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Alison Tammany April 20, 2011

Intra- versus inter-colony competition in bumble bee foraging specificity

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

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1. The level of generalization or specialization of bumble bees affects their foraging behaviors and therefore plant pollination. Optimal foraging theory (OFT) predicts that increased competition among various bee species results in more specialization.
2. Bumble bees of the same species compete differently when competing with their same colony (intra-colony competition), versus different colonies (inter-colony competition). OFT predicts that intra-colony competition results in increased generalization. In contrast to this theory, I predicted that inter-colony competition would increase specialization of foraging behavior.
3. I tested the difference between inter- and intra-colony competition using two colonies of Bombus impatiens by running foraging experiments at high and low densities. Bumble bees either foraged with their own respective colony, or foraged along with bees from a different colony. I analyzed the videos of the trials and recorded exact foraging patterns of individual bees. The level of specificity was measured using the Fisher's exact test and was measured for inter- and intra-colony competition.
4. I found that inter-colony competition resulted in an increase of specialization among bumble bees, as predicted by OFT. By contrast, bees in the same colony (intra-colony competition) displayed higher generalization in flower type.
5. Synthesis. My study reveals the difference in intra- versus inter-colony competition on foraging specificity in bumble bees, where in the past only differences among species has been examined. Higher inter-colony competition could increase specificity, for example in agricultural contexts.

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INTRA- VERSUS INTER-COLONY COMPETITION IN BUMBLE BEE FORAGING SPECIFICITY

ALISON TAMMANY

SUMMARY

1. The level of generalization or specialization of bumble bees affects their foraging behaviors and therefore plant pollination. Optimal foraging theory (OFT) predicts that increased competition among various bee species results in more specialization.
2. Bumble bees of the same species compete differently when competing with their same colony (intra-colony competition), versus different colonies (inter-colony competition). OFT predicts that intra-colony competition results in increased generalization. In contrast to this theory, I predicted that inter-colony competition would increase specialization of foraging behavior.
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4. I found that inter-colony competition resulted in an increase of specialization among bumble bees, as predicted by OFT. By contrast, bees in the same colony (intra-colony competition) displayed higher generalization in flower type.
5. *Synthesis*. My study reveals the difference in intra- versus inter-colony competition on foraging specificity in bumble bees, where in the past only differences among species has been examined. Higher inter-colony competition could increase specificity, for example in agricultural contexts.

KEY TERMS: *Bombus impatiens*, bumblebees, competition, Constancy Index, foraging behavior, foraging patterns, inter-colony competition, intra-colony competition, optimal foraging theory, resource partitioning

INTRODUCTION

Bees have principle importance as pollinators of both the human agricultural enterprise and also for the functioning of native ecosystems (Allen-Wardell et al., 1998). Currently, there is extensive evidence that bee populations are declining (Biesmejier et al., 2006)—bumblebees in particular (Grixti et al., 2009). One imperative factor of underlying successful plant pollination is specialization in bee foraging of flowers. Specialization is indispensable for plant pollination because it is only successful when pollinators sequentially visit the same species of plant, therefore transferring the right kind of pollen (Morales and Travaset, 2008). By contrast, if a bee were to visit five different species of plants in a row, it would not transfer the proper pollen to any of them and none would be successfully pollinated. A component to help solve this environmental worry rests in the knowledge of bumble bee foraging behavior. The more we discover about foraging behaviors, the better we can understand their integrative role in our agriculture systems.

Optimal foraging theory (OFT) is a general model that is applicable to bumble bees. OFT states that animals have a three-prong approach to optimizing foraging behavior, including choosing a food source, choosing an appropriate cost-benefit situation, and then deciding where to forage based on the trade offs (Pyke 1977). OFT therefore predicts that if bumblebees have a reduction in resource availability, or an increase in competition, they will become more generalized. OFT can be applied and tested under two different pretexts of competition: inter/intraspecific and inter/intra-colony. Fontaine (2008) used OFT as a predictor to show that when multiple species of bumble bees foraged, they were more generalized than if bumble bees foraged within their own species. Fontaine (2008) also found that intra-colony (within) competition resulted in increased competition and higher generalization among the bees, yet he did not investigate the counter argument. To date, there have been few, if any, studies comparing inter-colony competition and intra-colony competition among bumblebees. In my experiment, I investigated the opposite phenomenon to test if inter-colony competition resulted in higher specificity (and lower generalization) in foraging behavior.

Another factor in my research concerns the long-standing debate over whether generalization or specialization is a more prevalent pattern in plant-pollinator systems. The traditional view is that specialization is the more logical direction of pollinators as in accordance with evolution: it is evolutionarily favorable for specialization as it leads to niche development and evolutionary radiation. Specialization would also favor the plant, as it would enjoy more reliable and efficient pollination and thus reproduction. On the other side, Waser (1996) and Fontaine (2008) argue that generalization is more common than previously established. Generalization is a reasonable behavior for foraging bumble bees when they analyze their cost/benefits in comparison to specialization. When population density increases, Waser (1996) notes that bumble bees tend to generalize rather than specialize because they are less selective over flower preference. In specific, bumble bees tend to generalize in their pollination patterns when the cost of pollen extraction is too high, travel costs increase, and/or when the reward does not exceed the energy invested.

Additionally, there is an overarching pattern that density correlates with specialization in all of ecology, which is often discussed in the context of "habitat selection theory" (reviewed by Rosenzweig 1991). Habitat selection theory states that increased intraspecific competition, via increased density, leads to more generalization in habitat selection, which affects foraging behavior (Rosenzweig 1991). Usually in higher density situations (i.e. with more bumble bees in the same area with the same resources), it is logical that for the most part, generalization will occur. An explanation for this is that more individuals will have fewer options for foraging if there is increased competition. As the density of bees decreases, then more flowers will be available for individual foraging and specialization is favored. To test for differences in this context, I used two different densities of bumble bees in the experiment while maintaining an equal number of flowers.

Specialization can be dependent on inter-specific (between species) versus intra-specific (within a species) competition. This study investigates whether or not this same pattern operates at a finer taxonomic scale, i.e. within one species. The majority of studies to date concerning foraging competition among bumble bees has focused on inter- versus intra-species differences but have largely ignored colony competition. As Fontaine (2008) displayed that intra-species competition leads to a decrease in specialization, and that an increase in inter-specific competition should contrastingly lead to an increase in specialization. Fontaine (2008) also notices that at high densities "competition for resources led different individuals within colonies to forage consistently on somewhat different sets of plant species." By contrast, when considering interspecific rather than intraspecific competition, theory predicts and empirical evidence suggests greater specialization at high densities in a wide range of organisms and locations (Rosenzweig 2001). There is some evidence that this may be true in plant-pollinator systems, which is exactly what I aim to investigate. In particular, Inouye (1978) found that when one species of bumble bee (*Bombus sp.*) was selectively removed from a meadow that a competitor species broadened the number of plant species it focused on, and vice-versa (i.e. the same principle applied when the other species of bumble bee was removed).

This study focuses on a measure of specificity in foraging behavior, defined as floral constancy. Flower constancy is the habit of pollinating animals to limit their visits to a specific flower type even if nectar rewards might be higher elsewhere (Waser 1986). To measure the specificity of bumblebees I calculated proportions and the Fisher's exact test, which will be examined later in the paper. It is in this manner that my findings relate to a novel study: the effects of between versus within *colony* competition on foraging specialization.

METHODS

In order to explore a difference in foraging behaviors of inter-colony and intra-colony competition behavior, I designed an experiment that controlled for specific bumblebee densities and colonies. Using two separate colonies of *Bombus impatiens,* ordered from different suppliers in the United States, I set up 12 experiments. By using distinct suppliers, I ensured that the bumblebees were not closely related. I housed the bumblebees inside so that weather and pollen/nectar collection would not act as stressors. They were placed inside a wooden-framed enclosure with mesh curtain sealing each colony in and I differentiated the two colonies by labeling them A and B. The bees were allowed to forage freely on nectar, pollen, and water while in their separate sides.

Artificial Flower Foraging

In a separate enclosure (48 inches by 48 inches, 46 inches tall), I set up 24 artificial flowers—12 with yellow acetate and 12 with blue acetate. The yellow flowers were smaller (2.5 cm diameter) and had 2 μL 1M sucrose solution with lemongrass oil. The larger blue flowers (5 cm diameter) had 2 μL 2M sucrose solution with clove oil. The solution was placed into the lid of a micro-pipette and then taped onto the center of the acetate. The acetate was then attached to a 1 inch tall plastic cylinder and placed into the enclosure. I staggered the flowers arranging them into columns (4 yellow, 3 blue) and rows (3 yellow, 4 blue) to create maximal distance from each other. These locations were marked and reused for each experiment.

I ran six experiments at a low density of bumblebees, using six bumblebees. For the low-density experiments, I used 3 inter-colony trials and 3 intra-colony trials. I also ran six experiments at a high density of bumblebees, using twelve bumblebees per trial. Three of these high-density trials were inter-colony and three were intra-colony runs. To run the trials, I collected the bees (keeping colonies A and B separate) in tubes and caped them with mesh squares and a rubber band. I then placed the bees in the refrigerator for 20 minutes to temporarily anesthetize them (Thomson & Plowright 1980). I removed the bees, one by one, and marked them with a paint-marker—red for colony A, and white for colony B. This removed any pseudo-replication in the experiment because once bees were marked I did not reuse them. I placed the bees in dark cabinets, starving them for an additional 55 minutes to encourage them to forage once inside the enclosure.

After the hour and half of starvation, I added the bees into the enclosure. For inter-colony trials, I added all the bees from colony A and then from colony B so that I could distinguish the bee colonies for video analysis. I video recorded the trials using a HD webcam for 20 minutes after the last bee entered the enclosure (Fontaine 2008). After each trial, I collected the bees and released them back into their respective colony enclosures. I then rinsed all of the flowers and wiped them with ethyl alcohol before refilling them to remove any pheromones from previous visitors.

Video Analysis & Computation of Results

To analyze the bumblebees' foraging patterns, I reviewed all twelve videos of my trials. I would start each video and follow bees one by one until I followed all 6 or 12 bumblebees. For each bee, I would record the entry time (e.g. 32 seconds) and then would watch the bee and record whenever it foraged. I recorded what flower number, flower color, and time spent (start and stop) during each foraging visit. I had to often slow the video down to follow certain bees and used a 40-inch screen LCD television to better track the exact locations of the bumblebees.

I organized the data into a summation table where I calculated the total number of foraging switches (i.e. from yellow to blue, or blue to yellow) as well as the number of foraging constants (i.e. blue to blue or yellow to yellow) (see appendix). If a bee did not forage at all or only made one foraging trip, I did not use its data in my calculations. To calculate the difference in competition, I used the Fisher's exact test because I had some small sample sizes of foraging trips (less than 10). The test provides an exact P-value and analyzes the significance of the relationship between intercolony foraging and intracolony foraging using a contingency table. I performed a power analysis after calculating my initial values for the Fisher's exact test to see if using the same proportions, I could find a statistically significant relationship between inter- and intra-colony foraging competition.

RESULTS

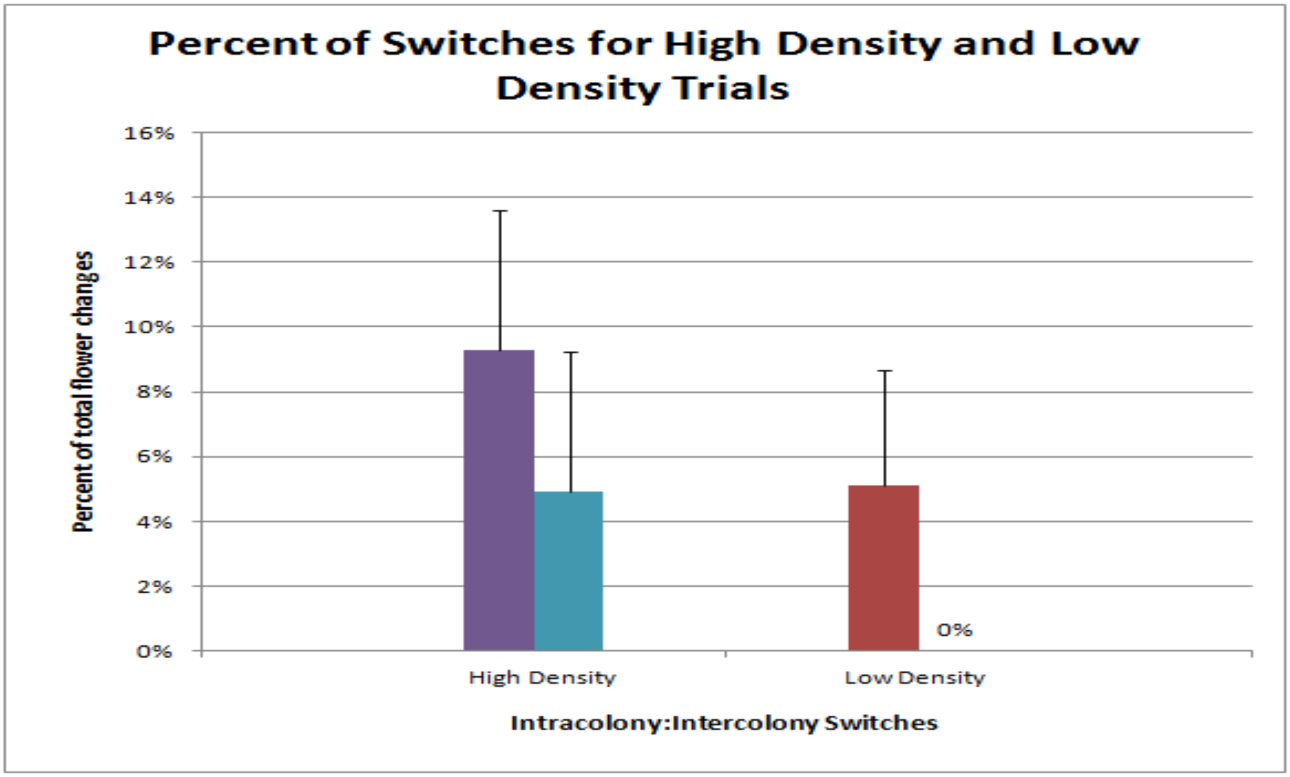
In order to fairly tally up the numbers to test for inter-versus intra-colony competition, I made no distinction between colony A or colony B in summing up either the interclonal or intraclonal flower trips (See Table 1). Because I included two colonies in all of my interclonal trials, there is no need distinguish colony A from colony B and to then analyze the foraging habits of the separate colonies in comparison to one another.

Table 1. Summations of trial trips between flowers

TRIAL	COLONY	DENSITY	TOTAL SWITCHES	TOTAL CONSTANCY	TOTAL TRIPS
1	B	Low	1	14	18
2	A	Low	1	19	24
12	A	Low	0	4	7
3	A & B	Low-a	0	4	5
		Low-b	0	0	0
7	A & B	Low-a	0	0	0
		Low-b	0	4	6
11	A & B	Low-a	0	0	0
		Low-b	0	0	1
4	B	High	6	47	63
5	A	High	2	25	35
10	A	High	1	16	22
6	A & B	High-a	1	5	9
		High-b	0	14	18
8	A & B	High-a	0	13	17
		High-b	0	5	7
9	A & B	High-a	2	8	14
		High-b	0	13	17

The statistical methods used to analyze my data included summing up the number of trips to the same flower type in addition to trips to different flower types of both intracolony and intercolony trials. I calculated the percentage of bumblebee flower switches that were generalized and would forage anywhere versus the percentage of bees that specifically chose one flower type. I then used a two-tailed Fisher's exact test to test my hypothesis that interclonal foraging is more specialized than intraclonal foraging. Finally, I determined the standard error of difference separately for the high and low-density of the inter- and intra-colony trials. (See Figure 1). I chose the Fisher's exact test over a Chi squared test because not all of my sample sizes were greater than 30.

Figure 1: Graph of intra-versus inter-colony generalization to specialization for high and low density trials



Low Density Trials—For the low density trials using six bumblebees I created a contingency table with my two variables: inter/intra-colony trials and constant/switched flower visits. After calculating the Fisher's exact test, I found a p-value of 1.000 for the six trials at a 95% confidence interval (see Table 2). This p-value signifies that there is no relationship between specialization and inter-versus intra-colony competition. With this p-value, I cannot definitively support or refute my hypothesis. For the intracolony trials (within the same colony), there were 39 total flower movements. Two of these were from one color to another, while the other 37 were switches to the same flower type. In this sense, the bees had a 5% tendency to switch flower type (i.e. were 95% specialized). The intercolony trials only had eight flower switches—none of which were to a new color (i.e. all eight trips were between the same colored flower). This shows that 100% of the trips were specialized. Looking at these percentages only and ignoring the p-value, this data set supports my hypothesis that interclonal foraging has higher specificity (100%) than intraclonal foraging (5%). While the p-value of 1.000 shows that the data set does not differ from inter to intra colony competition: this could be explained by the small sample size of intercolony competition.

High Density Trials—For the high-density trials of twelve bees per experiment, the contingency table was set up in the same way as before. I found a p-value of 0.3722 at 5% confidence, which is not significant enough to support my hypothesis (see Table 2). In order for the test to find a statistically significant relationship between specialization and inter versus intracolony competition, the p-value should be less than 0.05. The intracolony trials had 97 total flower movements, with nine of them to different flower types and 88 of them to the same flower type.

Therefore, intracolony bees were 9.3% generalized and specialized 90.7% of the time. Of the 61 interclonal trials, three trips were to different flower types while 58 trips were to the same flower type. This value supports my hypothesis because the intercolony bees specialized 95.1% of the time and generalized 4.9% of the bouts. With the data from the high-density trials, the intercolony bees specialized more than the intracolony bees. Even so, more data is needed to explore if there is a statistically significant relationship between the variables. Because the data follows my hypothesis's expected direction, I used power analysis to see how large of a sample size would be needed to find a statistically significant difference, keeping original proportions the same.

Table 2. Calculation of Fisher's exact test for low density and high density inter- versus intra-colony specialization/generalization

Fisher's Exact Test			
LOW DENSITY			
	Constant	Switches	Total
Intracolony	37	2	39
Intercolony	8	0	8
Total	45	2	47
p value=1.0000			
The association between rows (groups) and columns (outcomes) is considered to be not statistically significant			
HIGH DENSITY			
	Constant	Switches	Total
Intracolony	88	9	97
Intercolony	58	3	61
Total	146	12	158
p value=0.3722			
The association between rows (groups) and columns (outcomes) is considered to be not statistically significant			

Power Analysis—I performed power analyses at two times, three times, and four times magnification to see how large of a sample size I would need to find a statistically significant difference in inter- versus intra-colony specialization. Doubling the numbers for the low density kept the p-value at 1.0000—likely due to the zero switches of intercolony bumblebees. The high-density p-value dropped to 0.1927 when values were doubled—displaying a trend that supports my hypothesis. For the 3rd magnification, I added 3 switch trips to the inter-colony low-density switches column, to see if the zero was causing a problem in the statistics. The p-value decreased to 0.3699 with the 24:3 (8:1) ratio and the high density p-value dropped to 0.1080. Finally, at the fourth power analysis, the low-density (now with four switches in the intercolony column) had a p-value of 0.2431, while the high-density had a p-value of 0.0459 (see Table 3). This value for high-density displays a statistically significant difference of inter- versus intra-colony competition, thus supporting that intercolony foraging is more specialized than intracolony foraging. Increasing the sample size and keeping the proportions the same eventually show this result when the sample size is much larger (i.e. 584 total constant trips and 48 switch trips). The low-density trial p-values do decrease towards a statistically significant outcome when I added one switching trip per power, but it is impossible to know for sure what would happen due to my raw data recording zero trips for one column without additional experimentation.

Table 3. Powers of Fisher's Exact Test with p-values

POWER x2	
	p-value
Low Density	1.0000
High Density	0.1927
POWER x3 + 3 to Low Intercolony switches	
Low Density	0.3699
High Density	0.1080
POWER x4 + 4 to Low Intercolony switches	
Low Density	0.2431
High Density	*0.0459*

DISCUSSION

While the p-values for both low and high-density trials failed to show that intercolony foraging was significantly more specialized than intracolony competition, the data set does seem to follow this trend as supported by my power analysis. While the p-value of 1.000 shows pretty definitively that there is no relationship between my variables, it is difficult to find a relationship due to the small sample size. However, when I hypothesized that some switches would eventually occur with my power analysis, the p-value started to decrease towards a significant value. All eight trips displayed 100% specialization in intercolony trips and despite the faulty p-value, the statistical percentages do support my hypothesis that intercolony foraging is more specialized that intracolony foraging.

The high-density trial percentages did agree with my hypothesis even though the p-value failed to show a significant relationship (p-value=0.3722). Intracolony competition resulted in higher generalization and therefore lower specialization than intercolony competition. This p-value supports my hypothesis with 62.78% confidence. This number is rather inconclusive, as most scientific experiments require a 95% confidence interval in order to support or refute definitively a hypothesis. The power analysis showed that at a larger sample size, this relationship does become statistically significant. Overall, in order to get a more specific answer, additional trials would need to be performed to support that intercolony competition is more specialized than intracolony competition.

Errors in the methodology of this experiment mostly lie in the low number of foraging switches by the intercolony bumblebees. Future experimentation should plan to use multiple trials in order to get a sample size of at least 5 so that Fisher's exact test will give more conclusive p-values. The high number of bumblebees that did not forage at all was rather large considering the bumblebees had been starved for 90 minutes. Of the intercolony low density trials, 13 of 18 bees did not forage, two bees visited one flower each (and could not be used), and the remaining bees actually foraged from flower to flower—for a total of 8 flower switches. Of the intracolony low density trials, six bees did not forage, two bees only foraged once, and the remaining eight of 18 bees foraged various flowers. During the high-density intercolony bouts, 11 bees did not forage, six bees foraged once, and the remaining 19 bees foraged actively. Finally, during the high-density intracolony trials, ten bees did not forage at all, two bees foraged once, and the other 24 bees foraged on multiple flowers. Perhaps if the bees were starved for longer periods of time, the number of bees that foraged would increase. Moreover, the bumblebees from colony B began dying rapidly at least two weeks before they were meant to expire, so the bees used in the last experiments (10-12) could have utilized less healthy bees that were not very willing to forage (see Appendix).

Despite the p-values neither supporting nor refuting my hypothesis, the overall percentages do hint at a relationship between intracolony and intercolony competition among bumble bees. In agreement with optimal foraging theory, when bumblebees compete with other species or colonies (i.e. bees that are nonrelated to the group in question), they are likely to specialize their foraging habits more than if they competed with their own group. This makes sense from an ecological standpoint because the more groups present in a system, the higher the competition and the more animals will specialize to preserve their own resources. However, Daniel Bolnick (2001) found the opposite result is true. His experiment with *Drosophilia melanogaster* showed that less interspecific competition (fewer species) favors more intraspecific competition. This result may not relate to my study because it examines the fitness of the flies, stating that in areas of high fly density with multiple species, the fitness of individual species decreases. In a more applicable paper studying generalist foraging of pollinators, Fontaine found that bee density affects specialization at the colony and species level. Bumblebees will expand their diet at high densities than at low densities. My data support this because a more significant difference is observed at high densities than at low densities. Moreover, Fontaine found that at high bumblebee density, more plant species were visited in intraspecific trials.

The amount of nectar in the flowers also affects bumblebee foraging. Logically, the greater the reward a flower has, the more likely a bee is to visit that flower (Waser 1986). In my experiment, the blue flowers were more rewarding than the yellow flowers. While each flower was filled with 2 μL of sucrose solution, the blue flowers had 2 M sucrose concentration while the yellow flowers had 1 M sucrose. According to theory, bumblebees have the ability to determine which flower offers the maximum reward (Harder 1990). In my case, the bumblebees were able to realize that the blue flowers had more energetic value than the yellow flowers. Moreover, bees are intelligent animals that can change foraging behavior with regard to reward availability while in flight (Harder 1990). Under restraints of increased competition, bees can practice floral constancy in which they choose to be highly specialized even if their chosen flower does not offer the greatest reward (Waser 1985). Flower constancy is the behavior in which bees choose a more dependable reward than one that varies flower to flower (Real 1981). In my experiment, the bumblebees that specifically foraged on the yellow flowers displayed flower constancy.

Future research possibilities in studying the foraging differences of inter- versus intra-colony competition lays in replicating additional foraging trials. Understanding bumblebee foraging behavior is becoming more important as bee populations dwindle. If we do lose bumblebee biodiversity, then our ecosystems and agriculture will be negatively affected (Pfisterer 2006). The connection between the health of our pollinators and the health of our crops is an easy one to observe. Even though my p-values were a bit high, the ambiguity of a statistically significant result being set at 95% confidence might not really apply perfectly to ecological patterns. For instance, in the long term, if bumblebees have a tendency to specialize in intercolony settings at 70% confidence, this pattern will have large implications for a pollination system. Based on my preliminary research, if we use two distinct colonies of the same species (*Bombus impatiens* in this case) then there will be higher specialization of foraging. The more specialized bees are, the higher the chances of successful pollination for the plant: for example, if a bee specializes on flower A, then it will mostly visit flower A and increase the chances of pollen transfer and therefore reproduction of the plant (Waser 1996). This pattern of specialization can thus be utilized to increase agricultural yields if properly employed by greenhouses and small farms.

Acknowledgements

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Appendix. Foraging trips of individual bees in the 12 trials of two densities

LOW DENSITY TRIALS

Intracolony foraging

Trial	Density	Colonies	
1	low	B	
Constancy			
Bee #	# of switches	# constant	# trips
1	N/A		1
2	1	3	5
3	0	6	7
4	N/A		0
5	0	5	6
6	N/A		1

Trial	Density	Colonies	
2	low	A	
Constancy			
Bee #	# of switches	# constant	# trips
1	N/A		0
2	0	9	10
3	0	3	4
4	0	4	5
5	N/A		0
6	1	3	5

Trial	Density	Colonies	
12	low	A	
Constancy			
Bee #	# of switches	# constant	# trips
1	0	2	3
2	N/A		0
3	N/A		0
4	0	1	2
5	N/A		0
6	0	1	2

Intercolony foraging

Trial	Density	Colonies	

HIGH DENSITY TRIALS

Intracolony foraging

Trial	Density	Colonies	
4	high	B	
Constancy			
Bee #	# of switches	# constant	# trips
1	N/A		0
2	0	4	5
3	0	8	9
4	0	3	4
5	0	5	6
6	0	6	7
7	2	4	7
8	0	2	3
9	0	6	7
10	0	7	8
11	4	2	7
12	N/A		0

Trial	Density	Colonies	
5	high	A	
Constancy			
Bee #	# of switches	# constant	# trips
1	1	4	6
2	0	3	4
3	N/A		0
4	0	2	3
5	N/A		0
6	0	2	3
7	N/A		0
8	1	3	5
9	0	4	5
10	0	4	5
11	N/A		0
12	0	3	4

Trial	Density	Colonies	

3	low	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	N/A		0
2A	0	4	5
3A	N/A		0
4B	N/A		0
5B	N/A		0
6B	N/A		0

Trial	Density	Colonies	
7	low	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	N/A		0
2A	N/A		0
3A	N/A		0
4B	0	3	4
5B	0	1	2
6B	N/A		1

Trial	Density	Colonies	
11	low	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	N/A		0
2A	0	0	1
3A	N/A		0
4B	N/A		0
5B	N/A		0
6B	N/A		0

10	high	A	
Constancy			
Bee #	# of switches	# constant	# trips
1	0	6	7
2	0	2	3
3	0	3	4
4	N/A		1
5	1	3	4
6	0	1	2
7	N/A		0
8	N/A		0
9	N/A		1
10	0	1	2
11	N/A		0
12	N/A		0

Intercolony foraging

Trial	Density	Colonies	
6	high	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	0	1	2
2A	N/A		1
3A	N/A		0
4A	1	0	2
5A	N/A		1
6A	0	4	5
7B	0	6	7
8B	N/A		0
9B	0	3	4
10B	0	1	2
11B	N/A		0
12B	0	4	5

High density-Intercolony

Trial	Density	Colonies	
9	high	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	2	3	6
2A	0	5	6
3A	N/A		1
4A	N/A		1
5A	N/A		0
6A	N/A		0
7B	0	7	8
8B	0	1	2
9B	N/A		0
10B	0	2	3
11B	0	3	4
12B	N/A		0

Trial	Density	Colonies	
8	high	A & B	
Constancy			
Bee #	# of switches	# constant	# trips
1A	N/A		1
2A	N/A		1
3A	0	2	3
4A	0	4	5
5A	0	5	6
6A	0	2	3
7B	N/A		0
8B	N/A		0
9B	N/A		0
10B	N/A		0
11B	0	3	4
12B	0	2	3