Reversal of apparent feeding preferences of bumble bees by aggression from *Vespula* wasps[1]

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In field experiments, the nectar and pollen levels of *Aralia hispida* inflorescences were independently manipulated. In the absence of *Vespula* spp., *Bombus* spp. workers (the primary pollinators) appeared to prefer nectar-enriched inflorescences, learning their locations and visiting them at a higher rate, but did not respond to variation in pollen. In the presence of *Vespula*, however, *Bombus* appeared to prefer inflorescences with more pollen, showing no response to nectar variation. *Vespula* responded strongly to nectar level, aggressively patrolling the nectar-enriched plants and preventing *Bombus* from feeding.

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Les concentrations de nectar et de pollen dans des inflorescences d'*Aralia hispida* ont été manipulées indépendamment au cours d'expériences en nature. En l'absence de *Vespula* spp., les ouvrières de *Bombus* spp. (pollinisateurs primaires) semblent préférer les inflorescences enrichies de nectar, dont elles apprennent la position et qu'elles visitent plus souvent, mais elles ne réagissent pas aux variations des concentrations de pollen. En présence de *Vespula*, cependant, les *Bombus* semblent préférer les fleurs qui contiennent plus de pollen et ne réagissent pas aux variations des concentrations de nectar. Les *Vespula* réagissent fortement aux concentrations de nectar et elles patrouillent agressivement les plants enrichis de nectar pour empêcher les *Bombus* de s'y nourrir.

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Introduction

Within a flowering season, the andromonoecious plant *Aralia hispida* Vent. (Araliaceae) goes through alternating male and female phases (Thomson and Barrett 1981). This species forms clonal patches through rhizomatous spreading, and the sex-phase shifts tend to be synchronized within clones; thus, pollinators experience stands of *A. hispida* as temporally and spatially shifting mosaics of male-phase patches, which offer nectar and pollen, and female-phase patches, which offer nectar only. Bumble bees (Hymenoptera: Apidae), the primary pollinators, tend to forage in specific areas, visiting a series of particular flowering shoots in a more or less consistent sequence or "trapline" (Thomson et al. 1982; Thomson et al. 1987). Under normal conditions, these traplines are stable for periods of several days, although individual shoots may be added or dropped by the bees, causing gradual changes in trapline structure.

In 1983 and 1984, I conducted field experiments in which the pollen and nectar status of *Aralia hispida* inflorescences were varied in a factorial design. The primary question concerned the response of bumble bees to the reward variation, and the implications of that response for the evolution of floral characters; this question is addressed elsewhere (Thomson 1988) using 1984 data. The experimental design implicitly assumed that any differences in visitation shown by the bumble bees to particular reward treatments accurately reflected their preferences for certain pollen or nectar levels. In fact, it was apparent that visitation rates in 1983 were more strongly influenced by interference competition from *Vespula* wasps (Hymenoptera: Vespidae) than by the nectar content of the flowers. This paper shows that the presence of *Vespula* has the effect of switching the behavior of *Bombus* from a preference for nectar enrichment to a preference for pollen enrichment.

Methods

Identical experiments were performed in July of 1983 and 1984 in large populations of *Aralia hispida* in recently logged areas near Wesley and Northfield, Maine. Eight "stations" were established at 5- to 15-m intervals along the periphery of a dense *Aralia* stand. At each stations, four artificial "inflorescences" were placed at the corners of a 0.5-m square. Each inflorescence was a 0.5-m tall green bamboo wand fitted with short pieces of clear plastic tubing at the top to hold two cut umbels of *A. hispida* at a normal height and angle. Insects visited these umbels in an apparently normal manner, without obvious hesitation. To provide maximum uniformity of umbels, they were all secondary umbels (Thomson and Barrett 1981) gathered early in the male phase from a single clone; all were initially trimmed to present eight open flowers, and this size was maintained by occasional trimming as new flowers opened throughout the experiments.

Nectar and pollen supplies of the flowers were altered to create two levels of each. Pollen treatments were (*i*) removal of all anthers, denoted as −P, or (*ii*) intact anthers (+P). Nectar was (*i*) left alone, subject to normal removal and evaporation (−N), or (*ii*) supplemented at approximately 30-min intervals with 1 μL of 35% sucrose solution per flower, delivered by a Hamilton microsyringe with a repeating dispenser attachment (+N).

During a pre-experimental period on the first of 2 days, all eight stations were supplied with identical treatments, one inflorescence each of −P−N, −P+N, +P−N, and +P+N. Immediately after setup, a team of observers sat at the stations, rotating positions every 15 min, and watched insects. Because this paper concerns insects' decisions about where to forage, the analyses are based on station visits rather than inflorescence visits or flower visits (which depend on the nectar standing crops encountered (Thomson 1988)). Because the stations offered identical rewards, I attribute any differences in visitation among stations to neighborhood effects (most likely, varying local densities of flowers) that resulted in different amounts of insect traffic in the different localities. Thus, the pre-experimental data provide a base line against which to compare

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changes in visitation following experimental changes in station quality.

For the experimental period on the following day, all four inflorescences within each station received the same treatment, but stations varied. There were two stations each of the four treatments, −P−N, −P+N, +P−N, and +P+N. Differences in visitation between the pre-experimental and experimental periods were expected to reflect the insects' ability to discover and return to especially rewarding plants. Observations proceeded as in the pre-experimental period. Counts of visits were analyzed by goodness of fit tests and tests of two- and three-way contingency tables following Sokal and Rohlf (1981).

Results

The most common visitors in 1983 were bumble bees, including *Bombus ternarius* Say, *B. vagans* F. Smith, *B. sandersoni* Fkln., and *B. terricola* Kirby, and *Vespula* wasps, including the bald-faced hornet, *V. maculata* (Linn.), and a number of yellowjackets that we did not identify to species. Based on other collections nearby, the yellowjacket category may have included *V. arenaria* Fabr., *V. acadica* (Sladen), *V. consobrina* (Saussure), and *V. arctica* Rohmer. The *Vespula* were considerably more common than usual at the experimental site in 1983; a yellowjacket nest was discovered near the array of stations. A variety of other insects constituted a minor proportion of visitors (see Thomson et al. 1982). In the following analyses, I lump all the *Bombus* spp. into one category and the yellowjackets into another, but keep the hornet *V. maculata* separate because it is an active predator which has been reported to attack *Bombus* for reasons unrelated to floral food sources (Heinrich 1984).

In 1983, it appeared that the +N stations were discovered and defended by yellowjackets during the experimental period. These wasps would remain near the nectar-enriched stations between feeding bouts, often chasing and occasionally colliding with bumble bees that attempted to feed. Hornet attacks on *Bombus* were not noted, perhaps because of the rarity of *V. maculata* (Table 1; but see Heinrich 1984). In repeating the experiments in 1984, I planned to net and remove as many *Vespula* as possible to study the bees' response alone, but in 1984, *Vespula* were extremely rare at the site and none were recorded during our observations. Thus, within-year comparisons were impossible, and I present the data as the results of a "natural experiment" over the two seasons.

Table 1 gives the total number of visits recorded in both years. Data are pooled for the pairs of stations that had the same experimental treatments. There was no significant ($p < 0.05$) heterogeneity between the two replicate stations for either *Bombus* or yellowjackets in either year (based on *G*-tests of 2 × 2 contingency tables: (2 stations) × (pre- vs. post-experimental)). Yellowjacket visits approached between-station heterogeneity ($G = 3.67$, df = 1) for the −P−N treatment. In both years, visitation rates per unit time increased from the 1st to the 2nd day (for all insects a 20% increase in 1983, 19% in 1984), which might be expected, given that the enriched stations represented new resources. However, because various other uncontrolled factors could also affect these numbers (weather, observations at different times of day, changing population sizes), the following analyses treat only relative visitation rates to the different treatments.

First, it is apparent that pre-experimental visits to the uniform stations deviated significantly from a uniform expectation in 1983 for the more abundant species (for *Bombus*, $G = 41.5$, $p < 0.001$; for yellowjackets, $G = 20.3$, $p < 0.001$; for the rarer hornet, $G = 2.6$, ns; df = 3 in each case). Although pre-experimental *Bombus* visits did fit a uniform expectation in 1984 ($G = 2.8$, ns), the large departures from expectation in 1983 point up a potential underlying spatial heterogeneity in visitation probabilities and the desirability of comparing experimental results with base-line data rather than uniform distributions.

Comparison of pre-experimental and experimental visit frequencies to the four treatments via 2 × 4 contingency tables shows no significant response by *Bombus* in 1983 ($G = 6.33$, df = 3, $0.05 < p < 0.1$), but a highly significant change by yellowjackets that year ($G = 36.7$, df = 3, $p < 0.001$). Again, the few hornet observations show no pattern ($G = 0.5$, df = 3, ns). In 1984, with *Vespula* absent, the *Bombus* response was significant ($G = 10.9$, df = 3, $p < 0.025$). By casting the *Bombus* data for both years into a three-way contingency table ((1983 vs. 1984) × (pre-experimental vs. experimental) × (the 4 treatment combinations)) and fitting log-linear models, it can be seen that there is a significant three-way interaction ($G = 11.6$, df = 3, $p < 0.01$), indicating that the bumble bees responded differently to the experiment in the 2 years. Examination of the trends in Table 2 shows that the *Bombus* appeared to be responding primarily to pollen level in 1983; they increased their visits to both of the +P treatments and decreased their visits to the −P treatments. The significance of this apparent response can be assessed by examining the three-way contingency table ((pre-experimental vs. experimental) × (+N vs. −N) × (+P vs. −P)) for a specific effect of pollen level, i.e., testing the hypothesis that the relationship between nectar treatment and experimental period is independent of pollen level. For the 1983 data, this test of conditional independence reveals a marginally significant pollen level effect ($G = 5.90$, df = 2, $p \sim 0.05$), whereas the corresponding test for a nectar effect is insignificant ($G = 1.5$, df = 2).

In 1983, however, it is clear that yellowjackets responded strongly to nectar level. They increased their visits to both +N treatments and decreased their visits to both −N treatments. Tests of specific effects similar to those described for *Bombus* yield a highly significant nectar-level effect ($G = 34.4$, df = 2, $p < 0.001$) and a marginally significant pollen-level effect ($G = 6.3$, df = 2, $p < 0.05$) for *Vespula*. Hornets showed no effects.

In 1984, the reaction of bumble bees was quite different from their reaction in 1983; they increased their visits to both +N treatments and decreased their visits to both −N treatments. There was a significant effect of nectar level ($G = 10.8$, df = 2, $p < 0.005$) but not of pollen level ($G = 1.1$). In 1984, therefore, *Bombus*, in the absence of *Vespula*, behaved qualitatively similarly to the way *Vespula* behaved the previous season.

Discussion

Previous work on *Aralia hispida* suggests that most of the bumble bees were traplining, and that the observed responses to the experimental treatments were due to individual foragers changing the frequency of their visits to particular stations (Thomson et al. 1987). However, no individuals were marked in the present experiment, so the observed responses are most conservatively interpreted as preferences of the *Bombus* fauna as a whole, and I use the term "preference" in this sense.

TABLE 1. Numbers of visits by *Bombus* and two categories of *Vespula* (see text) to semi-artificial inflorescences of *Aralia hispida* in which nectar and pollen levels were independently manipulated

	−P−N	+P−N	−P+N	+P+N	Total
1983					
Pre-experimental (13 July, 8 h)					
Bombus	95	132	194	108	529
Yellowjackets	91	115	58	99	363
Hornets	9	7	5	11	32
Total	195	254	257	218	924
Experimental (14 July, 4.5 h)					
Bombus	71	109	118	101	399
Yellowjackets	27	40	70	67	204
Hornets	6	7	3	7	23
Total	104	156	191	175	626
1984					
Pre-experimental (21 July, 2.25 h)					
Bombus only	90	69	81	80	320
Experimental (22 July, 1.0 h)					
Bombus only	38	21	56	54	169

NOTE: Data are pooled for the two stations of each of the four treatments. The total number of hours that each station was observed are given.

TABLE 2. Responses, in terms of visitation, to the establishment of the experimental conditions

	−P−N	+P−N	−P+N	+P+N
1983				
Bombus	0.989	1.092	0.807	1.240
Yellowjackets	0.520	0.613	2.145	1.215
Total	0.787	0.905	1.097	1.186
1984				
Bombus	0.801	0.574	1.308	1.280

NOTE: Values are given as the fraction of visits to the two stations of each treatment during the experimental period divided by the equivalent fraction for the pre-experimental period; thus, a value greater than unity indicates an increase in relative visits.

Given that yellowjackets were observed to patrol the nectar-enriched stations and attack approaching bees, the best interpretation of these data is that *Bombus* truly prefer nectar enrichment to pollen "enrichment," at least at the levels supplied in this experiment. (Because these levels were arbitrary, the results imply nothing about pollen versus nectar preferences in general.) The 1984 data showed that *Bombus*, by themselves, located the nectar-enriched stations and paid more visits to them. In 1983, however, the *Vespula* showed a similar preference for nectar enrichment, located those stations, and prevented the *Bombus* from displaying the preferences that they presumably would have displayed in isolation. However, the monopolization of the nectar-enriched stations by the *Vespula* did not simply result in the *Bombus* being relegated to the nectar-unenriched stations. Had that been the case, the *Bombus* would have displayed a significant nectar-level effect, opposite in direction from that of the *Vespula*. Instead, the *Bombus* displayed a different kind of selectivity, responding to pollen level instead. This suggests a hierarchy of preferences: if nectar enrichment was available, that preference overrode the pollen preference; if access to nectar enrichment became more difficult, the pollen preference emerged (Table 2).

This result points up the probable involvement of exploitative competition by *Vespula*, along with the more visible interference effects. Assuming that the wasps, which feed on sugar but not pollen, defended both the +P+N and the −P+N treatments with equal vigor, two extreme cases can be proposed to explain the displacement of the bees. The *Vespula* may have removed only trivial amounts of nectar, but put up such a strong defense that the bees would only tolerate the attacks if they could gain a pollen reward as well as the nectar. In this case, active interference is the dominant mode of competition. On the other hand, the bees may have been oblivious to the attacks, but the wasps may have drained all the nectar from both treatments, so that the pollen in the +P+N treatment provided the only profit for the bees. In this case, exploitative competition dominates. Presumably, the real situation lies between these extremes, but separating the two types of competition would require precise data on reward-level depression during the experiment (see Gill et al. 1980).

Upon encountering a nectar-rich plant of *Aralia hispida*, bumble bees typically work very systematically, feeding from all the flowers and then searching for other plants in the immediate vicinity (Thomson et al. 1982; Thomson et al. 1987; see Pyke 1978; Heinrich 1979; Morse 1980). Thus, in many cases, the only bees to experience a nectar "bonanza" would have been the first bees to visit a station after the half-hourly refillings. This implies that most of the increase in visitation in the preferred treatments may be attributable to a small number of frequently returning insects.

This study suggests some cautions for future work, especially field experiments on flower choices by pollinators. First, the ability of bumble bees and wasps to learn the specific localities of especially rewarding plants suggests caution in applying foraging models that assume that incoming pollinators are ignorant of a plant's probable reward content (see Thomson et al. 1982). Other pollinators are also apparently capable of remembering the locations of specific plants, and traplining hermit hummingbirds (*Phaethornis*) show a refined ability to adjust their visitation rate to the nectar-reward rates of artificial feeders (Gill 1988).

Second, the significant heterogeneity in visitation rates to uniform inflorescences shows patchiness in pollinator activity within a stand. In such circumstances, the appropriate null hypothesis for a feeding preference experiment may not be one of uniform visits to all stations, but one of homogeneity with pre-experimental base-line variation.

Third, the possibility of aggressive interactions among pollinators may complicate the interpretation of "pollinator preferences" in field experiments. *Vespula* are well known as active, aggressive defenders of feeding sites (Kalmus 1954; Parrish 1984), as are trigonid stingless bees (Johnson and Hubbell 1974) and many flower-feeding birds (e.g., Gill and Wolf 1975; Carpenter and MacMillen 1976; Kodric-Brown and Brown 1978). Other interactions may be less subtle: bumble bees very seldom attack each other or engage in overt aggression while foraging (Inouye 1978; personal observation), yet Morse (1977) showed that some displacements do occur in nature, and Brian (1957) elicited aggressive interspecific behavior on artificial flowers. In the present case, my 1983 data have described not the "preferences" of bumble bees, but rather what the bees do when they are prevented from demonstrating their preferences.

Fourth, the sharp distinction between the 1983 and 1984 experiments underscores the danger of drawing conclusions from a single field site or a single season. The *Vespula* densities at the experimental site in 1983 were the highest I have seen in seven seasons of fieldwork on *A. hispida* in Maine and New Brunswick. In both 1983 and 1984, *Bombus* densities on *Aralia hispida* were comparable to those of each year since 1979, but in 1985 there was a nearly complete local absence of *Bombus*, probably because of rain during the period of nest establishment. Large yearly fluctuations of bee (Inouye 1976) and other pollinator populations, and spatial patchiness of colonial species, must be considered natural hazards in the study of insect pollination systems that can affect both quantitative and qualitative aspects.

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