

# DIFFERENCES IN HONEY BEE AND BUMBLE BEE FORAGING BEHAVIOR

## INTRODUCTION

Optimal foraging theory is one of several cost/benefit analysis used to predict or explain animal behavior. Optimal foraging theory predicts that animals will behave in such a manner as to maximize their energy intake (benefit) with the minimal output of energy (cost). Foraging by bees provides an area where optimal foraging can be tested. When bees forage they are faced with much stimuli in a short period of time (Chittka et al., in press). Depending on the diversity of flowers in a particular area, bees are faced with stimuli of color, smell, size, flower complexity and distance between flowers. If optimal foraging theory holds, bees should choose flowers whose cost of obtaining nectar is less than the energy gain from the nectar. Costs may include energy used in searching for the food source and the time it takes to manipulate a food source.

Four experiments were conducted on bumble bees (*Bombus spp*) and honey bees (*Apis spp*) in the field. Two of the experiments, floral advertising and nectar rewards, were designed to determine whether the bees do make a choice on which flowers they forage. This is determined by seeing if there is a preference shown for the treated or untreated flowers. A third experiment on the effects of pheromones on bee behavior was also included. Although it does not have a direct impact on optimal foraging theory because the bees theoretically would be attracted to the pheromone for mating purposes and not making choices based on cost/benefit of foraging, it is included here as a matter of interest. The fourth experiment looks at the floral constancy of a bee to a particular flower species. The constancy experiment used here tests a bees preference between two species of goldenrod (*Solidago canadensis* and *Solidago rugosa*). The hypothesis

being tested is that bees do make active choices while foraging, and that bees will show a certain degree of constancy to minimize cost.

## MATERIALS AND METHODS

Four experiments were conducted in the field: flower constancy, floral advertising, nectar rewards and pheromone attraction. Data were collected over three years by students in Ecology and Behavioral Ecology labs at SUNY Stony Brook. Data for flower constancy were gathered in 1999 only. Data were grouped differently depending on the year. In 1997-1998, the number of landings of bees were counted, which included landings where probing occurred (visits) and landings where no probing occurred (rejects). In 1999 landings were separated into visits and rejects.

All experiments were carried out with an interview stick as described by Thomson (1981). For each experiment, a choice between two flowers was offered to an individual bee. An attempt was made to standardize the flowers in size and age so that the treatment would be the only difference between the two flower choices.

The flower constancy experiment was conducted at Weld Preserve in Nissequogue, NY in a field of mixed-species goldenrod. Primary species found in the field were *Solidago rugosa* and *Solidago canadensis*. These two species were used in the choice experiments.

All other experiments were carried out in an area near the Life Sciences building at Stony Brook with knapweed (*Centaurea maculosa*). For the floral advertising experiment, we removed the ray florets from one flower while leaving the other flower untouched. In the nectar reward experiment flowers were selected from a plant that had been screened off for several days. The second flower for the nectar rewards experiment was selected from flowers that the observer had seen drained by a bee. BeeScent, a honey bee pheromone, was used on one flower in the

pheromone experiment, with the other flower left untreated. Flowers were replaced after each visit.

## RESULTS

Data for floral advertising, nectar rewards and pheromone attraction were analyzed using a chi-squared goodness-of-fit test. The null hypothesis for each was that there would be no difference in which flower was selected, so there should be a 50:50 split of visits between each choice offering. Floral constancy was analyzed using 2x2 contingency tables to test independence. The null hypothesis is that the flower the bee flies to is independent of the flower the bee flies from.

Data were analyzed in three groups: 1997-1998 landings (visits + rejects), 1999 visits only, 1997-1999 landings (visits + rejects including 1999 rejects). Rejects for 1999 are not analyzed separately for floral advertising or nectar rewards because in almost all cases the expected numbers were  $< 3$ . Only in the pheromone attraction and flower constancy experiment are rejects analyzed separately due to a larger sample size for rejects. The 1999 rejects were not added to the 1999 visits data but were added in the 1997-1999 cumulative data. I kept rejects separate from the 1999 visits because they rejects can dilute the numbers (i.e., make it seem like there are more visits (probing) when some of them were rejects). Rejects were added to the cumulative data because previous years included them and there was no way to separate them out from the 1997-1998 data.

Table 1 shows the chi-squared values for the data for floral advertising, nectar rewards and pheromone attraction experiments. In the paragraphs below, the term preference is used to indicate that bees landed on one type of treatment more than another.

### *Floral Advertising*

In data from 1999, honey bees showed a significant preference for flowers with rays, while bumble bees showed no preference between the two flowers. In 1997-1998 honey bees show an even stronger preference for flowers with rays. Bumble bees also showed a significant preference for flowers with rays during 1999, but at a much lower level ( $P = .022103$ ) than honey bees. Figure 1 illustrates the cumulative 1997-1999 data, where we can see a significant difference between honey bee and bumble bee preference. Honey bees show a much stronger preference than bumble bees for flowers with rays.

#### *Nectar rewards*

Neither honey bees nor bumble bees showed preference for either enriched or drained flowers in the 1999 data. However, data from 1997-1998, and the cumulative data (Figure 2) do show a significant preference by both honey bees and bumble bees for enriched flowers. In this experiment, bumble bees showed a stronger preference for enriched flowers than honey bees, but both showed significant preferences.

#### *Pheromone attraction*

The pheromone data for 1999 rejects had sufficient numbers to analyze separately. All tests of the data (1999 visits, 1999 rejects, 1997-1998 landings and 1997-1999 visits and rejects) are significant for both honey bees and bumble bees. However, the manner in which they are significant is opposite to what is expected (Figure 3). The bees preferred the flowers with no pheromones rather than the treated flowers. The number of bumble bees observed in 1999 is quite small, but when looking at the cumulative data neither the honey bees nor the bumble bees showed a greater preference ( $P = 19.94$  and  $P = 19.84$  respectively).

Table 1. Analysis of data gathered over three years for floral advertising, nectar reward and pheromone attraction experiments.

(A) Floral advertising: choice between flowers with ray florets and flowers whose ray florets were removed.

	Rays	No rays	X <sup>2</sup>	P-value
<i>Honey bees</i>				
1997-1998 (visits + rejects)	99	44	21.15385	4.24 x 10 <sup>-6</sup>
1999 (visits only)	52	25	9.467532	0.002091
1997-1999 (visits + rejects)	153	71	30.01786	4.28 x 10 <sup>-8</sup>
<i>Bumble bees</i>				
1997-1998 (visits + rejects)	62	39	5.237624	.022103
1999 (visits only)	19	17	.111111	.738883
1997-1999 (visits + rejects)	83	58	4.4326241	.0352583

(B) Nectar rewards: choice between flowers enriched by screening off a plant for several days and flowers recently drained by bees.

	Enriched	Drained	X <sup>2</sup>	P-value
<i>Honey bees</i>				
1997-1998 (visits + rejects)	56	29	8.576471	0.003405
1999 (visits only)	26	18	1.454545	.2278
1997-1999 (visits + rejects)	83	53	6.617647	0.010097
<i>Bumble bees</i>				
1997-1998 (visits + rejects)	67	42	5.733945	0.01664
1999 (visits only)	23	13	2.777778	0.095581
1997-1999 (visits + rejects)	92	58	8.591549	.003377

(C) Pheromone attraction: choice between flowers treated with BeeScent, and untreated flowers.

	Pheromones	No Pheromones	X <sup>2</sup>	P-value
<i>Honey bees</i>				
1997-1998 (visits + rejects)	32	83	22.61739	1.98 x 10 <sup>-6</sup>
1999 (visits only)	2	46	40.33333	2.14 x 10 <sup>-10</sup>
1999 (rejects only)	34	2	28.44444	9.64 x 10 <sup>-8</sup>
1997-1999 (visits + rejects)	68	131	19.94472	7.97 x 10 <sup>-6</sup>
<i>Bumble bees</i>				
1997-1998 (visits + rejects)	25	72	22.7732	1.82 x 10 <sup>-6</sup>
1999 (visits only)	4	12	4	.0455
1999 (rejects only)	7	1	4.5	0.033895
1997-1999 (visits + rejects)	36	85	19.84298	8.41 x 10 <sup>-6</sup>

### Floral Constancy

Data were available from 1999 only and both visits and rejects were analyzed separately. Visits by honey bees did show a correlation between from and to flowers (P = 0.013525). Rejects for honey bees were not significant (P = 0.062942). With bumble bees there is not a correlation between from and to flowers for either visits or rejects (P = 0.05637 for visits and P = 0.808605 for rejects).

Analysis using Bateman's index as described by Waser (1986) did not seem to show a strong difference in constancy between honey bees (BI = 0.185) and bumble bees (BI = 0.162). In Bateman's index, the range is from -1 to +1. A rating of -1 is completely inconstant, 0 is random interactions and +1 is completely constant (Waser 1986). The Bateman's index for both honey bees and bumble bees is much closer to random than constant.

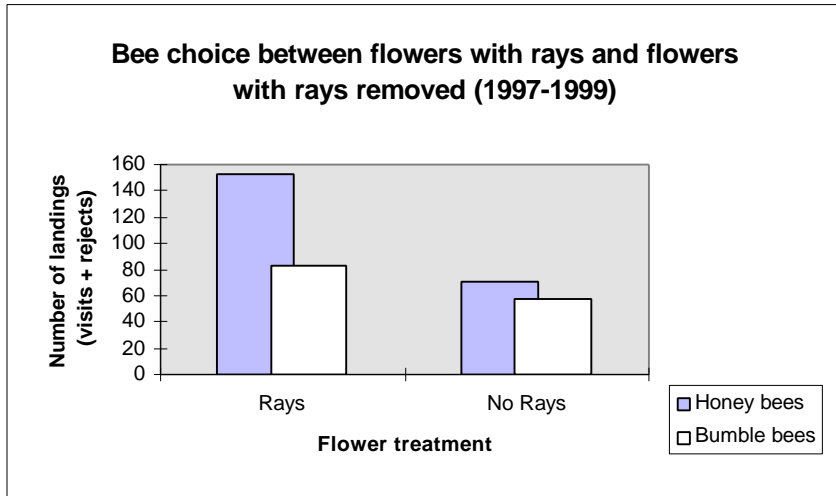


Figure 1. Differences in bee choice between flowers with ray florets and without ray florets.

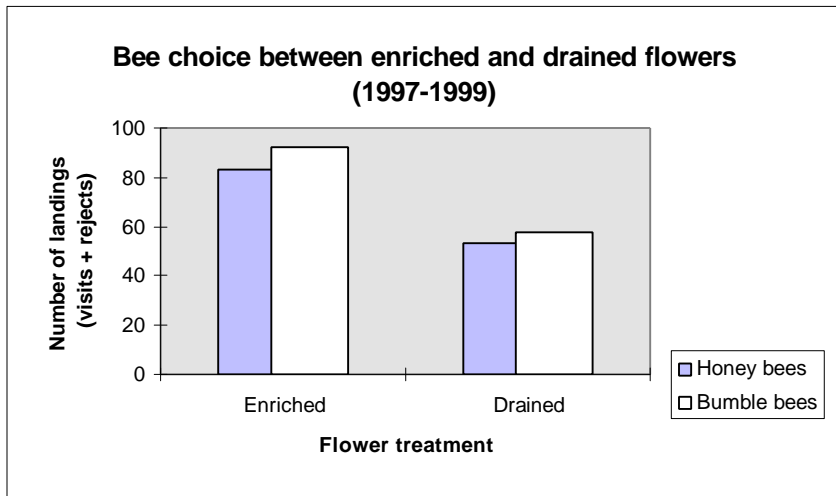


Figure 2. Differences in bee choice between enriched and drained flowers.

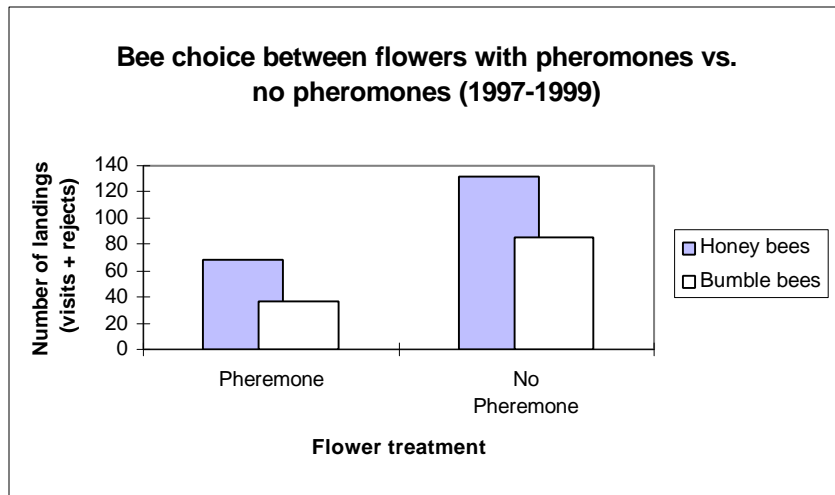


Figure 3. Differences in bee choice between flowers treated with pheromones and untreated flowers.

## DISCUSSION

Experiments on floral advertising and nectar rewards should indicate whether bees are able to make a choice as to which flower to forage on based on sensory cues from a distance. Many experiments have been done that show that bees do use visual and olfactory cues when foraging. Thomson (1981) found definite indications in bumble bees that choices were being made based on color of flower.

Visual cues were examined in the floral advertising experiment. The untreated flower was much more attractive to honey bees than the treated flower, where ray florets were removed. Because diameter was not controlled for (as it was in a similar experiment by Thomson et al., 1982) it is difficult to tell whether the honey bees were attracted to the ray florets or simply to the largest flower. Bumble bees showed a much lower preference for flowers with ray florets than honey bees. Thomson et al. (1982) found that diameter was not as important to bumble bees as the number of flowers within that diameter.

Experiments using nectar rewards can show whether a bee is able to sense the nectar from a distance. It is also possible to examine the behavior of the bee once the initial choice is made to see if reward level affects its next foraging choice. In the 1999 data, neither honey bees nor bumble bees showed a significant preference for the enriched flowers. One factor that may have contributed to the lack of significance in the 1999 data was the procedure for selecting the drained flowers. Because the drained flower was chosen by picking a flower that a bee just visited, it may still have had a substantial amount of nectar in it when picked. The 1997-98 and cumulative data do show preference for both the bumble bee and honey bee for enriched flowers, which may indicate that they can sense the presence of nectar from a distance. In our study bumble bees showed a slightly more significant preference than honey bees. Thomson et al. (1982), however, found no preference in bumble bees for enriched flowers.

It is difficult to apply the nectar experiment as conducted here to optimal foraging theory. If nectar cannot be sensed at a distance, then one would have to look at the behavior of the bee after it encountered the enriched or drained source. If a bee encounters an enriched flower, it would be most cost effective to probe a flower of the same species if located nearby. We did not collect sufficient data on second moves. Number of probes per flower were collected, but the data will not be analyzed here.

Floral constancy experiments are more helpful when considering optimal foraging theory. On the surface, floral constancy may be seen as sub-optimal, causing a bee to pass up flowers that may have valuable nectar rewards. The additional flight cost could only be made up for by increased rewards upon arrival. However, if one considers handling time, staying constant is the optimal foraging pattern. According to Waser (1986), bees passing up flowers that may be



rewarding are actually being more efficient even though they may have to travel farther because of reduced handling time.

To apply floral constancy to optimal foraging theory is not straight-forward, however. One problem is that individuals of a species have different preferences (Waser 1986), so it may be difficult to generalize constancy data to an entire species. Also, in looking at foraging costs it is necessary to look beyond simplistic handling time experiments and examine the learning process of bees to get a better understanding of their limitations (Chittka et al., in press). Chittka et al. (in press) reviewed many experiments and found that apparent reported limitations in learning or memory capacity in bees may be due to experimental design. They also suggested that it may not be a limit of the bees' capacity to learn per se that would increase the handling time, but the time it takes for a bee to retrieve the information from long term memory.

An additional complication is how to categorize inconstant moves. Should they be classified as "wrong" moves, which may hurt an individuals' fitness by increasing handling time per reward gained? Or should they be viewed as sampling (Chittka et al., in press) where a bee has a chance to increase its fitness because sampling may indicate that there are more rewarding species than the one they are currently constant to?

In our floral constancy experiments only honey bees showed significant floral constancy. They also visited many of the "wrong" species of flower (Figures 4 & 5). Bumble bee behavior showed inconstancy. However, in figure 5 honey bee and bumble bee movement from *S. canadensis* show similar behavior (slopes of the lines on graph are very similar).

The Weld Preserve field contained both species of goldenrod intermixed. Several previous experiments showed conflicting results as to a bees' behavior in mixed-species fields. A prediction made by Waser (1986) is that as diversity of flower morphology increases, we should

see an increase in constancy due to handling time problems. Waser found that constancy was higher in areas of higher floral diversity in both the bumble bees he studied, and data analyzed from honey bee observations by Bateman. Thomson (1981) observed that there was a higher degree of inconstancy when diversity of flower type is increased but Wilson and Stine (1996) found that bumble bees foraging in a mixed-species area did show a strong floral constancy, but that morphological differences in flower type were not a factor. *S. rugosa* and *S. canadensis* have the same color (to the human eye) and a similar arrangement of flowers on each inflorescence, although their color may be different to a bee (Chittka et al., in press) and the flower morphology may be different. Our study found that constancy was not high (see Bateman's index) in a mixed-species field for either honey bees or bumble bees, but the similarities between the two flower species may have made it easier to switch between them with no added cost.

If floral constancy is an appropriate measure of optimal foraging, then our experiment indicates that honey bees should do better as individuals than bumble bees. But what explains the difference in behavior between the two bee genus', and is one using a tactic that is superior, or just different from the other. Wilson and Stine (1996) attribute floral constancy to sensory cues that trigger a specific search image. Chittka et al., (in press) go much further in examining the learning and memory process in bees. Chittka et al., (in press) found that bees foraging in mixed-species areas had less constancy, and proposed that the bees could hold more than one flower image in their short term memory if given equal opportunity to learn both flower species. The honey bees in our study could have a stronger search image than bumble bees, which would make them more constant. Alternatively bumble bees could have better short term memories than honey bees. Bumble bees could also have found that a higher sampling rate (Chittka et al., in press) may be a more beneficial to them than a strong floral constancy pattern. Other factors not

tested here may be that bumble bees in the Weld Preserve had territories that encompassed more of the mixed-species areas than honey bees, giving them a greater opportunity to learn both species or that the energy costs of foraging are different enough between honey bees and bumble bees to promote differences in behavior.

The pheromone attraction experiment is outside the scope of the above discussion due to the reasons mentioned earlier, but does provide some unusual results. Although it would be expected to have some effect on honey bees but no effect on bumble bees, it in fact had a strong effect on both. However the effect was for the bee to prefer the untreated flowers. I can only speculate as to why this may have occurred. The pheromone may have been old, or improperly stored, so was no longer effective. If this were true we should see no preference for either flower by the bees. If when aging the pheromone lets off a smell that is distasteful it may have caused the reaction shown, which was avoidance and high rejection rate.

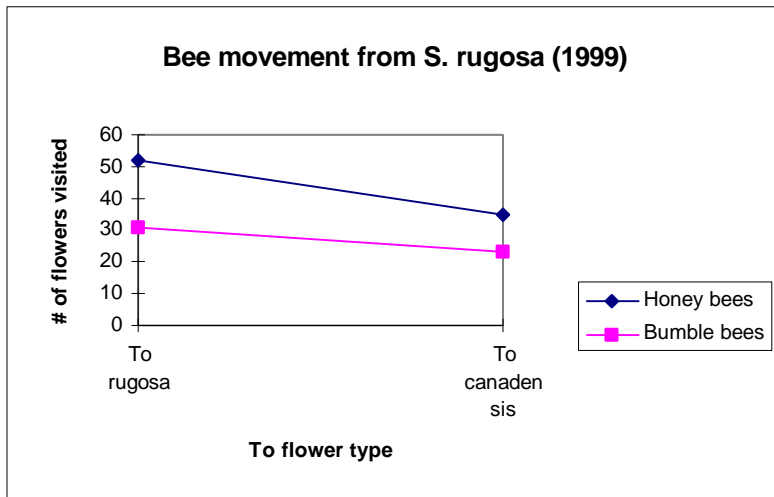


Figure 4. Movement of bees from *S. rugosa* to either *S. rugosa* or *S. canadensis*

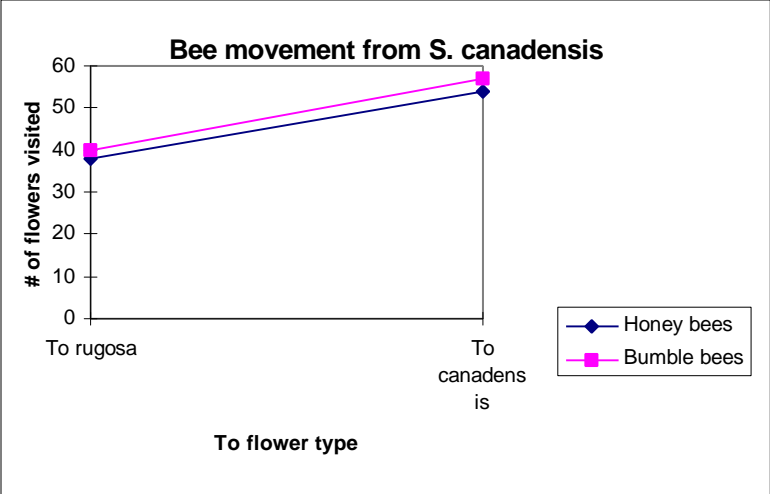


Figure 5. Movement of bees from *S. canadensis* to either *S. canadensis* or *S. rugosa*.

## LITERATURE CITED

- Chittka, L., J. D. Thomson, and N. M. Waser. 1999. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften*, in press.
- Thomson, J. D. 1981. Field measures of flower constancy in bumblebees. *Am. Midl. Nat.* 105:377-380.
- Thomson, J. D., W. P. Maddison and R. C. Plowright. 1982. Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54:326-336.
- Waser, N. M. 1986. Flower constancy: definition, cause, and measurement. *Am. Nat.* 127:593-603.
- Wilson, P and M. Stine. 1996. Floral constancy in bumble bees: handling efficiency or perceptual conditioning? *Oecologia* 106:493-499.