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Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency

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Summary. In field experiments, we mapped the regular foraging routes (traplines) of marked bumble bees visiting *Aralia hispida*. When other bees were removed to create localized "competitive vacuums", the marked bees shifted their feeding activity toward the removal areas. Bees foraging in these competitive vacuums probed more flowers per inflorescence than control bees. One bee's foraging was studied intensively before and after its local competitors were removed. Compared to four nestmates foraging elsewhere, the focal bee's trip times were shorter ($p<0.005$) and its food collection rate was marginally higher ($P=0.064$) during the removal, although all the bees foraged similarly before the removal. These observations indicate that traplining bumble bees opportunistically modify their use of space in response to the activities of other bees in a highly competitive environment.

Key words: *Aralia* – *Bombus* – Competition – Energy budget foraging – Niche shift – Trapline

Ecological studies of competition often concentrate on ultimate effects such as population dynamics or resource use patterns (summarized by Schoener 1983). The consequences of competition for the time and energy budgets of marked individual animals are seldom investigated, although it must be through such proximate consequences that ultimate effects are produced. There are few proximate studies because few animals are well-suited for field competition experiments that require simultaneous manipulation of density, complete observation of foraging behavior, and complete quantification of foraging success. Bumble bees (Hymenoptera, Apidae, *Bombus*) are an exception.

Worker bumble bees often confine their feeding to small areas and may "trapline", or repeatedly visit, certain subareas in a predictable sequence within their feeding areas (Manning 1956, Heinrich 1976a, Thomson et al. 1982, Corbet et al. 1984). When feeding from *Aralia hispida* Vent. (Araliaceae), they develop traplines of specific favored flowering shoots, and they revisit these many-flowered shoots several times during a foraging trip. Individual workers use the same foraging area over at least several days, but trapline structure changes gradually through additions and deletions of shoots. Thomson et al. (1982) provided maps of typical traplines, showing these day-to-day changes.

Although statistical evaluation of the degree of traplining is difficult, in practice it soon becomes apparent to an observer whether a marked bee is repeatedly visiting certain shoots in sequence. For example, our most closely observed bee, Yellow (see below), consistently flew directly from the hive to a clump of several shoots in the far corner of the grid, approximately 35 m from the hive, to begin foraging. From this point, she would make several regular circuits spanning an area of about 10 × 15 m, visiting major clumps of flowers and larger isolated shoots in a highly, but not perfectly, repeatable sequence. She typically concluded each bout by flying to the top of a particular 3 m aspen sapling within her foraging area to groom before flying to the hive. If an observer familiar with a bee's trapline loses sight of the bee, he can usually relocate the bee by moving to the next stop on the trapline.

We exploited the foraging patterns of bumble bees on *A. hispida* in designing two experiments to determine (1) whether these bees live in a competitive environment, and (2) how any observed competition affects a bee's foraging behavior and efficiency. Although intensive studies of individuals necessarily entail small sample sizes, the unique mechanistic insights obtainable may be worth the sacrifice (cf. Corbet et al. 1984). Our results provide the first demonstrated link between patterns of use of space by worker bees and the economy of the hive.

Methods

We conducted field experiments during July 1983 and 1984, in recently logged sites near Wesley, Maine (44° 52′ N; 67° 33′ W), where *A. hispida* was primarily visited by *Bombus ternarius*, *B. vagans*, *B. terricola* and *B. sandersoni*. *Bombus vagans* and *B. sandersoni* are too similar in appearance to distinguish in the field, and we treated both taxa as "*vagans*-type" (see Thomson et al. 1982). Observations over several years suggest that B. ternarius and "*vagans*-type" workers typically trapline, as described above; whether *B. terricola* traplines is uncertain.

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Aralia hispida forms especially dense flowering stands in logged areas where the soil has been scarified. Rhizomatous spreading produces clonal clumps of various size that bear numerous umbels of small greenish-white flowers. Plants are andromonoecious and highly dichogamous; a large plant typically passes through three cycles of sexual alternation as three orders of umbels each pass through a synchronized staminate, then pistillate, phase. Because this protandrous blooming behavior is fairly synchronized within clones, bees experience a stand of *A. hispida* as a slowly shifting mosaic of patches of male- and female-phase flowers. Both sex phases produce nectar, but only male-phase flowers offer pollen; bees typically collect both nectar and pollen. Thomson and Barrett (1981) gave further details on flowering in *A. hispida.*

The 1984 study site was an open rectangle, bordered by young aspen (*Populus tremuloides* and *P. grandidentata*) thickets on three sides and a logging road on the fourth. We laid out a 20 × 44 m grid of 2 × 2 m squares, filling this area. On three days during our experiments, we counted the numbers of open male- and female-phase flowers in each grid square. The 1983 site was a 30 × 30 m grid in which we mapped the locations of all flowering shoots in the central 10 × 10 square.

In both years, we netted foraging bumble bees, marked them between the wing bases with unique color combinations of Floquil hobby paint, and released them immediately. We applied the paint through the net while holding a bee immobilized against the mesh, thus minimizing our handling of the bees. Many marked bees returned to forage in the plots.

Foraging area experiments – 1983 and 1984

The 1984 experiment explicitly examined whether sharing *A. hispida* plants with many other bees affects the spatial distribution of a bee's foraging effort. After paint-marking many individual bees and observing them for several days, we chose 4 *B. ternarius* workers with stable foraging areas as experimental subjects. On 17 July 1984, observers followed each bee as continuously as possible from 0900 until 1800, tape recording the time spent in each grid square and the number of umbels "accepted" or "rejected" (a measure of foraging success: see below). At 1250, we began removing bees other than our experimental bees from one quarter of the grid (Figs. 1 and 3). We removed 18 *Bombus* during the first 30 min, and 31 more during the remainder of the afternoon.

We performed similar experiments as pilot studies in 1983. Because the 1984 experiments were more carefully performed, and because the results were similar, we cite only one 1983 experiment here. It provides greater detail on the response of a single intensively-studied *Bombus ternarius* worker ("Red"). On 12 July after observing Red working a stable trapline for several days, we recorded the number of visits she made to each shoot in the mapped center of our square plot. After accumulating data from several foraging trips, we removed other *Bombus* from the central area, while continuing to observe Red as continuously as possible. Beginning at ~1300, we removed bees, storing them alive in an ice chest. We continued observing Red for the next two days; at ~1500 on 13 July, we marked the captured bees and released them.

During our 1984 experiments observers classified all umbel visits into one of three categories: (a) *accepted,* (b) *rejected,* and (c) *ambiguous.* A rejection consisted of a bee probing one or two flowers and then leaving the plant; during an acceptance the bee probed all open flowers in a systematic fashion and then visited nearby umbels on the same plant. Rejections could not be distinguished from acceptances on umbels with only one or two open flowers, but most umbels had enough flowers that acceptances and rejections were clearly separable. *Ambiguous* observations were not included in the analysis.

From previous work (Thomson et al. 1982) we suspected that a bee usually rejects an umbel that has been recently drained of nectar. To test this expectation that acceptances and rejections reflect nectar stocks in flowers, one observer followed bees on the grid throughout the experiment on 17 July. The observer sampled nectar from unvisited flowers on accepted and rejected inflorescences, using the following protocol. If a bee visited one or two flowers on an umbel and then left, five unvisited flowers were sampled. If a bee visited all flowers on two successive umbels of a ramet and then moved to a third umbel and started feeding, she was shooed away and five unvisited flowers on the third umbel were sampled. Because nectar volumes were too small for the standard capillary tube/refractometer method of estimating volume and concentration, we used filter paper wicks to extract the nectar from each flower. The wicks were air-dried and the sugars were later dissolved and quantified colorimetrically (McKenna and Thomson, in prep.). The five flowers from each umbel were pooled for analysis. Unvisited flowers from accepted inflorescences contained significantly more sugar ($\bar{x}=10.6$ μg; $n=12$ inflorescences) than unvisited flowers on rejected inflorescences ($\bar{x}=3.2$ μg; $n=11$; $U_s=121$; $P<0.001$, Mann-Whitney *U*-test).

To minimize the effects of different observers using different criteria in scoring rejections, a particular observer was assigned to each bee. Thus, all data for a particular bee should be consistent and we do not compare rejection rates between bees. At intervals throughout the day, the rejection rates of numerous unmarked bees were recorded at a control stand of *A. hispida* 250 m from the grid. Approximately 4 umbel visits were scored for each of at least 25 bees per sample period in the control stand.

Food collection rate experiment – 1984

Prior to this experiment, we marked the workers of a captive *Bombus affinis* colony that we had established in a nestbox, and set the colony out near a corner of the grid. Several marked workers established traplines within the grid; several other individuals fed on *Aralia hispida* elsewhere (based on microscopic analysis of pollen loads). The nestbox was fitted with a special entrance tube that allowed us to catch incoming or outgoing bees in vials for weighing. We used a 6V dry cell battery to power an Ainsworth analytical balance in the field (the only electrical part is a light bulb). We would weigh a returning forager with her nectar and pollen loads, then remove the corbicular pollen pellets, reweigh the bee (now with nectar only), allow her to enter the hive and deposit her nectar load in a honeypot, and then weigh her again as she left for another foraging trip. Departing weights were quite consistent for individual bees; this probably indicates that they left the hive "empty".

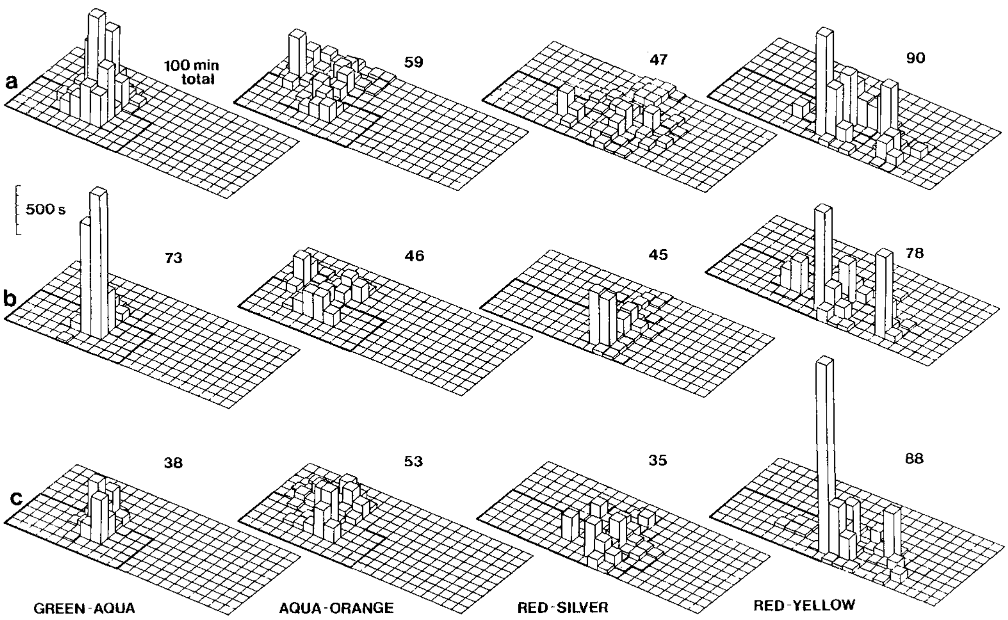

Fig. 1 A–C. Space-time budgets of 4 color-marked *Bombus ternarius* workers on 17 July 1984. The 20 × 44 m grid contained a discrete population of plants. Heights of the vertical bars indicate the time a bee spent in each 2 × 2 m section while under observation. Row **A** shows preremoval data (0900–1250); rows **B** and **C** show early (1300–1530) and late (1530–1800) postremoval data. The heavy outline indicates the removal area. Total observation time is given for each period, which included multiple trips from the hive

We used this system to examine the effect of competition on the rate at which foragers supplied food to the hive. On 13 July, we measured trip times and load weights for Yellow and for four control bees that fed on *Aralia hispida* away from the grid. At 1300 we began removing bees from Yellow's portion of the grid, taking out 36 during the afternoon. We kept Yellow under continuous observation, in and out of the nest, and recorded umbel acceptance/rejection data as previously described.

Results and analysis

Foraging areas experiments

After the removal of other bees from one quarter of the grid, the observers of all four experimental bees reported that their animals seemed to be moving into the removal area more often than before, spending more time there, or both. Figure 1 shows the time allocated to each grid section by each bee during preremoval (0900–1250), early postremoval (1300–1530), and late postremoval (1530–1800) periods. Although all four bees maintained most of their original foraging areas through the day, each shifted its activity within that area toward the removal area during early afternoon. All bees abandoned some 2 × 2 m squares that they had visited in the morning. These squares were always distal to the removal area. In late afternoon, each bee reverted slightly to its morning position.

This apparent change in the bees' allocation of feeding time to the removal area was examined statistically by considering observations as a repeated measures design with two within-subjects factors, Period (before or after the removal) and Location (inside or outside the removal area). Given this design, a change in the use of space after the removal should be reflected in a significant interaction between Period and Location. The analysis of variance we conducted on this design considered the proportion of each bee's total observed foraging time spent in the two locations during pre- and post-removal. Because these proportions sum to 1 and are not independent of each other, we conducted 1,000 analyses of variance on random data with the same dependencies as the original observations. The observed test statistic for the interaction between Period (P) and Location (L) ($F' = MS_{P \times L}/MS_{P \times L \times B} = 19.04$, where B is the effect associated with each bee) was larger than all but 20 of the randomization tests (i.e., $P \sim 0.02$). We conclude that the removal of competing bees caused a significant shift in these bees' use of their foraging areas. Specifically, while bees spent equivalent proportions of their total observed foraging time outside ($\bar{x} \pm SE = 0.194 \pm 0.025$) and inside ($0.198 \pm 0.044$) the removal area before the removal, they spent more time inside the removal area after experimental manipulation (outside $= 0.214 \pm 0.059$; inside $= 0.393 \pm 0.044$).

The above analysis is rather coarse in that it implicitly considers the removal area to be homogeneous. In fact, nectar and pollen availabilities, as judged by counts of open flowers, were extremely patchy in the grid as a whole (Fig. 2), and in the removal area in particular (Fig. 3). Rather than anticipating bees to simply move into the removal area in general, a more specific expectation is that they would move toward especially flower-rich areas within the removal area. There were two especially dense flower concentrations within the area, denoted in Fig. 3 as "A" and "B". Area A was a prominent mound, covered by a profusely-flowering patch of *Aralia*. During the removal experiment, most flowers at A were in female phase (Fig. 2). Flowers were less dense at concentration B, but a greater proportion of them were in the more attractive (Thomson et al. 1982) male phase (Fig. 2). Figure 3 also gives the mean positions (i.e., the "centers of gravity" of the space-time budgets of Fig. 1) of each bee before and during the removal. The shift in position of each bee (from pre- to postremoval periods) is oriented toward the nearest concentration of flowers in the removal area within ±15°. Under a hypothesis of random movement direction, it would be extremely unlikely for four bees to display this degree of directionality ($P < 0.0001$).

The 1983 data (Fig. 4) show the gradual nature of bee Red's shift toward the removal area. She sampled previously unvisited shoots on each trip, and then returned to them on the following trip. After the removed bees were

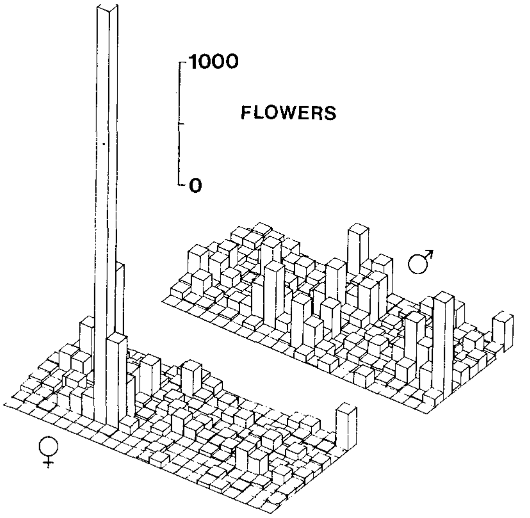

Fig. 2. Flower census data from 18 July 1984. Flower densities during the experiment on 17 July were very similar. The upper panel gives the number of open staminate-phase ("male") flowers in each 2 x 2 m grid square; the lower panel enumerates pistillate-phase flowers. In addition to pollen, male-phase flowers provided more nectar than female-phase flowers

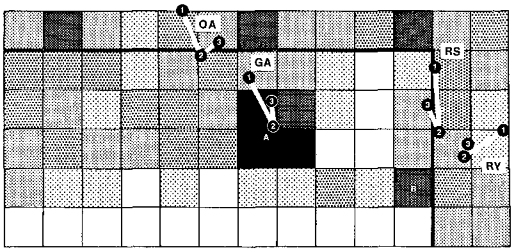

Fig. 3. Detail of part of the grid from Figs. 1 and 2 showing the removal area (heavy outline). The mean positions of the bees for the three time periods are given by the sequentially-numbered points connected by vectors of change. Flower density classes in 2 x 2 m grid squares are indicated by stippling: no stippling = 0 flowers; progressively darker stippling = 1–49, 50–149, 150–349, 350–1000; black = >1000 flowers. *A* and *B* denote the two local peaks of flower abundance toward which the bees apparently shifted

released in the afternoon of 13 July, several of them resumed foraging in the area from which they had been removed. By next morning, Red's foraging area had receded toward its preremoval location.

The foraging shifts observed in all removal experiments were greater in magnitude and developed faster than spontaneous shifts (described earlier) that we have observed for unmanipulated bees. Based on many observations in 1979–1984, natural shifts were seldom greater than those illustrated by Thomson et al. (1982). Such shifts involve deletion or addition of a few plants per day, so that the "center of gravity" hardly moves at all.

In 1984, the bees that shifted toward the removal area appeared to improve their foraging success relative to control bees that were unaffected by the experiment. Figure 5 summarizes the temporal pattern of the frequency of umbel rejections for both sets of bees. Analysis of the 3-way interaction in a 2 x 2 x 2 contingency table [(control vs. experimental bees) x (preremoval vs. postremoval) x (accepted vs. rejected umbels)], indicates that the pattern of umbel rejec-

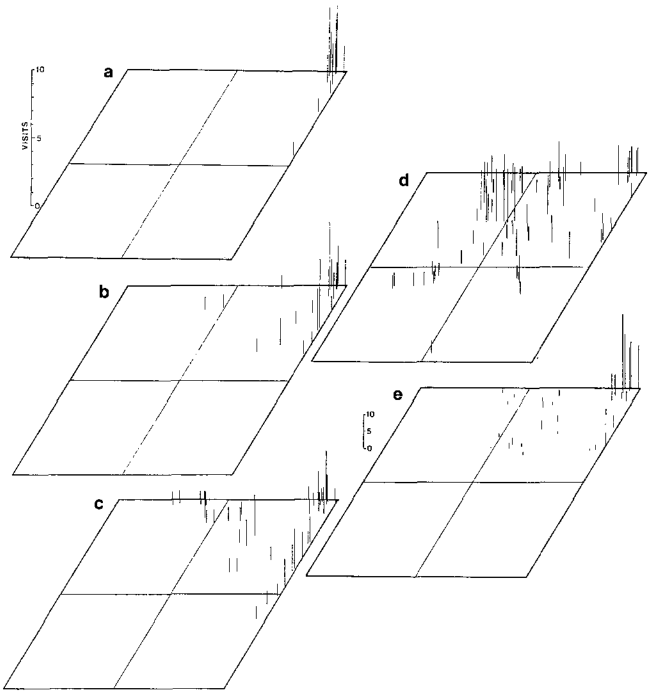

Fig. 4a–e. Pattern of plant visits within a mapped 10 x 10 m area by a *Bombus ternarius* worker ("Red") during a competition experiment (12–14 July 1983). The vertical bars show the number of visits recorded at a plant during an observation period. Panel **a** gives the visitation pattern observed before the experiment (12 July, 1100–1300, $n = 27$ visits); Red had established a foraging trapline that included only a few plants in the upper right corner of the mapped area. Panels **b–d** depict successive observation periods after removal of other bees (see text) from the mapped area (**b**: 12 July, 1300–1500, $n = 37$; **c**: 12 July, 1500–1700, $n = 51$; **d**: 13 July, 0800–1200, $n = 129$). Panel **e** (14 July, 0800–1200, $n = 139$) shows a partial return to the preexperimental pattern after the release of the removed bees. Note the different vertical scale in panel **e**

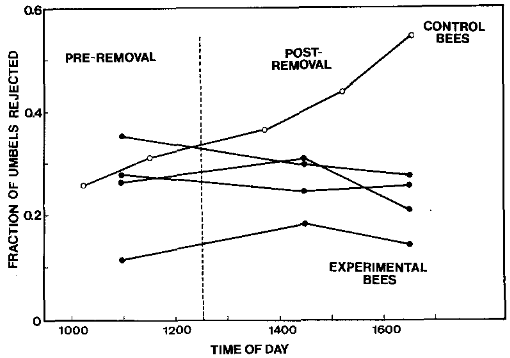

Fig. 5. Umbel rejection rates through the day for control (open circles) and experimental bees (i.e., those affected by the removal experiment; closed circles) on 17 July 1984. For the experimental bees, the overall rejection fraction for each of the three observation periods (0900–1250, 1300–1530, and 1530–1800) is plotted at the midpoint of the interval. Control bees were scored for 5 periods of 25 min each; again, rejection fractions are plotted at the midpoints of each observation period. Sample sizes for controls range from 96 to 119 umbels (no more than 4 umbel visits scored per bee). Sample sizes for experimental bees range from 274 to 836 umbel visits

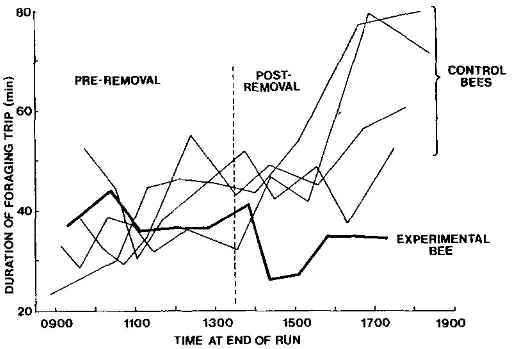

Fig. 6. The durations of foraging trips of 5 *Bombus affinis* workers foraging from a nestbox on 13 July. The experimental bee ("Yellow") foraged in the mapped grid, from which competing bees were removed at 1330. The control bees fed on *Aralia hispida* elsewhere

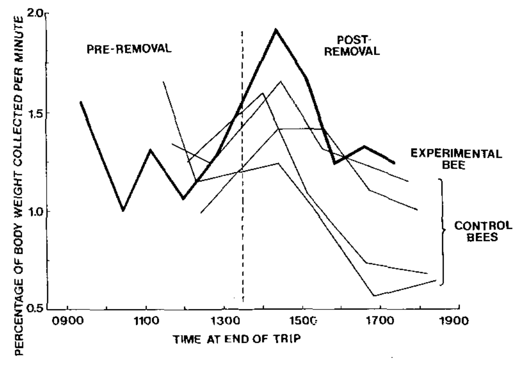

Fig. 7. Foraging efficiency [(total weight of pollen and nectar returned to the hive) (live weight of the bee)$^{-1}$ (duration of foraging trip)$^{-1}$] of the bees shown in Fig. 3

tion by experimental bees differed significantly from that of control bees ($G = 68.3$, 1 *d.f.*, $P < 0.001$). Resources in the control areas become more depleted, relative to demand, later in the day. The lower rejection rates suggest that experimental bees shifted their activity toward the removal area because flowers there contained more nectar than flowers in the more thoroughly exploited non-removal portion of the grid.

Food collection rate experiment

Four marked bees from the *Bombus affinis* colony established regular traplines on the grid; however, as we prepared for the 13 July experiment, one of these disappeared, one (probably parasitized) began foraging extremely sluggishly, and one appeared to have incurred a leg injury that prevented her from collecting pollen. We therefore concentrated on the remaining healthy bee, "Yellow". For several days, Yellow had maintained a well-defined trapline (see introduction), and she was particularly easy to track.

Figure 6 compares the temporal pattern of Yellow's foraging trip times to those of four other marked bees from the same hive who were feeding on *Aralia hispida* but not on the experimental grid. Yellow maintained roughly constant trip times through the day, whereas the control bees took longer trips during the afternoon depression of floral rewards. We assessed statistical significance of these effects by breaking the observation period into intervals, using midpoints of Yellow's foraging trips as breakpoints. All data (trip times or load weights) for control bees were compared to the corresponding value for Yellow for the interval in which they fell, and were analyzed as 2 × 2 contingency tables [(less than Yellow vs. greater than Yellow) × (preremoval vs. postremoval)]. The interaction is highly significant ($G = 9.1$, 1 *d.f.*, $P < 0.005$, Yates' correction).

Figure 7 shows the temporal pattern of food collection efficiency for Yellow and the same control bees. The pattern is similar to that of trip length in that control bees brought back less food per unit time later in the day, whereas Yellow continued to forage efficiently. We tested these patterns in the same way as the trip time data. Unfortunately, we obtained only 6 preremoval data points for control bees and the test of interaction between load weight and experimental period falls slightly short of conventional statistical significance ($P = 0.067$; Fisher's exact test).

The above analyses compare the control bees to the experimental bee over a series of time periods to correct for the daily trends apparent in Figs. 6 and 7. An alternative approach, dividing the data into pre- and post-removal periods only, sacrifices some knowledge about temporal trends but allows a specific test of individual differences among all bees. We conducted separate Kruskal-Wallis tests between the five bees for the pre- and post-removal periods, followed by planned contrasts among the control bees and between the control bees as a group and yellow (Marascuilo and McSweeney 1977). For trip durations (Fig. 6), there was no difference among the bees during the pre-removal period ($X^2 = 3.97$, 4 *d.f.*, $P > 0.1$), but significant variation after the removal ($X^2 = 12.83$, 4 *d.f.*, $P < 0.025$). The post-removal contrast among the control bees was not significant ($X^2 = 1.52$, 3 *d.f.*, $P > 0.5$), but that between yellow and the control bees was highly significant ($X^2 = 11.32$, 1 *d.f.*, $P < 0.001$). Thus, the control bees behaved homogeneously during the experiment, but Yellow's trip durations differed from theirs. Similar tests of food collection rate indicated no significant variation among the bees in either period. Inspection of Fig. 7 suggests that this is because during late afternoon Yellow collected nectar and pollen slower than control bees had early in the afternoon, even though Yellow's rates were typically higher than any control bees during any specific portion of the afternoon.

All of these analyses treat data from separate trips as independent, and it is unfortunate that only one experimental bee could be monitored. Because we had a clear a priori prediction that the single experimental bee would diverge from the other four, we can still attach a probability of $0.5^5 = 0.03$ to the pattern observed for trip durations. Thus, although Yellow may have deviated from the other 4 bees by chance rather than because of our experiment, it is unlikely that this is the case.

During the preremoval period, Yellow rejected 346 of 1055 umbels scored (32.8%). Afterwards, she rejected a significantly smaller fraction (260 of 945 (27.5%); 2 × 2 contingency table, $G = 6.36$ (Yates' correction), $P < 0.025$). Although we have no data on control bees during this experiment, comparison of Yellow's data to the rejection rate patterns of the control bees on 17 July (Fig. 5) suggests that the removal had a strong effect on Yellow's rejection rate, bolstering our contention that the patterns in Figs. 6 and 7 are indeed results of the removal treatment.

Discussion

Although numerous studies of competition in nectar- and pollen-feeders have been essentially observational in nature (e.g., Brian 1957; Heinrich 1976b; Ranta et al. 1981; Pyke 1982, Corbet et al. 1984), there have been several field experiments in which densities have been altered. There are two possible types of responses to competition experiments involving removal; the remaining individuals can change what they have been doing, or they can become more successful at it. Both responses have been taken as evidence of competition, although they are not strictly equivalent (Thomson 1980).

To date, competition experiments on nectarivores have generally looked for short-term, behavioral niche shifts: for example, Inouye (1978) showed that one species of *Bombus* switched preferred flower species after removal of a competing *Bombus* species. Laverty and Plowright (1985) outlined a complex set of density-related shifts in resource use by hummingbirds and bumble bees visiting *Impatiens biflora*. Morse (1977) suggested that interference competition from a larger *Bombus* species forced a smaller species to forage more distally on *Solidago* inflorescences than when it foraged alone.

Our experiments differ from previous studies in that we have simultaneously demonstrated changes in foraging area and foraging success (via rejection rates, trip times, and load weights). Our results are consistent with those of other studies: competition for floral resources is important to bumble bees in some, perhaps most, situations. In our particular situation, the primary mode of competition seems to be exploitation simply because bees encounter recently emptied flowers far more often than they encounter the animals that emptied them. Since nectar and pollen are the only resources needed by a *Bombus* colony for reproduction, decreased foraging efficiency of individual workers in such a competitive environment will directly affect colony output.

The late-afternoon reversions shown by the 4 bees on 17 July deserve comment. Continuous removal of bees through the afternoon may have eventually depressed bee densities throughout the grid, so that the experimental bees found good foraging everywhere. The first bees to be removed would be those that maintained foraging areas within the removal area; those taken out later may have strayed in after originally feeding elsewhere. Even if a removal area is sharply defined, it will not produce a sharply bounded area of low competition, but rather a directional gradient. Nonetheless, the bees show a refined ability to locate and fill the sorts of competitive vacuums that occur naturally as plants start and stop flowering, and as bees die.

As the 1983 data from bee Red show most clearly, this ability stems from a tendency to sample new shoots and to return systematically to rewarding inflorescences. Most models of bee foraging (e.g., Pyke 1978; reviewed by Waddington 1983, Plowright and Laverty 1984) do not include the spatial memory that these flexibly traplining workers seem to display. A trapline is inherently conservative, and seems best suited for efficient exploitation of resources that are patchy in space (Thomson et al. 1982, Waddington 1983); the opportunistic way that these bees shift their traplines also allows them to adjust to patchiness in time.

Consequently, we expect that the negative effects of exploitative competition for food will be evenly spread across all bees feeding on *Aralia hispida*. Aside from individual differences in flower handling ability, one individual could gain a consistent competitive advantage over others by discovering underused plants more quickly. However, more sampling of new shoots may necessitate less complete exploitation of shoots already included in the trapline.

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