5-2007

The Long Term Effect of Time-Memory on Forager Honey Bee (*Apis mellifera*) Recruitment.

Matthew Walter Otto
East Tennessee State University

The Long Term Effect of Time-Memory on Forager Honey Bee (*Apis mellifera*) Recruitment

---

A thesis

presented to

the faculty of the Department of Biological Sciences

East Tennessee State University

In partial fulfillment

of the requirements for the degree

Masters of Science in Biology

---

by

Matthew W. Otto

March, 2007

Dr. Darrell Moore, Chair

Dr. Karl H. Joplin

Dr. Tim McDowell

Keywords: foraging behavior, time-memory, *Apis mellifera*, recruitment

ABSTRACT

The Long Term Effect of Time-Memory on Forager Honey Bee (*Apis mellifera*) Recruitment

by

Matthew W. Otto

Experiments were performed to determine the influence of the honey bee time-memory on a forager bee's sensitivity to recruitment. Two groups of foragers from one colony were trained to separate food stations at the same restricted time of day for several consecutive days. Feeding then was canceled at one station but continued for four more days at the other. Bees with more days of training at a non-productive source were significantly less likely than foragers with less training to be recruited to an alternative food source presented at the same time of day. Furthermore, the ability of a forager to be recruited recovered after several days, but this recovery period was longer for bees with greater experience. These findings demonstrate a long-term influence of time-memory on subsequent foraging behavior, in contrast to currently accepted models for the allocation and re-allocation of honey bee foragers to food patches in the environment.

ACKNOWLEDGEMENTS

First, I would like to thank all the research assistants that helped during the two summers of research. There would be no results without their help and sacrifices. These wonderful people are Samara Miller, Guy Kramer, Forrest Harrison, Jeremey Whitaker, Jaime McManus, Nathan Humphrey, Caleb Paquette, Byron van Nest, and Bobby Jo Otto.

Second, I would like to thank my committee members for all their help in proofreading and editing this manuscript. I would especially like to thank Dr. Moore, my chair, for all his help in all phases of my research. He played a pivotal role in the development, implementation, and analyses of these experiments. Without his assistance, none of this would have been possible.

Third, this research would not have been possible without the funding provided by two graduate departmental awards. These awards include both the William Harvey Fraley and Nina M. Fraley Memorial Research Award and the Dr. Denise Pav Scholarship Award. This funding provided for beekeeping equipment as well as the materials to build 4 more observation hives, both of which were essential to the research.

Last but not least, I would like to thank my wife and children (dogs) for their never-ending support. They suffered through the low moments of this research right along side me. They gave me support when I needed it most, provided me with a distraction at the perfect times, and kept me on track when I did not want to go any further. For everything they have done, I dedicate this thesis to them. Bobby Jo, Reba, Marley, and Kodiak, I love you all and thanks.

CONTENTS

List of Tables

List of Figures

CHAPTER 1

INTRODUCTION

The order Hymenoptera is known for its diversity of social structures. This order, which includes ants, wasps, and bees, exhibits degrees of sociality that range from solitary individuals to large complex colonies containing thousands of individuals. In these large colonies, there is a need for social organization if the colony is to survive as a whole. This organization is normally a caste system in which the members of each caste are responsible for specific duties in the colony. The common honey bee (*Apis mellifera*) is one of the most well studied examples of a large colony social structure.

Honey bee colonies, when fully functional, can vary in size from a few thousand individuals to well over 50,000 individuals, with a typical colony containing roughly 30,000 bees (Seeley 1995). There are three morphologically distinct castes: the queen, the drones, and the workers, with each having a specific role in the colony's survival. The determination of each bee's future caste is determined at the time the egg has been laid. If the queen fertilizes the egg, the result will be diploid offspring that are morphologically female. The female offspring become either workers or another queen depending on the size of the cell into which the egg is deposited. If the egg is deposited into a standard cell, the result will be a worker. If the egg is deposited into the larger queen cells, which normally hang off the bottom of the comb, the result is a new queen. If the egg is not fertilized, the haploid offspring will become a drone (male bees).

Besides the donation of sperm by the drones, the reproductive caste is the sole domain of one individual queen bee. She is the only reproductively active female in the hive and is thus responsible for all reproduction. When a new queen is needed in a hive, either because of a future swarm or the deteriorating health of the current queen, a certain procedure is followed. The workers will build multiple larger than average queen cells into which the queen will deposit an egg. As the larva develops, workers feed it only royal jelly, a food product made by the workers that consists of sugars, lipids, and many vitamins (Michener 1974). After 16 days, the new adult queen emerges. She first hunts the hive for and eliminates any other rival queens including any that have hatched from the other queen cells.

On her sixth day of adulthood the queen will leave the hive to copulate with multiple drones (male bees). Drones from multiple hives, including the virgin queen's hive, gather at mating assemblies (Franck et al. 2002). During the nuptial flight, the queen is swarmed by a cloud of hundreds of drones and normally mates with 8-20 drones (Tarpy and Page 2002). Of these spermatozoa, 95% of it is subsequently expelled from the queen prior to storage in the spermatheca (Franck et al. 2002). As the queen uses sperm from all of the drones (Haberl and Tautz 1998) and the order they inseminate her does not influence sperm preference (Franck et al. 2002) each drones genetic make-up is equally represented. This increases genotypic variation (Tarpy and Page 2002) in the hive and thus greatly decreases any influence from possible inbreeding. Upon returning from her nuptial flight, the queen assumes the one duty that will consume the rest of her life, reproduction. She can lay around six eggs an hour and lives for as many as five years. As she is cleaned, fed, and cared for by the workers, she has no need to perform any other in-hive tasks, forage, or defend the hive.

The male honey bees are called drones. They are the product of an unfertilized egg being laid in slightly larger cells constructed around the edges of the colony. It has been found that drone production is normally timed to coincide with new queen production (Michener 1974). The drones take, on average, about 26 days to emerge as adults and are much larger in size when compared to the worker. The drone's only responsibility is to copulate with a queen. This includes any queen that arrives at the mating assemblies. They do not forage or do any other chores around the hive. They are fed and cared for by the workers until the weather begins to deteriorate in the fall, at which time they are killed or expelled from the hive.

The final caste, the workers, is arguably the most important resource in the hive. They perform all the day-to-day tasks for the hive to run properly. As stated earlier, workers are the product of a fertilized egg deposited in regular brood cells. They are fed royal jelly for the first three days of their life, after which they are switched to a combination of pollen, nectar, and bee milk, a food product made by other worker bees (Michener 1974). After 21 days, the workers emerge as adults and begin to perform the rest of the tasks needed for survival. Because they perform all the tasks not associated with reproduction and also comprise more than 90% of the hive, they have been the focus of most of the studies done over the years. They also show many amazing behaviors and abilities that have fascinated scientists all over the world.

Upon emergence as an adult, the new worker immediately begins to carry out the required in-hive tasks. These tasks have been found to be generally divided up between different workers depending on age. For the first three days after emergence, the workers spend most of their time cleaning cells and preparing them for new eggs (Lindauer 1961; Seeley 1995). From day 4 to day 10, the worker takes on the duty of feeding and tending to the brood (young larvae) as well as tending to the queen's needs. Day 10 to day 15 are spent building and repairing the honeycomb. From day 15 until the onset of foraging, the worker splits its time between the duties of a "receiver bee" and a "guard bee." A receiver bee receives the nectar, pollen and water brought back by the foragers and stores it, while the guard bee protects the entrance so that no intruders can enter the hive. Normally by day 21, the worker has made the transition from an in-hive worker to a forager.

The age-related sequence of tasks (age polytheism) is the general rule but is not always followed by all bees and all colonies (Winston and Neilson Punnett 1982). Each individual worker bee has its own time table for scheduling tasks. For example, some worker bees have been shown to shorten or even skip the cell cleaning stage (Seeley 1995). Other times, workers will become nurse specialists and spend almost the entire time in-hive tending to brood and queen. Some workers specialize in grooming (Kolmes 1989), with one example specializing in it for life (Moore et al. 1995). There has even been documentation of workers specializing in guarding (Moore et al. 1987). A new hive may have a greater need for receiver bees and foragers than nurse bees as the number of brood is still low, while an old hive may need more nurse bees to compensate for the number of brood in the hive. This versatile demographic structure allows for great flexibility to deal with multiple in-hive factors.

External environmental factors can also lead to a change in age polytheism. During good conditions with ample sources of nectar and pollen, the time between emergence and foraging can be shortened to 8 to 10 days (Lindauer 1961). The shortening depends upon both the amount of external forage and the number of workers in the hive. As the proportion of foragers decreases, the likelihood of developmental acceleration increases. In other words, the time between emergence and the onset of foraging decreases. In one study, the addition of a cohort of younger bees to a hive of 8-13 day-old workers induced early foraging by workers (Page et al. 1992). Early foraging is also paralleled by an increase in the level of juvenile hormone, the main hormone involved in behavioral development (Robinson et al. 1989). If a hive has a large food surplus but an inadequate amount of nurse bees, the older workers or even foragers can revert to nurse status to increase the numbers (Lindauer 1961; Robinson 1992; Seeley 1995). These examples show the great adaptability that the worker caste has to ensure that all duties are performed as needed.

A circadian rhythm is a process that occurs with a periodicity of approximately one day. Specifically, it is when an organism settles into a daily cycle of physiological processes (for example, plant leaf movement and floral production) or behavioral actions that regularly include an active period and an inactive period. In the absence of external cues, the organism cycles under the direction of it endogenous biological clock – it is said to "free run". The actual length of its endogenous "day" varies between species and is typically close to but not equal to 24 hours. Many animals use sunlight as an environmental cue that re-sets their circadian clock each day. Some organisms are active at night (nocturnal) whereas others are active during the day (diurnal).

The honey bee has a circadian rhythm of locomotor activity with a period that is roughly 24 hrs (Moore and Rankin 1985). In constant light, the period is greater than 24 hrs and in constant darkness it is less than 24 hrs. It is assumed but not demonstrated that the same circadian oscillator controls general locomotor activity, measured under laboratory conditions, as well as foraging behavior, measured under natural conditions in the field (Moore 2001). Circadian rhythmicity plays a key role in a honey bee's ability to forage, influencing both its time-memory and its time-compensated sun compass (both will be discussed later). However, the presence of circadian rhythmicity would have a negative impact on the workers ability to perform in-hive tasks. Most of the in-hive tasks, especially the brood and queen care, must be continued through the night. If the workers demonstrated a diurnal circadian rhythm that developed at emergence, no work would be accomplished at night and thus the honey bee colony would not survive. There are two possibilities that could allow the in-hive workers to continue work at night. The workers could either be arrhythmic early in life and then develop a circadian rhythm prior to foraging, or the workers could divide themselves in shifts with, for example, half of the workers on the “day” shift and the other half on the “night” shift (Moore et al. 1998). Studies have shown that a new worker is active at all times of the day with work being intermingled with short rest periods and thus does not show a circadian rhythm (Moore et al. 1998; Moore 2001). As the worker ages, however, it begins to rest more at night and work during the day which is evidence of a developing circadian rhythm (Moore 2001). In a healthy hive under normal environmental conditions this rhythm is fully functional by day 14, but has developed as early as day 7 (Toma et al. 2000). This functional rhythm matches almost perfectly with the worker’s switch to a receiver/guard bee, both duties that are most important during the day. So by having this delayed circadian rhythm, the honey bee is able to perform all the tasks required in the hive and then develop the necessary rhythm prior to the onset of foraging.

At the onset of foraging, the honey bee worker begins to use multiple unique behaviors that maximize the overall effectiveness of a forager sub-group. As they are responsible for the collection of all essential external products, they must have mechanisms in place that allow them to allocate their efforts towards the most profitable food sources. These also need to be the most necessary products for the hive at that particular time. Through the individual choices of foragers, which are influenced by many in-hive feedback loops (Seeley et al. 1991; de Vries and Biesmeijer 1998; Anderson and Ratnieks 1999; Sumpter and Pratt 2003), the foragers maximize their overall effort to the appropriate sources.

The first of these unique behaviors that are essential for forager success is the use of recruitment dances. The foragers have many different “dances” that are used to inform other foragers of good food sources in the surrounding landscape. The first and most basic of these is the round dance. This dance, first interpreted by Karl von Frisch (1967), is used to recruit foragers to a food source close to the hive. The returning forager will circle around on the dance floor (an area on the comb near the entrance to the hive where all the dances take place), making sure to reverse directions, while vibrating its abdomen. After making multiple circuits, the recruiter will stop and offer a sample of its food to the followers. The follower then decides if she wants to go out to find that source or not. As the follower cannot assess the profitability of the source by taste, and at times does not follow the whole dance to the point when the sample is given, the choice to go to a source has been shown to be random (Seeley 1995).

The next dance, and probably the most well known, is the waggle dance. This dance, again first interpreted by von Frisch (1967), is used for sources greater than about 60 meters distant from the colony. This dance consists of a waggle run (the forager moves across the honeycomb in a specific direction shaking its abdomen from side to side) followed by a return to the starting point. The waggle run is done again and then the bee returns to the start in the opposite direction, creating a "figure-eight" path. Through this repeated sequence, the bee not only tells the follower that a food source is out there, she also gives the direction and distance to the source. Studies have shown that the duration of the waggle run is proportional to the distance to the source (von Frisch 1967; Seeley 1995; de Vries and Biesmeijer 1998). The direction is specified by the angle of the waggle run. For example, if the angle of the waggle run is 45° to the left of vertical, then the food source would be 45° to the left of a line drawn from the hive to the sun's azimuth. This angle will change with the sun's apparent motion across the sky, but the bees will compensate for that and will change the angle as the day progresses. This compensation can occur without the bee actually seeing the change in the sun's position

(Lindauer 1960). Bees can compensate for the sun's change in position without viewing the sun because they can continuously keep track of the time of day from their internal circadian clock. This ability is known as the time-compensated sun compass.

Besides the round dance and waggle dance, the two primary communication dances, there are a few more dances that should be mentioned. The tremble dance is one that has just recently been receiving more attention (Seeley et al. 1996; Anderson and Ratnieks 1999; Thom 2003). It is used by foragers that encounter a long wait to be unloaded by receiver bees. The forager will walk around on the comb periodically vibrating (or trembling) its entire body. This is a signal that more receivers are needed and leads to a rapid increase in the number of receiver bees. The other "dance" that is receiving more attention is the shaking signal. If a forager has returned from a source that had stopped producing but now is once again profitable, the returning forager will grab on to other foragers and "shake" them. It is interpreted as a way to urge other foragers to return to the old source (Beismeijer 2003). Both of these dances have not been as well studied as the round and waggle dance and thus are not completely understood.

Another essential component of foraging behavior is the foragers' time-memory. As stated earlier, the development of a strong circadian rhythm just prior to foraging has several advantages. First, it allows the forager to anticipate when a food source is most profitable and then focus its efforts at that time on following days (Moore and Rankin 1983). This ability of a forager honey bee to remember the time when a food source is profitable is referred to as its time-memory. Also called the foraging rhythm, time-memory apparently functions by a mechanism in which the bee consults its circadian clock. This time-memory allows each individual bee to focus its energy at the most productive time. This is essential as honey bees have a short lifetime and need to maximize their energetic efficiency (Seeley 1994, 1995; Visscher and Dukas 1997).

Studies of time-memory have shown that there is a connection between the time of day and the accuracy of the memory. Forager honey bees have the most accurate arrival time (when a forager initially arrives at a food source) in the morning but it becomes less accurate through the rest of the day (Moore and Rankin 1983). The variation in timing accuracy according to time of day has also been shown to be an endogenous component of time-memory (Moore et al. 1989). Time-memory and each individual bee’s willingness to recruit more hive mates are affected by many factors including the quality of the food source (Seeley et al. 1991; Seeley 1995; Weinselboim et al. 2002) as well as the amount of experience at a food source (Moore 2001). The honey bee time-memory decays over time, but the pattern of this decay is influenced by the number of days of experience accumulated by the individual forager at the feeding station (Moore unpublished; Fig. 1). When this decay reaches a point where the forager appears to have completely forgotten the previous food source, it is referred to as time-memory extinction.

Both the process of recruitment and foraging based on time-memory play a role in the allocation of foragers to productive food sources. Both of these behaviors are influenced by external as well as in-hive factors. A forager’s willingness to perform recruitment dances (its dance threshold) is affected by environmental factors. For example, when forage is plentiful, the threshold will be increased (Seeley 1994) and only bees going to highly profitable food sources will perform recruitment dances. Conversely, when food is sparse, not only is the dance threshold lowered (Seeley 1997) but the foragers will also go farther afield to gather nectar

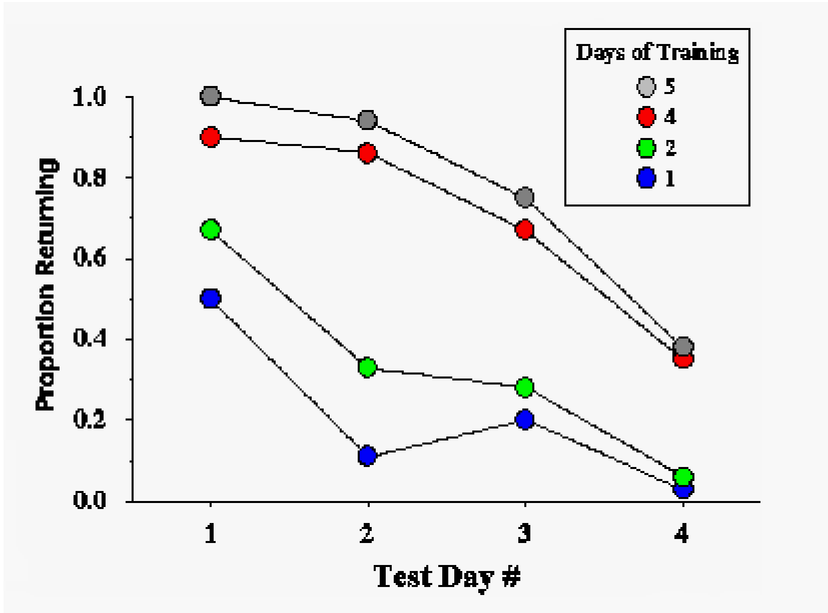

Figure 1 Time memory extinction (Moore, unpublished). The proportion of living individuals returning to the feeding station on four unrewarded test days was documented. The foragers were divided into separate cohorts according to the number of consecutive days of experience they received at the food source. Note that the bees with higher experience arrived in higher proportion on all test days. Also, the bees with less training (1 and 2 days) have a greater rate of decay from test day 1 to 2.

(Schneider and McNally 1993). Foragers have also been shown to decrease their overall activity when foraging at a food source that shows diminishing productivity (Wainselboim et al. 2002).

Internal factors also play a part in the forager's dance threshold. Studies have shown that trophallaxis, the passing of nectar from a returning forager to other bees, influences the dance threshold and other recruiting behaviors (Farina 2000; Gil and Farina 2002; Fernandez et al. 2003). Farina (2000) demonstrated that the number of trophallactic events an individual forager has decreases its dance threshold. In this study, foragers were returning from multiple sources with some being of low profitability levels that did not elicit a dance behavior. Upon entering the hive, these bees did not dance. It was not until after trophallaxis events with multiple hive mates that they started to perform recruitment dances. Their hive mates were possibly telling them that there was a need for more nectar in the colony which then triggered this decreased threshold.

There is also a distinct feedback loop involving receiver bees. As a forager returns from a food source, it attempts to unload its nectar to a receiver bee. These bees have been shown to deferentially unload better sources first and worse sources last (Seeley et al. 1991). This differential unloading will lead to a delay in unloading the foragers coming from a poor source. The forager will use this delay as a way of judging how good her food source is. If she is coming from a poor food source, she is less likely to perform a recruitment dance. If the source is very poor, she may not dance at all or may even abandon the source and become susceptible to recruitment. Presumably this involves the loss of the time-memory for that particular food source, but this has never been tested. Through this mechanism, the foragers are directed to the most profitable sources. As these sources are constantly changing, the criteria for defining a profitable source are also changing and thus this feedback loop is important in always keeping the flow of food into the hive at its maximum.

Forager honey bees use the same mechanisms regardless of the type of forage. Both pollen and nectar foragers perform the recruitment dances to recruit more foragers to a source. They also determine the source profitability from the quickness by which they are unloaded. Nectar foragers (von Frish, 1967) develop a time-memory for food source availability. Increasing experience at the source strengthens this memory (Moore, unpublished). Water is only used by honey bees as a thermoregulator and thus is collected only when the hive's internal temperature is becoming too hot (Lindauer 1961). However, it has been shown that there are always at least a small number of bees foraging for water (Visscher et. al. 1996). When temperatures increase past a threshold, the receiver bees unload water foragers first and the nectar and pollen foragers last. This lets the water foragers know that there is a need and they begin to recruit more foragers. At the same time, the nectar/pollen foragers decrease their recruiting or switch over to water foraging (von Frisch 1967).

This wealth of knowledge accumulated on the mechanisms of forager allocation has led to many questions that have yet to be answered. The factors affecting recruitment have been well studied. Time-memory has also received a large amount of attention. What has not been looked at is the effect that time-memory has on recruitment. It has been shown that more experience at a food source strengthens the time-memory that, in turn, increases the time it takes to go extinct. What influence does a strong time-memory have on an individual bee's willingness to be recruited?

We have developed three hypotheses on how the forager honey bee's time-memory can influence its recruitability. First, the time-memory could play no part in the individual forager's susceptibility to recruitment. If this "extinction-irrelevant" hypothesis is the case, then we would predict that every forager will demonstrate the same willingness to switch to a new food source, no matter how strong its memory is. Previous thoughts and models on allocation/re-allocation of foragers suggest that this would be the case (Seeley et al. 1991; Bartholdi et al. 1993; de Vries and Biesmeijer 1998; Saunders 2002). On the other hand, the time-memory could influence recruitment in various ways. A second hypothesis, the "incomplete extinction" hypothesis, states that a strong time-memory could inhibit recruitment to a new food source but only when the memory is fresh and still strong. If this is the case, then we would predict that foragers with a strong time-memory will be more likely to remain loyal to the old food source. However, as the time-memory begins to weaken because of apparent extinction (Moore unpublished) the receptivity to recruitment will increase and the forager bees will begin to switch to new food sources. In the final hypothesis, the "complete extinction" hypothesis, the time-memory might completely block a forager bee's ability to be recruited to a new food source. If this is the case, then we would predict that a forager's time-memory would have to decline to complete extinction before the bee could switch to a new food source. It is the goal of this study to discern between these hypotheses.

CHAPTER 2

MATERIALS AND METHODS

Study Area

All experiments occurred at the old Marine Corps Armory, west of State of Franklin Rd. and bounded on the south by McKinley Rd. in Johnson City, Tennessee [36°20'7"E, 82°22'22"W] (Fig. 2). This 30-acre site has a mix of wooded areas and grassy open areas that support a large variety of flowering plant species. These plants include: blackberry, joe-pye-weed, iron weed, butterfly weed, dogbane, Clematis, everlasting pea, sumac, and a variety of asters and goldenrods. A variable number of colonies were housed on site, either in one of five standard commercial bee hives, or in one of three observation hives (two four frame hives and one three frame hive). The commercial hives were located along the perimeter of the site while the observation hives were set up in sheds located in the southwest corner of the property.

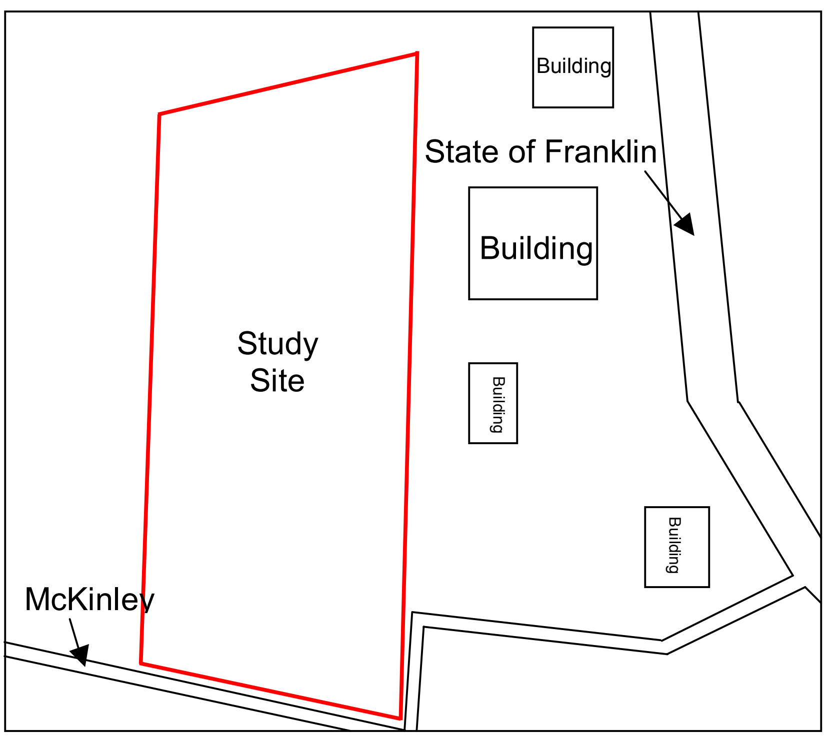

Figure 2 Map of study site.

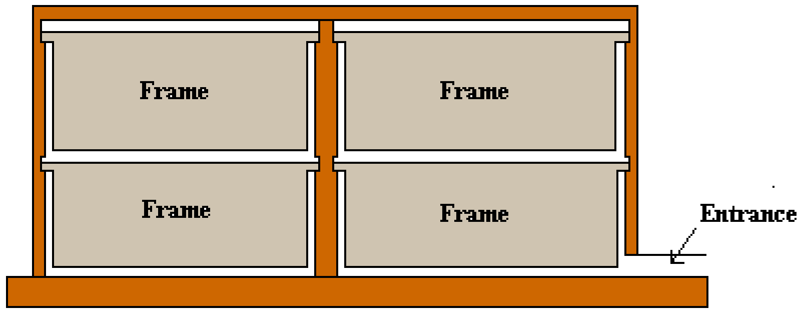

Figure 3 Observation hive. A pane of glass covers each side that allows for viewing of in-hive activities and behaviors.

Training Procedure

There is a standard procedure used to train forager bees to a specific artificial feeder (von Frisch 1967) which was followed in the present study. The standard table used in these experiments has a foot square top with four legs, each a foot tall. The first step was to place a training table within one meter of the hive entrance with a level ramp leading from the entrance to the table. Droplets of sucrose were placed at the hive entrance. Once the forager bees were regularly feeding off of the first droplets, other droplets were placed farther away, thus slowly leading the foragers down the ramp and to the training table. A full Petri dish of sucrose solution was placed in the middle of the table on a circular piece of filter paper. When 7 to 10 bees were consistently returning to the Petri dish, the table was moved away from the hive in increments of one meter for the first 10 to 20 meters so that the forager bees did not lose track of the dish. After the initial 20 meters, the table was then moved at 10 meter increments until the desired distance was reached. A distance of 100m was chosen, ensuring that the majority of forager bees would perform the waggle dance for recruitment (von Frisch 1967). This behavior contains both information on distance and direction and serves to recruit hive-mates to the proper station.

Experimental Design

To test the hypotheses and their predictions, the following series of experiments were performed. For each experiment, two different groups of forager bees were trained to two separate feeding stations using the general procedure discussed above with a slight variation. We started at the hive with one table and petri dish where foragers were trained to the sucrose solution as stated above. After the table had been moved out 7 to 10 meters from the hive entrance, a second dish was placed next to the first one. Once bees were feeding from both dishes, the second dish was slowly moved to the second table. If at any time we lost a response to either dish, the dishes were moved next to each other again. At this time the tables were moved away from each other in different directions. When the tables were separated by two to three meters, different essential oils were applied to the filter paper under the two petri dishes to scent the different food sources. This scent was only used to assist the forager honey bees in differentiating between to two sources and returning to the correct source. Now that the tables were split, each was moved out to 100m using the above described method.

In three of the four experiments, the honey bees were housed in an observation hive (Fig. 3). In the fourth experiment, a commercial hive was used to confirm that the observed trends persisted in larger colonies. A previous study had reported that foraging behavior varied little between large and small colonies (Beekman et al. 2004). The feeding stations were located in different directions from the hive with a minimum of 60° angle separating them (Fig. 4). At the same time each following day, a Petri dish containing a 2M sucrose solution was set out at both stations and each was monitored for the duration of the training time that varied from one to two hours depending on the experiment. It has been shown previously that honey bee foragers' response to artificial food sources is statistically similar to their response to natural sources

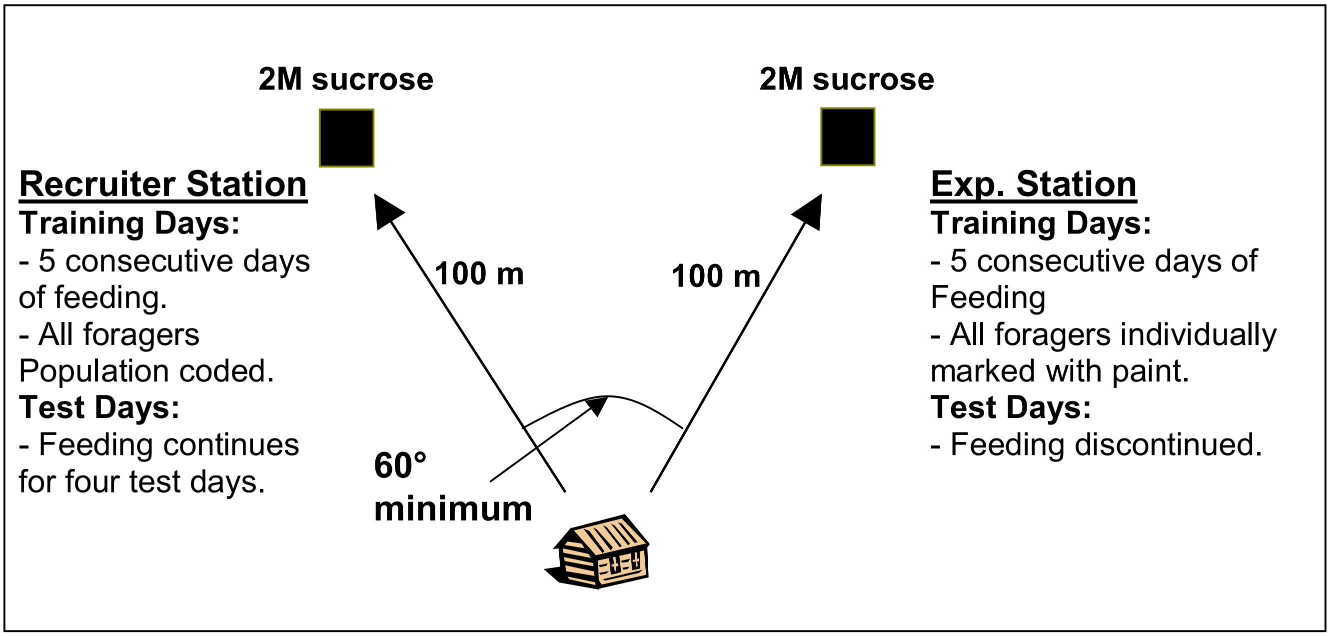

Figure 4 Diagram of experimental design

(Butler et. al. 1943). The training time duration needed for each experiment was determined on the first day of the experiment, depending on the amount of time required to recruit the necessary number of forager honey bees (at least 20 new recruits each day). All bees arriving at the experimental station were individually marked. Specific color combinations (Testors pla enamel) were painted in dots on the abdomen and thorax of each bee as it fed. This marking allowed us to record all arrivals of each individual forager through out the experiment as well as document the number of rewards (successful feeding at the artificial food source) on each training day. This also allowed for the census of the observation hive for the remainder of the experiment. If at any time, the arrival of new recruits became too great to paint all new individuals; those that did not get marked were eliminated using a pair of forceps. Bees arriving at the recruiter station were not individually marked but were given the same population code with color dots painted on their thoraces for location identification. This training procedure was continued for five training days (days when food was set out at both stations at the specified time).

After five days, the food source at the experimental station was discontinued while the food at the recruiter station remained the same. This new feeding protocol was continued for a total of four test days (days when food was set out only at the recruiter station). Both stations were monitored for a minimum of four hours prior to and four hours after the initial training time during the test days. This allowed for all forager visits during the day to be recorded. A detailed visual census of the observation hive for all living marked bees was performed a minimum of three times each test day, with one occurring during the original training time. The proportion of bees returning each day was calculated as the total number of marked bees that returned to the feeding stations divided by the total living number determined by the census. When the commercial box hive was used (Experiment 3), a different procedure was used to determine the number of living bees. As a hive census was not possible, a "re-recruitment" day was added at the end of the experiment. On the re-recruitment day, the bees were once again fed and the

Table 1 Specific information on each experiment

Experiment #	Test day dates	Scent used	Hive used
1	August 4th – 7th 2003	Exp. = Anise[a] Rec. = Peppermint[b]	4-frame observation hive
2	July 29th – Aug. 1st 2005	Exp. = Lavender Rec. = Lilac	3-frame observation hive
3	July 29th – Aug. 1st 2006	Exp. = Anise Rec. = Almond	Commercial box hive
4	Sep. 27th – 30th 2006	Exp. = Anise Rec. = Almond	3-frame observation hive

[a]Exp. = experimental station
[b]Rec. = recruiter station

original scent was used at both stations during the training time. Bees initially trained to the station were recruited to it once again. These bees were counted to provide the total number of living bees. Four experiments were completed: three using observation hives and one using a commercial field hive (Table 1).

Data Analysis

All data from each individual experiment were analyzed separately and the results compared. Each bee was categorized according to its number of consecutive training days. This resulted in five distinct cohorts with either five, four, three, two, or one day(s) of training. These cohorts were further subdivided according to the stations visited during each separate test day, with possibilities being experimental station only, recruiter station only, or both stations. This process gave a total of sixty distinct groups. These numbers were compared to the total number of living bees in each cohort on each test day which yielded proportions of bees returning for all test days, locations, and training cohorts.

Statistical tests included χ^2 tests on 2 x 2 contingency tables to test for differences in proportions between training cohorts for each test day. These tests were used to show if there were significant differences in abandonment of the experimental station and recruitment to the recruiter station between foragers with different amounts of training to the original training station setup. A multiple comparison of arcsine transformed proportions (Zar 1996) was performed for each cohort to determine if there were any trends in arrivals from test day to test day. In these comparisons, data from each cohort for all four experiments were pooled to increase the sample size in each training cohort. These combined results were then analyzed using the same methods described above. The combined mean rewards were then compared to see if the number of rewards influenced the forager bee’s behavior. A Kruskal-Wallis multiple comparison was performed on these means. If significance was determined, then Mann-Whitney pair-wise comparisons were used to pinpoint the significant differences.

CHAPTER 3

RESULTS

For each of the experiments, the forager bees were divided into cohorts according to the number of days of training they received. For a bee to be included in a specific cohort, it had to have returned for at least one reward every training day after the initial day it was painted. The complete reward and arrival history of the bee was required for it to be included in one of the cohorts; bees with incomplete data were excluded. All data from all training days were collected and then condensed into tables showing total number of rewards per day allowing for only bees that fit the qualifications to be included (see Table 11-13, 22-24, 33-35, 44-46 in the appendices). The total number of bees in each cohort varied between experiments (Table 2). Bees with one day of training consistently had the largest total numbers. This would make sense as they needed only a single trip from the hive after the initial painting to be counted, which would minimize their probability of death. They were also recruited to the experimental station by the largest number of previously recruited foragers.

These cohorts were then subdivided according to their arrivals at the two different stations over the next four test days. All arrival data were collected and then condensed into arrival proportions for each cohort at the experimental station only, the recruiter station only, or

Table 2 Total marked bees in each cohort prior to Test Day 1

Experiment #	5 Day Bees	4 Day Bees	3 Day Bees	2 Day Bees	1 Day Bees
1 (August 2003)	15	28	5	20	41
2 (July 2005)	10	11	17	22	27
3 (July 2006)	16	18	12	16	36
4 (September 2006)	25	15	19	9	39
Totals	66	72	53	67	143

at both stations for each test day (see figures 14-18, 25-29, 36-40, 47-51 in the appendices). Because the individual cohort numbers were relatively small, the cohorts were then combined into high and low experience groups. Bees with five and four days of training comprised the high experience group while bees with two and one day(s) of training comprised the low experience group. The three day bees showed similarities with both high and low experience bees and thus were treated as intermediates. Data analyses were then performed on each individual experiment.

Experiment 1

Figure 5 shows the proportions of high and low experience bees arriving at either the experimental station only, the recruiter station only, or both stations for each test day. A larger proportion of the high experience bees (five and four day bees) remained loyal to the experimental station than the low experience bees. The proportion visiting the experimental station decreased in each group over time (Fig. 5: yellow graphs). By test day two, an increased proportion of high experience visited both stations (Fig. 5: green graphs). In contrast the low experience bees were more likely to be recruited to the recruiter station and showed a faster increase in their proportion arriving at the recruiter station than the high experience bees (Fig. 5: black graphs).

A multiple comparison of arcsine transformed proportions (Zar 1996) was performed for each individual graph in Figure 5. Any significant difference between proportions returning on each test day was signified by a different letter above the bar on the graph. The proportion of high experience bees returning to the experimental station was significantly higher on test day one in comparison to test day three and four (Fig. 5: top graph, column A). The proportion of high experience bees being recruited to the recruiter station was significantly lower on test day

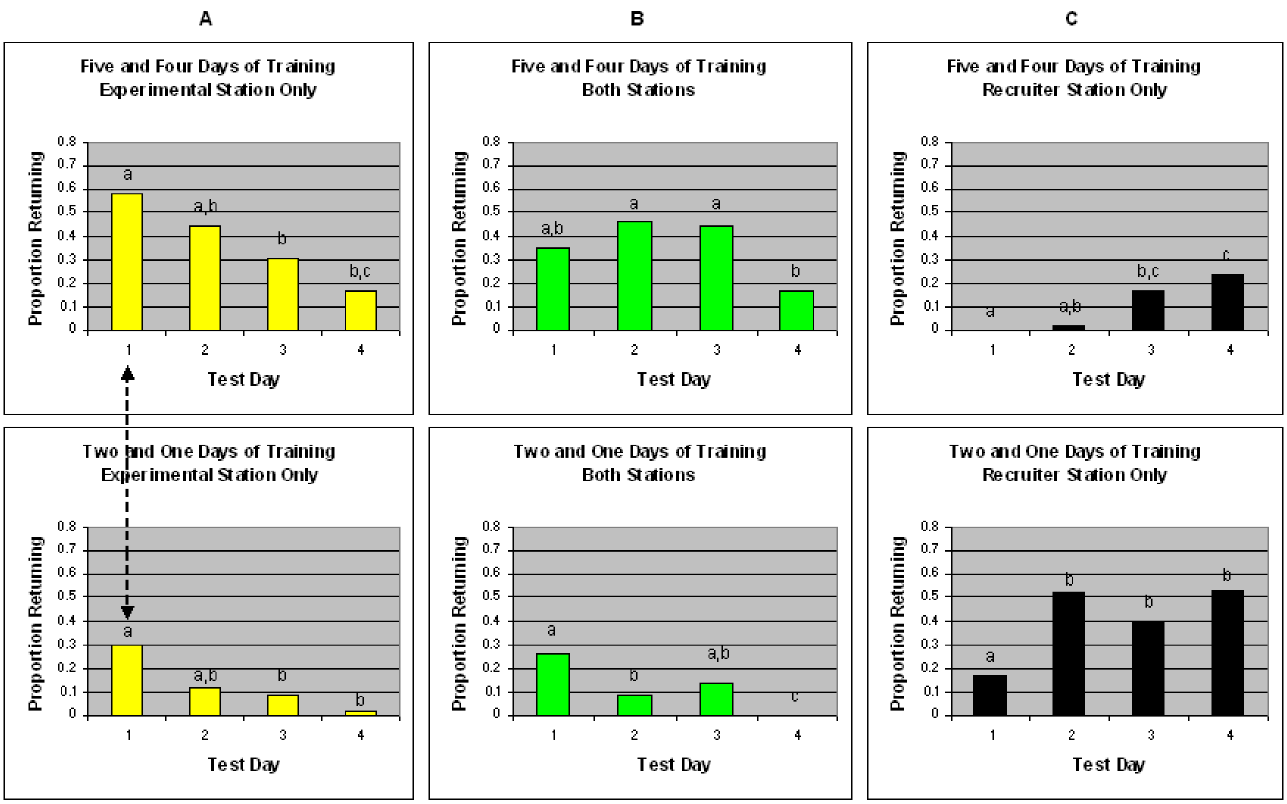

Figure 5 Experiment 1, July 31st-August 7th 2003. Proportion of foragers returning on each test day. The foragers arrivals were divided into those that only arrived at the experimental station (A), those that only arrived at the recruiter station (C), and those that arrived at both stations on a given test day (B). The arrivals were further divided into high experience bees (five and four days of training, upper graphs) and low experience bees (two and one days of training, lower graphs). Chi-square analysis was performed between high and low experience bees for each test day and arrival location(s) (see dashed arrows) Trend analysis using multiple comparison of proportions (Zar, 1996) was performed for each separate graph. Within each graph, bars that do not share letters are significantly different from each other ($P \leq 0.05$).

one in comparison to test day three and four (Fig.5: top graph, column C). The proportion of high experience bees visiting both stations was significantly higher on test days two and three in comparison to test day four (Fig. 5: top graph, column B). The proportion of low experience bees returning to the experimental station was significantly higher on test day one in comparison to test day three and four (Fig 5: bottom graph, column A). The proportion of low experience bees being recruited to the recruiter station was significantly lower on test day one in comparison to all other test days (Fig.5: bottom graph, column C). The proportions low experience bees visiting both station was significantly higher on test day one in comparison to test day two and four with test day four being significantly lower than any other day (Fig.5: bottom graph, column B).

Chi-square analyses were performed to test for significant differences in arrivals of high experience bees versus low experience bees (Table 3). A separate test was conducted for each test day as well as for arrivals at the experimental, recruiter, or both stations (see dashed line in Fig. 5 for example). High experience bees arrived at the experimental station in significantly higher proportions than did low experience bees on every test day (Table 3: left column). Low experience bees were recruited to the recruiter station in significantly higher proportions on every test day (Table 3: right column). High experience bees were able to go to both stations in significantly higher proportions on every test day except test day 1 (Table 3: center column).

Table 3 Experiment 1 Chi square analysis: August 2003

	Experimental Station Only	Both Stations	Recruiter Station Only
Test Day 1			
Chi-square score[a]	7.040	0.461	6.150
P value	**0.008**[b]	0.497	**0.013**
Test Day 2			
Chi-square score	12.032	17.449	26.846
P value	**<0.001**	**<0.001**	**<0.001**
Test Day 3			
Chi-square score	6.468	10.146	5.391
P value	**0.011**	**0.001**	**0.020**
Test Day 4			
Chi-square score	5.371	7.844	7.188
P value	**0.020**	**0.005**	**0.007**

[a]Degrees of freedom = 1 for all Chi-square analyses
[b]Numbers bolded in red are significant

The total number of arrivals for each cohort at either the experimental station or recruiter station on each test day was also examined. These arrivals were divided by time into 15 min. increments and displayed in figure 6 and 7.

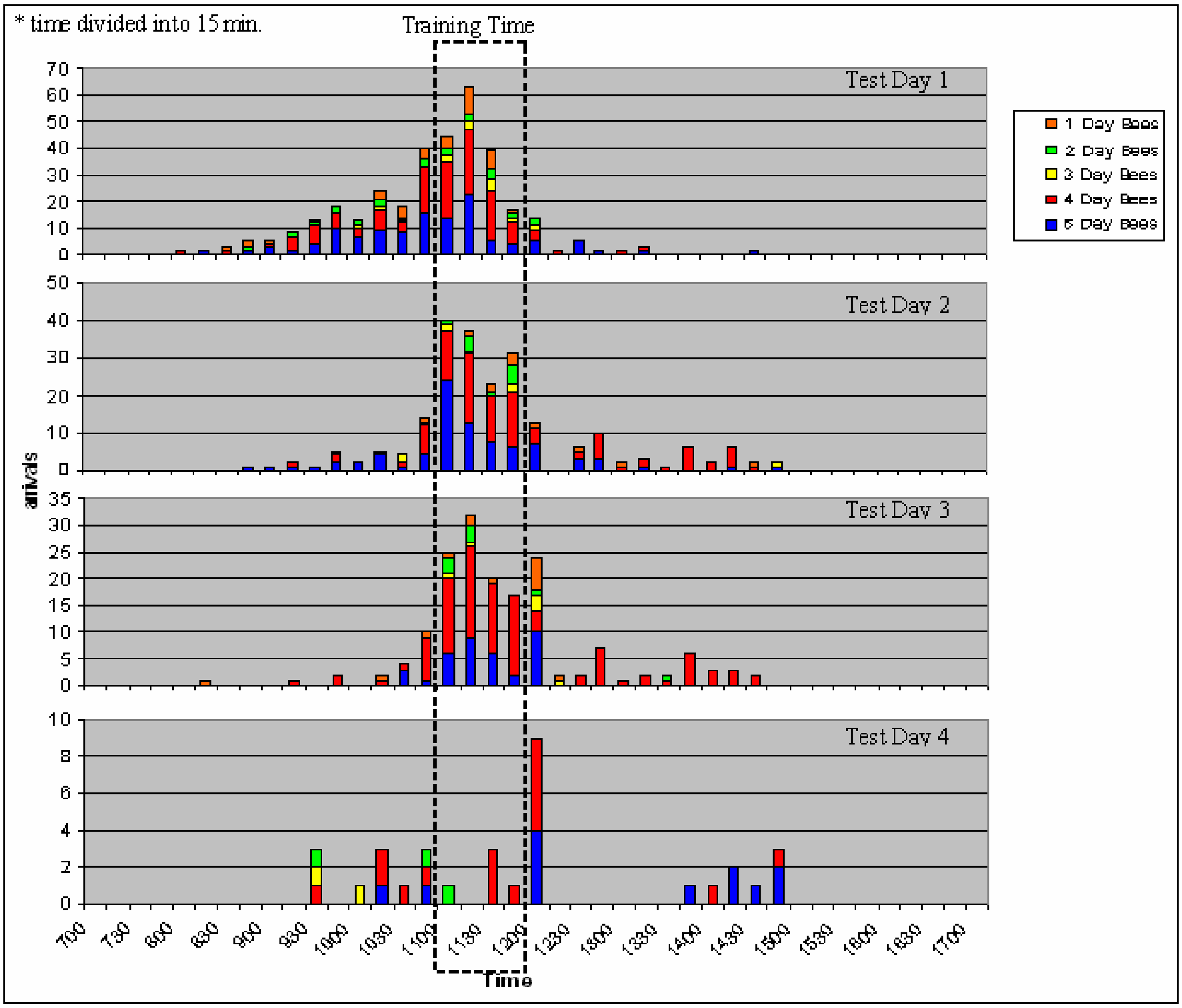

Figure 6 Test day arrivals at experimental station during experiment 1, August 2003. All arrivals were divided and color coded by cohort (see legend). Arrivals were totaled for each 15 minute increment from the start of observations to the end of each test day. The proportion of total arrivals was then found for high experience and low experience bees for each test day (Table 4).

Table 4 Proportion of total arrivals at the experimental station

	Test Day 1	Test Day 2	Test Day 3	Test Day 4
High Experience Bees (5 and 4 days of training)	0.755	0.849	0.833	0.848
Low Experience Bees (2 and 1 days of training)	0.195	0.114	0.131	0.091

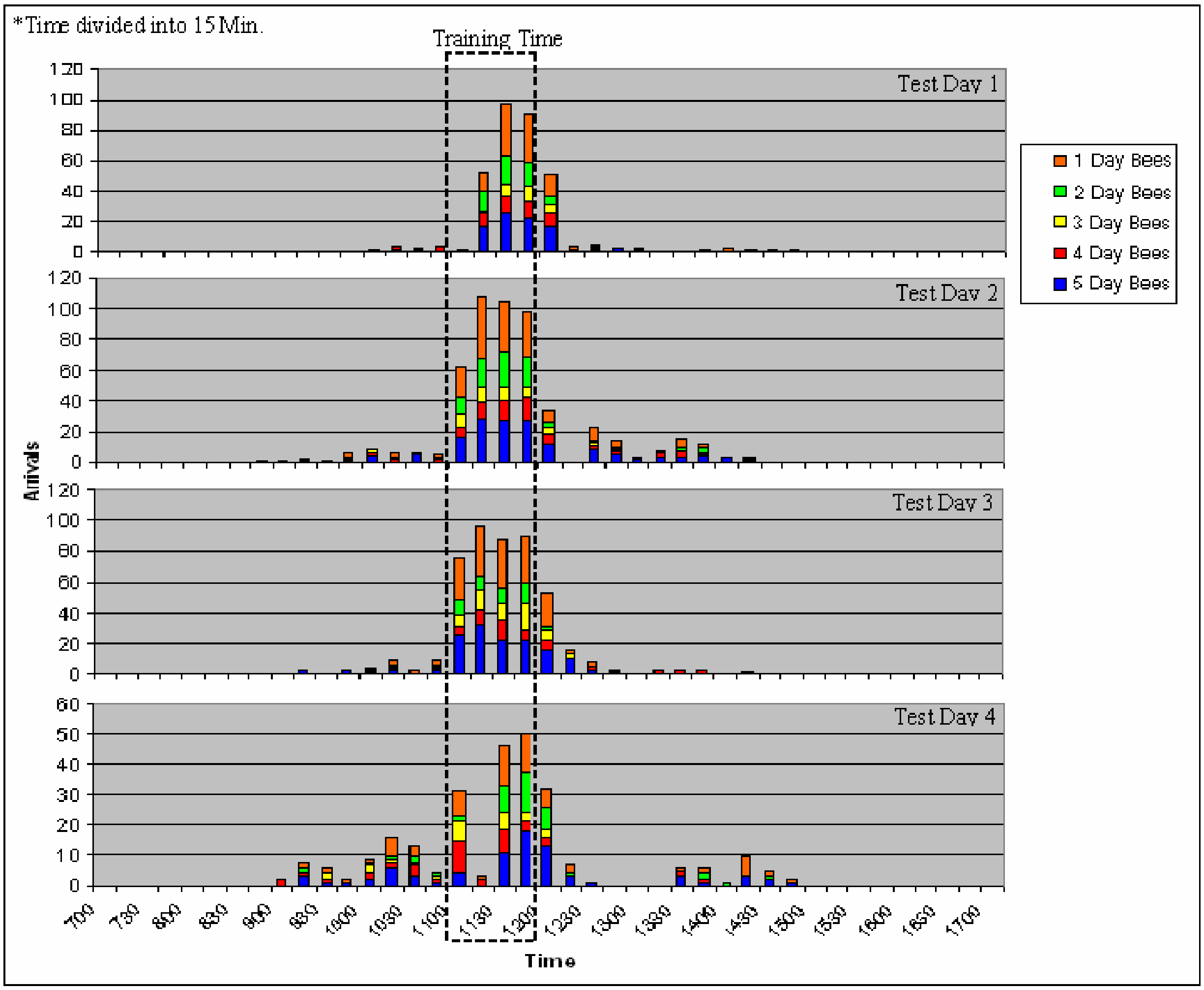

Figure 7 Test day arrivals at the recruiter station during experiment 1, August 2003. See Figure 6 for details.

Table 5 Proportion of total arrivals at the recruiter station

	Test Day 1	Test Day 2	Test Day 3	Test Day 4
High Experience Bees (5 and 4 days of training)	0.422	0.430	0.439	0.462
Low Experience Bees (2 and 1 days of training)	0.494	0.480	0.433	0.442

The foragers arrived at the experimental station in the greatest numbers during the training time on test days one, two, and three demonstrating that they were indeed time-trained to the food source (Fig. 6). High experience bees made up a larger proportion of these arrivals, on all test days (Fig. 6: blue and red bars; table 4). Low experience bees were recruited in greater proportions to the recruiter station (see Table 3; right column) but shared roughly an equal proportion of total arrivals on all test days (Fig. 7: orange and green bars; Table 5). This result is surprising because with higher proportions being recruited, one would have expected the low experience bees to have a higher proportion of total arrivals. The recruiter station arrivals in this experiment were the exception when compared to the other three experiments. In the other three experiments, the low experience bees made up the greater proportion of total arrivals on test days one and two (see figures 21, 24, & 27 in the appendices). As the foragers time-memory decays, their receptivity to recruitment increases and thus by test days three and four, the high experience bees make up an equal proportion of the total arrivals (see figures 21, 24, & 27 in the appendices).

After analyzing all four experiments, many similarities were noticed in the separate results (see Appendices A-D). These similarities include: **1)** all experiments had high proportions returning to the experimental station on test day one that decreased over the four test days (Fig. 5: yellow graphs); **2)** high experience bees had higher proportions returning to the experimental station then low experience; **3)** all experiments had low proportions initially being recruited to the recruiter station which then increased over time (Fig. 5: black graphs); **4)** low experience bees had higher proportions being recruited to the recruiter station in comparison to the high experience bees; **5)** high experience bees were able documented going to both stations in higher proportions then low experience bees; **6)** all experiments had very similar total arrival graphs (Fig. 6 & 7), and proportions of total arrivals (Table 4 & 5). The one main inconsistency among the four experiments was the amount of significance found in our chi-square analyses. Experiment 1 had the greatest amount of significance (Table 3), while other showed very little significance (see figures 30, 41, 52 in the appendices). This variation could have been due to the low sample sizes in the individual experiments. Because of the many similarities between experiments and to alleviate any possible errors because of small sample size, we pooled the data and then re-analyzed these larger numbers.

Pooled Results

Figure 8 shows the pooled proportions of high and low experience bees arriving at either the experimental station only, the recruiter station only, or both stations for each test day. These pooled results show even greater trends in proportions arriving at the different stations from test day to test day (letters above individual bars; see discussion of procedure earlier in results). As in each individual experiment, a larger proportion of high experience bees (five and four day bees) remained loyal to the experimental station then the low experience bees with the proportion decreasing in each group over time as the time-memory went extinct (Fig. 8: yellow graphs). By test day two, a greater proportion of high experience bees also visited both stations at once (Fig. 8: green graphs). In contrast, the low experience bees were more likely to be recruited to the recruiter station and showed a faster increase in their proportion arriving at the recruiter station

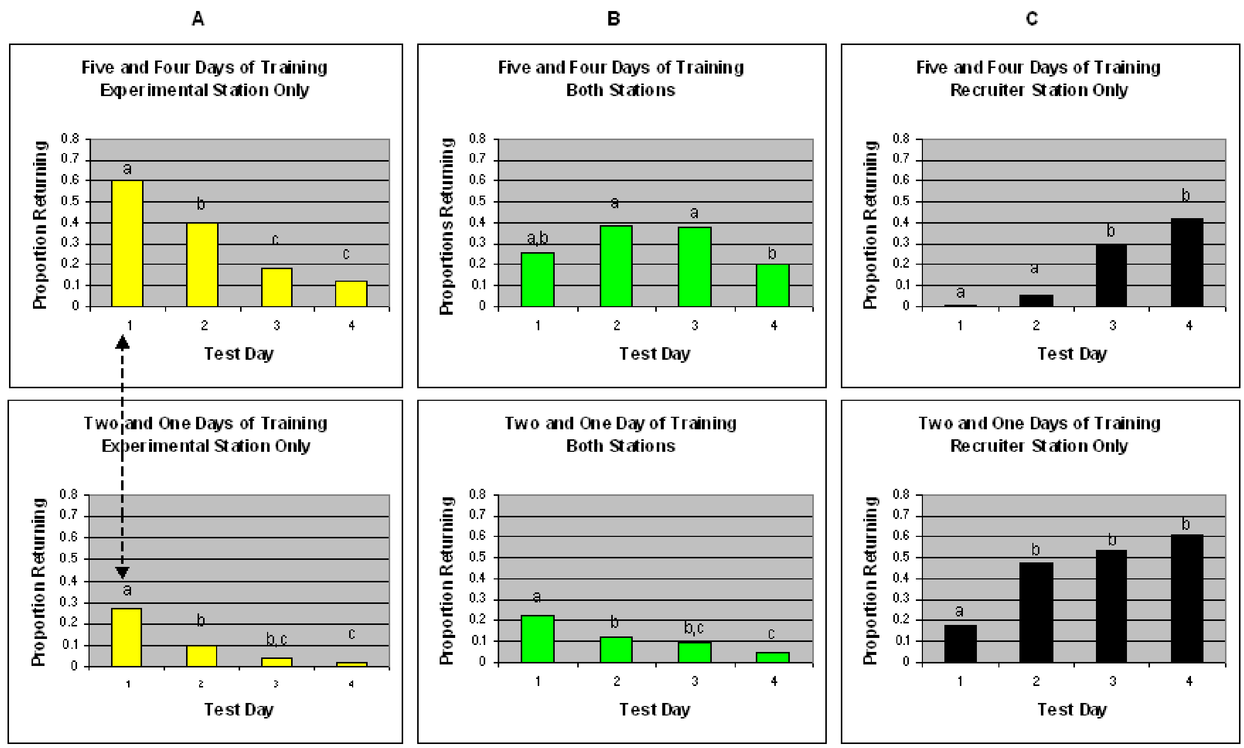

Figure 8 Pooled results of all four experiments, 2003 - 2006. Proportion of foragers returning on each test day. See Fig. 5 for details.

then the high experience bees (Fig. 8: black graphs). By pooling the data, the differences between high and low experience bee arrivals has been increased and is reflected in the Chi-square analysis. The pooled Chi- square analysis show extreme significance for arrivals at either station (or both stations) for almost every single test day (Table 6).

To further analyze these pooled data, we looked at the number of rewards foragers received over the training days to determine if rewards played a part in recruitment. The mean number of rewards received by high and low experience bees over the training days was determined for each individual test day (Table 7). The means were then seperated by the bee's arrivals at the experimental station only, recruiter station only, and both stations. These means were then used in a Kruskal-Wallis multiple comparison to determine if there was any difference between mean rewards of bees in the high and low experience cohorts that remained loyal to the experimental station, switched to the recruiter station, or went to both stations. The results

Table 6 Pooled results Chi-square analysis

	Experimental Station Only	Both Stations	Recruiter Station Only
Test Day 1			
Chi-square score[a]	34.341	0.325	21.797
P value	**<0.001**[b]	0.569	**<0.001**
Test Day 2			
Chi-square score	40.617	29.181	60.350
P value	**<0.001**	**<0.001**	**<0.001**
Test Day 3			
Chi-square score	14.426	32.473	16.360
P value	**<0.001**	**<0.001**	**<0.001**
Test Day 4			
Chi-square score	10.698	14.722	8.376
P value	**0.001**	**<0.001**	**0.004**

[a]Degrees of freedom = 1 for all Chi-square analyses
[b]Numbers bolded in red are significant

showed significance only in the low experience bee's arrivals at the different stations on test day one and two (Table 8). There was no significant difference in the number of rewards received by high experience bees that went to different stations. Through the Mann-Whitney pair-wise comparison (Table 9) we were able to determine that low experience bees with fewer rewards were significantly more likely to abandon the old food source and be receptive to recruitment. In other words, the number of rewards influenced the forager bee's time-memory and thus its loyalty to the original food source, but only to a point. After a certain number of rewards, or a certain number of days, the rewards no longer play a significant role in time-memory and loyalty. However, this possibility was not directly tested in this experiment.

Table 7 Mean number of rewards over the training days[a]

Test Day #	High Experience Bees: Experimental Station	Both Stations	Recruiter Station	Low Experience Bees: Experimental Station	Both Stations	Recruiter Station
1	27.63	23.59	19.00	5.17	4.61	2.00
2	27.88	23.55	23.43	8.00	6.30	2.90
3	24.32	26.00	20.97	4.75	3.83	3.51
4	20.85	33.36	23.13	10.00	5.86	3.29

[a]The mean was calculated for arrivals at each station for each test day

Table 8 Kruskal-Wallis multiple comparison analysis[a]

	High Experience Bees	Low Experience Bees
Test Day 1		
H (test value) [b]	0.818	18.403
Probability	0.664	**<0.001**[c]
Test Day 2		
H (test value)	1.530	23.003
Probability	0.464	**<0.001**
Test Day 3		
H (test value)	2.750	4.580
Probability	0.252	0.101
Test Day 4		
H (test value)	3.360	1.830
Probability	0.186	0.400

[a]High experience bees and low experience bees were both analyzed separately
[b]Degrees of freedom = 2 for all analyses
[c]Significant numbers shown in red

Table 9 Mann-Whitney pair-wise comparison[a]

	Experimental vs. Both Station Bees	Experimental vs. Recruiter Station Bees	Both Station vs. Recruiter Station Bees
Test Day 1			
U =	968.50	499.00	266.50
z-score	0.029	3.590	4.060
P value	0.977	**<0.001**	**<0.001**
Test Day 2			
U =	165.00	322.50	575.00
z-score	1.103	4.019	3.280
P value	0.270	**<0.001**	**0.001**

[a] Tests were performed between the experimental and both station bees, experimental and recruiter station bees, and then both station and recruiter station bees

[c]Significant numbers shown in red

CHAPTER 4

DISCUSSION

The results from this experiment demonstrate that the honey bee time-memory exerts an inhibitory influence on forager receptivity to recruitment. Foragers with a stronger time-memory (i.e., more days of experience) are significantly more likely to remain loyal to the original food source and are less likely to be recruited. In accord with this finding, foragers with a weaker time-memory (fewer days of experience) are significantly less likely to remain loyal to the original food source and are more receptive to recruitment. Consequently, significantly higher proportions of low-experience bees compared to high-experience bees are recruited sooner to the new food source. However, for both low- and high-experience bees, as the forager's time-memory decays, receptivity to recruitment does increase while loyalty to the old food source decreases (see Fig. 8). Our results demonstrated that, even after four unrewarded test days, high-experience bees still arrived at the experimental station in higher proportions than low-experience bees. Also, low-experience bees were still recruited in higher proportions to the recruiter station than high experience bees. With these results in mind, what hypotheses are supported or refuted by the data?

Figure 9 illustrates a simple model for the relationship between time-memory and recruitment sensitivity. This represents the first attempt at conceptualizing the possible organization of behavioral controls and relationships. The circadian oscillator (upper box) is the master timekeeper. Different forms of experience influence subsequent foraging behavior. In the case of our experiments, one type of experience is a successful foraging trip to the food source. Previous studies (Moore unpublished; Fig. 1) have shown that experience at a food source influences the strength of the time-memory as well as the rate of decay. This experience

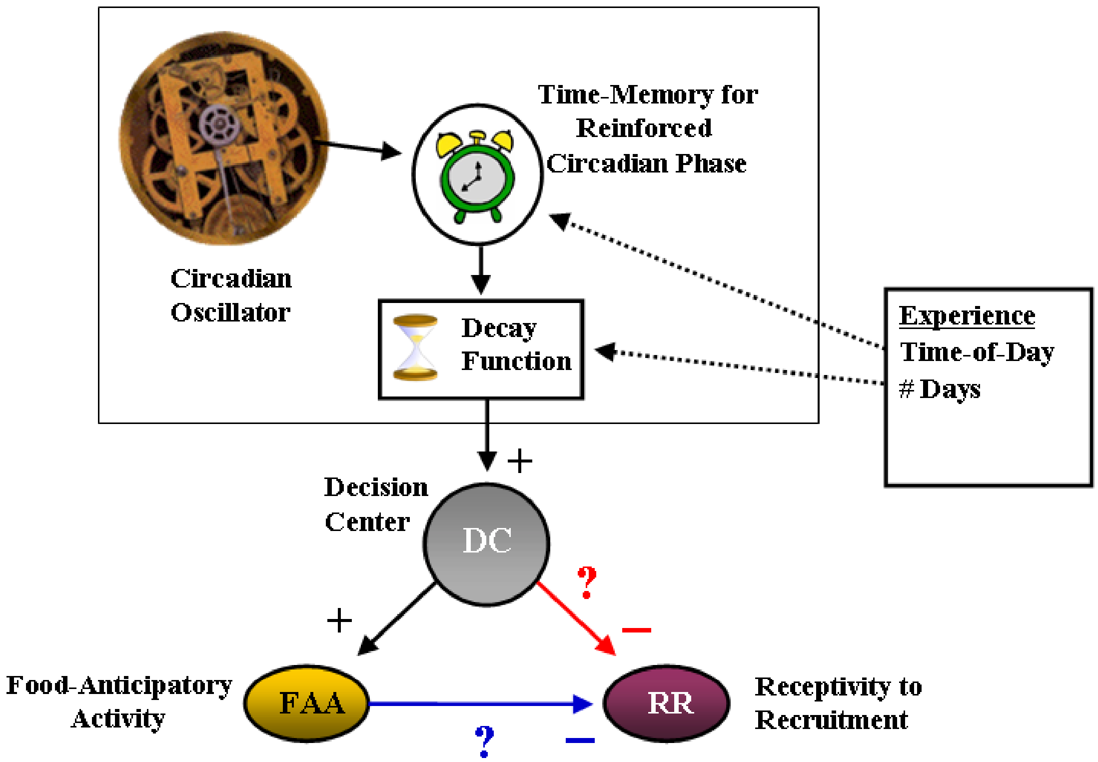

Figure 9 Simple model of the possible interactions between experience, time-memory, food-anticipatory activity and receptivity to recruitment. Experience has been shown to set the phase of time-memory and influence the decay function which then influences (+ signs) food-anticipatory activity. Possible inhibitory affects (- signs) on receptivity are shown with a red and blue line and question mark.

affects the honey bee forager in two ways. First, the experience of being rewarded at a particular time-of-day sets the phase of the time-memory represented by the alarm clock. In other words, the bee now remembers the time and place that it successfully foraged. Increasing the number of days of experience at a time of day serves to strengthen the accuracy of the time-memory (Moore and Doherty, in preparation). Second, the number of days also influences the rate decay of its time-memory – its apparent extinction (Moore et al., in preparation). More experience leads to a slower initial rate of decay as well as a higher initial proportion of returning foragers and a longer time before reaching extinction (see Fig. 1). The elevated time-memory response and extended decay then influences a forager bee's food anticipatory activity (forager bees returning to a food source at or often before its peak profitability) and potentially the foragers receptivity to recruitment. The ultimate goal of this project is to determine how this neuro-behavioral process affects the forager bee's receptivity to recruitment as well as the allocation of foragers to food sources in the environment. Does time-memory directly affect receptivity independent of food-anticipatory activity (Red-line, Fig. 9)? Does the time-memory directly influence food anticipatory activity which then must decay to a certain level before receptivity is permitted (Blue-line, Fig. 9)? Or, does time-memory have no influence at all on receptivity?

Our first hypothesis, the extinction-irrelevant hypothesis (Fig. 10), proposes that there is no linkage between a forager bee's time-memory and its receptivity to recruitment. If this is the case, then any forager is as likely to be recruited as the next, regardless of the strength of its time-memory. Our results have shown a difference in recruitment between the high and low experience bees and thus this hypothesis cannot be supported.

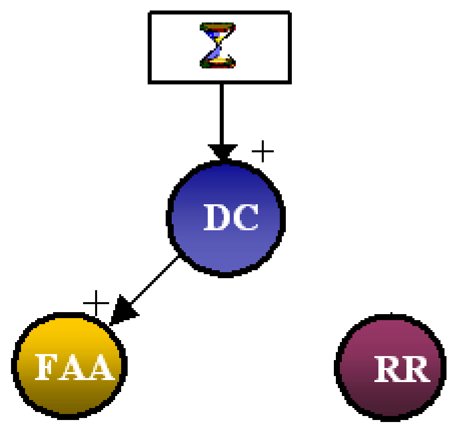

Figure 10 Extinction-irrelevant hypothesis. Note that there is no direct link between time-memory and receptivity to recruitment.

Our second and third hypotheses, the complete extinction (Fig. 11) and incomplete extinction (Fig. 12) hypotheses, both posit a linkage between a forager bee's time-memory and its receptivity to recruitment. In the complete extinction hypothesis, time-memory must decay to the point of complete extinction before the forager bee can be receptive to recruitment. At that time, the bee can be recruited to

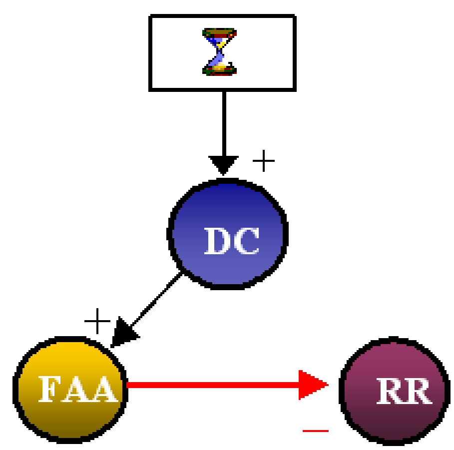

Figure 11 Complete extinction hypothesis. Note that the extinction of the time-memory eliminates the food anticipatory activity which then eliminates any inhibition on receptivity to recruitment.

and switch to a new food source. Furthermore, because its original time-memory has decayed to extinction, it will not return to the old food source. Similarly, in the incomplete extinction hypothesis, the time-memory must decay toward extinction before recruitment can occur. However, the complete extinction of the time-memory is not required (as in the complete extinction hypothesis): the receptivity to recruitment increases concurrent with the decline in food anticipatory activity. Under these conditions the forager bee potentially could be recruited to a new food source while maintaining reconnaissance to the old food source.

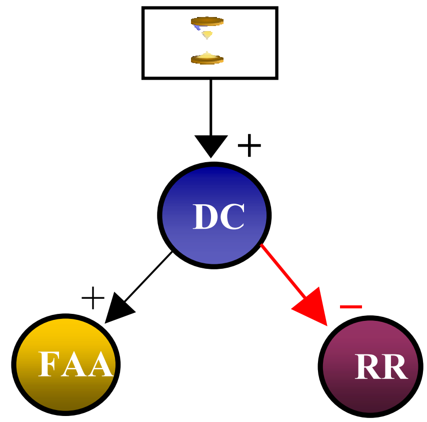

Figure 12 Incomplete extinction hypothesis. Note that time-memory has separate affects on food anticipatory activity (FAA) and receptivity to recruitment (RR). As time-memory decays towards extinction, the FAA decreases at the same time that RR increases.

To discern between the complete and incomplete extinction hypotheses, the forager bees that were documented at both stations on the same day must be examined in more detail. If these bees switch to the new food station (are recruited) and then never return, then the complete extinction hypothesis is supported. On the other hand, if the bees show an ability to go back and forth between both stations (i.e. are recruited while maintaining a memory for the old source) then the incomplete extinction hypothesis is supported. Through the four experiments, 185 forager bees were documented (Table 10) arriving at both stations on the same test day.

Table 10 Behavior of forager bees documented at both stations

Recruited and Done[a]	Dual Memory[b]	Unsuccessful Recruitment[c]	Total
62	110	13	185

[a]Bees that were recruited and never returned to the original station.
[b]Bees that were documented going back and forth between stations
[c]Bees that arrived at the recruitment station but never received a reward

Of those bees, 110 returned to the old food source after being recruited to the new food source. This ability to develop a new memory while still maintaining the old memory supports the incomplete extinction hypothesis and not the complete extinction hypothesis. Bees with more experience at a food source remain loyal to the original food source longer. However, as their time-memory decays towards apparent extinction, their receptivity increases and they will be recruited with a proportion of them still returning to the old food source.

This result was unexpected. It had been previously accepted that once a bee was not actively foraging at a profitable site it was now "unemployed" and could be recruited immediately to a different source (Seeley 1995). This definition then seemed to be used in the framework of many different models of foraging and forager allocation among different food sources (Bartholdi et al. 1993; de Vries and Biesmeijer 1998; Anderson and Ratnieks 1999; Biesmeijer and de Vries 2001). In these studies, experience and time-memory strength were neglected as variables. The forager bees' memory for an old source was not considered to play a role in subsequent foraging behavior. Saunders (2002) even went further to say, "The fact that the rhythm is fairly easily extinguished without positive reinforcement, however, is also of biological importance because there is an ever-changing array of nectar sources, and there is little selective advantage in continuing to arrive at flowers long past their best". If this had been the case, our data would have supported the extinction irrelevant hypothesis. Our data instead indicate a robust influence of previous foraging experience on subsequent foraging behavior.

Why would a forager bee expend the energy to return to an unsuccessful foraging location when there has not been a reward at that location for days? This observed "non-profitable" behavior could be a side affect of an extended time-memory that serves a beneficial purpose in other situations. Saunders (2002), while assuming that the foraging rhythm is quickly extinguished, also theorized that the time-memory persists over a day or two as an adaptive behavior to deal with inclement weather. An extended time-memory would allow the forager honey bee to remember the time and place of a profitable food source over several days of bad weather that has kept them in the hive (Saunders 2002). This would then allow the bee to return days later (after the rain has passed) without having to waste energy relearning the site of this food source. This would be an adaptive behavior to rainy days, but why would a bee continue to return day after day when weather is not an issue?

A second possibility for this "non-profitable" behavior focuses on the ever changing world that the bees inhabit. Flowers produce and cease production of nectar at varying times and for varying reasons throughout their life. Flowering plants also produce flowers in certain conditions and at certain times of the year. They also could stop floral production based on the environmental conditions that they are currently faced with. With the possibility of environmental conditions affecting the availability of food sources, forager bees could be remaining loyal to what was once a profitable food source because there is the possibility that that particular source will rejuvenate. In other words, are the high experience forager bees just waiting for the source to become profitable again because of improved environmental conditions?

After an extensive search of the scientific literature, no studies were found that specifically looked at any possible long term effects that environmental conditions may have on nectar or floral production. On the other hand, there have been other studies that have linked temperature and rainfall to other plant functions and structures. One study found that drought conditions can lead to a decrease in both grain yield and leaf surface area (Passioura 1996). Another found that high temperatures will decrease floral bud size and development in broccoli

(Bjorkman and Pearson 1998). A third study found that water stress will lead to decreased flower production as well as a decrease in the number of ovules per ovary (Frazee and Marquis 1994). Finally, a study found that increases in temperature can lead to a decreased time to abscission (the loss of plant parts, including flowers) (Ascough et al. 2005). With environmental functions affecting a large number of other functions and structures in plants, it is not hard to believe that such factors could lead to fluctuations in nectar and floral production. If future studies find this to be the case, then high experience forager bees are not just returning to an unprofitable source for no reason, they are actually just waiting for the source's profitability to return. This would then give a competitive advantage to the honey bee foragers.

Further Research

Besides the unanswered botanical questions posed above, many other ideas for further research have been stimulated from the results of the current study. These future paths have also been included into an expanded simple model from earlier version (Fig. 13).

Perceived source profitability has previously been shown to influence honey bee forager recruitment (Seeley 1995). During multiple experiments there were unforeseen factors that may have influenced this perceived profitability. During experiment 2 (July 2005), there was a massive recruitment to the recruiter station. This recruitment led to hundreds of bees as well as wasps and yellow jackets trying to forage off of the Petri dishes. Perhaps because of this elevated activity there was a decline in the proportion of arrivals of high experience bees as well as a leveling off of proportion of low experience bee arrivals (Fig. 14). It may be that competition has an inhibitory affect on both food anticipatory activity as well as recruitment (Fig. 13: upper left box; yellow lines).

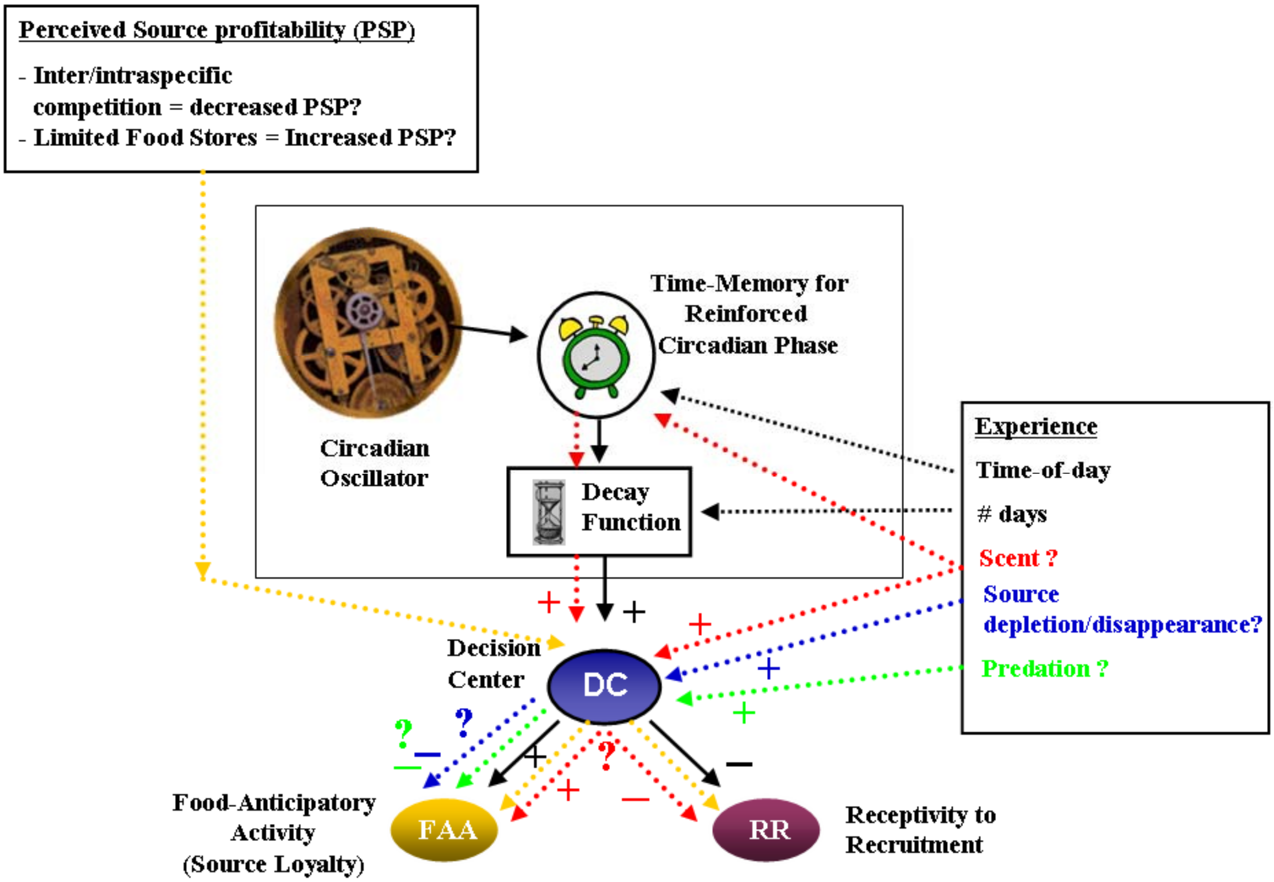

Figure 13 Expanded simple model with other possible interactions included.

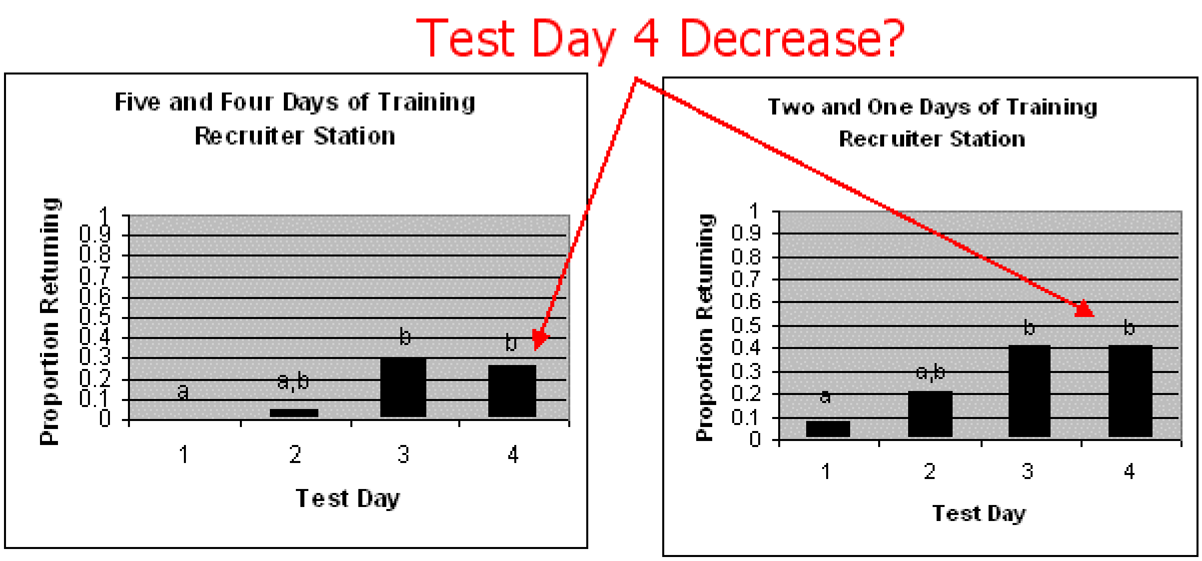

Figure 14 Decline in proportion returning on test day four during experiment 2 (July 2005).

In Experiment 4 (September 2006) the observation hive used had very little food stores and thus had a great need to forage at profitable sources at all cost. This led to a relatively rapid decline in loyalty to the experimental station when compared to a hive with ample food stores (Fig. 15). This in hive factor (lack of food) seemed to influence the perceived source profitability which then inhibited its food anticipatory activity (Fig. 13: upper left box; yellow lines).

Another possible factor influencing forager recruitment is scent. Scents were used in this series of experiments only to differentiate between the two stations, but what affect does scent play in this food anticipatory activity/receptivity to recruitment dynamic? As the scent reminds foragers of the source that was previously profitable, it could have a detrimental affect on receptivity to recruitment while strengthening food anticipatory activity (Fig. 13: red lines and symbols). Possibly the time-memory decay is influenced as much by the absence of the known scent as by the loss of the food source.

Figure 15 Comparison of decline in proportion returning to the experimental station between a hive with ample food stores and one with no food stores.

Perhaps the memory for the non-profitable source did not decay; instead, a new memory was formed from the lack of food at the old site (Fig. 13: blue lines and symbols). The forager is now associating the old known site with a wasted foraging flight. As more flights are made, this association becomes stronger until it causes the forager to abandon the site. In this way the forager bee's observed behavior seem to support the idea that the old time-memory decays toward extinction, but it is instead a new memory altering the forager's behavior while the old memory remains. This would give further light on the behavior demonstrated by those bees that were recruited to the recruiter station while retaining a memory to the old food source (Table 10; dual memory bees).

Finally, in a study conducted by Samara Miller and others, predation by giant robber flies (*Promachus fitchii*) greatly reduced the food anticipatory activity of foragers trained to an artificial food source (Fig. 13: green lines and symbols). Does the present of predators affect the perceived profitability of the source? From the normal recruitment during that experiment, the answer is probably no. Maybe the presence of predators plays a part in an increased decay function or in a more rapid formation of the new memory of a lack of food discussed above.

All of these possible influences show the complexity of the forager honey bee behavior. Research has just begun to scratch the surface of all the possible interactions that can affect this behavior. As is the case in all biology, when one answer is found, many more questions arise.

REFERENCES

Anderson C & Ratnieks FLW 1999: Worker allocation in insect societies: coordination of nectar foragers and nectar receivers in honey bee (*Apis mellifera*) colonies. Behav. Ecol. Sociobiol. 46: 73-81.

Ascough GD, Nogemane N, Mtshali NP, van Staden J 2005: Flower abscission: environmental control, internal regulation and physiological responses of plants. South African Journal of Botany 71: 287-301.

Bartholdi JJ, Seeley TD, Tovey CA, Vande Vate JH 1993: The pattern and effectiveness of forager allocation among flower patches by honey bee colonies. J. Theor. Biol. 160: 23-40.

Beekman M, Sumpter DJT, Seraphides N, Ratnieks FLW 2004: Comparing foraging behavior of small and large honey-bee colonies by decoding waggle dances made by foragers. Functional Ecology 18: 829-835.

Biesmeijer JC 2003: The occurrence and context of the shaking signal in honey bees (*Apis mellifera*) exploiting natural sources. Ethology 109: 1009-1020.

Biesmeijer JC & de Vries H 2001: Exploitation of food sources by social insect colonies: a revision of the scout-recruit concept. Behav. Ecol. Sociobiol. 49: 89-99.

Bjorkman T, Pearson KJ 1998: High temperature arrest of inflorescence development in broccoli (*Brassica oleracea* var. *italica* L.). Journal of Experimental Botany 49: 101-106.

Butler CG, Jeffree EP, Kalmus 1943: The behavior of a population of honeybees on an artificial and on a natural food crop. Journal of Experimental Biology 20: 65-73.

de Vries H & Beismeijer JC 1998: Modelling collective foraging by means of individual behavior rules in honey-bees. Behav. Ecol. Sociobiol. 44: 109-124.

Farina WM 2000: The interplay between dancing and trophallactic behavior in the honey bee *Apis mellifera*. J Comp. Physiol. 186: 239-245.

Fernandez PC, Gil M, Farina WM 2003: Reward rate and forager activation in honeybees: recruiting mechanisms and temporal distribution of arrivals. Behav. Ecol. Sociobiol. 54: 80-87.

Franck P, Solignac M, Vautrin D, Cornuet J, Koeniger G, Koeniger N 2002: Sperm competition and last-male precedence in the honeybee. Animal Behavior 64: 503-509.

Frazee JE, Marquis RJ 1994: Environmental contribution to floral trait variation in *Chanaecrista fasciculata* (Fabaceae: Caesalpinoideae). American Journal of Botany 81: 206-215.

Gil M & Farina WM 2002: Foraging reactivation in the honeybee *Apis mellifera L.*: factors affecting the return to known nectar sources. Naturwissenschaften 89: 322-325.
Haberl M, Tautz D 1998: Sperm usage in honey bees. Behav. Ecol. Sociobiol. 42: 247-255.

Kolmes SA 1989: Grooming specialists among worker honey bees, *Apis mellifera*. Animal Behavior 37: 1048-1049.

Lindauer M 1960: Time-compensated sun orientation in bees. Cold Springs Harbor Symposia on Quantitative Biology 25: 371-377.

Lindauer M 1961: Communication among social bees. Oxford University Press, London UK.

Michener CD 1974: The social behavior of the bees. The Belknap Press of Harvard University Press, Cambridge Mass.

Moore AJ, Breed MD, Moor MJ 1987: The guard honey bee: ontogeny and behavioural variability of workers performing a specialized task. Anim. Behav. 35: 1159-1167.

Moore D 2001: Honey bee circadian clocks: behavioral control from individual workers to whole-colony rhythms. Journal of Insect Physiology 47: 843-857.

Moore D & Rankin MA 1983: Diurnal changes in the accuracy of the honeybee foraging rhythm. Biol. Bull. 164: 471-482.

Moore D & Rankin MA 1985: Circadian locomotor rhythms in individual honeybees. Physiological Entomology 10: 191-197.

Moore D, Siegfried D, Wilson R, Rankin MA 1989: The influence of time of day on the foraging behavior of the honeybee, *Apis mellifera*. Journal of Biological Rhythms 4: 305-325.

Moore D, Angel JE, Cheeseman IM, Robinson GE, Fahrbach SE 1995: A highly specialized social grooming honey bee (Hymenoptera: Apidae). Journal of Insect Behavior 8: 855-861.

Moore D, Angel JE, Cheeseman IM, Fahrbach SE, Robinson GE 1998: Timekeeping in the honey bee colony: integration of circadian rhythms and division of labor. Behav. Ecol. Sociobiol. 43:147-160.

Page Jr. RE, Robinson GE, Britton DS, Fondrk MK 1992: Genotypic variability for rates of behavioral development in worker honeybees (*Apis mellifera* L.). Behav. Ecol. 3: 173-180.

Passioura JB 1996: Drought and drought tolerance. Plant Growth and Regulation 20: 79-83.

Robinson GE 1992: Regulation of division of labor in insect societies. Annu. Rev. Entomol. 37: 637-665.

Robinson GE, Page Jr. RE, Strambi C, Strambi A 1989: Hormonal and genetic control of behavioral integration in honey bee colonies. Science 246: 109-112.

Saunders DS with Steel CGH, Vafopoulou X, Lewis RD 2002: Insect Clocks. Elsevier Science B.V., Amsterdam, the Netherlands.

Schneider SS & McNally LC 1993: Spatial foraging patterns and colony energy status in the African honey bee, *Apis mellifera scutellata*. Journal of Insect Behavior 6: 195-210.

Seeley TD 1994: Honey bee foragers as sensory units of their colonies. Behav. Ecol. Sociobiol. 34: 51-62.

Seeley TD 1995: The wisdom of the hive: the social physiology of honey bee colonies. Harvard University Press, Cambridge Mass.

Seeley TD 1997: Honey bee colonies are group-level adaptive units. The American Naturalist 150: S22-S41.

Seeley TD, Camazine S, Sneyd J 1991: Collective decision-making in honey bees: how colonies choose among nectar sources. Behav. Ecol. Sociobiol. 28: 277-290.

Seeley TD, Kühnholz S, Weidenmüller A 1996: The honey bee's tremble dance stimulates additional bees to function as nectar receivers. Behav. Ecol. Sociobiol. 39: 419-427.

Sumpter DJT & Pratt SC 2003: A modeling framework for understanding social insect foraging. Behav. Ecol. Sociobiol. 53: 131-144.

Tarpy DR, Page Jr. RE 2002: Sex determination and the evolution of polyandry in honey bees (*Apis mellifera*). Behav. Ecol. Sociobiol. 52: 143-150.

Thom C 2003: The tremble dance of honey bees can be caused by hive-external foraging experience. The Journal of Experimental Biology 206: 2111-2116.

Toma DP, Bloch G, Moore D, Robinson GE 2000: Changes in *period m*RNA levels in the brain and division of labor in honey bee colonies. PNAS 97: 6914-6919.

Visscher PK, Crailsheim K, Sherman G 1996: How do honey bees (*Apis mellifera*) fuel their water foraging flights? J. Insect Physiol. 42: 1089-1094.

Visscher PK, Dukas R 1997: Survivorship of foraging honey bees. Insectes Soc. 44: 1-5.

von Frisch K 1967: The dance language and orientation of bees. The Belknap Press of Harvard University Press, Cambridge Mass.

Wainselboim AJ, Roces F, Farina WM 2002: Honeybees assess changes in nectar flow within a single foraging bout. Animal Behavior 63:1-6.

Winston ML & Neilson Punnett E 1982: Factors determining temporal division of labor in honeybees. Can. J. Zool. 60: 2947-2952.

Zar JH 1996: Biostatistical Analysis 3rd Ed. Prentice Hall, Upper Saddle River NJ.

APPENDICES

Appendix A
Experiment 1: August 2003 Experiment

Table 11 Five day experience bees; bees marked July 31st 2003							
				Number of Rewards per Training Day			
Training	Day 1	Day 2	Day3	Day 4	Day5	Total	Reward/day
BB	3	1	X	2	3	9	1.8
BG	5	5	5	2	3	20	4
BP	5	3	X	X	X	8	1.6
BR	5	X	X	1	X	6	1.2
BW	1	1	2	4	2	10	2
BY	5	9	4	5	6	29	5.8
GB	1	3	3	9	6	22	4.4
GG	2	4	1	5	5	17	3.4
GR	1	10	1	5	5	22	4.4
PB	1	3	2	4	9	19	3.8
PG	2	4	3	X	1	10	2
PP	1	2	X	3	4	10	2
PR	1	X	X	1	6	7	1.4
PW	2	X	X	X	X	2	0.4
PY	2	X	X	X	3	5	1
RG	1	X	X	X	X	1	2
RP	2	4	4	6	5	21	4.2
RR	3	5	2	6	5	21	4.2
RW	3	6	5	X	1	15	3
RY	2	2	5	7	6	22	4.4
WB	1	3	1	1	2	8	1.6
WG	1	4	5	6	3	19	3.8
WP	1	10	X	3	X	14	2.8
WR	1	4	6	X	5	16	3.2
WY	1	X	X	1	X	2	0.4
YB	3	5	4	X	4	16	3.2
YG	3	6	3	5	10	27	5.4
YP	1	X	2	1	X	4	0.8
YR	3	7	X	8	8	26	5.2
YW	2	6	7	5	8	28	5.6
YY	3	2	3	5	5	18	3.6
Bold lettering = Individuals that arrived on all training days.							
X = No arrival at feeding station							

Table 12 Four and three day experience bees; bees marked August 1st & 2rd 2003

Number of Rewards per Training Day

Four Day Bees							**Three Day Bees**					
Training	Day2	Day 3	Day 4	Day 5	Total	#/Day	Training	Day 3	Day 4	Day 5	Total	#/day
BBB	6	2	1	5	14	3.5	**BPG**	1	2	4	7	2.34
BGB	3	1	7	5	16	4	GGB	1	X	1	2	0.67
BPB	1	X	X	X	1	0.25	PBP	2	X	X	2	0.67
BRB	3	5	8	8	24	6	PGP	2	X	X	2	0.67
BWB	1	1	3	3	8	2	**PYB**	1	1	10	12	4
BYB	1	7	4	9	21	5.25	RGR	2	X	X	2	0.67
GBB	1	1	1	2	5	1.25	**RPR**	2	8	2	12	4
GGG	2	X	X	2	4	1	RWP	1	X	X	1	0.34
GGP	1	1	X	X	2	0.5	**RYR**	2	2	5	9	3
GP	2	3	8	5	18	4.5	**WGP**	3	7	5	15	5
GW	10	7	7	10	34	8.5						
GWW	2	4	X	X	6	1.5						
GY	4	2	8	3	17	4.25						
GYG	2	5	8	7	22	5.5						
PBB	3	X	X	X	3	0.75						
PPG	1	X	X	X	1	0.25						
PPP	2	2	X	X	4	1						
PRP	1	2	4	5	12	3						
PWP	1	3	3	4	11	2.75						
PYP	1	5	6	7	19	4.75						
RB	6	9	3	3	21	5.25						
RBB	4	5	9	4	22	5.5						
RRP	3	1	2	3	9	2.25						
RRR	3	4	6	6	19	4.75						
RRW	1	X	1	4	6	1.5						
RRY	1	1	1	4	7	1.75						
RWR	1	2	5	11	19	4.75						
WBB	4	4	4	4	16	4						
WBW	1	X	X	X	1	0.25						
WGW	1	4	X	2	7	1.75						
WPW	1	2	2	5	10	2.5						
WRW	3	X	X	X	3	0.75						
WW	3	2	8	5	18	4.5						
WWW	1	X	X	8	9	2.25						
WYW	2	2	7	7	18	4.5						
YBB	5	2	X	4	11	2.75						
YBY	1	X	2	X	3	0.75						
YRY	1	4	6	4	15	3.75						
YGG	1	X	1	X	2	0.5						
YGY	2	2	3	7	14	3.5						
YWY	1	1	8	8	18	4.5						
YYR	1	1	3	6	11	2.75						
YYY	5	5	3	3	16	4						

Bold lettering = Individuals that arrived on continuous training days.

X = No arrival at feeding station

Table 13 Two and One Day Experience Bees; Bees marked August 3rd & 4th 2003

			Number of Rewards per Training Day			
Two Day Bees					**One Day Bees**	
Training Day 4		Day 5	Total	#/day	Day 5	
BBG	2	7	9	4.5	**BGG**	3
BBP	3	2	5	2.5	**BPP**	3
BBR	4	3	7	3.5	**BRP**	2
BBW	3	X	3	1.5	**BWW**	3
BBY	1	3	4	2	**BWY**	1
BRR	1	5	6	3	**BYY**	2
BWP	1	X	1	0.5	**GBG**	2
BWR	3	5	8	4	**GGR**	1
GGY	1	1	2	1	**GGW**	1
GPP	1	X	1	0.5	**GPB**	3
GRR	1	2	3	1.5	**GPG**	3
GYY	1	X	1	0.5	**GRB**	1
PPP	7	5	12	6	**GRG**	2
PPY	1	1	2	1	**GWB**	2
PRR	1	3	4	2	**GWG**	4
PWW	1	3	4	2	**GYB**	2
RBG	2	X	2	1	**PGB**	1
RBP	1	X	1	0.5	**PGG**	3
RRB	2	1	3	1.5	**PPB**	3
RRG	1	X	1	0.5	**PPW**	1
WGR	1	X	1	0.5	**RBR**	1
WPP	1	X	1	0.5	**RGG**	2
WWB	1	X	1	0.5	**RGW**	1
WWP	2	3	5	2.5	**RPP**	5
WWR	2	6	8	4	**RWW**	1
WWY	3	3	6	3	**RYY**	2
WYY	2	4	6	3	**WBG**	1
YPP	1	8	9	4.5	**WGG**	2
YPY	1	X	1	0.5	**WPR**	2
YRR	1	2	3	1.5	**WRB**	1
YWW	1	3	4	2	**WRR**	2
YYB	2	X	2	1	**WWG**	1
YYP	2	6	8	4	**WYR**	1
					YGB	3
					YPB	1
					YPR	1
					YRB	2
					YRP	1
					YWB	1
					YYW	2

Bold lettering = Individuals that arrived on continuous training days.

X = No arrival at feeding station

Table 14 Five Day Bee Test Day Arrivals, August 4th- August 7th 2003

Anise = Experimental Station, Peppermint = Recruiter Station

	Test Day1		Test Day 2		Test Day 3		Test Day 4	
	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint
BG	X		X	X	X	X	X	X
BW	X		X			LIVING		LIVING
BY	X	X	X	X		X		X
GB	X	X	X	X	X	X	X	X
GG	X	X	X	X	X	X	X	X
GR	X		X		X			LIVING
PB	X		X	X	X	X		LIVING
RP	X	X	X	X	X	X	X	X
RR	X	X	X	X	X	X		X
RY	X		X		X			LIVING
WB	X	X	X	X	X	X	X	X
WG	X		X		X			LIVING
YG	X	X		X		X		X
YW	X		X	X	X			LIVING
YY	X		X			X		LIVING
Missed day three only								
BB	X	X	X	X	X			LIVING
PP	X	X		X	X	X	X	X
YR	X	X		X	X	X		LIVING
Missed day four only								
PG	X	X		X	X	X		X
YB	X	X	X	X	X	X	X	X
WR	X		X	X	X	X		X
RW	X		X		X		X	
Missed multiple random days								
BP		X	X	X		X		UNKNOWN
BR	X			X		UNKNOWN		UNKNOWN
PR	X		X	X		LIVING		LIVING
PY	X	X	X	X		X		X
WP		LIVING		X		LIVING		LIVING
WY		LIVING		X		LIVING		LIVING
YP	X	X		X		X		LIVING
Showed up day one only								
PW	X		X	X		X		X
RG		LIVING		LIVING		X		X
		15						
	Anise Only: 8/15 = .533		Anise only: 5/15 = .333		Anise Only: 4/15 = .267		Anise only: 0	
	Both Stations: 7/15 = .467		Both Stations: 9/15 = .600		Both Stations: 7/15 = .467		Both Stations: 5/15 = .333	
	P-mint only: 0		P-mint only: 1/15 = .067		P-mint only: 3/15 = .200		P-mint only: 3/15 = .200	
	0 Living		0 Living		1 Living		7 living	

Table 15 Four Day Bee Test Day Arrivals, August 4th- August 7th 2003									
					Anise = Experimental, Peppermint = Recuiter				
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Anise	Peppermint	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint
BBB		X		X		X	X	X	
BGB		X		X		X			LIVING
BRB		X		X	X	X	X		X
BWB			LIVING	X	X		X		X
BYB		X		X		X			LIVING
GBB		X	X	X	X		X		X
GP		X	X	X	X	X			LIVING
GW		X	X	X	X	X	X	X	
GY		X		X			LIVING	X	
GYG		X		X	X	X		X	
PRP		X			LIVING	X	X	X	X
PWP		X		X		X	X		LIVING
PYP		X	X	X	X	X	X	X	X
RB		X	X	X	X	X	X		X
RBB		X		X		X			LIVING
RRP		X			LIVING	X	X	X	
RRR		X			LIVING	X			LIVING
RRY			LIVING	X			LIVING		LIVING
RWR		X		X		X	X		X
WBB		X		X		X			LIVING
WPW		X	X	X	X	X	X		X
WW		X		X	X	X	X	X	
WYW		X		X		X	X	X	
YRY		X		X		X			LIVING
YGY			LIVING	X		X			LIVING
YWY		X	X	X			LIVING		LIVING
YYR		X	X	X	X		X		X
YYY		X		X			X		UNKNOWN
Missed day four only									
WGW		X			LIVING		LIVING		LIVING
YBB			LIVING		LIVING		LIVING		LIVING
Missed day 4 & 5									
GGP		X			UNKNOWN		UNKNOWN		UNKNOWN
GWW			X		X		LIVING		UNKNOWN
PPP			X		LIVING		X		UNKNOWN
Missed day three only									
RRW		X			LIVING		LIVING		LIVING
Missed day 3 & 4									
WWW		X			UNKNOWN		UNKNOWN		UNKNOWN
Missed multiple random days									
GGG			X	X			X		X
YBY		X			UNKNOWN		UNKNOWN		UNKNOWN
YGG			LIVING		LIVING		LIVING		LIVING
Showed up day two only									
BPB		X		X		X			X
PBB		X			LIVING		LIVING	X	
PPG			LIVING		LIVING		LIVING		UNKNOWN
WBW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WRW			LIVING	X			UNKNOWN		UNKNOWN
		Anise Only: 17/28 = .607		Anise only: 14/28 = .500		Anise Only: 9/28 = .321		Anise only: 7/27 = .259	
		Both Stations: 8/28 = .286		Both Stations: 11/28 = .393		Both Stations: 12/28 = .429		Both Stations: 2/27 = .074	
		P-mint only: 0		P-mint only: 0		P-mint only: 4/28 = .143		P-mint only: 7/27 = .259	
		3 Living		3 Living		3 Living		11 Living	

Table 16 Three Day Bee Test Day Arrivals, August 4th- August 7th 2003

Anise = Experimental station, Peppermint = Recruiter Station

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Anise	Peppermint	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint
BPG		X	X		X		X		X
PYB		X	X		X		X		X
RPR			LIVING	X		X			LIVING
RYR		X		X			X		X
WGP		X	X		X	X	X	X	X
Missed Day Two									
GGB		X			UNKNOWN		UNKNOWN		UNKNOWN
Showed up day one only									
PBP		X	X	X	X		X	X	X
PGP			LIVING		LIVING		LIVING		LIVING
RGR		X	X		X	X	X		X
RWP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
		Anise Only: 1/5 = .200		Anise only: 2/5 = .400		Anise Only: 1/5 = .200		Anise only: 0	
		Both Stations: 3/5 = .600		Both Stations: 0		Both Stations: 1/5 = .200		Both Stations: 1/5 = .200	
		P-mint only: 0		P-mint only: 3/5 = .600		P-mint only: 3/5 = .600		P-mint only: 3/5 = .600	
		1 Living		0 Living		0 Living		1 Living	

Table 17 Two Day Bee Test Day Arrivals, August 4th- August 7th 2003

Anise = Experimental Station, Pepperment = Recruiter Station

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Anise	Peppermint	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint
BBG			LIVING	X		X	X		X
BBP			X		X		X		X
BBR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
BBY		X			LIVING		LIVING		X
BRR		X	X	X	X		X		X
BWR		X		X		X		X	
GGY			LIVING		LIVING		LIVING		LIVING
GRR		X	X		X		X		X
PPP			***SCRATCH***		***SCRATCH***		***SCRATCH***		***SCRATCH***
PPY			LIVING		X		LIVING		X
PRR		X	X		X		X		X
PWW			LIVING		LIVING		LIVING		LIVING
RRB		X	X		X		LIVING		X
WWP		X	X		X		X		X
WWR		X	X		X		X		X
WWY		X		X			LIVING		LIVING
WYY		X	X		X		X		X
YPP			LIVING		X		LIVING		LIVING
YRR		X	X	X		X			LIVING
YWW		X			LIVING	X			LIVING
YYP		X		X	X	X			LIVING
Showed up day one only									
BBW		X			UNKNOWN		UNKNOWN		UNKNOWN
BWP			LIVING		LIVING	X			UNKNOWN
GPP			LIVING	X			LIVING	X	
GYY			X		X		X		UNKNOWN
RBG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RBP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RRG			LIVING		LIVING		X		UNKNOWN
WGR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WPP		X		X			LIVING		X
WWB			LIVING		X		LIVING		LIVING
YPY		X	X		X	X			X
YYB		X			LIVING		UNKNOWN		UNKNOWN
		Anise Only: 5/19 = .263		Anise only: 4/19 = .211		Anise Only: 4/19 = .211		Anise only: 1/19 = .053	
		Both Stations: 8/19 = .421		Both Stations: 2/19 = .105		Both Stations: 1/19 = .053		Both Stations: 0	
		P-mint only: 1/19 = .053		P-mint only: 9/19 = .474		P-mint only: 7/19 = .368		P-mint only: 11/19 = .579	
		5 Living		4 Living		7 Living		7 Living	

Table 18 One Day Bees Test Day Arrivals, August 4th- August 7th 2003

Anise = Experimental, Peppermint = Recuiter

	Test Day1		Test Day 2		Test Day 3		Test Day 4	
	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint	Anise	Peppermint
BGG		X		X		X		X
BPP		LIVING	X	X	X	X		LIVING
BRP		X		X	X	X		X
BWW	X	X		X		X		X
BWY		LIVING		LIVING		LIVING		LIVING
BYY		X		X	X	X		X
GBG	X			LIVING		LIVING		LIVING
GGR		LIVING		LIVING		LIVING		LIVING
GGW		X		X		X		LIVING
GPB	X	X		X		X		X
GPG	X			X		LIVING		LIVING
GRB	X			LIVING		LIVING		LIVING
GRG		X	X	X	X	X		X
GWB		X		X		X		X
GWG	X	X		X	X	X		X
GYB	X	X		X	X	X		X
PGB		X		X		X		X
PGG	X	X		X		X		X
PPB	X		X			LIVING		LIVING
PPW	X			X		X		X
PRB		LIVING		LIVING		LIVING		X
RBR	X	X		X		X		X
RGG		X		X		X		LIVING
RGW		LIVING		LIVING		LIVING		LIVING
RPP	X			LIVING	X			LIVING
RWW	X			LIVING		LIVING		LIVING
RYY	X	X		X		X		X
WBG	X			LIVING		LIVING		LIVING
WGG	X		X			LIVING		LIVING
WPR		LIVING		UNKNOWN		UNKNOWN		UNKNOWN
WRB		LIVING		LIVING		LIVING		LIVING
WRR		X		X		X		LIVING
WWG		LIVING		LIVING		X		LIVING
WYR	X			X		X		X
YGB	X			X		LIVING		LIVING
YPB	X	X		X		X		LIVING
YPR		LIVING		X		LIVING		X
YRB		LIVING		X		X		X
YRP	X		X	X		UNKNOWN		UNKNOWN
YWB		LIVING		LIVING		LIVING		UNKNOWN
YYW	X		X		X	X		X
	Anise Only: 13/41 = .317		Anise only: 3/40 = .075		Anise Only: 1/39 = .026		Anise only: 0	
	Both Stations: 8/41 = .195		Both Stations: 3/40 = .075		Both Stations: 7/39 = .179		Both Stations: 0	
	P-mint only: 9/41 = .220		P-mint only: 22/40 = .550		P-mint only: 16/39 = .410		P-mint only: 19/38 = .500	
	11 Living		12 Living		15 Living		19 Living	

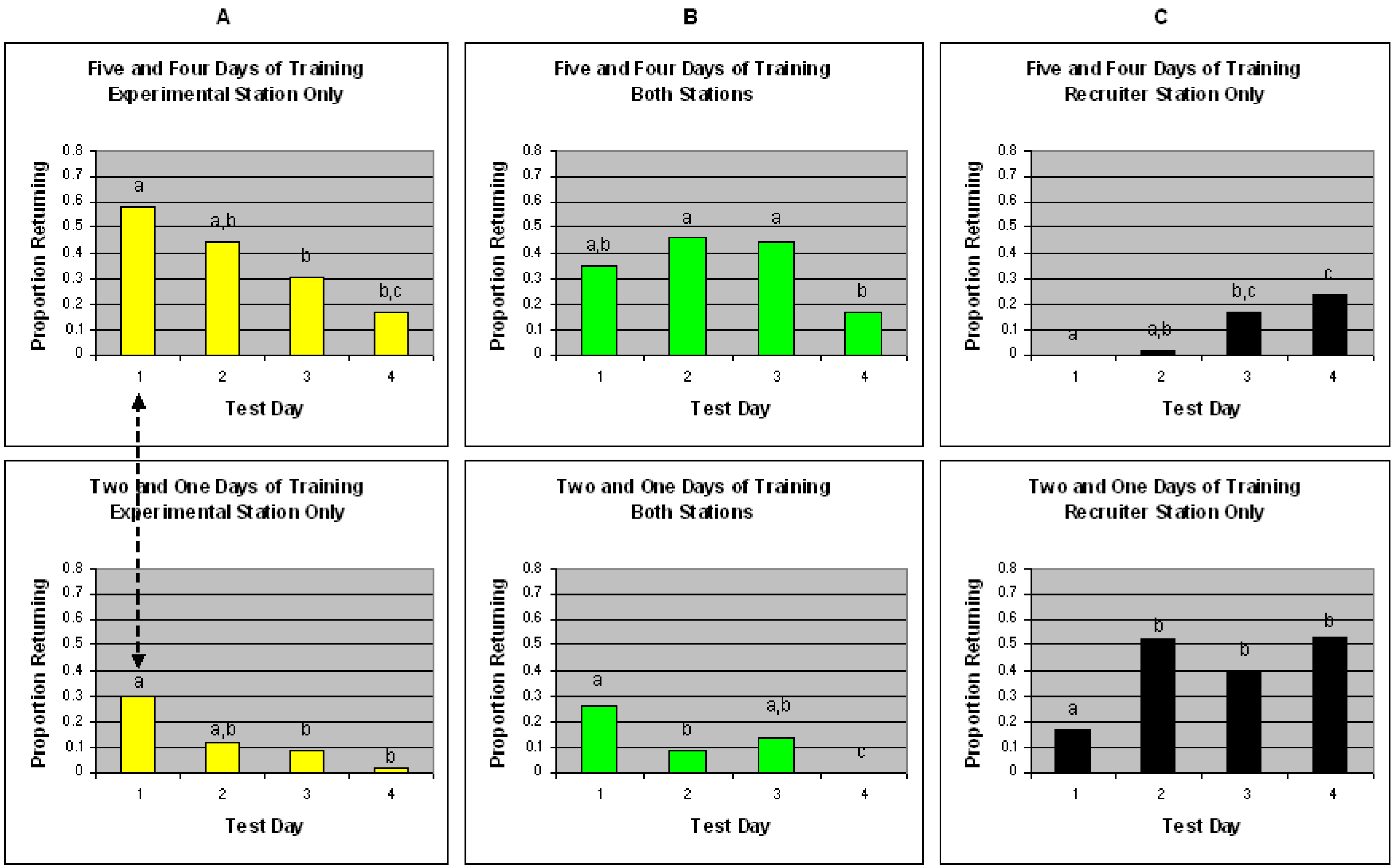

Figure 16 Initial experiment, July 31st-August 7th 2003. Proportion of foragers returning on each test day. The foragers arrivals were divided into those that only arrived at the experimental station (A), those that only arrived at the recruiter station (C), and those that arrived at both stations on a given test day (B). The arrivals were further divided into high experience bees (five and four days of training, upper graphs) and low experience bees (two and one days of training, lower graphs). Chi-square analysis was performed between high and low experience bees for each test day and arrival location(s) (see dashed arrows) Trend analysis using multiple comparison of proportions (Zar, 1996) was performed for each separate graph. Bars that do not share letters are significantly different from each other (P=0.05).

Table 19 Experiment 1 chi-square tests

Experimental Station Only			Both Stations			Recruiter Station Only		
Test Day 1			**Test Day 1**			**Test Day 1**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	25	18	5 and 4	15	28	5 and 4	0	43
2 and 1	18	42	2 and 1	16	44	2 and 1	10	50
	DF=1			DF=1			DF=1	
	$\chi^2 = 7.040$	$P = 0.008$		$\chi^2 = 0.461$	$P = 0.497$		$\chi^2 = 6.150$	$P = 0.013$
Test Day 2			**Test Day 2**			**Test Day 2**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	19	24	5 and 4	20	23	5 and 4	1	42
2 and 1	7	52	2 and 1	5	54	2 and 1	31	28
	DF=1			DF=1			DF=1	
	$\chi^2 = 12.032$	$P < 0.001$		$\chi^2 = 17.449$	$P < 0.001$		$\chi^2 = 26.846$	$P < 0.001$
Test Day 3			**Test Day 3**			**Test Day 3**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	13	30	5 and 4	19	24	5 and 4	7	36
2 and 1	5	53	2 and 1	8	50	2 and 1	23	35
	DF=1			DF=1			DF=1	
	$\chi^2 = 6.468$	$P = 0.011$		$\chi^2 = 10.146$	$P = 0.001$		$\chi^2 = 5.391$	$P = 0.020$
Test Day 4			**Test Day 4**			**Test Day 4**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	7	35	5 and 4	7	35	5 and 4	10	32
2 and 1	1	56	2 and 1	0	57	2 and 1	30	27
	DF=1			DF=1			DF=1	
	$\chi^2 = 5.371$	$P = 0.020$		$\chi^2 = 7.844$	$P = 0.005$		$\chi^2 = 7.188$	$P = 0.007$

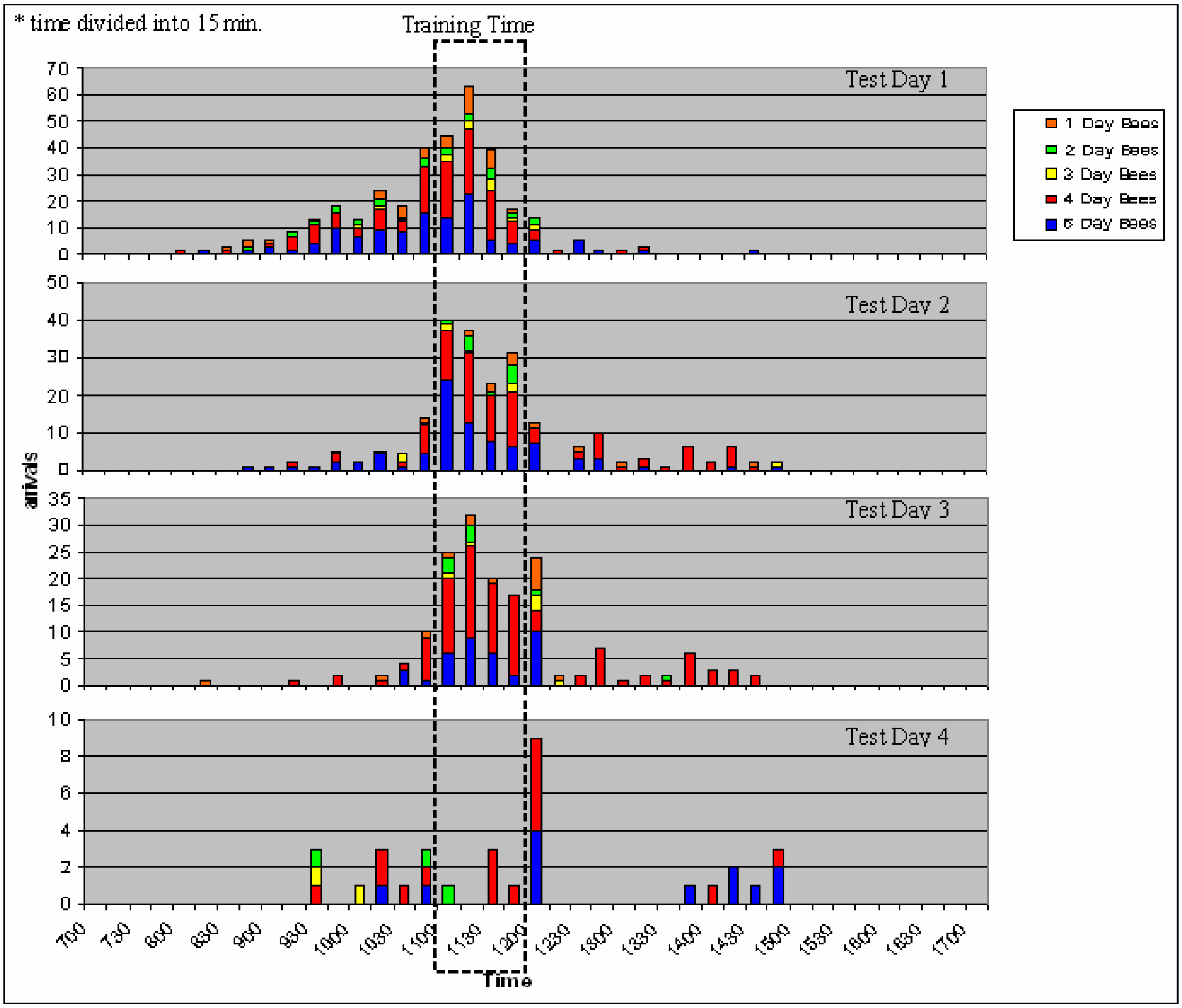

Figure 17 Arrivals at experimental station, August 2003. All arrivals were divided and color coded by cohort (see legend). Arrivals were totaled for each 15 minute span of time from the start of observations to end of each day. The proportion of total arrivals was then found for high experience and low experience bees for each test day (Table 10A).

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.755	.849	.833	.848
Low Experience Bees (2 and 1 Days of Training)	.195	.114	.131	.091

Table 20 Proportion of total arrivals at the experimental station, August 2003.

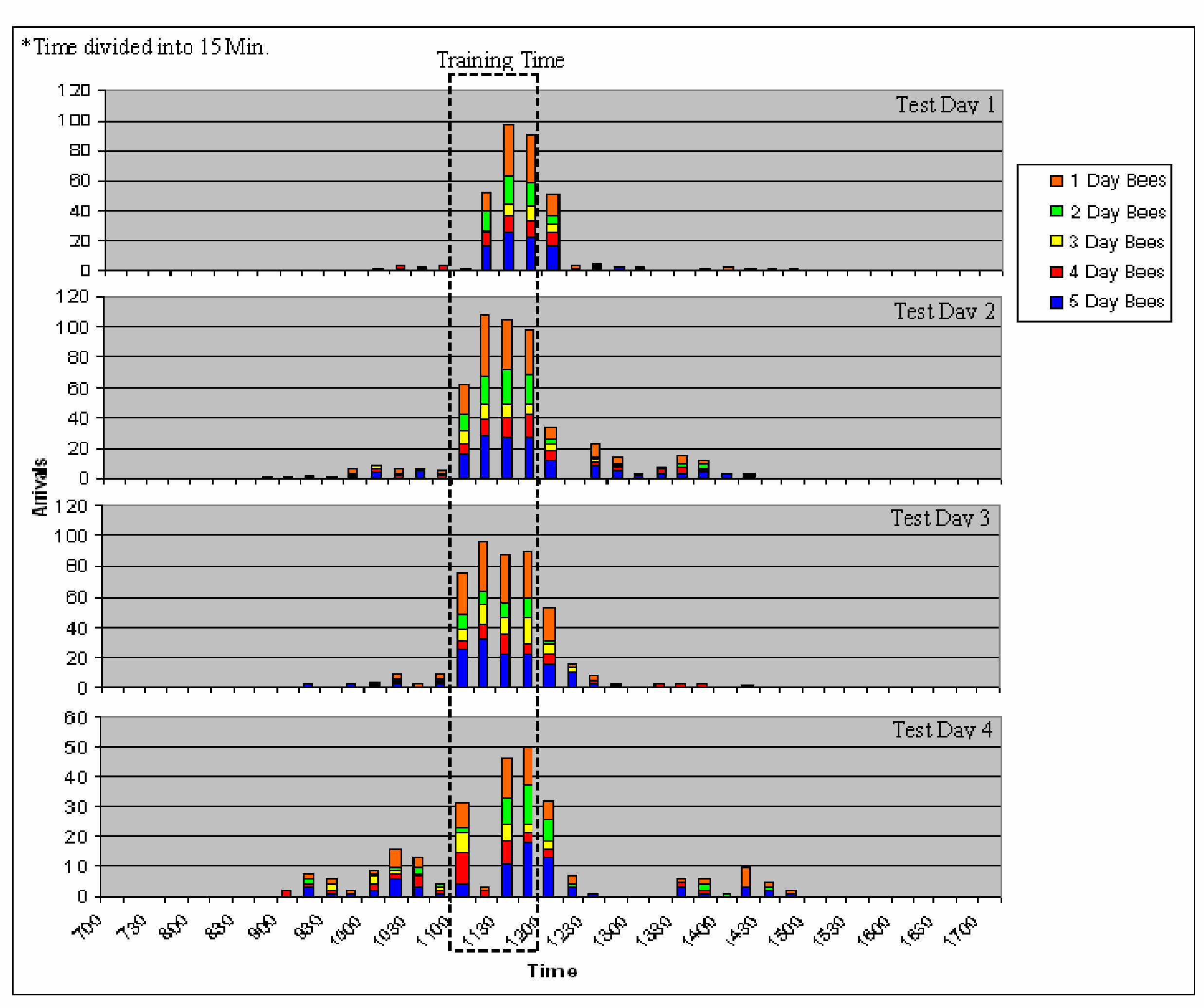

Figure 18 Arrivals at recruiter station, August 2003. See Figure 2A for Details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.422	.430	.439	.462
Low Experience Bees (2 and 1 Days of Training)	.494	.480	.433	.442

Table 21 Proportion of total arrivals at the recruiter station, August 2003.

Appendix B
July 2005 Experiment

Table 22 Five day experience bees; Bees marked July 24th 2005							
				Number of Rewards per Training Day			
Training day 1		Day 2	Day3	Day 4	Day5	Total	Reward/day
GWG	2	6	X	2	X	10	2
WGW	3	16	10	21	26	76	15.2
GWW	2	X	X	X	X	2	0.4
WGG	3	4	2	6	X	15	3
WRW	6	23	22	30	28	109	21.8
WRR	3	4	1	X	X	8	1.6
RWR	5	Tweezed		X	X	dead	
BWG	4	9	7	18	15	53	10.6
BWB	1	X	1	X	2	4	0.8
WBB	7	X	3	17	12	39	7.8
WBW	1	1	X	X	X	2	0.4
BWW	3	9	12	18	24	66	13.2
GYB	1	1	x	1	3	6	1.2
BYB	1	2	5	X	1	9	1.8
YBY	5	14	21	28	21	89	17.8
YBB	2	4	X	X	X	6	1.2
BYY	4	X	X	X	X	4	0.8
GYY	5	X	X	X	1	6	1.2
GYG	2	X	X	X	X	2	0.4
YGY	3	19	2	3	X	27	5.4
YGG	2	X	X	X	X	2	0.4
YBG	1	5	3	3	X	12	2.4
BGG	1	X	X	X	X	1	0.2
GBB	1	4	7	16	18	46	9.2
GBG	5	20	17	20	16	78	15.6
YWY	3	10	9	6	7	35	7
YWW	1	X	X	1	X	2	0.4
WYW	1	11	X	X	X	12	2.4
WYY	2	11	18	24	22	77	15.4
YRR	1	9	9	6	10	35	7
YRY	4	11	23	X	14	52	10.4
RR	1	X	X	X	X	1	0.2
BGY	3	X	1	4	1	9	1.8
RYB	1	X	X	X	X	1	0.2
RYW	1	12	X	X	X	13	2.6
?YW	?		20	20	16		
?GG	?	3	14	20	14		
?GY	?	2	1	X	X		
Bold lettering = Individuals that arrived on all training days.							
X = No arrival at feeding station							

Table 23 Four and three day experience bees; Bees marked July 25th & 26th 2005												
							Number of Rewards Per Training Day					
Four Day Bees							**Three Day Bees**					
Training Day 2		Day 3	Day 4	Day 5	Total	#/Day	Training Day 3		Day 4	Day 5	Total	#/day
PRP	22	1	1	X	24	6	**RWW**	2	1	1	4	1.33
RPB	4	X	X	1	5	1.25	**GRW**	13	13	15	41	13.67
RPR	11	19	26	20	76	19	**RGW**	6	8	12	26	8.67
RPP	5	X	X	X	4	1	**GWR**	9	12	19	40	13.33
PRR	1	X	X	X	1	0.25	**RWG**	2	9	15	26	8.67
BRR	2	5	24	17	48	12	WRG	2	2	X	4	1.33
RBR	4	5	X	X	9	2.25	**RWR**	3	12	14	29	9.67
RBB	3	1	X	X	4	1	BRW	1	2	X	3	1
BRB	2	2	X	X	4	1	RWB	2	3	X	5	1.67
PBP	3	X	X	X	3	0.75	**WRB**	3	6	18	27	9
PRB	3	3	7	18	31	7.75	**WGR**	3	7	5	15	5
PBR	3	5	2	X	10	2.5	**WBR**	2	1	1	4	1.33
PBB	2	X	1	X	3	0.75	**BRG**	2	11	18	31	10.33
BPP	2	4	4	11	21	5.25	BGR	1	X	X	1	0.33
BPB	3	1	5	X	9	2.25	**RBG**	2	2	10	14	4.67
GRG	4	X	X	X	4	1	**GBR**	3	9	7	19	6.33
GRR	5	18	18	16	57	14.25	RBW	4	3	X	7	2.33
RGG	3	5	9	15	32	8	**GRB**	1	7	9	17	5.67
RGR	2	2	5	7	16	4	**RGB**	2	9	16	27	9
PGP	2	2	1	3	7	1.75	PGB	3	1	X	4	1.33
GPG	1	4	7	9	21	5.25	GPB	3	10	X	13	4.33
PGG	1	2	3	X	6	1.5	GBP	2	1	X	3	1
GPP	2	X	X	X	2	0.5	**PBG**	2	6	5	13	4.33
YPY	2	11	13	13	39	9.75	BGP	1	X	X	1	0.33
YPP	1	X	X	X	1	0.25	BPG	1	X	X	1	0.33
PYR	2	X	X	X	2	0.5	**GBY**	1	6	14	21	7
PYP	1	1	1	X	3	0.75	**YGB**	1	9	11	21	7
PYY	1	5	1	2	9	2.25	BWR	1	6	X	7	2.33
RBP	1	3	5	X	9	2.25						
BRP	1	1	X	X	2	0.5						
BPR	1	1	X	X	2	0.5						
PPP	1	X	X	X	1	0.25						
YYY	1	X	X	X	1	0.25						
BBB	1	X	X	X	1	0.25						
P?P	?	21	21	19								
?BB	?	WEEZE	X									
?BB	?	14	16	9								
??B	?	6	13	13								
PB?	?	2	7	X								
B?B	?	weeze	X	X								
?B?	?	2	X	1								
?RG	?	4	8	7								
?RP	?	10	20	7								
?PB	?	7	14	5								
_BP	?		20	17								
Bold lettering = Individuals that arrived on continuous training days.												
X = No arrival at feeding station												

Table 24 Two and One Day Experience Bees; Bees marked July 27th & 28th 2005

			Number of Rewards per Test Day			
Two Day Bees					**One Day Bees**	
Training	Day 4	Day 5	Total	#/day	Day 5	
WYP	1	5	6	3	**GYR**	5
WPY	5	9	14	7	**YGR**	6
YWP	2	9	11	5.5	**RYG**	7
PWY	5	X	5	2.5	**YRG**	7
PYW	6	13	19	9.5	**RGY**	4
YPW	1	4	5	2.5	**GRY**	3
WPB	10	18	28	14	**RYY**	8
WBP	1	X	1	0.5	**GPY**	7
PBW	5	6	11	5.5	**YPG**	5
PWB	2	5	7	3.5	**PYG**	2
PWP	5	X	5	2.5	**PGY**	4
BWP	2	X	2	1	**GYP**	4
WPP	5	16	21	10.5	**YGP**	3
WPW	3	3	6	3	**YWG**	1
WPG	1	1	2	1	**WGY**	2
BPW	5	4	9	4.5	**WYG**	3
PWW	3	13	16	8	**YGW**	4
PWG	7	13	20	10	**GYW**	4
WGP	6	X	6	3	**GW?**	2
GWP	3	2	5	2.5	**GWY**	3
PGW	2	X	2	1	**BWY**	1
GPW	2	1	3	1.5	**WBY**	2
WPR	2	9	11	5.5	**?YB**	2
PWR	4	4	8	4	**??W**	1
PRW	3	8	11	5.5	**YBW**	3
RWP	1	1	2	1	**BYW**	5
WRP	1	6	7	3.5	**YWB**	4
RPW	1	7	8	4	**WY?**	2
RYR	1	7	8	4	**BGB**	4
??P	?	X			**?BR**	?
P_G or _P	2	X			**RP?**	?
_BY	?	X				
_RY	?	X				
?YY	?	4				
Bold lettering = Individuals that arrived on continuous training days.						
X = No arrival at feeding station						

Table 25 Five day bee test day arrivals, July 29th- August 1st 2005

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
Five Day Bees		Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter
WGW		X	X		LIVING		LIVING		LIVING
WRW		X		X	X	X	X	X	X
BWG		X			LIVING		LIVING		LIVING
BWW		X		X	X		LIVING		LIVING
YBY		X		X		X	X	X	X
GBB		X		X			X		X
GBG		X		X			LIVING		X
YWY		X		X	X		X		X
WYY		X		X		X	X		X
YRR			LIVING		LIVING		LIVING		LIVING
?YW		X		X		X		X	X
?GG		X		X	X		X		X
Missed day two only									
WBB		X			LIVING	X			UNKNOWN
BGY			LIVING		LIVING		LIVING		UNKNOWN
Missed day three only									
GYB		X			UNKNOWN		UNKNOWN		UNKNOWN
Missed day four only									
YRY		X			LIVING		LIVING		LIVING
BYB			LIVING		LIVING		LIVING		LIVING
Missed final day only									
WGG			LIVING		LIVING		UNKNOWN		UNKNOWN
YGY			LIVING		X		UNKNOWN		UNKNOWN
YBG			LIVING		LIVING		LIVING		X
Missed multiple random days									
GWG			LIVING		LIVING		LIVING		UNKNOWN
WRR		X		X	X	X	X		X
BWB			LIVING		LIVING		LIVING		LIVING
WBW			LIVING	X	X		X		X
YBB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GYY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
YWW			LIVING		LIVING		LIVING		X
WYW			LIVING		LIVING		X		UNKNOWN
RYW			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
?GY			LIVING	X			LIVING		X
Showed up day one only									
GWW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
BYY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GYG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
YGG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
BGG			LIVING	X			UNKNOWN		UNKNOWN
R_R	RR		LIVING	X			X		X
RYB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
		Experimental:	8/10 = .80	Exp.:	4/10 = .40	Exp.:	0	Exp.:	0
		Both:	1/10 = .10	Both:	3/10 = .30	Both:	3/10 = .30	Both:	2/10 = .2
		Recruiter:	0	Recruiter:	0	Recruiter:	2/10 = .20	Recruiter:	4/10 = .40
		Living:	1	living:	3	Living:	5	Living:	4

Table 26 Four day bee test day arrivals, July 29th- August 1st 2005									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter
RPR X			LIVING		LIVING		UNKNOWN		UNKNOWN
BRR		X		X		X	X		X
PRB		X		X	X	X	X	X	X
BPP			LIVING	X	X	X	X	X	X
GRR		X	X	X	X		X	X	X
RGG		X	X	X	X		X		LIVING
RGR		X		X	X		X		UNKNOWN
PGP		X			LIVING		LIVING		LIVING
GPG		X			LIVING	X			LIVING
YPY		X			X		X	X	X
PYY		X	X		LIVING		LIVING		LIVING
P?P		X	X	X	X	X	X		X
?BB		X			X	X	X	X	X
??B		X		X		X	X	X	X
?RG		X		X	X		X		X
?RP			LIVING		LIVING		LIVING		UNKNOWN
?PB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
_BP		X		X			LIVING		UNKNOWN
Missed day four only									
?B?			LIVING		LIVING	X	X	X	X
Missed day 4 & 5									
RBR			LIVING		LIVING		LIVING		LIVING
RBB			LIVING		LIVING		LIVING		UNKNOWN
BRB		X			LIVING		X		UNKNOWN
BRP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
BPR			LIVING		LIVING		LIVING		LIVING
Missed final day only									
BPB			LIVING		LIVING		LIVING		UNKNOWN
PBR			LIVING		LIVING		LIVING		X
PGG			LIVING		LIVING	X			UNKNOWN
PYP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RBP			LIVING		LIVING		LIVING		LIVING
PB?		X	X		LIVING	X			LIVING
PRP			LIVING	X			LIVING		LIVING
Missed multiple random days									
RPB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PBB			LIVING		LIVING		LIVING		X
Showed up day one only									
RPP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PRR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PBP			LIVING		LIVING		LIVING		UNKNOWN
GRG			LIVING		LIVING		LIVING		UNKNOWN
GPP			LIVING		LIVING		LIVING		LIVING
YPP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PYR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PPP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
YYY			LIVING		LIVING		LIVING		LIVING
BBB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
		Experimental:	6/11 = .545	Exp.:	1/11 = .091	Exp.:	1/10 = .100	Exp.:	0
		Both:	3/11 = .273	Both:	5/11 = .455	Both:	3/10 = .300	Both:	4/9 = .444
		Recruiter:	0	Recruiter:	1/11 = .091	Recruiter:	4/10 = .400	Recruiter:	1/9 = .111
		Living:	2	living:	4	Living:	2	Living:	4

Table 27 Three day bees test day arrivals, July 29th- August 1st 2005									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter
RWW			LIVING		LIVING		LIVING		UNKNOWN
GRW		X		X	X		X		X
RGW		X		X	X		LIVING		X
GWR		X		X		X		X	
RWG		X			X	X	X		X
RWR		X		X	X		X		X
WRB		X		X	X		X		X
WGR			LIVING	X		X	X		X
WBR			LIVING		LIVING		LIVING		LIVING
BRG		X		X			LIVING		X
RBG		X	X	X	X		X		X
GBR		X		X	X	X	X		X
GRB		X		X			X		LIVING
RGB		X		X	X	X	X		UNKNOWN
PBG			LIVING		X		X		X
GBY		X		X	X	X	X	X	
YGB		X			X		X		X
Missed final day only									
WRG			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
BRW			LIVING		LIVING		LIVING		X
RWB			LIVING		LIVING		LIVING		X
RBW			LIVING		LIVING		UNKNOWN		UNKNOWN
PGB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GPB			LIVING		LIVING		LIVING		LIVING
GBP			UNKNOWN	X	X		UNKNOWN		UNKNOWN
BWR			LIVING		LIVING		LIVING		X
Showed up day one only									
BGR			LIVING		LIVING		LIVING		X
BGP			LIVING		LIVING		LIVING		UNKNOWN
BPG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
		Experimental:	12/17 = .706	Exp.:	4/17 = .235	Exp.:	1/17 = .059	Exp.:	2/15 = .133
		Both:	1/17 = .059	Both:	8/17 = .471	Both:	5/17 = .294	Both:	0
		Recruiter:	0	Recruiter:	3/17 = .176	Recruiter:	7/17 = .412	Recruiter:	11/15 = .733
		Living:	4	living:	2	Living:	4	Living:	2

Table 28 Two day bees test day arrivals, July 29th- August 1st 2005

	Test Day1		Test Day 2		Test Day 3		Test Day 4	
Two Day Bees	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter
WYP		LIVING		X		X		X
WPY	X			LIVING		LIVING		LIVING
YWP		LIVING		X		X		X
PYW	X		X	X		X		X
YPW		LIVING	X			LIVING		LIVING
WPB	X	X	X	X		LIVING		LIVING
PBW		LIVING		LIVING		X		LIVING
PWB	X	X		LIVING		LIVING		UNKNOWN
WPP	X		X			LIVING	X	
WPW		LIVING		LIVING		LIVING		LIVING
WPG		LIVING		LIVING		LIVING		LIVING
BPW	X			X		LIVING		LIVING
PWW	X		X		X	X	X	X
PWG		LIVING	X			LIVING		X
GWP		LIVING		LIVING		LIVING		LIVING
GPW		UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WPR		LIVING	X			LIVING		LIVING
PWR	X		X			X		X
PRW	X			LIVING		X		LIVING
RWP		LIVING		UNKNOWN		UNKNOWN		UNKNOWN
WRP		LIVING		LIVING		X		X
RPW		X		X		X		UNKNOWN
RYR	X	X	X	X		X		LIVING
?YY		LIVING		LIVING		X		X
Showed up day one only								
PWY		LIVING		LIVING		LIVING		X
WBP		LIVING		LIVING		LIVING		X
PWP		LIVING		LIVING		LIVING		X
BWP		LIVING		LIVING		LIVING		LIVING
WGP		LIVING		LIVING		LIVING		X
PGW		LIVING		LIVING		LIVING		LIVING
??P		LIVING		LIVING		LIVING		X
P_G or _PG		LIVING		X		LIVING		UNKNOWN
_BY		UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
_RY		LIVING		LIVING		LIVING		X
	Experimental:	7/22 = .318	Exp.:	6/21 = .286	Exp.:	0	Exp.:	1/19 = .053
	Both:	3/22 = .136	Both:	3/21 = .143	Both:	1/21 = .048	Both:	1/19 = .053
	Recruiter:	1/22 = .045	Recruiter:	4/21 = .190	Recruiter:	9/21 = .429	Recruiter:	6/19 = .316
	Living:	11	living:	8	Living:	11	Living:	11

Table 29 One day bee test day arrivals, July 29th- August 1st 2005

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter	Exp.	Recruiter
GYR		X	X	X	X		X		UNKNOWN
YGR		X	X		LIVING		LIVING		X
RYG		X			X		X		UNKNOWN
YRG		X			LIVING		LIVING		LIVING
RGY			LIVING		LIVING		X		X
GRY		X			X		UNKNOWN		UNKNOWN
RYY			X		LIVING		LIVING		UNKNOWN
GPY		X		X			LIVING		LIVING
YPG			UNKNOWN	X	X		UNKNOWN		UNKNOWN
PYG			LIVING		LIVING		X		LIVING
PGY			LIVING		LIVING		LIVING		LIVING
GYP			LIVING		X		X		X
YGP			LIVING		LIVING		LIVING		X
YWG		X			LIVING		LIVING		LIVING
WGY			LIVING		LIVING		LIVING		LIVING
WYG			LIVING		LIVING		LIVING		LIVING
YGW			LIVING		LIVING		X		X
GYW			LIVING		LIVING		X		X
GW?			X		X		X		X
GWY			LIVING		LIVING		LIVING		LIVING
BWY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WBY			LIVING		LIVING		UNKNOWN		UNKNOWN
?YB		X		X			UNKNOWN		UNKNOWN
??W			X	X	X	X	X	X	X
YBW			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
BYW			LIVING		LIVING		UNKNOWN		UNKNOWN
YWB			LIVING		X	X			X
WY?			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
BGB			LIVING		X	X			X
?BR			LIVING		LIVING		LIVING	X	
RP?			LIVING		LIVING		LIVING		X
		Experimental:	6/27 = .222	Exp.:	2/26 = .077	Exp.:	2/21 = .095	Exp.:	0
		Both:	2/27 = .074	Both:	3/26 = .115	Both:	1/21 = .048	Both:	1/18 = .055
		Recruiter:	3/27 = .111	Recruiter:	6/26 = .231	Recruiter:	8/21 = .381	Recruiter:	9/18 = .5
		Living:	16	living:	15	Living:	10	Living:	8

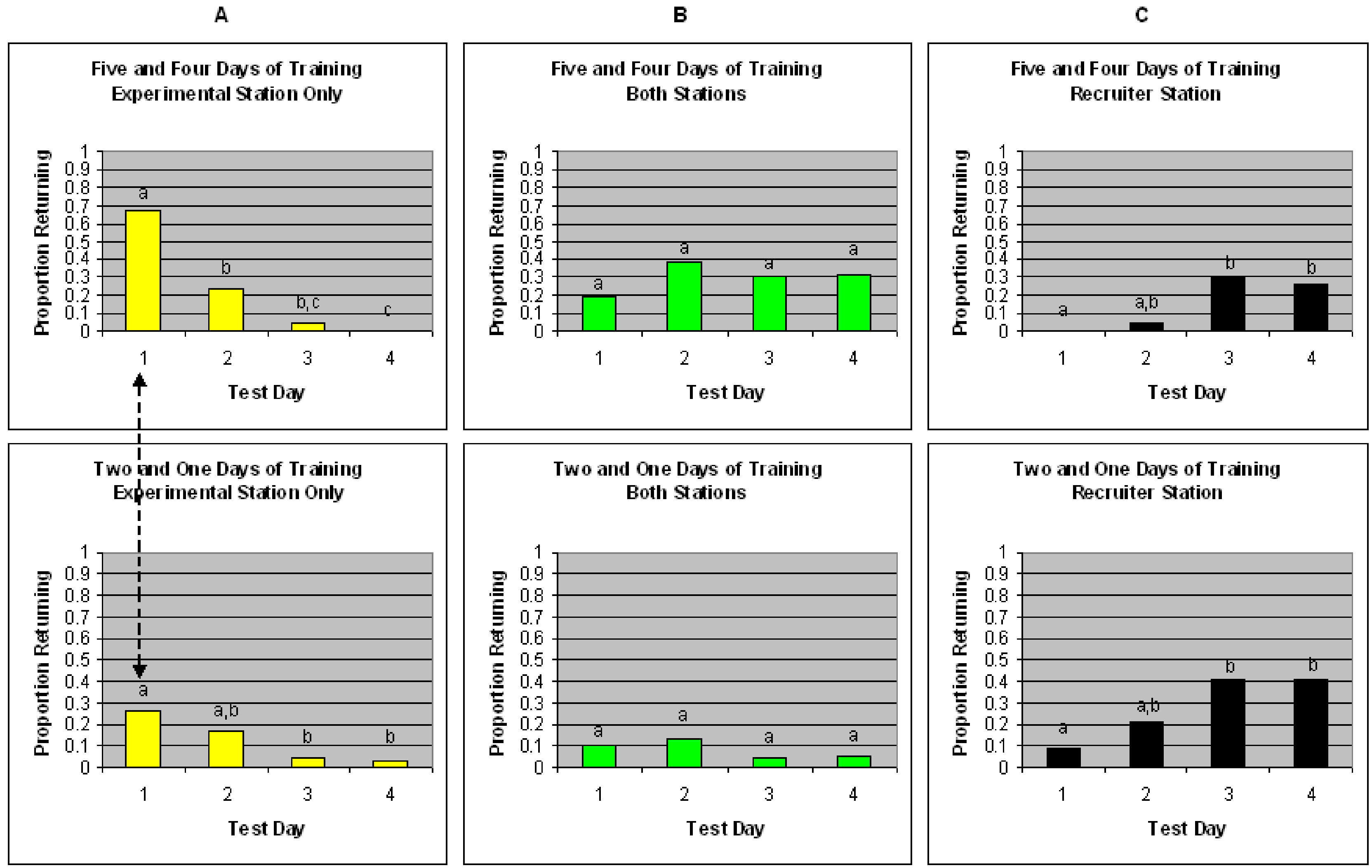

Figure 19 Experiment #2, July 24th - August 2nd 2005. Proportion of Foragers returning on each test day. See Figure 16 for details.

Table 30 Experiment 2 chi-square tests

Experimental Station Only			Both Stations			Recruiter Station Only		
Test Day 1			**Test Day 1**			**Test Day 1**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	14	7	5 and 4	4	17	5 and 4	0	21
2 and 1	13	36	2 and 1	5	44	2 and 1	4	45
	DF=1			DF=1			DF=1	
	χ^2 =8.372	P = 0.004		χ^2 =0.389	P = 0.533		χ^2 =0.619	P = 0.432
Test Day 2			**Test Day 2**			**Test Day 2**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	5	16	5 and 4	8	13	5 and 4	1	20
2 and 1	8	39	2 and 1	6	41	2 and 1	10	37
	DF=1			DF=1			DF=1	
	χ^2 =0.105	P = 0.746		χ^2 =4.25	P = 0.039		χ^2 =1.829	P = 0.176
Test Day 3			**Test Day 3**			**Test Day 3**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	1	19	5 and 4	6	14	5 and 4	6	14
2 and 1	2	40	2 and 1	2	40	2 and 1	17	25
	DF=1			DF=1			DF=1	
	χ^2 =0.351	P = 0.554		χ^2 =5.597	P = 0.018		χ^2 =0.267	P = 0.605
Test Day 4			**Test Day 4**			**Test Day 4**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	0	19	5 and 4	6	13	5 and 4	5	14
2 and 1	1	36	2 and 1	2	35	2 and 1	15	22
	DF=1			DF=1			DF=1	
	χ^2 =0.117	P = 0.732		χ^2 =5.048	P = 0.025		χ^2 =0.573	P = 0.449

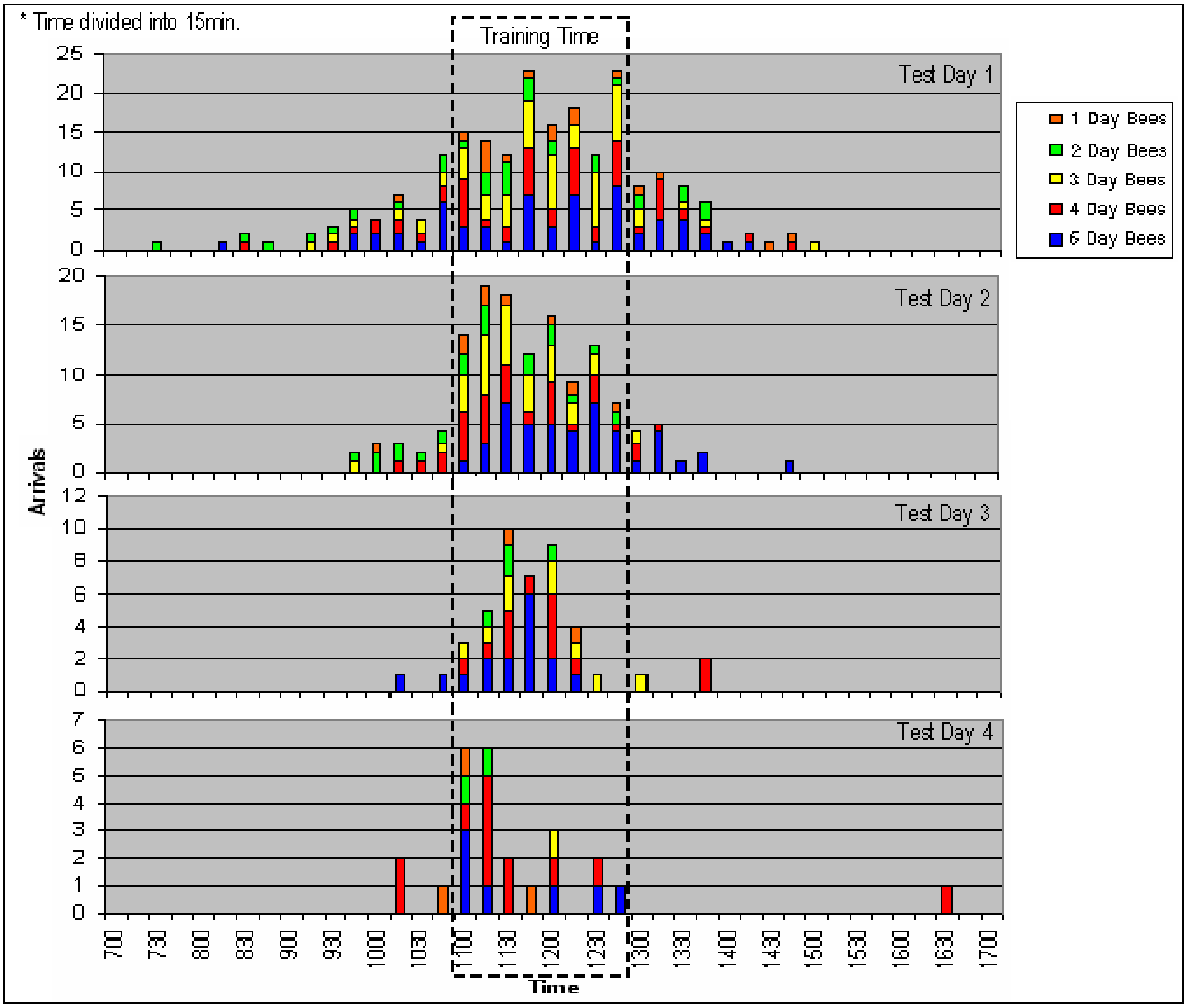

Figure 20 Arrivals at experimental station, July 2005. See Figure 17 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.523	.563	.659	.750
Low Experience Bees (2 and 1 Days of Training)	.224	.207	.136	.208

Table 31 Proportion of total arrivals at the experimental station, July 2005

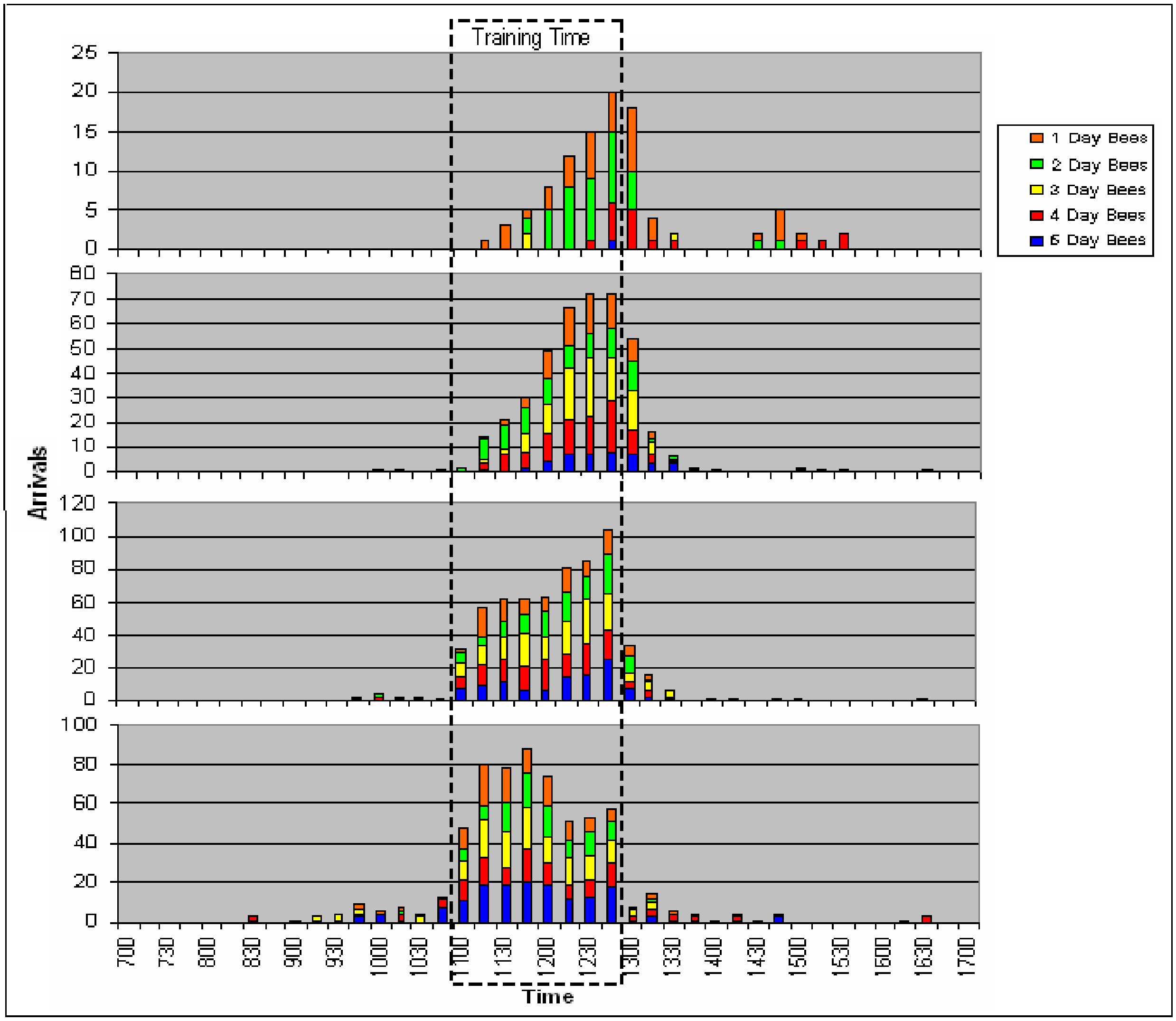

Figure 21 Arrivals at Recruiter Station, July 2005. See Figure 18 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.180	.331	.386	.432
Low Experience Bees (2 and 1 Days of Training)	.790	.406	.355	.347

Table 32 Proportion of total arrivals at the recruiter station, July 2005

Appendix C
July 2006 Experiment

Table 33 Five day experience bees; Bees marked July 24th 2006							
				Number of Rewards per Training Day			
Training day 1		Day 2	Day3	Day 4	Day5	Total	Reward/day
__W	1?	11	9	10	9	40	8
BB	1	3	2	1	2	9	1.8
BRR	2	4	9	5	1	21	4.2
BRW	2	13	1	5	14	35	7
BW	2	X	X	X	X	2	0.4
BWB	2	3	3	8	9	25	5
BWR	3	8	7	9	18	45	9
BWW	3	10	X	X	X	13	2.6
BWY	1	4	4	X	X	9	1.8
BYW	1	8	X	2	10	21	4.2
BYY	1	1	X	2	5	9	1.8
RBW	2	12	14	12	X	40	8
RWB	2	3	3	TWEEZED	X	8	1.6
RWR	1	X	X	X	X	1	0.2
WB	3	9	15	11	17	55	11
WBB	3	5	4	3	4	19	3.8
WBR	3	6	10	X	X	19	3.8
WBW	3	9	10	13	14	49	9.8
WBY	4	6	9	12	18	49	9.8
WRB	3	6	X	TWEEZED	X	9	1.8
WY	1	5	5	2	1	14	2.8
WYB	1	4	4	3	5	17	3.4
WYW	1	1	X	1	1	4	0.8
WYY	2	3	9	11	12	37	7.4
YBB	1	X	X	X	X	1	0.2
YBW	1	TWEEZED		RETURNED ?	X	1	0.2
YBY	1	X	X	2	5	8	1.6
YW	1	2	5	8	8	24	4.8
YWB	1	X	X	X	X	1	0.2
YWW	1	5	X	X	2	8	1.6
YWY	1	3	3	10	13	30	6
YY	1	2	2	4	12	21	4.2
Bold lettering = Individuals that arrived on all training days.							
X = No arrival at feeding station							

Table 34 Four and three day experience bees; Bees marked July 25th & 26th 2006

Number of Rewards Per Training Day

Four Day Bees							**Three Day Bees**					
Training Day 2		Day 3	Day 4	Day 5	Total	#/Day	Training Day 3		Day 4	Day 5	Total	#/day
BP	2	1	5	5	13	3.25	__R	1	TWEEZED		1	0.33
BPB	2	3	X	1	6	1.5	__W	1	X	X	1	0.33
BPP	4	5	3	13	25	6.25	GPR	1	X	X	1	0.33
BPY	2	6	8	12	28	7	GPW	3	TWEEZED		3	1
BYP	4	X	X	X	4	1	GRP	3	X	X	3	1
G__	1	X	1	X	2	0.5	**GWP**	1	1	1	3	1
GG	1	X	X	X	1	0.25	**GWW**	1	1	X	2	0.66
GP	3	1	6	3	13	3.25	**GWY**	1	9	X	10	3.33
GPG	1	2	6	7	16	4	**GYW**	1	4	4	9	3
GPP	2	1	X	1	4	1	**PGR**	1	2	5	8	2.66
GR	1	X	1	2	4	1	PGW	2	X	X	2	0.66
GRG	1	2	X	X	3	0.75	PRG	4	X	X	4	1.33
GRR	1	X	X	X	1	0.25	**PWG**	5	5	7	17	5.66
GY	4	5	X	X	9	2.25	RGP	1	TWEEZED		1	0.33
GYG	1	1	1	6	9	2.25	RPG	2	X	1	3	1
GYP	2	2	TWEEZED		4	1	WG	1	1	X	2	0.66
GYY	2	X	X	X	2	0.5	**WGG**	2	3	2	7	2.33
P__	3	2	X	X	5	1.25	WGP	2	TWEEZED		2	0.66
PB	2	6	7	5	20	5	**WGW**	1	3	5	9	3
PBB	1	Tweezed		X	1	0.25	**WGY**	3	5	8	16	5.33
PBP	5	9	13	15	42	10.5	WPG	2	X	X	2	0.66
PBY	3	X	X	X	3	0.75	WYG	2	1	1	4	1.33
PG	1	X	X	X	1	0.25	**YGW**	1	6	17	24	8
PGG	2	X	X	X	2	0.5	**YWG**	1	8	1	10	3.33
PGP	2	X	X	X	2	0.5						
PP	5	8	13	19	45	11.25						
PR	1	2	2	2	7	1.75						
PRP	1	X	X	X	1	0.25						
PRR	1	X	X	X	1	0.25						
PYB	1	3	4	6	14	3.5						
RG	2	3	3	12	20	5						
RGG	1	X	X	1	2	0.5						
RGR	2	5	2	4	13	3.25						
RP	4	X	X	X	4	1						
RPP	1	X	X	X	1	0.25						
RPR	1	X	2	X	3	0.75						
RR	1	X	6	1	8	2						
WRR	1	1	3	1	6	1.5						
YBP	2	6	6	9	23	5.75						
YG	1	1	2	5	9	2.25						
YGG	2	6	12	12	32	8						
YGY	1	2	5	3	11	2.75						
YPB	4	X	X	X	4	1						

Bold lettering = Individuals that arrived on all training days.

X = No arrival at feeding station

Table 35 Two and one day experience bees; bees marked July 27th & 28th 2006

			Number of Rewards per Test Day			
Two Day Bees					**One Day Bees**	
Training Day 4		Day 5	Total	#/day	Day 5	
BG	4	4	8	4	**_GR**	2
BGB	7	X	7	3.5	**AA**	2
BGR	8	6	14	7	**AG**	1
BR	7	X	7	3.5	**AGA**	1
BRB	2	5	7	3.5	**AGG**	1
BY	2	10	12	6	**AR**	1
BYB	1	2	3	1.5	**ARA**	2
G__	1	X	1	0.5	**ARR**	1
GBB	7	3	10	5	**AW**	2
GBR	8	X	8	4	**AWA**	1
GRB	5	X	5	2.5	**AWW**	1
GW	2	1	3	1.5	**AY**	1
GWW	3	X	5	1.5	**AYA**	3
PW	2	1	3	1.5	**AYY**	1
PWP	2	X	2	1	**BRY**	2
PWW	3	X	3	1.5	**BYR**	2
RB	7	1	8	4	**GA**	1
RBB	2	1	3	1.5	**GAA**	1
RBG	9	X	9	4.5	**GAG**	1
RBG	2	X	2	1	**GRY**	2
RBR	1	X	1	0.5	**GYR**	1
RGB	3	X	3	1.5	**RA**	2
RR	1	2	3	1.5	**RAA**	2
RW	2	X	2	1	**RAR**	1
RWW	3	4	7	3.5	**RBY**	1
RY	3	X	3	1.5	**RGY**	1
RYR	3	X	3	1.5	**RYB**	7
RYY	2	X	2	1	**RYG**	1
WP	2	1	3	1.5	**WA**	2
WPP	2	X	2	1	**WAA**	1
WPW	1	4	5	2.5	**WAW**	2
WR	1	X	1	0.5	**YA**	1
WRR	2	3	5	2.5	**YAA**	3
WRW	3	X	3	1.5	**YBR**	2
YB	1	2	3	1.5	**YRB**	2
YR	1	X	1	0.5	**YRG**	2
YRR	1	X	1	0.5		
YRY	1	X	1	0.5		

Bold lettering = Individuals that arrived on all training days.

X = No arrival at feeding station

Table 36 Five day bee test day arrivals, July 29th- August 1st 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp	Recruit	Exp	Recruit	Exp	Recruit	Exp	Recruit
Eight Days Of Training									
SO		X		X		X		X	X
Five Day Bees									
__W		X		X		X	X	X	X
BB			Living		X	X	X		X
BRR			Living	X		X			Unknown
BRW		X		X		X		X	X
BWB		X		X	X		Unknown		Unknown
BWR		X	X	X			Unknown		Unknown
WB		X		X		X		X	X
WBB		X		X	X	X	X		X
WBW		X		X			Unknown		Unknown
WBY		X			Unknown		Unknown		Unknown
WY		X		X	X		X		X
WYB		X		X	X	X	X		X
WYY		X		X		X		X	
YW		X		X		X		X	
YWY		X		X		X		X	
YY		X		X		X	X		X
Missed Final Day Only									
RBW			Unknown		Unknown		Unknown		Unknown
Missed day Four and Five									
BWY			Unknown		Unknown		Unknown		Unknown
WBR			Unknown		Unknown		Unknown		Unknown
Arrived Day One and Two									
BWW			Unknown		Unknown		Unknown		Unknown
Arrived Day One Only									
BW			Living		Living	X			Unknown
RWR			Unknown		Unknown		Unknown		Unknown
YBB			Unknown		Unknown		Unknown		Unknown
YWB			Unknown		Unknown		Unknown		Unknown
Missed Random Days									
BYW		X	X	X			Living	X	
BYY			Living		X		X		X
WYW			Unknown		Unknown		Unknown		Unknown
YBY		X		X			Unknown		Unknown
YWW			Unknown		Unknown		Unknown		Unknown
Dead Bees									
RWB			Dead		Dead		Dead		Dead
WRB			Dead		Dead		Dead		Dead
YBW			Dead		Dead		Dead		Dead
	Experimental:	13/16 = 0.813		Exp.:	10/15 = .667	Exp.:	6/12 = .500	Exp.:	3/11 = .273
	Both:	1/16 = 0.063		Both:	4/15 = .267	Both:	5/12 = .417	Both:	3/11 = .273
	Recruiter:	0		Recruiter:	1/15 = .067	Recruiter:	1/12 = .083	Recruiter:	5/11 = .455
	Living:	2							

Table 37 Four day bee test day arrivals, July 29th- August 1st 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
BP		X			X	X	X	X	X
BPP		X		X	X	X	X		X
BPY		X		X		X	X		X
GP		X	X	X	X		X		X
GPG		X		X	X	X	X		X
GYG			Living	X	X		X		X
PB		X		X			Living	X	
PBP		X		X		X		X	X
PP		X			X		X		X
PR			Living		Living		X		X
PYB		X			Unknown		Unknown		Unknown
RG		X	X	X	X		X		X
RGR			Living		Living	X	X	X	X
WRR		X		X	X	X	X		Unknown
YBP		X			Unknown		Unknown		Unknown
YG			Living		Living		X		X
YGG		X		X			Unknown		Unknown
YGY			Living	X			Unknown		Unknown
Missed days four and five									
GRG			Unknown		Unknown		Unknown		Unknown
GY			Unknown		Unknown		Unknown		Unknown
P__			Unknown		Unknown		Unknown		Unknown
Missed day 3 or 4 only									
RR			Living		Living		Living		X
GR		X			X		X		X
BPB			Unknown		Unknown		Unknown		Unknown
GPP			Living	X	X		Living		X
Missed days 3 & 5 or 3 & 4									
G__			Unknown		Unknown		Unknown		Unknown
RGG			Unknown		Unknown		Unknown		Unknown
RPR			Unknown		Unknown		Unknown		Unknown
Arrived Day two only									
BYP			Living		Living		Living		X
GG			Living		Living		Living		X
GRR			Unknown		Unknown		Unknown		Unknown
GYY			Unknown		Unknown		Unknown		Unknown
PBY			Unknown		Unknown		Unknown		Unknown
PG			Unknown		Unknown		Unknown		Unknown
PGG			Unknown		Unknown		Unknown		Unknown
PGP			Living		Living		Living		Living
PRP			Unknown		Unknown		Unknown		Unknown
PRR			Unknown		Unknown		Unknown		Unknown
RP			Living		Living		Living		Living
RPP			Living		X		Unknown		Unknown
YPB			Living		Living		Living		Living
Dead Bees									
GYP			Dead		Dead		Dead		Dead
PBB			Dead		Dead		Dead		Dead
	Experimental:	11/18 = 0.611		Exp.:	5/16 = .313	Exp.:	1/14 = .071	Exp.:	1/13 = .077
	Both:	2/18 = 0.111		Both:	6/16 = .375	Both:	6/14 = .429	Both:	3/13 = .231
	Recruiter:	0		Recruiter:	2/16 = .125	Recruiter:	6/14 = .429	Recruiter:	9/13 = .692
	Living:	5		Living:	3	Living:	1		

Table 38 Three day bees test day arrivals, July 29th- August 1st 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
GWP			Unknown		Unknown		Unknown		Unknown
GWW			Unknown		Unknown		Unknown		Unknown
GWY		X		X		X		X	
GYW			Living	X		X		X	X
PGR		X	X	X	X		X		Unknown
PWG			Unknown		Unknown		Unknown		Unknown
WGG			Unknown		Unknown		Unknown		Unknown
WGW			Living		X		X		Unknown
WGY		X		X	X	X	X		X
WYG		X	X	X	X		Unknown		Unknown
YGW		X			Unknown		Unknown		Unknown
YWG			Unknown		Unknown		Unknown		Unknown
Missed Final Day Only									
WG		X			Unknown		Unknown		Unknown
Day Three Only									
__W			Unknown		Unknown		Unknown		Unknown
GPR			Unknown		Unknown		Unknown		Unknown
GRP			Unknown		Unknown		Unknown		Unknown
PGW			Unknown		Unknown		Unknown		Unknown
PRG			Unknown		Unknown		Unknown		Unknown
RPG			Living	X	X	X	X		X
WPG			Unknown		Unknown		Unknown		Unknown
Dead Bees									
__R			Living		Living		Living	X	X
GPW			Dead		Dead		Dead		Dead
RGP			Dead		Dead		Dead		Dead
WGP			Living		Living		Living		Living
	Experimental:	3/7 = .429		Exp.:	2/6 = .333	Exp.:	2/5 = .400	Exp.:	1/3 = .333
	Both:	2/7 = .286		Both:	3/6 = .500	Both:	1/5 = .200	Both:	1/3 = .333
	Recruiter:	0		Recruiter:	1/6 = .167	Recruiter:	2/5 = .400	Recruiter:	1/3 = .333
	Living:	2							

Table 39 Two day bees test day arrivals, July 29th- August 1st 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
BG		X		X	X		X	X	X
BGR		X		X			Unknown		Unknown
BRB		X	X		X	X	X	X	X
BY		X		X	X		X		Unknown
BYB			Living		X		Unknown		Unknown
GBB		X			Living		Living		Living
GW		X			X	X	X		X
PW		X	X		X		Living		Living
RB			Unknown		Unknown		Unknown		Unknown
RBB			Living		Living		Living		Living
RR			Unknown		Unknown		Unknown		Unknown
RWW			Unknown		Unknown		Unknown		Unknown
WP			Living		X	X	X		Unknown
WPW		X		X			Unknown		Unknown
WRR		X			X		X		Unknown
YB			Living		Living		Living		Living
Day four only									
BGB			Unknown		Unknown		Unknown		Unknown
BR		X		X		X		X	
G__			Unknown		Unknown		Unknown		Unknown
GBR		X		X			Unknown	X	
GRB		X		X		X			Living
GWW			Unknown		Unknown		Unknown		Unknown
PWP			Living	X			Unknown		Unknown
PWW		X			Unknown		Unknown		Unknown
RBG		X		X			Living		Living
RBG			Unknown		Unknown		Unknown		Unknown
RBR			Unknown		Unknown		Unknown		Unknown
RGB		X		X		X			Living
RW			Unknown		Unknown		Unknown		Unknown
RY			Unknown		Unknown		Unknown		Unknown
RYR			Unknown		Unknown		Unknown		Unknown
RYY		X			Living	X			Living
WPP			Unknown		Unknown		Unknown		Unknown
WR			Living		Living		Living		Living
WRW			Unknown		Unknown		Unknown		Unknown
YR			Unknown		Unknown		Unknown		Unknown
YRR			Unknown		Unknown		Unknown		Unknown
YRY			Unknown		Unknown		Unknown		Unknown
	Exp.:	7/13 = .538		Exp.:	2/13 = .15	Exp.:	0	Exp.:	0
	Both:	2/13 = .154		Both:	2/13 = .15	Both:	3/10 = .30	Both:	2/7 = .286
	Recruiter:	0		Recruiter:	6/13 = .46	Recruiter:	3/10 = .30	Recruiter:	1/7 = .143
	Living:	4		Living:	3	Living:	4	Living:	4

Table 40 One day bee test day arrivals, July 29th- August 1st 2006

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
_GR		X			Living		X		X
AA			Living		X		X		X
AG			Living		Living		Living		X
AGA			X		X		X		X
AGG			Living		X		X		X
AR		X	X		X		Living		X
ARA			Living	X			Unknown		Unknown
ARR			Unknown		Unknown		Unknown		Unknown
AW			Living		X		X		X
AWA			Living		X		X		X
AWW			X		X		X	X	X
AY		X	X		X		X		X
AYA		X			Living		Living		X
AYY			Unknown		Unknown		Unknown		Unknown
BRY		X			Unknown		Unknown		Unknown
BYR			Living		Living		X		X
GA			Living		X		X		X
GAA			Living		X		X		X
GAG		X	X		X		X		Unknown
GRY			Living		X		X		X
GYR			Unknown		Unknown		Unknown		Unknown
RA		X			Unknown		Unknown		Unknown
RAA			X	X	X	X	X		X
RAR			Living		X		X		X
RBY			Living		Living		X	X	X
RGY			Unknown		Unknown		Unknown		Unknown
RYB		X		X	X		X		X
RYG		X			Unknown		Unknown		Unknown
WA		X			Living		X		X
WAA			Living		Living		X		X
WAW			Unknown		Unknown		Unknown		Unknown
YA			Living		X		X		X
YAA			Unknown		Unknown		Unknown		Unknown
YBR		X			X		X		X
YRB			X		X		X		X
YRG		X		X	X		X		X
Experimental:		9/30 = .300		Exp.:	1/27 = .037	Exp.:	0	Exp.:	0
Both:		3/30 = .100		Both:	3/27 = .111	Both:	1/26 = .038	Both:	2/25 = .080
Recruiter:		4/30 = .133		Recruiter:	16/27 = .593	Recruiter:	22/26 = .846	Recruiter:	23/25 = .920
Living:		14		Living:	7	Living:	3		

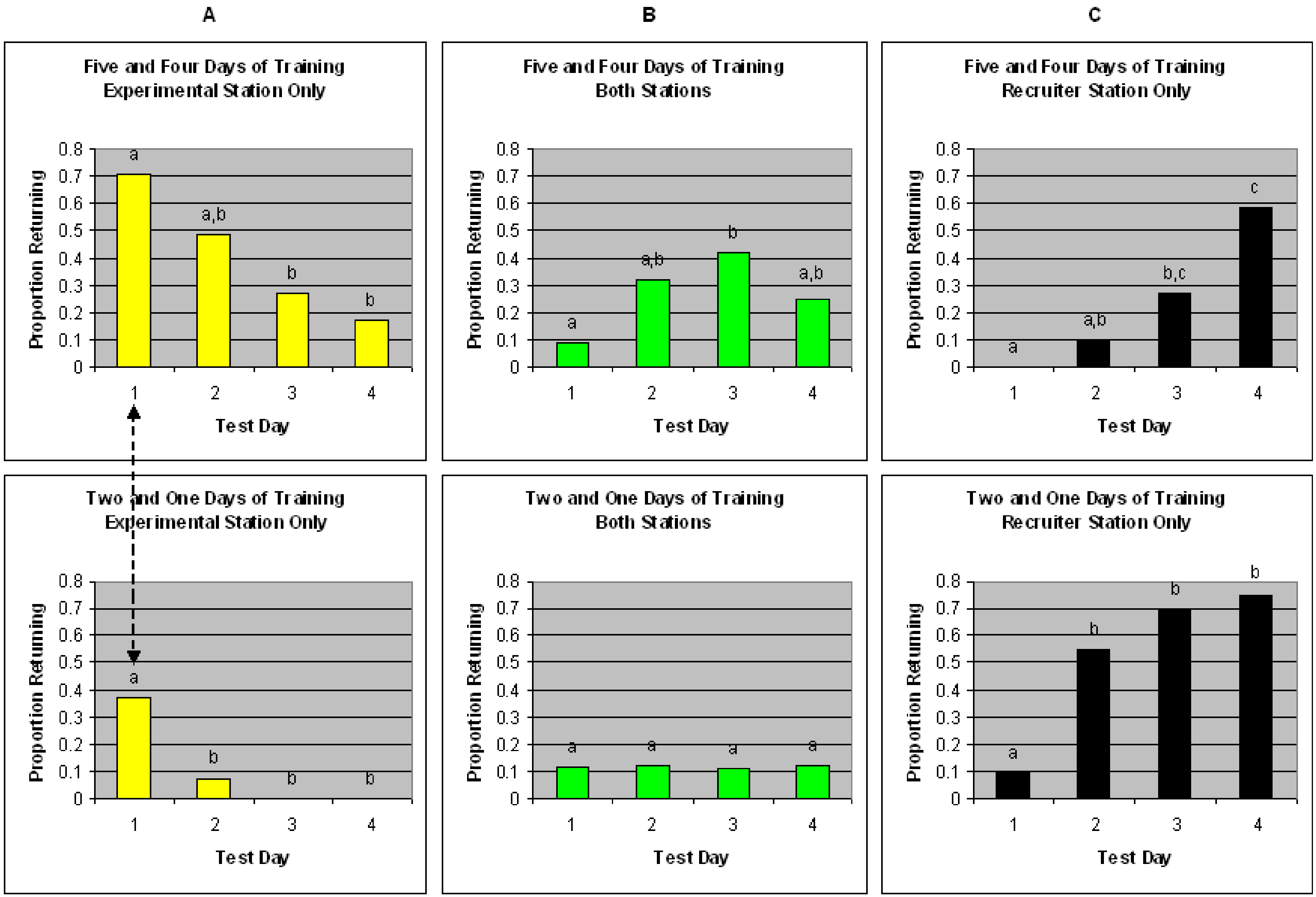

Figure 22 Experiment #3, July 24th - August 1st 2006. Proportion of foragers returning on each test day. See Figure 16 for details.

Table 41 Experiment 3 chi-square analysis

Experimental Station Only			**Both Stations**			**Recruiter Station Only**		
Test Day 1			**Test Day 1**			**Test Day 1**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	24	10	5 and 4	3	31	5 and 4	0	34
2 and 1	16	27	2 and 1	5	38	2 and 1	4	39
	DF=1			DF=1			DF=1	
	χ^2 =7.190	P = 0.007		χ^2 =0.0005	P = 0.981		χ^2 =1.715	P = 0.190
Test Day 2			**Test Day 2**			**Test Day 2**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	15	16	5 and 4	10	21	5 and 4	3	28
2 and 1	3	37	2 and 1	5	35	2 and 1	22	18
	DF=1			DF=1			DF=1	
	χ^2 =13.342	P < 0.001		χ^2 =2.992	P = 0.084		χ^2 =13.802	P < 0.001
Test Day 3			**Test Day 3**			**Test Day 3**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	7	19	5 and 4	11	15	5 and 4	7	19
2 and 1	0	36	2 and 1	4	32	2 and 1	25	11
	DF=1			DF=1			DF=1	
	χ^2 =8.403	P = 0.004		χ^2 =6.400	P = 0.011		χ^2 =9.293	P = 0.002
Test Day 4			**Test Day 4**			**Test Day 4**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	4	20	5 and 4	6	18	5 and 4	14	10
2 and 1	0	32	2 and 1	4	28	2 and 1	24	8
	DF=1			DF=1			DF=1	
	χ^2 =3.506	P = 0.061		χ^2 =0.733	P = 0.392		χ^2 =1.066	P = 0.302

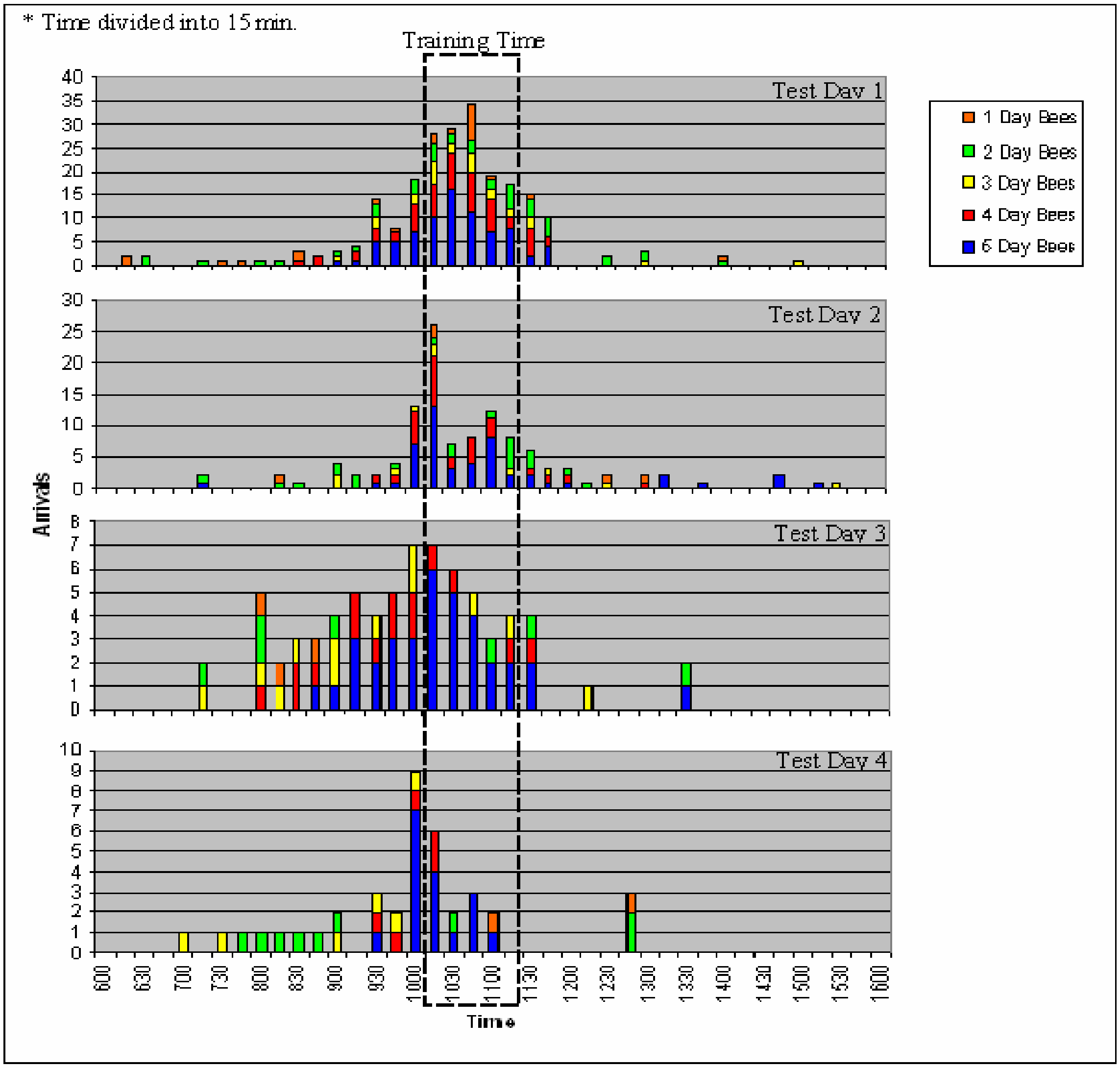

Figure 23 Arrivals at experimental station, July 2006. See Figure 17 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.606	.678	.694	.564
Low Experience Bees (2 and 1 Days of Training)	.285	.235	.135	.282

Table 42 Proportion of total arrivals at the experimental station, July 2006.

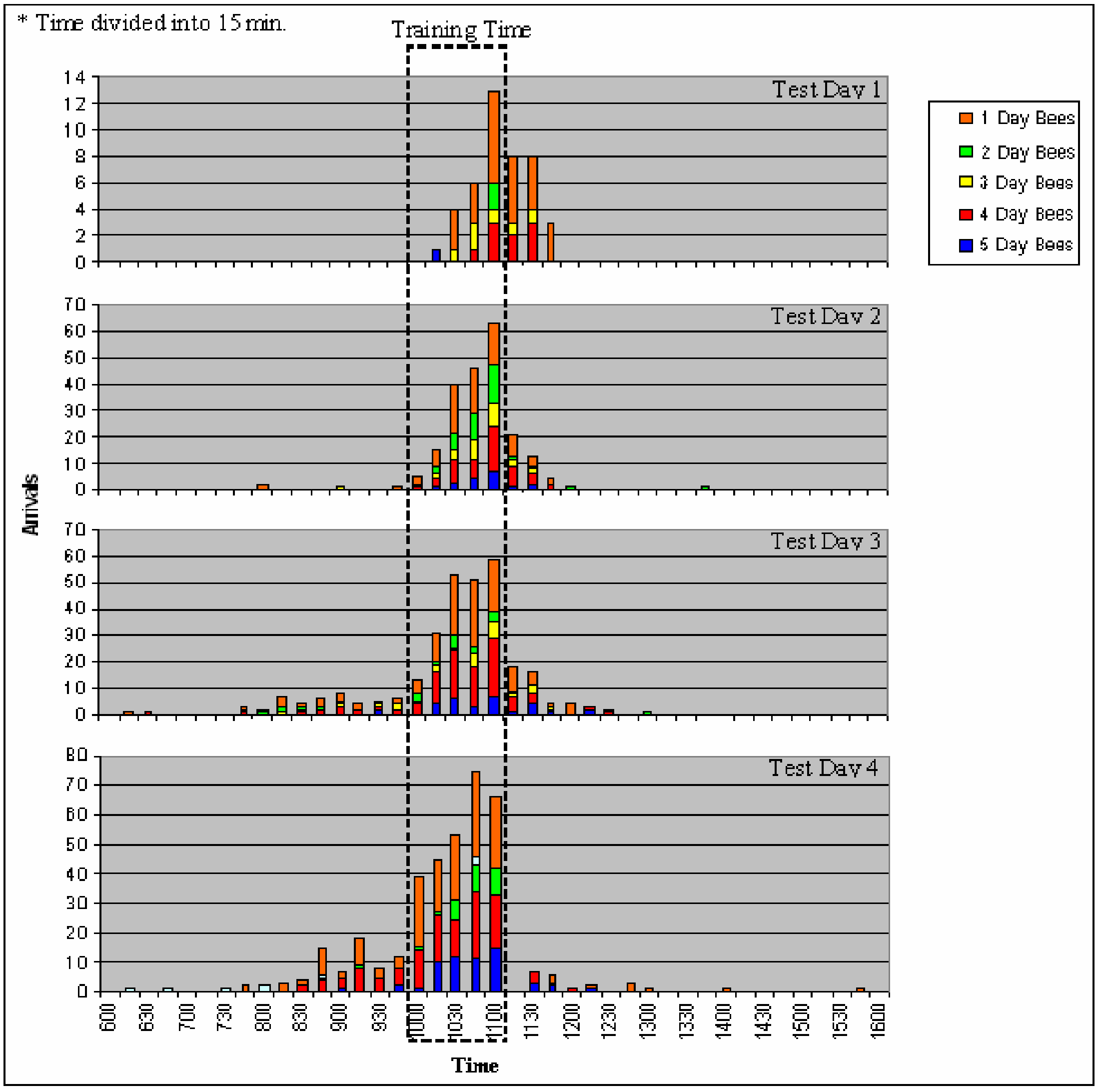

Figure 24 Arrivals at recruiter station, July 2006. See Figure 18 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.233	.324	.422	.472
Low Experience Bees (2 and 1 Days of Training)	.628	.540	.485	.453

Table 43 Proportion of total arrivals at the recruiter station, July 2006

Appendix D
September 2006 Experiment

Table 44 Five day experience bees; bees marked September 22nd 2006							
				Number of Rewards per Training Day			
Training day 1		Day 2	Day3	Day 4	Day5	Total	Reward/day
BB	5	9	8	5	7	34	6.8
BRW	7	7	X	6	3	23	4.6
BWB	3	6	6	5	6	26	5.2
BWR	5	9	4	5	11	34	6.8
BWW	5	5	6	7	9	32	6.4
GG	1	8	4	3	3	19	3.8
GP	1	1	X	X	7	9	1.8
GP_	2	X	X	X	X	2	0.4
GRG	1	X	X	X	X	1	0.2
GRR	1	1	5	7	6	20	4
GW	1	4	3	3	4	15	3
GWG	4	6	4	9	7	30	6
GWW	2	7	7	7	8	31	6.2
PG	1	6	2	DUP.	9	27	5.4
PGG	1	X	X	X	X	1	0.2
PP	1	3	X	1	X	5	1
PR	1	4	5	1	5	16	3.2
PRP	1	1	X	X	1	3	0.6
PRR	1	7	5	4	6	23	4.6
R__	3	6	X	7	12	28	5.6
RBW	1	X	X	X	1	2	0.4
RGG	4	6	2	7	3	22	4.4
RGR	2	4	X	X	X	6	1.2
RGW	3	5	3	5	6	22	4.4
RP_	1	X	X	X	X	1	0.2
RPP	1	3	9	6	6	25	5
RPR	1	3	7	6	5	22	4.4
RR	2	2	3	7	4	18	3.6
RW	2	3	4	6	1	16	3.2
RWB	8	10	5	11	X	34	6.8
RWG	2	X	X	X	X	2	0.4
RWR	2	X	X	X	X	2	0.4
RWR	DUP.	X	X	X	X	X	X
RWW	3	8	1	7	12	31	6.2
W__	1	X	Tweezed	X	X	X	X
WB	1	1	3	5	7	17	3.4
WBR	7	8	8	6	10	39	7.8
WBW	2	6	5	8	4	25	5
WG	1	X	3	6	5	15	3
WGG	2	3	3	4	11	23	4.6
WGW	2	5	8	7	8	30	6
WR	1	X	1	5	7	14	2.8
WRG	1	3	3	6	7	20	4
WRR	3	X	X	2	X	5	1
WRR	DUP.	8	X	X	X	X	X
WRW	3	4	6	3	7	23	4.6
WW	2	X	X	X	X	2	0.4
G__?		3	X	3	X	X	X
RG?		2	X	X	X	X	X
GR		5	X	1	X	X	X
B__		1	X	2	X	X	X
GW_		1	8	3	3	X	X
Bold lettering = Individuals that arrived on all training days.							
X = No arrival at feeding station							

Table 45 Four and three day experience bees; bees marked September 23th & 24th 2006

							Number of Rewards Per Training Day					
Four Day Bees							**Three Day Bees**					
Training Day 2		Day 3	Day 4	Day 5	Total	#/Day	Training Day 3		Day 4	Day 5	Total	#/day
BG_	?	1	X	X	1	0.25	BP	1	X	X	1	0.33
BG	3	5	7	7	22	5.5	BPB	1	X	X	1	0.33
BGB	2	5	6	7	20	5	BPP	1	X	X	1	0.33
BGG	2	1	X	X	3	0.75	**BR**	1	4	1	6	2
BY	1	4	2	1	8	2	BRB	1	X	4	5	1.67
BYB	2	6	4	9	21	5.25	**BRR**	1	4	3	8	2.67
BYY	1	1	1	X	3	0.75	**GWY**	2	8	5	15	5
GBB	1	X	X	X	1	0.25	GYW	2	X	X	2	0.67
GBY	2	4	5	2	13	3.25	PB	1	X	X	1	0.33
GRY	1	X	4	X	5	1.25	PBB	1	6	X	7	2.33
GY	1	4	4	5	14	3.5	PBP	1	X	X	1	0.33
GYG	2	5	2	6	15	3.75	PRW	3	1	X	4	1.33
GYR	3	X	4	2	9	2.25	**PW**	3	6	1	10	3.33
GYY	3	3	6	7	19	4.75	PWP	2	X	X	2	0.67
RG_	3	X	2	1	6	1.5	PWR	1	X	X	1	0.33
RY	1	X	X	X	1	0.25	PWW	3	X	X	3	1
RYG	3	6	5	3	17	4.25	**PY**	3	5	4	12	4
RYR	4	X	X	1	5	1.25	**PYP**	2	1	1	4	1.33
RYY	2	X	X	X	2	0.5	PYW	1	X	X	1	0.33
YB	2	X	X	X	2	0.5	PYY	4	6	X	10	3.33
YBB	1	5	X	X	6	1.5	**RB**	1	6	6	13	4.33
YBY	1	3	X	1	5	1.25	RBB	1	X	X	1	0.33
YG	1	2	2	2	7	1.75	**RBG**	1	1	1	3	1
YGB	1	X	1	X	2	0.5	RBR	1	4	X	5	1.67
YGG	1	5	2	3	11	2.75	**RG**	1	2	1	4	1.33
YGR	1	X	X	X	1	0.25	RGY	2	X	X	2	0.67
YGY	1	5	X	X	6	1.5	**RPW**	2	6	5	13	4.33
YR	6	4	6	5	21	5.25	**RWP**	1	2	3	6	2
YRG	4	8	3	5	20	5	**WGY**	1	3	1	5	1.67
YRR	1	3	4	6	14	3.5	**WP**	1	1	5	7	2.33
YRY	6	6	9	8	29	7.25	WPP	1	3	X	4	1.33
YWW	3	1	X	X	4	1	**WPR**	3	5	3	11	3.67
YWY	1	3	2	X	6	1.5	WPW	1	X	X	1	0.33
BYG?	?	1	X	X	X	X	**WRP**	4	5	6	15	5
GYB ?	?	?	1	1	X	X	WY	1	1	X	2	0.67
GR?	?	?	6	9	X	X	WYG	1	2	X	3	1
G__	?	?	5	X	X	X	**WYW**	6	3	7	16	5.33
GB?	?	?	2	1	X	X	**WYY**	2	1	4	7	2.33
RG?	?	?	1	X	X	X	YG	1	X	1	2	0.67
GBG	?	?	2	X	X	X	YP	1	X	X	1	0.33
							YPP	1	X	X	1	0.33
							YPY	3	1	7	11	3.67
							YW	2	8	10	20	6.67
							YWB?	1	X	X	1	0.33
							YWG	2	1	2	5	1.67
							PRG?	?	1	X	X	X
							RB_	?	4	6	X	X
							BPR	?	1	X	X	X
Bold lettering = Individuals that arrived on all training days.												
X = No arrival at feeding station												

Table 46 Two and one day experience bees; bees marked September 25th & 26th 2006

			Number of Rewards per Test Day			
Two Day Bees					**One Day Bees**	
Training Day 4		Day 5	Total	#day	Training Day 5	
BGB	1	4	5	2.5	**AB**	2
BGR	2	X	2	1	**ABA**	1
BGY	1	3	4	2	**ABB**	3
BRG	1	1	2	1	**AG**	1
BYG	DUP.	X	X	X	**AGA**	1
GB	2	2	4	2	**AGG**	1
GBR	3	4	7	3.5	**AP**	1
GPB	1	3	4	2	**APA**	1
GPG	2	X	2	1	**APP**	2
GPP	4	X	4	2	**AR**	6
GPR	1	X	1	0.5	**AR_**	3
GR	1	3	4	2	**ARA**	1
GRB	1	X	1	0.5	**ARR**	4
GRP	1	X	1	0.5	**AW**	1
GYB	DUP.	X	X	X	**AW_**	2
P__	3	X	3	1.5	**AWA**	4
PBG	1	X	1	0.5	**AWW**	1
PG	DUP.	2	3	1.5	**AY**	2
PGB	1	X	1	0.5	**AYA**	4
PGP	1	2	3	1.5	**AYY**	1
PGR	1	X	1	0.5	**BA**	1
PR_	2	X	2	1	**BAA**	1
PRG	DUP.	X	X	X	**BAB**	2
RBG	1	X	1	0.5	**GA**	2
RG	1	DUP.	X	X	**GAA**	1
RGB	1	X	1	0.5	**GAG**	1
RGP	2	8	10	5	**PA**	2
RPG	1	X	1	0.5	**PAA**	3
YBG	4	X	4	2	**PAP**	2
GBW?	?	1	X	X	**RA**	1
GWP?	?	1	X	X	**RAA**	1
RP?	?	4	X	X	**RAR**	5
PGY?	?	1	X	X	**W__**	3
GWB?	?	1	X	X	**WA**	1
GR_?	?	2	X	X	**WA_**	1
RRW?	?	1	X	X	**WAA**	1
					WAW	3
					YA	2
					YAA	3
					YAA	3
					YAY	3
Bold lettering = Individuals that arrived on all training days.						
X = No arrival at feeding station						

Table 47 Five day bee test day arrivals, September 27th- September 30th 2006

		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp	Recruit	Exp	Recruit	Exp	Recruit	Exp	Recruit
BB		X	X	X		X	X		UNKNOWN
BWB		X	X	X			UNKNOWN		UNKNOWN
BWR		X		X			UNKNOWN		UNKNOWN
BWW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GG			X		LIVING		X		X
GRR			LIVING		LIVING		LIVING		X
GW			LIVING	X			UNKNOWN		UNKNOWN
GWG		X	X	X	X	X	X		X
GWW		X		X	X	X	X		X
PR		X		X		X	X	X	X
PRR			LIVING		LIVING		LIVING		X
RGG		X		X			X		X
RGW		X	X	X	X		X		X
RPP		X		X		X	X	X	X
RPR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RR		X	X	X	X		X		X
RW		X		X		X			UNKNOWN
RWW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WB		X		X			LIVING		UNKNOWN
WBR		X		X		X	X		LIVING
WBW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WGG		X			UNKNOWN		UNKNOWN		UNKNOWN
WGW		X	X	X	X	X	X	X	X
WRG		X		X			X		X
WRW		X			UNKNOWN		UNKNOWN		UNKNOWN
Missed Final Day Only									
RWB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Missed Day Three Only									
BRW		X	X	X	X		X		X
R__		X	X	X	X		X	X	X
Missed Day Two Only									
WG		X	X	X	X		X		X
WR		X		X			X		LIVING
Missed Day Four and Five									
GP		X		X	X	X	X		X
PRP			LIVING		LIVING		LIVING		LIVING
Missed Day Two, Three and Four									
RBW			LIVING	X					UNKNOWN
Arrived Day One and Two									
RGR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Arrived Day One Only									
GRG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PGG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GP_			LIVING		LIVING	X			UNKNOWN
RP_			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RWG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RWR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WW			LIVING		LIVING		X		UNKNOWN
Missed Random Days									
PP		X			UNKNOWN		UNKNOWN		UNKNOWN
WRR		UNKNOWN			UNKNOWN		UNKNOWN		UNKNOWN
Dead Bees, Duplictes and undocumented color codes									
B__			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
G_?			LIVING		LIVING		LIVING		LIVING
GR			LIVING		LIVING		LIVING		LIVING
GW_			LIVING	X			X	X	
PG		X		X		X		X	
RG?			X	X	X		X		LIVING
RWR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
W__			DEAD		DEAD		DEAD		DEAD
WRR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
	Experimental:	11/21=.523		Exp.:	11/19=.579	Exp.:	1/16=.063	Exp.:	0
	Both:	6/21=.286		Both:	5/19=.263	Both:	7/16=.438	Both:	3/13=.231
	Recruiter:	1/21=.048		Recruiter:	0	Recruiter:	5/16=.313	Recruiter:	9/13=.692
	Living:	3		Living:	3	Living:	3	Living:	1

Table 48 Four day bee test day arrivals, September 27th- September 30th 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
BG		X			LIVING	DEAD IN HIVE			DEAD
BGB			LIVING		LIVING		X	X	
BY			LIVING		LIVING		X	X	
BYB		X	X	X	X		X		X
GBY		X			UNKNOWN		UNKNOWN		UNKNOWN
GY		X			LIVING		LIVING		UNKNOWN
GYG		X		X			LIVING		LIVING
GYY		X		X	X		X		X
RYG		X	X		X		X		X
YG		X	X	X	X		X		X
YGG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
YR		X	X	X	X		X		X
YRG		X		X	X	X	X		X
YRR		X	X		X		X		X
YRY		X	X	X	X		X		X
Missed Final Day Only									
BYY			LIVING		LIVING		UNKNOWN		UNKNOWN
YWY			LIVING		LIVING		X		UNKNOWN
Missed days four and five									
BGG			LIVING		LIVING		LIVING		LIVING
YBB		X			LIVING		X		UNKNOWN
YGY		X			UNKNOWN		UNKNOWN		UNKNOWN
YWW			LIVING	X			LIVING		UNKNOWN
Missed day 3 or 4 only									
GYR		X		X			LIVING		LIVING
GRY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RG_			X		X		X		X
YBY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Missed days 3 & 5 or 3 & 4									
RYR		X			UNKNOWN		UNKNOWN		UNKNOWN
YGB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Arrived Day two only									
GBB		X			X		UNKNOWN		UNKNOWN
RY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RYY			LIVING		LIVING		LIVING		X
YB			X		UNKNOWN		UNKNOWN		UNKNOWN
YGR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Dead Bees, Duplictes and undocumented color codes									
BG_			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
BYG?			LIVING		LIVING		LIVING		LIVING
GYB ?			LIVING		LIVING		LIVING		UNKNOWN
GR?		X	X		X		X		X
G__		X			LIVING		LIVING		LIVING
GB?		X	X		LIVING		LIVING	X	
RG?			LIVING		LIVING		LIVING		X
GBG			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
		14							
Experimental:		6/14=.429		Exp.:	1/13=.077	Exp.:	0	Exp.:	2/11=.182
Both:		6/14=.429		Both:	6/13=.462	Both:	1/12=.083	Both:	0
Recruiter:		0		Recruiter:	2/13=.154	Recruiter:	9/12=.75	Recruiter:	8/11=.727
Living:		2		Living:	4	Living:	2	Living:	1

Table 49 Three day bee test day arrivals, September 27th- September 30th 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
BR			LIVING		LIVING		LIVING		LIVING
BRR		X	X	X	X		X		X
GWY		X	X	X	X		X		X
PW		X		X		X			UNKNOWN
PY		X		X		X			UNKNOWN
PYP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RB		X		X			UNKNOWN		UNKNOWN
RBG			X		X		X	X	X
RPW		X		X	X		X		X
RWP		X	X		X		X		X
WGY		X			LIVING		LIVING		LIVING
WP		X		X		X	X		X
WPR		X	X		X		UNKNOWN		UNKNOWN
WRP		X	X	X	X		X		X
WYW		X	X		X		X		X
WYY			LIVING		LIVING		LIVING		UNKNOWN
YPY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
YW		X	X	X	X		X	X	X
YWG		X	X		X		X		X
Missed Final Day Only									
PBB		X		X		X	X		X
PRW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PYY			UNKNOWN				X		LIVING
RBR		X			UNKNOWN		UNKNOWN		UNKNOWN
WPP			LIVING		LIVING		X		LIVING
WY			LIVING	X			UNKNOWN		UNKNOWN
WYG			LIVING		LIVING		LIVING		LIVING
Missed Day Four Only									
BRB		X			LIVING		LIVING		UNKNOWN
YG			X	X			X		X
Day Three Only									
BP			X		X		X		UNKNOWN
BPB		X			LIVING		LIVING		X
BPP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GYW			LIVING		LIVING		LIVING		LIVING
PB			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
PBP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PWP			LIVING		LIVING		LIVING		LIVING
PWR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PWW			LIVING		LIVING		X		X
PYW			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RBB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RGY		X			UNKNOWN		UNKNOWN		UNKNOWN
WPW			LIVING		LIVING		LIVING		LIVING
YP			LIVING		LIVING	X			UNKNOWN
YPP			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
Dead Bees, Duplictes and undocumented color codes									
YWB?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PRG?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RB_			X	X	X		LIVING		LIVING
BPR		X	UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RG		X	X		X		X		X
Experimental:		6/17=.353		Exp.:	4/17=.235	Exp.:	2/15=.133	Exp.:	0
	Both:	8/17=.471		Both:	5/17=.294	Both:	1/15=.067	Both:	2/12=.167
Recruiter:		1/17=.059		Recruiter:	5/17=.294	Recruiter:	9/15=.6	Recruiter:	8/12=.667
	Living:	2		Living:	3	Living:	3	Living:	2

Table 50 Two day bee test day arrivals, September 27th- September 30th 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
BGB			LIVING		LIVING		X		LIVING
BGY			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
BRG			X		LIVING		LIVING		X
GB		X	X		X		X		X
GBR		X	X	X	X		X	X	X
GPB		X	X		X		X		X
GR		X	X	X	X		X		X
PGP		X	X	X	X	X	X		X
RGP		X	X		X		X		X
Day four only									
BGR			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GPG			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
GPP			LIVING		LIVING		X		UNKNOWN
GPR			LIVING		LIVING		LIVING		LIVING
GRB			LIVING		LIVING		LIVING		UNKNOWN
GRP			LIVING		X		UNKNOWN		UNKNOWN
P__			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PBG			LIVING		LIVING		LIVING	X	
PGB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PGR			LIVING		LIVING		X		LIVING
PR_			LIVING		LIVING		X		X
RBG			X		X		X		X
RGB			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
RPG			LIVING		LIVING		X		X
YBG			LIVING		LIVING		X		X
Dead Bees, Duplictes and undocumented color codes									
GYB			LIVING		LIVING		LIVING		LIVING
BYG			LIVING		LIVING		LIVING		LIVING
PRG			LIVING	X			X		X
RG		X	X		LIVING		X		LIVING
GBW?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GWP?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
PG		X		X			X		LIVING
RP?		X	X		X		X		X
PGY?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GWB?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
GR_?			LIVING		LIVING		LIVING		LIVING
RRW?			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
	Exp.:	0		Exp.:	0	Exp.:	0	Exp.:	0
	Both:	6/8=.75		Both:	3/8=.375	Both:	0	Both:	1/8=.125
	Recruiter:	1/8=.125		Recruiter:	3/8=.375	Recruiter:	7/8=.875	Recruiter:	6/8=.75
	Living:	1		Living:	2	Living:	1	Living:	1

Table 51 One day bee test day arrivals, September 27th- September 30th 2006									
		Test Day1		Test Day 2		Test Day 3		Test Day 4	
		Exp.	Recruit	Exp.	Recruit	Exp.	Recruit	Exp.	Recruit
AB		X	X	X	X		X		X
ABA			X		LIVING		LIVING		X
ABB		X	X	X	X		UNKNOWN		UNKNOWN
AG			X		X		X		X
AGA			X		X		X		X
AGG			X		X		LIVING		LIVING
AP		X	X		LIVING		LIVING		LIVING
APA			LIVING		LIVING		LIVING		LIVING
APP			X		X		X		X
AR		X		X	X		X		X
AR_			X		X		LIVING		X
ARA			X		X		X		LIVING
ARR		X	X		X	X	X		X
AW		X			X		X	X	
AW_			X		X		X		UNKNOWN
AWA			X		X		X		X
AWW			X		X		X		X
AY		X			LIVING		X		X
AYA		X	X		X		UNKNOWN		UNKNOWN
AYY			LIVING		UNKNOWN		UNKNOWN		UNKNOWN
BA		X	X		X	X	X		X
BAA			X		X		X		X
BAB			X		X		X		X
GA		X	X		LIVING		X		X
GAA			X		X		X		X
GAG			X		X		X		X
PA		X			LIVING	X			X
PAA		X	X		X	X	X		X
PAP			X		X		X		X
RA		X			LIVING		X		X
RAA		X			LIVING		LIVING		LIVING
RAR		X			X		X	X	X
W__		X	X	X	X		X		X
WA		X	X		X		X		X
WA_			UNKNOWN		UNKNOWN		UNKNOWN		UNKNOWN
WAA			LIVING		LIVING		LIVING		X
WAW		X	X		X		X		X
YA		X	X		X		X		X
YAY			X		X		X		X
Dead Bees, Duplictes and undocumented color codes									
YAA		X	X		X		X		X
YAA		X	X		X		X		X
	Experimental:	7/38=.184		Exp.:	0	Exp.:	1/35=.029	Exp.:	1/34=.029
	Both:	12/38=.316		Both:	4/37=.108	Both:	3/35=.086	Both:	1/34 = .029
	Recruiter:	16/38=.421		Recruiter:	24/37=.649	Recruiter:	24/35=.686	Recruiter:	27/34=.794
	Living:	3		Living:	9	Living:	7	Living:	5

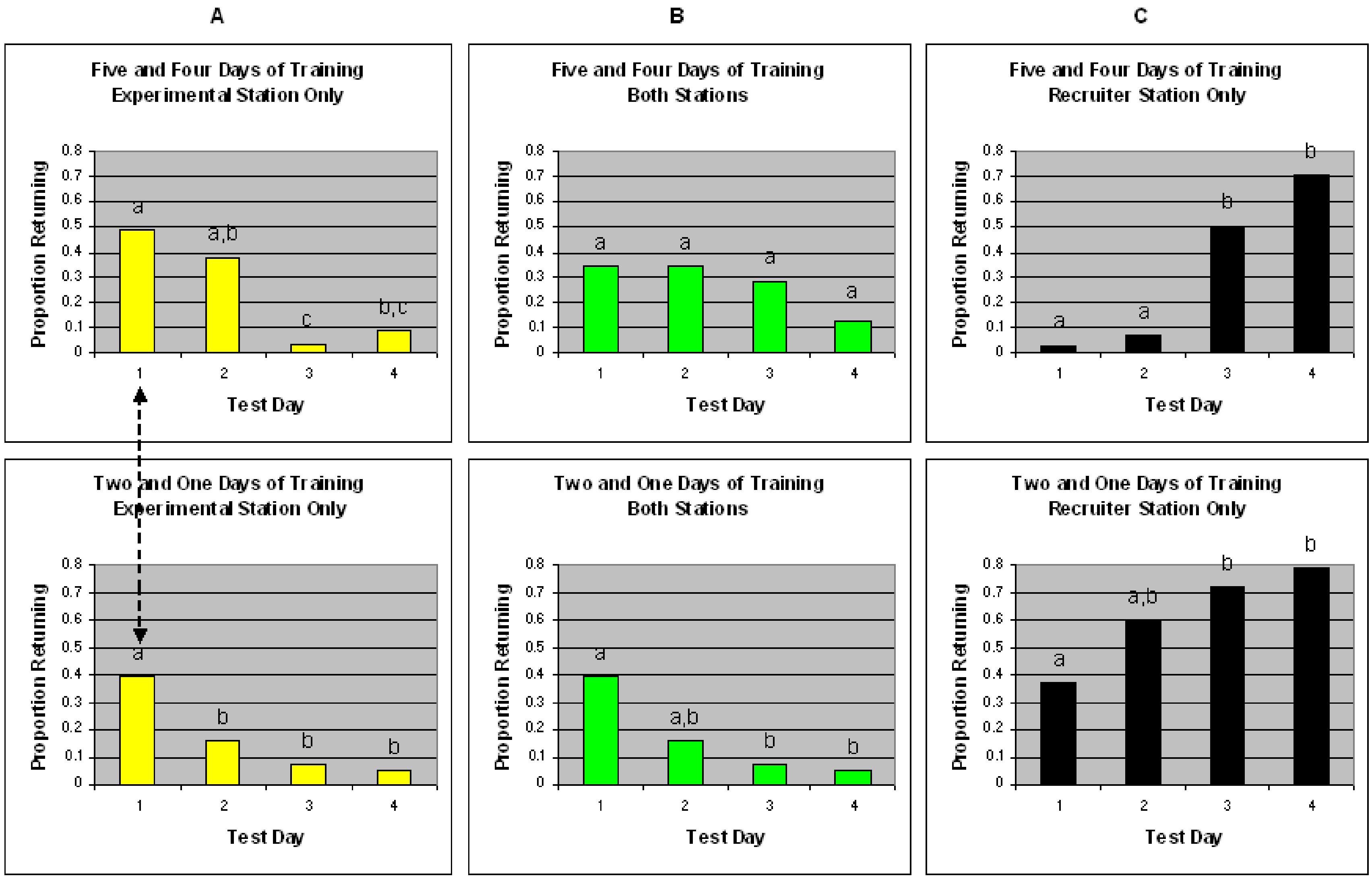

Figure 25 Experiment #4, September 27th - September 30th 2006. Proportion of foragers returning on each test day. See Figure 16 for details.

Table 52 Experiment 4 chi-square analysis

Experimental Station Only			Both Stations			Recruiter Station Only		
Test Day 1			**Test Day 1**			**Test Day 1**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	17	18	5 and 4	12	23	5 and 4	1	34
2 and 1	7	39	2 and 1	18	28	2 and 1	17	29
	DF=1			DF=1			DF=1	
	χ^2 =9.066	P = 0.003		χ^2 =0.046	P = 0.830		χ^2 =11.472	P < 0.001
Test Day 2			**Test Day 2**			**Test Day 2**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	12	20	5 and 4	11	21	5 and 4	2	30
2 and 1	0	45	2 and 1	7	38	2 and 1	27	18
	DF=1			DF=1			DF=1	
	χ^2 =17.242	P < 0.001		χ^2 =2.722	P = 0.099		χ^2 =20.780	P < 0.001
Test Day 3			**Test Day 3**			**Test Day 3**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	1	27	5 and 4	8	20	5 and 4	14	14
2 and 1	1	42	2 and 1	3	40	2 and 1	31	12
	DF=1			DF=1			DF=1	
	χ^2 =0.180	P = 0.672		χ^2 =4.503	P = 0.034		χ^2 =2.678	P = 0.102
Test Day 4			**Test Day 4**			**Test Day 4**		
	Arrived	No Arrival		Arrived	No Arrival		Arrived	No Arrival
5 and 4	2	22	5 and 4	3	21	5 and 4	17	7
2 and 1	1	41	2 and 1	2	40	2 and 1	33	9
	DF=1			DF=1			DF=1	
	χ^2 =0.253	P = 0.615		χ^2 =0.435	P = 0.510		χ^2 =0.166	P = 0.684

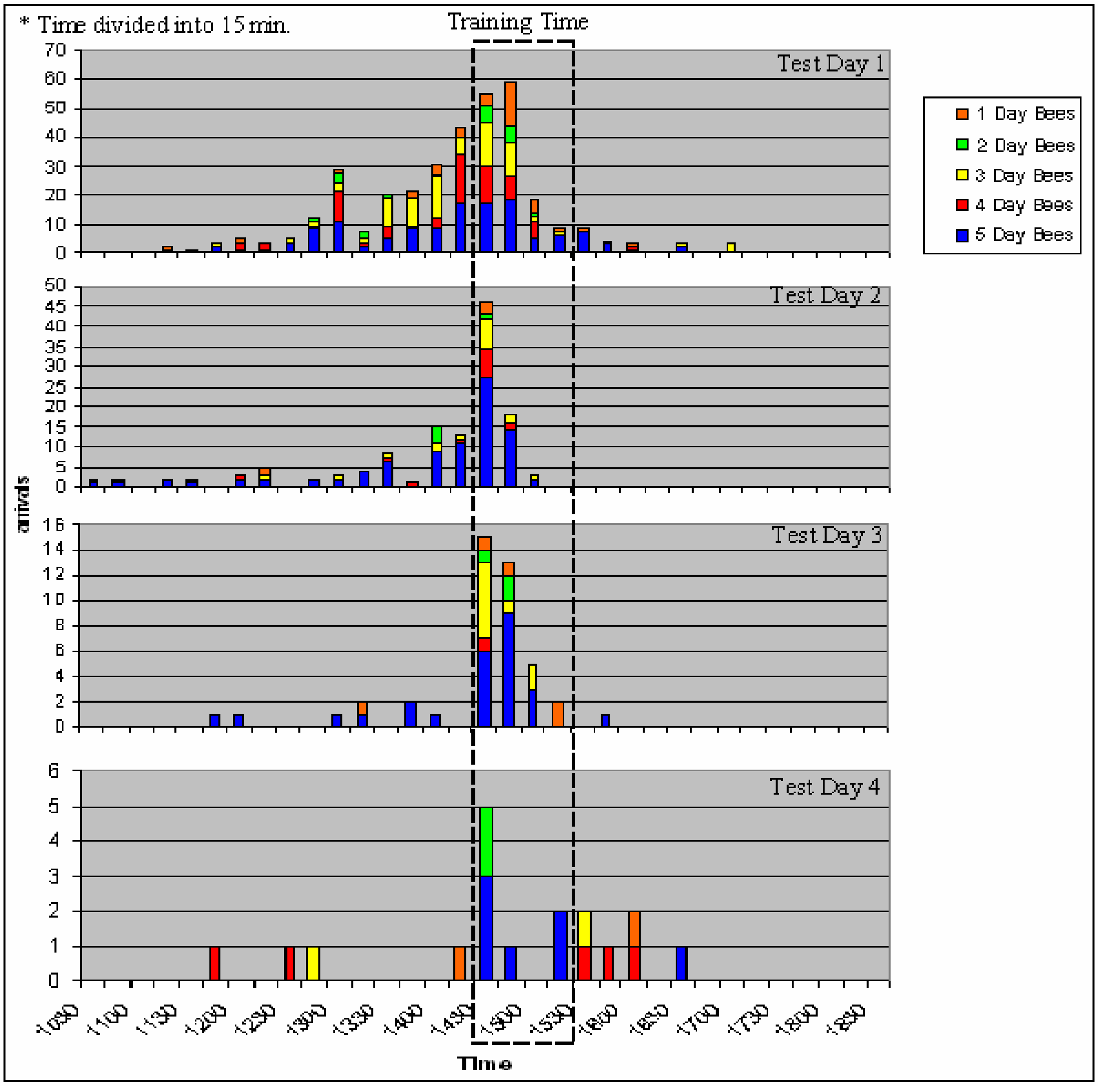

Figure 26 Arrivals at experimental station, September 2006. See Figure 17 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.574	.767	.614	.667
Low Experience Bees (2 and 1 Days of Training)	.178	.085	.182	.222

Table 53 Proportion of total arrivals at the experimental station, September 2006

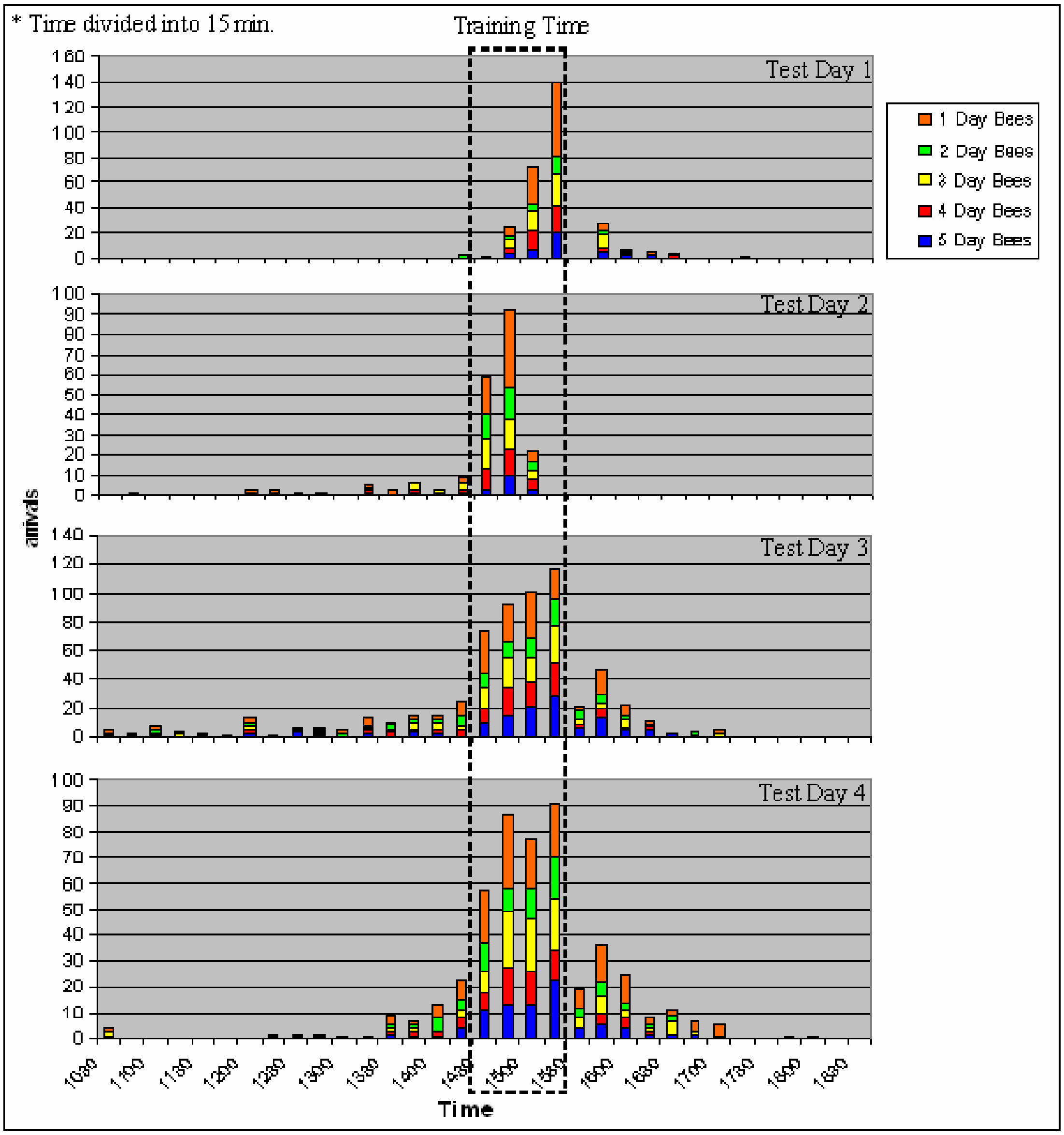

Figure 27 Arrivals at recruiter station, September 2006. See Figure 18 for details.

	TEST DAY 1	TEST DAY 2	TEST DAY 3	TEST DAY 4
High Experience Bees (5 and 4 Days of Training)	.308	.268	.350	.316
Low Experience Bees (2 and 1 Days of Training)	.490	.522	.457	.480

Table 54 Proportion of total arrivals at the recruiter station, September 2006

VITA

MATTHEW W. OTTO

Personal Data:	Date of Birth: November 6th, 1974 Place of Birth: Elgin, Illinois Marital Status: Married
Education:	Crystal Lake South H.S., Crystal Lake, Illinois B.S. Zoology, Eastern Illinois University, Charleston, Illinois 2000 M.S. Biology, East Tennessee State University, Johnson City, Tennessee 2007
Professional Experience:	Research Assistant, Eastern Illinois University; Charleston Illinois 2000 Biological Science Aid, U.S. Fish & Wildlife Service; Marquette Michigan 2001 Biological Science Technician, U.S. Park Service; Porter Indiana 2002-2003 Graduate Assistant, East Tennessee State University; Johnson City Tennessee 2004-2006
Honors and Awards:	William Harvey Fraley and Nina M. Fraley award for graduate research in organismal and cellular biology, Department of Biological Sciences, East Tennessee State University 2005 Dr. Denise Pav Research Award for graduate research in biological sciences, Department of Biological Sciences, East Tennessee State University 2006