlesworth and Charlesworth (1981), Lloyd (1984), and Charlesworth (1984) specify conditions for the spread of unisexuals in hermaphroditic populations. Assuming that female reproductive success is 'resource-limited' (i.e. increases linearly and through the origin with investment in female function), the essential requirement for the spread of males is that male reproductive success must be an accelerating function of investment. Female reproductive success (as seed set) does appear to be resource-limited in *A. hispida* (Thomson and Barrett, 1981a), as is commonly (Willson, 1979; Bell, 1985; Stanton *et al.*, 1986) but not universally (Bierzychudek, 1981) the case. Male reproductive success is harder to measure; it should increase with visitation rate over some range, but probably in a decelerating fashion (Lloyd, 1984). First, as visits increase due to increased flower numbers, it is more likely that pollen will be delivered redundantly to stigmas already pollinated by the same source. Second, if pollinators visit more flowers on a plant, relatively less pollen will leave the plant, due to self-pollination and grooming losses (Thomson, 1986). Third, pollen may be completely removed from anthers after one or a few visits (Harder *et al.*, 1985; Harder and Thomson, in prep.). Thus, for male fitness to be

positively accelerating with respect to investment, as required by the Bawa–Beach hypothesis, given that male reproductive success is a decelerating function of visitation, then visitation must also be accelerating with respect to investment. In fact, the nonlinearity of the visits vs investment curve would need to be more pronounced than that of the corresponding fitness curve.

To complicate the argument, there are two types of visits to consider, inflorescence visits and flower visits. It is not clear *a priori* which of these is more closely linked to successful pollen donation. At one extreme, a pollinator may accumulate an equal amount of pollen on its body for each flower it visits within an inflorescence, so that if it leaves after visiting 10 flowers, it will carry 10 times as much pollen as if it had visited only one flower. In this case, flower visit number would be closely related to pollen donation potential and, therefore, to male reproductive success. At the opposite extreme, a pollinator may groom off excess pollen during its stay or while in flight to the next plant. The number of residual grains left on the animal for delivery to stigmas may be uncorrelated with the number of flowers visited, in which case the number of flower visits is immaterial to male reproductive success, and inflorescence visits become all-important. Grooming losses are an important determinant of pollen transfer by bumble bees (Thomson, 1986), with grooming typically occurring when a bee leaves an inflorescence. The only quantitative data available (on *Erythronium* lilies) suggest that *Bombus* groom more vigorously immediately after acquiring large amounts of pollen, such that heavy pollen pickup actually results in a lower proportion of the removed grains reaching stigmas (Thomson, 1986; Harder and Thomson, in prep). These considerations suggest inflorescence visits probably are more closely linked to fitness than flower visits are. If so, male reproductive success certainly does not accelerate with increasing flower number, as required for the Bawa–Beach hypothesis for the evolution of dioecy through androdioecy. Even if flower visits are the better reproductive success currency, the data do not indicate the strong nonlinearity required by the hypothesis, at least over the range of variation tested. These experimental findings are thus in accord with Charlesworth's (1984) conclusion that androdioecy has been of little importance as an intermediate step in the evolution of dioecy.

Reward variation experiments, food competition, and selectivity

If bees do pick out the richest plants and then incorporate them into a trapline that ensures a high visitation rate, those plants might get a greater fitness return on their investment in flowers than they would if the bees foraged with less precise spatial memory; that is, traplining may magnify plant fitness differentials based on pollinator attractiveness. The inflorescence quality and station quality experiments tested pollinator selectivity at two spatial scales. Based on preliminary trials, I expected a station response only, but bees in fact located the more rewarding inflorescences within stations, as well as discovering the more rewarding stations. It appears that they actually learned the positions of sucrose-enriched plants, rather than responding directly to the appearance or scent (Thorpe *et al.*, 1975; Heinrich, 1979b) of the added nectar. First, the response developed slowly (analyses above); second, bumble bees do not discriminate between drained and sucrose-enriched umbels of *Aralia hispida* in pairwise choice tests (Thomson *et al.*, 1982).

In other experiments, Thomson *et al.* (1987) have shown that bees respond to even larger-scale differences in plant rewards by shifting their activities into areas from which other bees have been removed. Thus, at all scales, from pairwise choices of umbels to 200 m² competitive vacuums, bumble bees learn where more floral rewards are concentrated and adjust their behavior accordingly. It has frequently been shown that bees respond to increased floral reward (e.g. Hartling and Plowright, 1978; Waddington and Heinrich, 1981; Morse, 1980; Schaffer and Schaffer, 1979), but those observations do not consider a traplining context wherein a bee's experience on one foraging trip is likely to modify the plants visited on the succeeding trip. The

experiments of Thomson *et al.* (1987) demonstrated that bumble bees feeding on *Aralia hispida* competed for food; flowers were revisited at a high rate, and removing some bees increased the rate at which remaining bees brought food to their hives. The flexible traplining shown by foragers probably approximately equalizes the standing crops of floral rewards in the plants, such that more rewarding plants would receive a higher visitation rate (Heinrich, 1979a). Thus, selection for higher reward production could well be driven by selection for pollinator attraction. However, this highly competitive situation might also explain why visits seem to increase only linearly with flower production. Bees exploit *Aralia hispida* flowers so thoroughly that they discover and repeatedly visit even small, inconspicuous inflorescences. The high revisitation rate, spatial memory, and competition for food would act together to ensure that inflorescences of all sizes receive visits more or less in proportion to the rewards they offer, i.e. in proportion to their flower production. David Lloyd (pers. comm.) points out that such proportionality may be considered as one manifestation of the 'ideal free distribution' predicted to occur when competing foragers face a patchy environment (Fretwell, 1972), which can be considered an *a priori* argument against the Bawa–Beach hypothesis under such circumstances. In a less competitive situation, pollinators may have the luxury of being able to concentrate on only the largest inflorescences (Schaffer and Schaffer, 1979; Schemske, 1980). In such situations male fitness may be an accelerating function of flower number.

It would be incorrect to infer from the reward-level experiments reported here that bumble bees cannot or will not respond to pollen variation. In similar 'station quality' experiments done in 1983, a local concentration of Yellowjacket wasps (*Vespula* spp.) aggressively prevented *Bombus* workers from using nectar-enriched stations. Under those circumstances, the bees showed significant preferences for the higher-pollen reward stations (i.e. they preferred $+P-N$ to $-P-N$; Thomson, unpub. data). Apparently, bees can react to either kind of variation; the behavior they show in any particular circumstance may vary depending on the options open to them.

Umbel number and size tradeoffs

That 12 flowers distributed among three umbels should receive significantly more visits than 12 flowers in a single umbel is difficult to explain in terms of simple foraging efficiency, and could well be an idiosyncrasy of the stimulus–response behavior of bumble bees, without adaptive value in the present case. However, there could be consequences for the evolution of inflorescence architecture, in addition to previously cataloged selection pressures (Wyatt, 1982), in that the subdivision of a given flower crop into more but smaller subunits might increase pollinator service. A concomitant cost is that greater subdivision requires greater relative expenditure on supporting structures.

Inflorescence size, discriminating pollinators, and dioecy

Inflorescence-size discrimination by pollinators has been proposed as the basis for certain of the ecological correlates of dioecy. Bawa (1980) points out that many dioecious plants have small, whitish-green flowers and are visited by small generalist bees. The association of dioecy with small flowers of this sort is strongly confirmed by statistical analysis by Muenchow (1987 and pers. comm.). Bawa suggests that such bees may be especially keen discriminators of inflorescence size variation, and that this selectivity may partially account for the prevalence of dioecy in such taxa. However, as the present results show, bumble bees are also highly discriminating generalists. In fact, they select *Aralia hispida* umbels for size more reliably than small bees do (Thomson *et al.*, 1982). Plants specifically adapted for bumble bee pollination often have large, zygomorphic, blue or yellow flowers (Faegri and van der Pijl, 1979), characters not associated with dioecy. It

therefore seems that highly size-selective pollination is in itself insufficient to explain the observed correlation.

Trapline holdover effects

When flowers within cosexual plants have separate sex roles, as in monoecious plants, models usually assume that greater investment in one sex of flowers only increases reproductive success through that sex. However, the 22 July afternoon experiments show that female-phase inflorescences receive greater visitation than identical neighbors if they have been preceded by more rewarding males, due to continued microsite constancy by bees. This shift from male to female phase imitates the natural sex change in umbels of *A. hispida*. Such holdover effects greatly hinder any simple assignment of benefits to particular investments in pollinator attraction. Nectar secreted during one female phase, for example, could in principle benefit both current female and subsequent male reproductive success. In fact, because female reproductive success appears to be independent of visitation rate in *A. hispida*, female-phase nectar could have a much greater effect on male reproductive success than on female. A proper understanding of the relation between plant investment, visitation rate, and fitness requires knowledge of the way that pollinators respond to the whole temporal sequence of reward presentation and gamete deployment.

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