

ENERGY COSTS OF FORAGING BY HONEY BEES ON ARTIFICIAL FLOWER PATCHES
OF VARIABLE AND CONSTANT NECTAR DISTRIBUTIONS

A Thesis

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ABSTRACT

Experimentation with the honey bee, Apis mellifera, was performed with two artificial flower patches, located at a certain distance from an apiary. Patches were tested adjacent to each other and with a separation distance between them. Responses of foraging bees on the patches were measured by censusing at one-minute intervals in order to determine preferences by the bees for three factors which differed between patches; Nectar Distribution ("constant" or "variable" amounts per flower), Flower Color (blue or yellow), and Distance from the apiary (near or far). The bees preferred the "constant" nectar distribution and the blue flower color. Although a distance preference was not found, the data suggest that a preference for the nearer patch may be exhibited at distances greater than those used in these experiments.

Thesis Title: Energy costs of foraging by honey bees on artificial flower patches of variable and constant nectar distributions.

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2. Keywords.

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BEEES

HONEY BEES

BEHAVIORAL PREFERENCE

ENERGETICS

FEEDING PREFERENCE

FORAGING

OPTIMAL FORAGING

FLOWER PATCHES

CERTAINTY

NECTAR DISTRIBUTION

COLOR PREFERENCE

Energy costs of foraging by honey bees on artificial flower

patches of variable and constant nectar distributions

Introduction

Under natural conditions, an animal must expend considerable time and energy in searching for food. Any animal, while searching for food or foraging, must gain more energy than it expends in the process. The most efficient (or optimal) foraging involves maximizing the ratio of energetic benefit to cost. Optimal foraging occurs when an animal is able to assess the food resources available in the environment and apply a foraging "strategy" which will maximize the ratio of benefit to cost.

Such a "strategy" entails certain decisions. An animal must choose among the types of food available in the environment. Since food is not evenly distributed, it must choose among the various types of patches where food is to be found. It must decide how much time to allocate to each patch, and it must decide what pattern and at what speed to make its movements (Pyke, Pulliam and Charnov 1977). Optimal foraging theory has been developed from studies of animal foraging behavior. Optimal foraging theory predicts the way in which food resources are used.

Mathematical models have been developed to predict

foraging behavior (Caraco 1980, Charnov 1976, Emlen 1966, MacArthur and Pianka 1966, Oster 1976, Oster and Heinrich 1976, Plowright and Hartling 1981, Pulliam 1974, Waddington and Holden 1979). Various parameters have been considered, such as types of food items available, their density and distribution, their relative abundances, their energetic value, and the time spent in search for and consumption of them. No model yet proposed is sufficiently complex to predict behavior under all circumstances found in nature. However, for an animal which can be considered to forage primarily on one kind of food, models can be more reliably made. Thus, the foraging behavior of bees, which forage exclusively on plant nectar and pollen, has received much attention (Heinrich 1976, Oster 1976, Pyke et al. 1977, Pyke 1978a).

Close relationships exist between bee families and the flowering plants over which they forage. Many plant species depend upon bees to accomplish pollination. They produce in their flowers, nectars of varying amounts and of varying sugar compositions and concentrations. Bees depend upon nectar as their primary energy food. Bees scurry and fly from blossom to blossom, probing deep past the reproductive structures of flowers to the nectaries, and collecting the nectar. In the process, pollen from the anthers brushes off onto the hairy body of the bee. Bees often show fidelity to

particular flower species for long periods of time (Brittain and Newton 1933, Free 1970, 1963, Grant 1950, Heinrich 1976, Heinrich, Mudge and Deringis 1977, Thomson 1981). Therefore, when a bee moves to another flower, that flower will usually be of the same species as the previous flower. Pollen which adhered to the bee at the first flower often brushes off onto the stigma of the second flower, thus accomplishing cross pollination. Nectar is produced by flowers and attracts these pollinators. Furthermore, simultaneously flowering plant species "compete" for pollinator attention, through nectar production and other, secondary attractant mechanisms such as odor and color (Grant 1950; Levin 1970; Pleasants 1980; Waser 1978; Zimmerman 1980).

The pollinator-plant relationship has been studied in the field by both botanists and zoologists. They have investigated nectar properties, amounts, production and distribution in flower patches and populations (Baker and Baker 1975, Bond and Brown 1979, Brink 1982, Carpenter 1976, Corbet, Unwin and Prys-Jones 1979, Corbet et al. 1981, Feinsinger 1978, Inouye et al. 1980, Nunez 1977, Pleasants and Zimmerman 1979, Southwick and Southwick 1983, Southwick 1982a,b, Southwick, Loper and Sadwick 1981, Zimmerman 1981a, Zimmerman 1982), and pollinator activity and behavior (Butler, Jeffree and Kalmus 1943, Heinrich 1976, Heinrich 1979, Inouye 1978, Pleasants 1981, 1980, Pyke 1978a,b,

Thomson 1982, Zimmerman 1981b).

The foraging behavior of the honey bee (Apis mellifera) has long been of interest, both from an economic point of view (honey production and crop pollination (Farrar 1931, Gary, Witherell and Lorenzen 1980, Holm 1966, Kipp and Mason 1982, Southwick and Pimentel 1981, Tepedino 1981) and from a zoological and ecological point of view (Darwin 1859, Bond and Brown 1979, Nunez 1977, Ribbands 1949, Waddington and Holden 1979, Wells, Wells and Smith 1981) Natural flowers, and feeders containing sugar solutions, have been used by von Frisch (1967) and others (Butler et al. 1943, Robacker and Ambrose 1981) to study bee behavior. The sensory capabilities of the honey bee have been clearly defined. Bees can distinguish color (including ultraviolet and polarized light), pattern, odor, taste, and nectar sugar concentration (von Frisch, 1967, Waller 1972). They are able to associate the coloration and odor of flowers with the amounts of their nectar rewards (von Frisch 1967, Waddington 1979a, Waller 1977). They are even able to measure and communicate the distance from the hive to a food source (von Frisch, 1967).

In recent years, artificial flowers and flower patches have been devised in order to clarify aspects of bee foraging behavior. These devices allow investigation of bee foraging in the field or laboratory under more controlled conditions

than those existing in natural flower patches.

Characteristics of patches, flowers, and the nectar can be readily manipulated. Nectar characteristics of interest include the volume, flow (production) rate and pattern of presentation, composition, concentration and fragrance.

Flower characteristics include color (including color pattern, and reflectance in the ultraviolet), shape, depth, and inclination of the corolla. Important patch characteristics are inter-flower spacing, flower number, flower density, number of flower varieties, nectar-amount variance among flowers of one variety or among flower varieties, and distance between patches.

Several designs of artificial flowers and flower patches have been used and described in the literature. Hartling and Plowright (1979) described an artificial flower which consisted of a short (7.6 mm) capillary tube, which served as a nectary. Filling of the tube with sugarwater was remotely controlled by means of an electro-mechanical device, which dipped the capillary tube into a reservoir of sugarwater positioned below, thus refilling the tube. The entire apparatus was enclosed in a box, with only the upper end of the capillary tube and an artificial corolla (a white cardboard disk) exposed to the foraging bee. Twelve such flowers were arranged in two circular formations of six each, forming two flower patches. This design was used for study

of bumblebee foraging behavior.

Waller (1972) designed an artificial flower for study of honey bee responses to sugar solutions of various sugar and salt concentrations and pH's. It was made of seven 1.0 ml glass vials, held together by a rubber band and capped by a 3 mm thick plastic disc, 3.6 cm in diameter. Micropipettes extended into the vials through holes in the disc. Honey bees imbibed sugar solution through the pipettes from the vials below.

Kremer (1981) used a flower consisting of a capillary tube, filled with sugar solution by an electrically powered pump. The pump was activated by electrical impulses resulting from the breaking of a light beam by a feeding honey bee. He used two and three such flowers at various inter-flower separations.

Heinrich et al. (1977) used a 2.3 m² flower patch of green acrylic bearing white and blue flowers. The corolla of each flower consisted of thin transparent acrylic squares with "petals" of white or blue tape surrounding a hole drilled through the center. These corollas were centered over wells drilled into the sheet of acrylic 15 cm apart. The wells were filled with sugar solution by a PB-600 Hamilton push-button repeating dispenser through polyethylene tubing.

Waddington, Allen and Heinrich (1981) used a patch

similar to that of Heinrich et al. (1977) but smaller. Only four flowers were used, two yellow and two blue. Waddington (1979b) described another design for an artificial flower patch. It consisted of transparent acrylic (1.22 x 1.22m) laid on a sheet of paper on which 2208 possible flower positions were computer-printed, and arranged in rows and columns 2.54 cm apart. Positions designated as flowers, and flowers designated to receive sugar solution, could be randomly or non-randomly selected. Rubber stamps were used to apply flower-like shapes to the designated positions. Wells, for containment of sugarwater, were drilled into the acrylic over all of the possible flower positions. Waddington and Holden (1979) used this design to test a model of honey bee foraging in a patch of two varieties of flowers. They used 100 blue and 100 yellow flowers in a random distribution. Waddington (1980) used this design to study honey bee foraging flight patterns. Patches of 100, 200 and 400 purple flowers of both random and clumped distributions were used.

Waddington and Heinrich (1979) studied foraging movements of bumblebees on artificial vertical inflorescences. Each "inflorescence" consisted of a strip of dark green acrylic, 23 x 190 mm, bearing a row of five wells, 39 mm apart.

Wells et al. (1981) used a flower design in which 36

flowers were arranged in six columns and six rows 75 mm apart. Each flower consisted of a 30 mm² piece of acrylic 6 mm thick with a nectar well in its upper surface. The underside was painted yellow or blue. Each flower was supported by a 90mm wooden stem set into a hole in a sheet of plywood. Patches of all blue flowers, of all yellow flowers, or of equal numbers of blue and yellow flowers randomly mixed were used in a study of honey bee foraging behavior.

Real (1981) constructed a patch based on Waddington's (1979b) design. He used transparent acrylic, 1.2 x 1.2m x 6mm, containing 2304 wells, in rows and columns 2.5cm apart. He selected random coordinates for 200 flowers (100 blue, 100 yellow) and placed blue and yellow cardboard squares under them. Under all of this he placed a green sheet of plywood.

Real's experiments are described here in more detail, as I used a modification of his experiments in my studies of honeybee foraging. Real used the flower patch to examine the effect of variability of nectar reward on foraging behavior of bumblebees (Bombus sandersoni Fkln) and paper wasps (Vespula vulgaris L.). He performed three experiments with the bumblebees. Individual bees were allowed to forage alone on the patch inside a 1.5 x 6.4 x 1.5m tent of mosquito netting. In the first experiment, each blue and each yellow flower contained 2 ul of nectar. The bees showed a preference for the yellow flowers. In the second experiment,

each blue flower contained 2 ul (a "constant" volume of nectar per flower). The yellow flowers contained variable nectar amounts, with 6 ul in one third of the flowers and nothing in the rest. The total nectar volume in the blue flower patch was equal to the total volume in the yellow flower patch. The bees preferred the constant-yield blue flowers over the the variable-yield yellow flowers. Reversing the colors to make blue variable and yellow constant, he found the bees to prefer yellow constant.

In the third experiment, Real reduced the variability of the variable flowers by putting 5 ul in one-third and 0.5 ul in the rest. The constant flowers still contained 2 ul in each, so the total patch volumes were still equal (200 ul for each color patch). Again the bees preferred the constant flowers over the variable flowers, even when colors were reversed. The bees were able to distinguish the variable flowers from the constant flowers in a single foraging bout, and to adjust their foraging behavior so that they foraged more frequently on the constant variety.

Real performed two additional experiments with wasps. Wasp foraging was not restricted to individuals. Many wasps foraged simultaneously. In the first experiment, when blue and yellow flowers rewarded equally, the wasps showed preference for yellow. In the second experiment, the wasps showed preference for the constant flowers, of either

color.

Real concluded that although a pollinator forages so as to maximize the benefit to cost ratio, it also is sensitive to variation in nectar reward. Therefore, the forager minimizes uncertainty of finding reward by selecting a flower variety of less variability in nectar reward and avoiding a flower variety of more variability. "Certainty associated with receiving a reward may prove as important to pollinators as the reward itself" (Real 1981, p.25). Avoidance of uncertainty in foraging has been found in other studies. Bumblebees, in the study by Waddington et al.(1981), preferred a continuously rewarding flower-type over an intermittently rewarding type. Robacker and Ambrose (1981) found honey bees sensitive to levels of reinforcement at feeding dishes.

In a further study (Real, Ott and Silverfine 1982), bumblebees were again found to be sensitive to variability in nectar reward. Constant flowers were preferred over variable (when mean nectar rewards were equal). Yellow flowers were preferred over blue.

My Study

As an extension of Real's (1981) work, I decided to investigate the behavior of foraging honey bees on two artificial flower patches, of differing color and differing

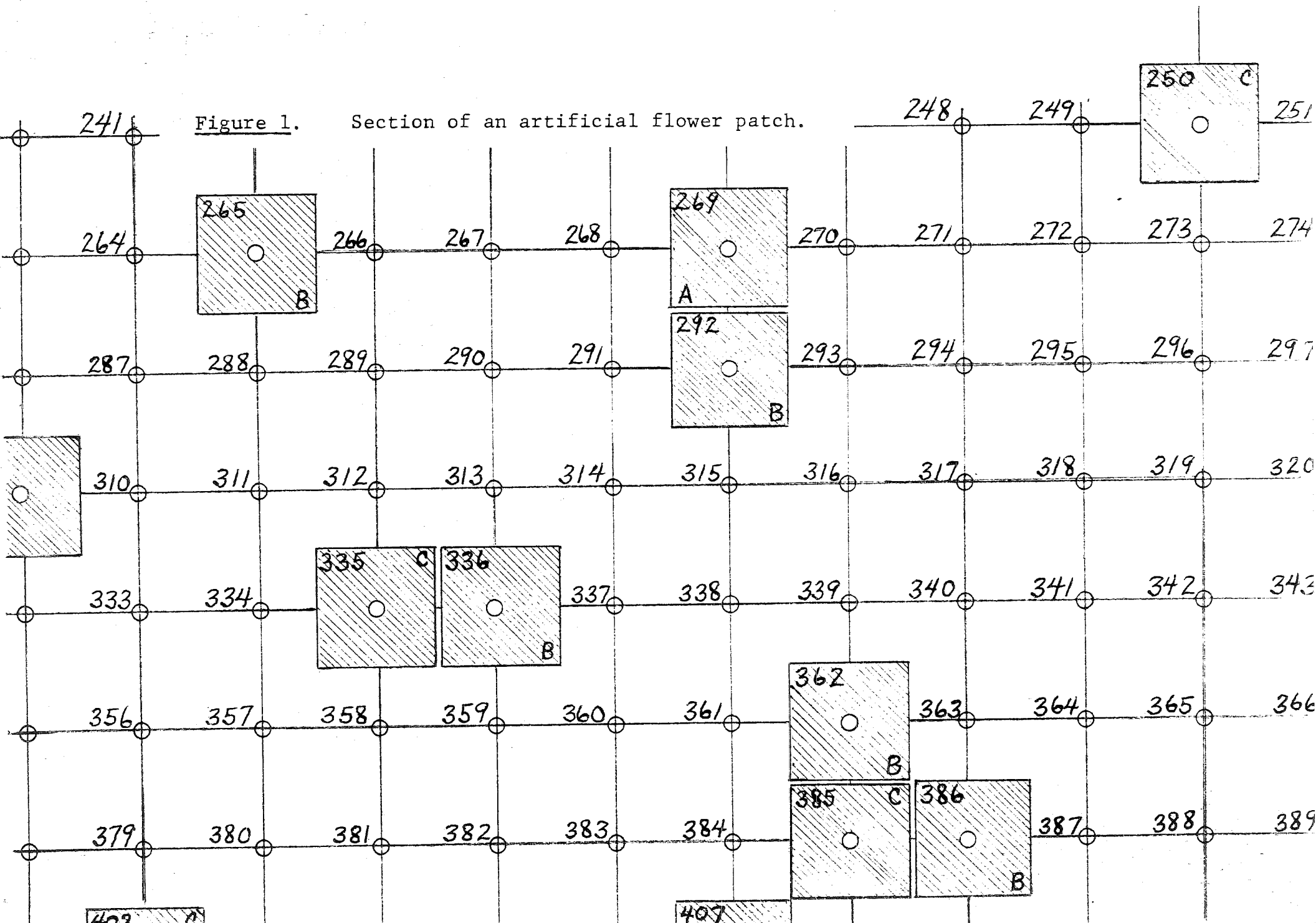
nectar distributions. I proposed that two patches could be set adjacent to each other at a specific distance from a beehive and exposed to foraging bees. One could then look for a preference of the bees for constant or variable nectar distributions. If a preference for either constant or variable were perceived, then the patch of the preferred distribution could be moved progressively farther away from the other patch in a direction away from the hive. At some specific separation between patches, the increased distance would cause the bees to cease to prefer the more distant patch due to the increased energy cost of foraging upon it. This would result in an increase in foraging upon the nearer patch.

I constructed two artificial flower patches in order to test two main hypotheses: (A) Honey bees prefer a patch of flowers of a constant nectar reward over a patch of variable nectar reward, (B) Honey bees prefer a patch of flowers closer to the hive over a patch farther away. Two other hypotheses were tested concurrently, as follows: Honey bees prefer either blue or yellow flowers, and honey bee foraging is affected by daily-varying environmental factors. (See Appendix A, Null and alternate hypotheses.)

Methods

The Artificial Flower Patches

I used two artificial flower patches, each consisting of a 0.61m x 0.61m sheet of acrylic 6mm thick, bolted to a plywood board of similar dimensions. On the surface of the plywood next to the acrylic, a grid of 2.5cm-squares was drawn in pencil. Each intersection of pencil lines was numbered. There were 483 such numbered intersections. This gridwork and the associated numbers were readily visible through the acrylic, as illustrated in Figure 1. An identical gridwork was laid out on the upper surface of the acrylic sheet and wells (3mm x 4.5mm deep) were drilled into the acrylic at each of the intersection points. Each well could therefore contain as much as 32.0 ul sugar solution.



Forty-eight intersection points were selected by a computer random number generator (MINITAB, 1980) to become flower locations. Blue and yellow cardboard squares were centered on the selected intersection points. Their numbers were written on their upper surfaces with a letter, A, B, or C. Sixteen (one-third of the total) on each patch were lettered "A", sixteen were lettered "B", and the remaining sixteen were lettered "C". The purpose of the letters was to make three readily distinguishable flower sub-groups on each patch. The lettering was also determined by the random number generator. The numbers and letters were visible through the acrylic. Blue squares were placed at the 48 numbered locations on one of the plywood boards, and yellow squares were placed on the corresponding locations on the other board. The acrylic sheets were laid on top of these and bolted into place at the four corners. The result was two artificial flower patches identical in numbering, lettering, and flower pattern. Only flower color was different.

When used in the field, these patches were set upon small three-legged round-topped metal tables, 47 cm high, having upper surfaces of lesser area (diameter = 49 cm) than the areas of the flower patches such that the table surfaces were not visible. Fitted screens of 3.5mm mesh were set over the patches to keep bees away from the sugarwater ("nectar")

when the flowers were being loaded or cleaned.

Nectar Distributions

I tested for a preference by the bees for a constant or variable nectar distribution on the two artificial flower patches. The constant distribution was 8.3 ul of nectar in all 48 flowers of one patch (termed "constant" hereafter). The variable distribution was 25.0 ul of nectar in one third (16) of the flowers of a patch and no nectar in the remaining two-thirds of the flowers (termed "variable"). In order to prevent bees from memorizing locations of rewarding flowers on the variable patch, the third of the flowers receiving nectar was switched from one trial to the next during the course of a day's testing. The three differently-lettered subgroups (A, B, C) were used for this purpose. The total amount of nectar in one patch was equal to the total in the other (e.g. $48 \times 8.3 \text{ ul} = 400 \text{ ul} = 16 \times 25.0 \text{ ul}$). As the flowers of one patch were blue and those of the other patch were yellow, it was necessary to repeat each test at each location after reversing nectar distributions, in order to control for a color bias, e.g., tests with all possible combinations of Nectar Distribution, Color, and Location were performed.

The Experiments

Eight experiments with the artificial flower patches were conducted at the apiary and bee laboratory of the State University of New York, College at Brockport, which is located in western Monroe County, New York. Two of these took place during the period from late June through mid-July 1982. Experiment I was conducted with the patches set adjacent to each other 83 meters from the apiary center. Experiment II was carried out at 83 and 158 meters (75 meter separation between patches). Three more experiments took place from mid-September through mid-October. Experiment III was done at a distance of 44 meters from the apiary center with adjacent patches. Experiment IV was conducted at 44 and 87 meters (43 meter separation between patches). Experiment V was conducted at 26 meters from the apiary center with adjacent patches. In these five experiments, all possible combinations of Nectar Distribution (Constant or Variable), Flower Color (Blue or Yellow), and Distance from the apiary (near or far) were tested (except in Experiments I, III, and V, in which the patches were adjacent and therefore Distance was not a factor that varied between patches; see Appendix E for experimental set-ups).

Three other, less extensive experiments were done. In early July, at the location of Experiment I, a yellow flower

patch with no nectar was tested adjacent to a blue patch with nectar in the Variable distribution. Also a yellow patch of Constant nectar distribution was tested adjacent to a blue patch with no nectar. This is hereafter referred to as Experiment Ia. Experiment Ib took place at the same location in early August. A Blue-Variable patch was tested adjacent to a Yellow-Variable patch. Experiment IIIa was conducted in September at the Experiment III location. A yellow patch was tested adjacent to a blue patch, both patches having Constant nectar distributions. This was repeated, but with both patches having Variable nectar distributions.

Training Bees

Before each of the experiments bees were trained to the "zero points" (the points where tests were begun with adjacent patches, i.e. at 26, 44, and 83 meters) by use of a hive entrance feeder containing 50% sugar solution. A drop of anise oil was added to the sugar solution to attract the bees by odor. When training bees, the feeder was initially placed near the entrance of a hive until bees discovered it and began to feed. This required no more than an hour, after which the feeder was gradually moved away from the hive in

ever increasing increments at a rate of about one meter per minute. It was moved only when bees were actually on it, so that there were always some bees which could communicate the location of the feeder in recruiting dances at the nest. Foragers not on the feeder at the time of the move returned to its former location and searched for it there. Gradually they widened their area of search until they found the feeder. A move consisted of picking up and carrying the feeder to a new location, always handling it gently so as not to disturb the feeding bees. It was left stationary for several minutes between moves so as to allow recruiting to occur. The training feeder was ultimately moved to the location at which testing was to take place and set upon a board and left there continuously, except for the times when testing with the patches was actually occurring. When testing was to occur at two separate locations (i.e., Experiments II and IV), a second feeder was used and bees were trained to both locations at the same time.

Daily Experimental Procedure

Each morning, at 0900, I refilled the training feeders at the predetermined location (zero point) or locations (zero point and one farther point). The purpose of this was to

maintain the attractiveness of those locations. Usually, within about 30 minutes there were many bees feeding. This active feeding continued until the sugarwater was exhausted or the feeders were removed.

I removed the feeders 30 to 60 minutes before the test start time, which was about 1230. From preliminary studies in January 1982 at Archbold Biological Station at Lake Placid, Florida, I had learned that if the feeders were removed at the same time as the presentation of patches, there would be more bees on the patches than one could visually count reliably, and the nectar content would be exhausted immediately. The early removal reduced the number of bees present at the feeding location to visually countable numbers (24 or fewer).

Between the time of feeder setting and the start of the testing on any given day, the nectar was freshly made by dissolving sugar (sucrose) in distilled water, yielding a 50% solution (50g sugar/100g solution). A drop of oil of anise was added to the solution (about 200 ml) to provide a scent attractive to bees. Part of the solution was poured into a small jar for easier manipulation of the micropipettor used to fill flower wells (Drummond digital microdispenser, No. 525, 0-25ul).

The flower patches, three small tables, and a box of equipment were carried to the field site after the feeders

were removed. The patches were set in position on two of the tables, and the third table was set aside and used as a work table. Two wood blocks were set on the patches under the covering screens to increase their effectiveness in preventing bees from reaching the nectar in the wells before the proper time.

When all was ready, I filled the flowers according to the predetermined pattern. The micropipettor was used to fill the desired number of flower wells. The micropipettor was then re-adjusted to dispense the volume desired for the flowers of the other patch and they were then filled. When loading of both patches was accomplished, the micropipettor tip was flushed in distilled water.

The screens were removed from the patches, and one minute later the first bee count was taken. Bees were counted simultaneously on both patches as rapidly as possible. To insure simultaneous counting, an assistant and I used voice communication and synchronised watches. We counted all the bees actually touching the surfaces of the patches at the minute-mark. After the tenth count, the screens were replaced and any remaining nectar was removed with hypodermic syringes. The patches were reloaded, and the next trial was begun. Nectar removal and reloading took about 15 minutes per trial.

After four trials (each day's test consisted of four

trials), the patches were removed and the feeders were placed at the same locations. If the following day's test required a separation of the patches, then the bees were trained to the new arrangement at this time or on the following morning.

Bees crossing between patches

It was hoped that the bees would respond to the artificial flower patches as they would to real flower patches. It was expected that they would quickly learn to associate color and odor with the presence of nectar, and ignore the unmarked, empty wells. Naive bees were seen investigating empty, unmarked wells. Soon, however, they learned to forage only on the color-marked wells. A bee on a patch, after leaving one flower, walked or flew to another flower, ignoring intervening empty wells.

On several mornings, I used enamel paints to mark individual bees (on the thorax or abdomen) at the feeders. I used several colors, so as to make individual bees recognizable. During our observations at the patches, we noted individuals at our respective patches and compared notes afterwards to see if the same bees were visiting both patches.

When patches were adjacent, I watched for bees crossing

between them. Most of them did so. I felt this to be important, as the determination of a preference depends on the knowledge of both options. When patches were separated, this was not easy to observe. We looked for distinctively marked bees at each of the patches. Also I watched for bees which left the nearer patch and flew along the mowed path in the direction of the farther patch. We did see a few marked individuals at both patches and frequently saw bees flying along the trail between patches in Experiment II.

In Experiment IV, we failed to observe marked individuals at both patches. Furthermore, we were fairly certain that bees from a hive lying in a different direction from that of the apiary, were coming to the patches.

Analysis of data

Bees were allowed to forage simultaneously on both patches. Other experiments with artificial flower patches have involved the use of enclosures around the patches, and foraging by single individuals has been observed in most cases (Heinrich et al. 1977, Real 1981, Real et al. 1982, Waddington and Heinrich 1979, Waddington and Holden 1979, Waddington 1980, Waddington et al. 1981). With one forager at a time, record of each flower visited can be made easily.

However, with many bees foraging simultaneously, this is impossible. No attempt was made to restrict the number of foragers to just one at a time in my experiments. Since the two varieties of flowers (blue and yellow, or constant and variable) were in separate patches, I reasoned that a preference by the bees for one variety or the other could be measured by periodically counting the numbers of foragers at each patch and statistically comparing them.

Analyses of variance (ANOVA's) were used to determine the significance of the effects of four independent factors on numbers of bees counted at the patches. These factors were Nectar Distribution (constant or variable), Flower Color (blue or yellow), Distance from the beehive (near or far), and "Day". "Day" was included in order to factor out differences in counts of bees due to environmental factors varying from day to day.

Consideration of these factors required a four-way ANOVA, using the computer program, Statistical Package for the Social Sciences (SPSS), at the State University College at Brockport, in Experiments II and IV. As the patches were adjacent in Experiments I, III, and V, Distance was not a factor, and therefore a three-way ANOVA was used. T-tests (Two-sample t-test, MINITAB, 1980) were used in analyses of Experiments Ia, Ib, and IIIa.

As the tests spanned a period of more than three months,

analysis of the effect of weather on bee counts was done. Weather data for the period were obtained from the Department of Earth Science, State University College at Brockport, New York. Mean counts of bees were regressed on total daily solar radiation, daily mean temperature, and time, separately (Figures 2, 3 and 4). Total daily solar radiation and mean temperature were regressed separately on time (Appendix D).

Results

The results are reported for adjacent patches and separated patches as summarized in Appendix E.

Experiments I, III, and V - Adjacent Patches

Experiments I, III, and V were conducted with adjacent patches only. No inter-patch separations were made. Therefore, the analyses of variance for these three experiments did not include the Distance factor. Nectar Distribution, Flower Color, and Day (independent factors) were analysed by a three-way ANOVA.

In each of the three experiments, all three independent factors were found to have significant effects on numbers of foraging bees. Table 1 shows that $P < 0.05$ in Experiments I, III, and V, indicating that the probability that the differences between means for each factor having occurred by chance alone is less than 5%. Patches with constant amounts of nectar per flower were preferred over patches with variable amounts, and blue flowers were preferred over yellow. The "Day" factor, although significant, does not vary between patches (only between days) and is not considered in this context (See below).

Table 1. Preferences of honey bees. Experiments I, III, and V.
Adjacent artificial flower patches.

Experiment I. (N = 120) D = 83 meters

<u>Factor</u>	<u>N</u>	<u>Mean</u>	<u>P</u>
Nectar Distribution			0.004
Constant *	60	2.73	
Variable	60	1.73	
Flower Color			<0.001
Blue *	60	2.97	
Yellow	60	1.50	
"Day"			<0.001

Experiment III. (N = 120) D = 44 meters.

<u>Factor</u>	<u>N</u>	<u>Mean</u>	<u>P</u>
Nectar Distribution			<0.001
Constant *	60	3.47	
Variable	60	2.08	
Flower Color			0.034
Blue *	60	3.10	
Yellow	60	2.45	
"Day"			<0.001

Experiment V. (N = 80) D = 26 meters

<u>Factor</u>	<u>N</u>	<u>Mean</u>	<u>P</u>
Nectar Distribution			<0.001
Constant *	40	10.38	
Variable	40	5.67	
Flower Color			<0.001
Blue *	40	9.88	
Yellow	40	6.17	
"Day"			<0.001

* Statistically significant preference.

Experiments II and IV - Separated Patches

Experiments II and IV were conducted with inter-patch separations. Experiment II was done at 83 and 158 meters from the apiary center, and Experiment IV was done at 44 and 87 meters from the apiary center. Nectar Distribution, Flower Color, Distance, and Day were analyzed by a four-way ANOVA.

In both experiments, Nectar Distribution, Flower Color, and Day produced significant differences in the numbers of bees at the two patches. Table 2 shows $P < 0.01$ for Nectar Distribution, Flower Color and Day, indicating that the probability that these phenomena occurred by chance alone is less than 1%. Blue flowers were preferred over yellow in both experiments. In Experiment II, "constant" was preferred over "variable", but in Experiment IV, "variable" was preferred over "constant". As above, the "Day" factor does not vary between patches and is not considered here (see below). In neither experiment is Distance significant (in Experiment II, $P = 0.084$; in Experiment IV, $P = 0.334$). In both cases, however, the means for the locations nearer to the apiary were higher than those for the farther locations. Although Distance was not significant in these experiments, the data are suggestive of an effect of Distance.

Table 2. Preferences of honey bees. Experiments II and IV.
Separated artificial flower patches.

Experiment II. (N = 240) D = 83 and 158 meters.

<u>Factor</u>	<u>N</u>	<u>Mean</u>	<u>P</u>
Nectar Distribution			0.001
Constant *	120	3.35	
Variable	120	2.53	
Flower Color			<0.001
Blue *	120	3.49	
Yellow	120	2.39	
Distance			0.084
Near (83m)	120	3.16	
Far (158m)	120	2.72	
"Day"			<0.001

Experiment IV. (N = 240) D = 44 and 87 meters.

<u>Factor</u>	<u>N</u>	<u>Mean</u>	<u>P</u>
Nectar Distribution			0.003
Constant	120	2.38	
Variable *	120	3.30	
Flower Color			0.008
Blue *	120	3.26	
Yellow	120	2.42	
Distance			0.334
Near (44m)	120	2.99	
Far (87m)	120	2.69	
"Day"			<0.001

* Statistically significant preference.

Experiments Ia, Ib, IIIa - Adjacent Patches

In Experiment Ia, the bees were very quickly able to to distinguish between a non-rewarding patch (containing no nectar) and a rewarding patch (containing nectar). They foraged almost exclusively on the rewarding patch. When the yellow patch with no nectar was tested adjacent to the blue patch of Variable nectar distribution, the blue was preferred ($P = 0.006$). When the yellow patch of Constant nectar distribution was tested adjacent to the blue patch with no nectar, the yellow patch was preferred ($P < 0.001$). (See Table 3)

Experiment Ib was a test for Flower Color preference. Nectar distributions were equal. A Yellow-Variable patch was tested adjacent to a Blue-Variable patch. Neither patch was preferred ($P = 0.522$). Experiment IIIa was also a test for Flower Color preference. When Yellow-Constant was tested against Blue-Constant, the blue patch was preferred ($P = 0.04$). When Yellow-Variable was tested against Blue-Variable, neither was preferred ($P = 0.28$). In both experiments, the mean numbers of bees visiting the blue patches of either nectar distribution were greater than those for the yellow patch. (Table 3)

Table 3 t-tests, Experiments Ia, Ib, IIIa.

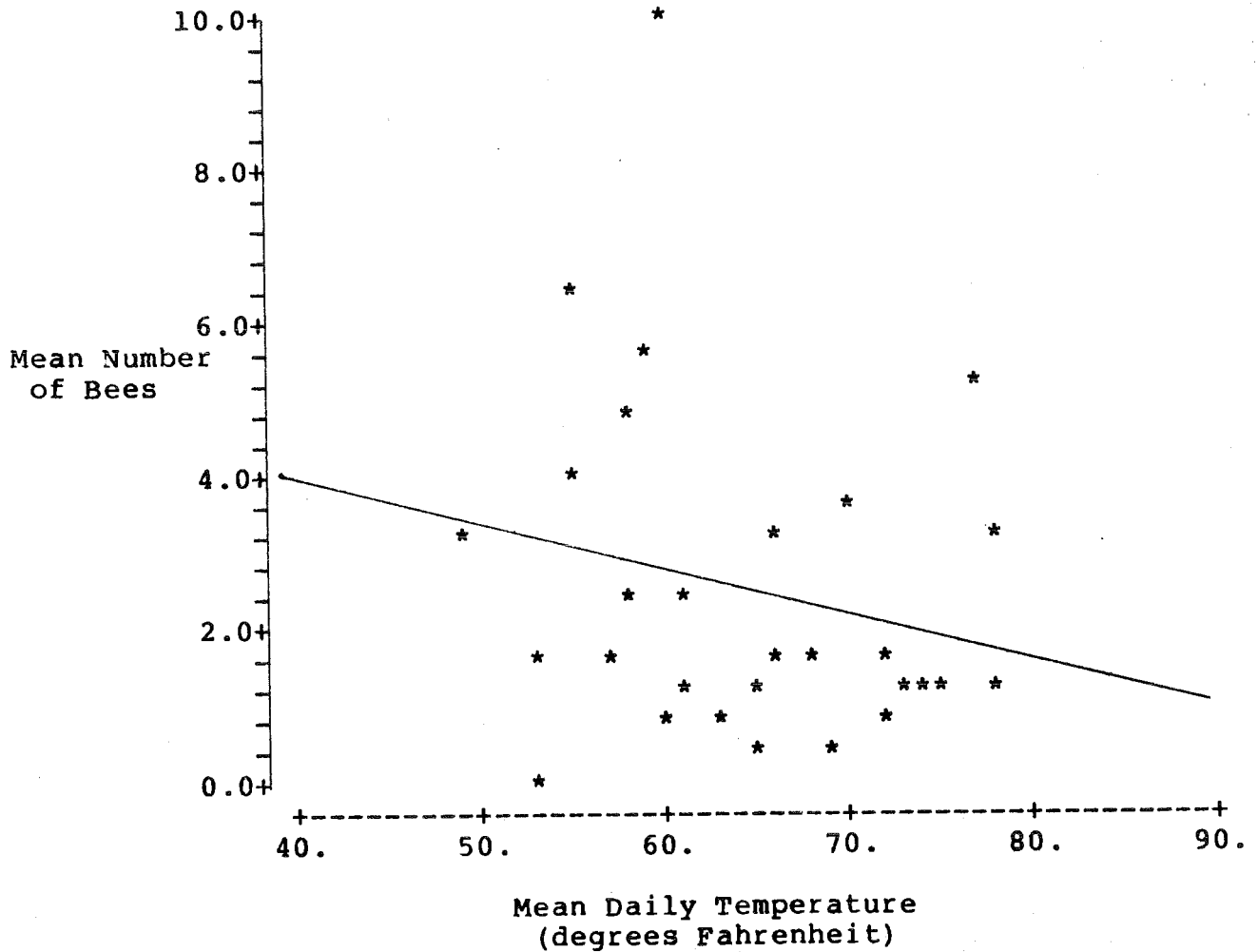
<u>Experiment</u>	<u>N</u>	<u>Mean</u>	<u>S.D.</u>	<u>t</u>	<u>P</u>
<u>Ia</u> D = 83 meters, 6 July 1982					
Yellow-empty	20	0.10	0.31		
Blue-Variable*	20	0.60	0.68	-2.994	0.006
Yellow-Constant*	20	1.35	0.93	5.688	<0.001
Blue-empty	20	0.10	0.31		
<u>Ib</u> D = 83 meters, 7 August 1982					
Yellow-Variable	30	0.73	0.87		
Blue-Variable	30	0.87	0.73	-0.644	0.522
<u>IIIa</u> D = 44 meters, 20-21 September 1982					
Yellow-Constant	30	0.50	0.63		
Blue-Constant*	30	0.97	1.03	-2.112	0.040
Yellow-Variable	40	4.28	2.52		
Blue-Variable	40	4.95	3.01	-1.087	0.281

* Statistically significant preference.

Effect of "Day"

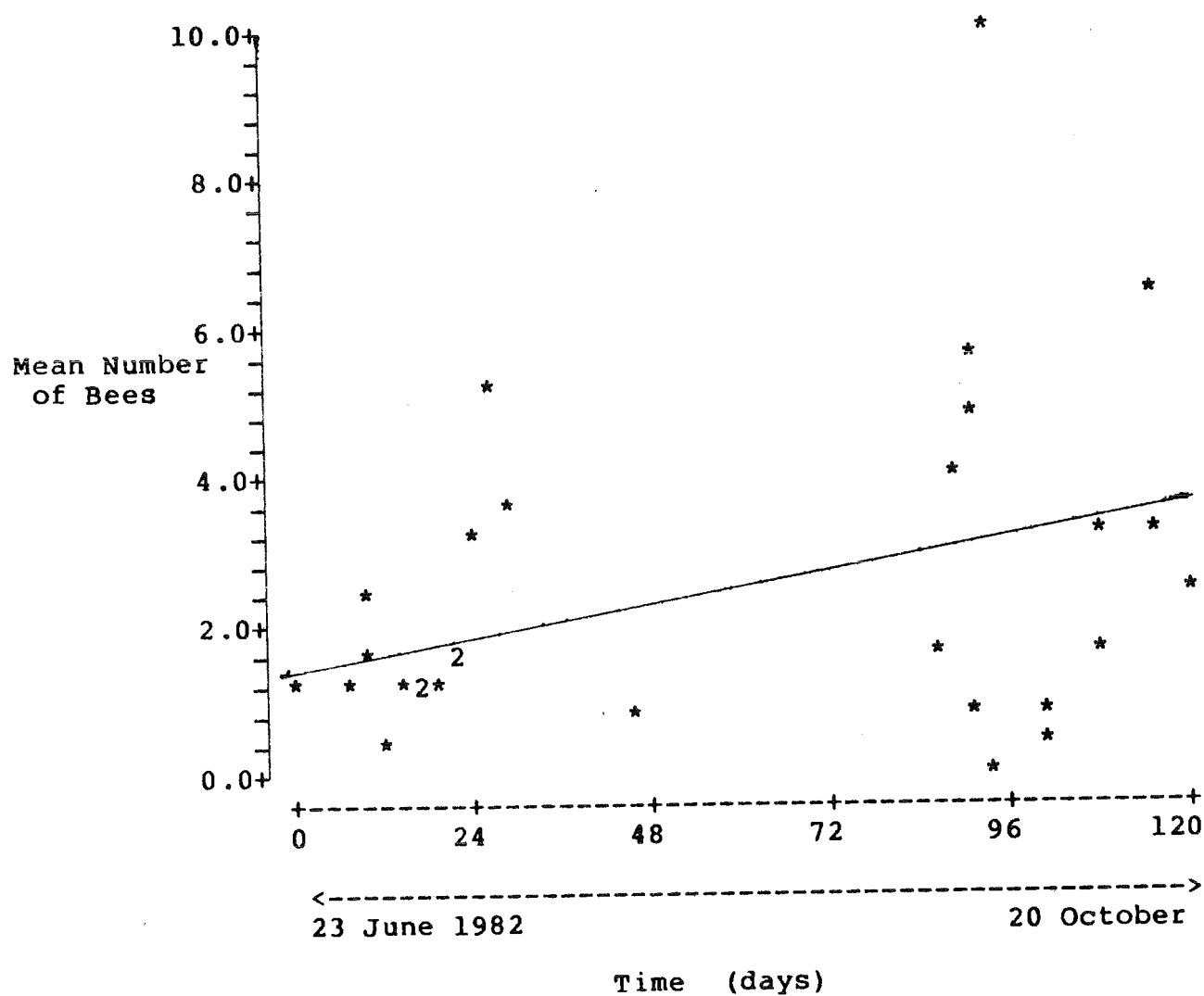
Figures 2 and 3 show some surprising results. They show a decline in mean number of bees foraging in the artificial flower patches with increasing solar radiation and increasing temperature. Figure 4 shows that mean number of bees increased with time. Total daily solar radiation and daily mean temperature decreased with time. (See Appendix D.)

Figure 3. Relationship between honey bee foraging at artificial flower patches and temperature.



The regression equation is
 $Y = 6.1 - 0.055 X$ $r = -0.21$

Figure 4. Effect of season on honey bee foraging at artificial flower patches.



Discussion

Nectar Distribution

The preference by the bees for the Constant nectar distribution in Experiments I, II, III, and V is in agreement with Real's (1981, 1982) results with bumblebees and wasps and with the results of Waddington et al. (1981) with bumblebees. The honey bees in this study demonstrated a sensitivity to the difference in nectar distribution and preferred the Constant distribution which provided greater certainty of reward.

At the beginning of each trial there was no difference between patches in terms of value of energetic reward offered. The concentrations and total amounts of "nectar" in the patches were equal. Theoretically there was also no difference between patches in cost of harvesting the nectar even though distributions of nectar differed. A single bee systematically visiting each flower on the "variable" patch should experience just as much energetic expenditure and energetic reward as a single bee systematically visiting each flower on the "constant" patch, assuming that they landed at each flower and probed the wells with their probosces.

However, even though there is no real difference between

patches, in either energetic reward or expenditure, there is a perceived difference. Each forager bases her preference for one patch or the other on the results of sampling in both patches. Sampling in the "variable" patch reveals a lower certainty of reward than does sampling in the "constant" patch. "Sampling necessarily involves a time-energy cost" (Heinrich, 1976). On the basis of a lower perceived benefit to cost ratio on the "variable" patch, the bees prefer the "constant" patch. Although this behavior is not necessarily advantageous in the context of artificial flower patches, it is advantageous in natural flower patches, as the bees adjust their foraging behavior to maximize their benefit to cost ratio.

However, the single result of Experiment IV, when "variable" was preferred over "constant", may show a tendency of the bees to accept greater risk when natural food resources are diminished, as they were during the time when Experiment IV was conducted (September and October). Ambient temperatures and solar radiation were reduced during this time as well. This may have contributed to the willingness to take greater risk (Caraco, Martindale and Whittam 1980). It is well-known to beekeepers that honey bee colonies are more aggressive in foraging in fall, when food sources are diminished. Consequently, colonies attempt to rob each other of food stores (Root 1975). On the other hand, the

"constant" patch was always available at the same time as the "variable" patch. If it were truly less energetically expensive to forage in the "constant" patch, then it should have been preferred even more in this experiment than in the other experiments.

Flower Color

The preference by the bees for the blue flowers was demonstrated in all of the experiments. Even when the effect of Flower Color was not statistically significant, there were more bees visiting the blue flowers, as in Experiments Ib and IIIa. Many years ago, Von Frisch (1914, as cited by Grant 1950) determined that honey bees have a physiologically-based preference for blue flowers. He determined that, to honey bees, blue contrasts more strongly than yellow with the surrounding foliage, which bees see "as almost colorless gray, in a highly unsaturated yellowish shade" (von Frisch 1967, p. 485). Other researchers have confirmed this preference for blue. Heinrich et al. (1977) found a preference by bumblebees for blue over white. As this white was not reflective in the ultraviolet (Heinrich et al. 1977), it would have been blue-green to the bees, according to von Frisch (1967). However, Real (1981) and Real et

al.(1982) found bumblebees and wasps to show preference for yellow over blue. He suggests that his yellow flowers contrasted more than the blue flowers against the green plywood background which he used. This is not in agreement with Daumer (1956, as cited in von Frisch 1967), who found bees unable to distinguish well between yellow and green. On this basis, Real's blue flowers should have been more easily distinguishable by the bees. I suspect that ultraviolet light may be an important factor here. Daumer (1956; as cited by von Frisch 1967) found that honey bees are most sensitive and responsive to ultraviolet. Perhaps the preference of the bumblebees and wasps for yellow in Real's work could be explained if the particular reflectance spectra of his "yellow" and "blue" flowers were known. If his yellow flowers reflected ultraviolet, then they would appear to the bees as "bee purple" and not as yellow (Daumer 1956; as cited by von Frisch 1967). They would then be more distinct from the green background than blue and more attractive.

Distance

Distance of the patches from the apiary was considered as a factor in Experiments II and IV. Although there were more bees visiting the closer patches, the effect of Distance

on numbers of bees was not significant (Table 2). In Experiment II, the distance effect was almost significant at $P = 0.084$, and in Experiment IV, $P = 0.334$. The fact that the Experiment II locations were farther from the apiary (83 and 158 meters) than the Experiment IV locations (44 and 87 meters) suggests that separation between patches had a greater effect on numbers of bees when both patches were located farther away from the apiary, i.e., when two separated patches are farther away from the apiary, bees are more likely to prefer the nearer of the two.

A scouting forager, upon locating a food source (such as nectar-rich flower patch, a feeder or an artificial flower patch), returns to the hive and communicates to her comrades specific information. By means of a "dance language" she communicates distance and direction of the food source from the hive, and by presentation of a nectar sample, she communicates odor, taste, and sugar concentration of the nectar to be found (von Frisch 1967). When the food source is less than 25 meters away from the hive, the scouts use a "round dance", which does not give directional information. When the food source is more than 100 meters away from the hive, a "tail-wagging dance" is used, which does give accurate directional and distance information. When the food source lies between 25 and 100 meters from the hive, dances which are intermediate to the "round" and "tail-wagging"

dances are used (von Frisch 1967). The foragers observe these dances in the hive and fly out to search for the food source.

The question may then be raised: how were the foragers recruited in the experiments which I conducted? Bees do not communicate color, and therefore the foragers would have searched for a particular odor (oil of anise, in this case) and for a particular location (if distance and direction were communicated). The distances in my experiments ranged from 26 meters to 158 meters from the apiary center. Therefore, the bees would have used the intermediate dances and the tail-wagging dance, although these were not actually observed.

Further questions can be raised. How did the scouts recruit foragers to two patches which were indistinguishable in communication? Did each forager actually know that there were two patches, or did she simply return to the site where she first found the nectar each time she received the message that the nectar was again available? This is an important question, because formation of a preference requires exposure to both options. When patches were adjacent (Experiments I, III and V), the bees were exposed to both patches, as indicated by their crossing between patches. However, when patches were separated (Experiments II and IV), all foragers may not have been exposed to both patches during the course

of a test. My assistant and I observed a few marked individuals at both sites in Experiment II and I observed bees flying along the path which ran between separated patches. In Experiments II and IV, feeders were left at both locations and bees were trained to both sites. Is it possible that there were two distinct groups of bees, foraging at the two feeders and "preferring" the patches set in place of their feeders? It has been found that within a colony there are different foraging groups which exploit specific nectar resources and heed only the dances of their own members (von Frisch 1967; Visscher and Seeley 1982). If there were two such groups, bees trained to the far feeder might have known also of the existence of the near feeder, as they had to pass over it on the way to the far feeder. The bees trained to the near feeder might have known only of the existence of the near feeder. Another factor which could have led to the formation of two foraging groups in Experiment II is that the far location (158 meters) was more than 100 meters from the hive and therefore the location-specific "tail-wagging" dance was probably used. The near location was less than 100 meters from the hive and a location-specific dance was probably not used. In Experiment IV, with patch distances of 44 and 87 meters, the less accurate intermediate dances were probably used for both patches.

These observations tend to cast some doubt on the validity of Experiments II and IV, however, they do not invalidate the results. Both training feeders were equally rewarding, so there was no difference between locations (other than distance) except during testing when the feeders were replaced by artificial flower patches, in which Nectar Distribution and Flower Color varied. Both feeders were initially located at the near location and bees from the near location were trained to the far location. All combinations of Nectar Distribution and Flower Color were tested at both locations. Finally, as Distance, of the three factors which varied between patches, was found to be the only factor which did not show a significant effect, the results of Experiments II and IV need not be rejected.

I believe that the bees which foraged on the patches were probably scouts for the most part, as the numbers of bees counted at both patches at any one time never exceeded 33 and the average was 5.3, while there were hundreds of bees at the feeders earlier in the day. There was ample time, during the two hours of testing on any given day, for those same hundreds of bees to have been recruited again, but this did not occur. Apparently the amounts of nectar in the patches were not sufficient to stimulate the intensity of recruiting stimulated by the much greater amounts provided by the feeders. Von Frisch (1967) speaks of a similar

phenomenon, when scouts foraged repeatedly at feeders of low reward but did not perform recruiting dances in the hive.

"Day" (daily-varying environmental factors)

"Day" was found to be a significant influence in Experiments I-V (Tables 1 and 2). "Day" was included as a factor in the analyses of variance to account for day-to-day variation in bee counts caused by environmental factors other than Nectar Distribution, Flower Color, and Distance. If "Day" had not been considered, then this variation would have been concealed among the three other factors.

The fact that mean number of bees counted at the patches on the days of testing varies inversely with solar radiation and temperature (Figures 2 and 3) does not mean that bee foraging is enhanced by dark, cold days. The degree of availability of natural food sources is influenced by these and other environmental factors, and it in turn influenced the mean number of bees at the feeders. When natural sources were less available, the patches were more attractive. When natural sources were more available, the patches were relatively less attractive in competition with them. The bees were including sources other than the patches in their colony foraging strategy (Visser and Seeley 1982). "During

times of rich nectar production only a few bees from a colony will forage at an artificial feeder provided them, whereas when the natural forage declines many bees from the same colony will forage vigorously at the same feeder" (Vissscher and Seeley 1982, p. 1800).

A possible source of error.

Bees were trained from a specific hive in the apiary. There is no certainty that bees from other hives did not also forage upon the patches. For this reason, we used a point in the center of the apiary for measurements of distance to the flower patch locations, rather than the hive itself. We observed bees leaving the patches and flying toward the apiary, and bees marked at the patch locations were observed leaving and entering the hive and also inside the hive during routine inspections. During Experiment IV, we were fairly certain that bees from a hive lying in a different direction from that of the apiary were foraging on the patches. This hive was 22 meters from the "near" patch and 45 meters from the "far" patch. The main error introduced into the experiment by this hive of bees would arise if they foraged more upon the near location. Whether or not they affected the Distance results is impossible to tell, but the result (P

= 0.334; near mean > far mean) is consistent with that of Experiment II ($P = 0.084$; near mean > far mean). The effect on the Nectar Distribution and Flower Color results probably varied with that of the apiary bees. Except for this, I have no reason to believe that the foragers counted came from any place other than the apiary.

Adaptive significance

The flower patches in this study correspond to patches of different "morphological variants of the same plant species" (Waddington, 1979, p. 279). From one patch to the other, flowers differ only in color and variability of nectar distribution. Odor, shape, and size of flowers are the same. In a natural situation, preference by the pollinators for one variety over the other would result in a greater frequency of pollination of the preferred variety, and consequently, selection for the unique characteristics of that variety. In this case, selection would be for blue flower color and uniformity of nectar reward (certainty) throughout the population.

Given that the pollinator prefers certainty of reward, it should be advantageous to plants to provide such certainty. Due to its increased affinity for pollinators, a

plant species providing certainty of reward will have a competitive advantage over sympatric species which do not provide certainty.

Where in nature do we find examples of constancy of nectar reward? There are reports of variability of nectar reward within plant populations and among blossoms on individual plants (Brink 1982, Corbet et al. 1981, Feinsinger 1978, Nunez 1977, Southwick et al. 1981, Southwick 1982) However, constancy in nectar secretion or standing crop among blossoms has not been reported. It has been suggested that variable patterns of nectar production may be energy-saving to plants (Southwick 1982). If only an occasional flower on a plant must produce nectar in order to maintain pollinator attraction to the species, then energy can be saved for fruit and seed production. Variability in nectar production might also result in a greater number of flowers becoming pollinated, as pollinators must visit more flowers to satisfy their energetic requirements.

For what reason does this preference by the bees for constancy exist, if constancy does not occur in nature? It seems contradictory to find pollinators demonstrating a preference for a phenomenon to which they could not have become adapted. However, although there may not be "constancy" and "variability" in such discrete forms as in the artificial flower patches, there may be degrees of

variability. If mean nectar rewards are equal, then flower varieties of low variability should be preferred over varieties of high variability. If the mean rewards are not equal, then a flower variety of high variability ("variable") but also high mean nectar reward may be preferred over a variety of low variability (or "constancy") and low mean nectar reward (Real et al. 1982).

Another example of "constancy" exists in nature. Natural flower patches are not static like artificial flower patches. In my study, the patches were physically distinct and clearly recognizable by color to both man and bee. According to Pleasants and Zimmerman (1979), natural patches cannot be recognized as discrete clumps but exist as a continuum of nectar-rich and nectar-poor areas within a field (patchiness). The pollinators themselves create patchiness by their foraging movement patterns (Zimmerman 1981). Bees' movements between flowers are influenced by the rewards they find. If consecutive rewards are high, bees turn aside more frequently from straight-line paths and visit flowers nearby. This tends to keep them in certain areas or "patches" of high rewards. If, however, consecutive rewards are low, then they turn less and make flights to flowers farther away. This serves to remove them from "patches" of poor reward and increases the probability of finding patches of rich reward (Heinrich 1979, Pyke 1978b). These behaviors create

patchiness by keeping bees within certain rich areas until they become depleted. On any given day, within a plant population, there are patches in which pollinators have not recently foraged, and therefore there is likely to be nectar in most of the producing flowers. There are also patches in which pollinators have recently foraged and most of the flowers in them are empty of nectar. There may be a few flowers which were missed and now contain relatively large quantities of nectar due to continued production and lack of harvesting. I suggest that the former might be considered "constant" or low variability patches, as there would be a greater certainty of reward from one flower to the next. The latter might be considered "variable" or high variability patches. Pollinators would then prefer the "constant" patches and forage in them until they became "variable", by which time the "variable" patches would have become more "constant" by production of new nectar.

Perhaps, however, the terms certainty and uncertainty, or high-risk and low-risk, should be used, rather than "constant" and "variable", which are artificially contrived and not found in nature. The entire matter of certainty versus uncertainty rests on the fact that there is not great abundance of nectar in natural flowers. If there were great abundance, there would be no uncertainty regarding nectar reward, as pollinators could easily find enough to satisfy

their energetic demand. However, plants usually produce only enough nectar to attract pollinators and not enough in one blossom or inflorescence to satisfy a pollinator. Therefore, the pollinator must visit many plants in order to meet its requirements (Heinrich and Raven 1972). While doing this, cross-pollination is accomplished. Preference by the pollinator for certainty of reward serves as a mechanism of competition between plant species, and also as a mechanism of insuring pollination within a species. It may be of more adaptive significance to the pollinators than to plants. If foragers are more efficient by preferred feeding on more certain resources, then they (or their colony) will be more likely to survive, prosper and pass on their selected-for traits to the succeeding generations.

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Appendix A. Null and alternate hypotheses

Ho: Nectar Distribution has no effect on Mean Number of bees.

Ha: Nectar Distribution has an effect on Mean Number of bees.

Ho: Flower Color has no effect on Mean Number of bees.

Ha: Flower Color has an effect on Mean Number of bees.

Ho: Distance from the hive has no effect on Mean Number of bees.

Ha: Distance from the hive has an effect on Mean Number of bees.

Ho: Daily-varying environmental factors have no effect
on Mean Number of bees.

Ha: Daily-varying environmental factors have an effect
on Mean Number of bees.

Appendix B. Analysis of variance of numbers of foraging bees on adjacent artificial flower patches. Experiments I, III, and V.

Experiment I (N = 120) D = 83 meters, June-July 1982

<u>Source of Variation</u>	<u>Sum of Squares</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>P</u>
Main Effects					
Nectar Distribution	30.000	1	30.000	8.493	0.004
Flower Color	64.533	1	64.533	18.270	<0.001
Day	145.200	1	145.200	41.108	<0.001
Error Within	409.729	116	3.532		

Cell Means

Total population

2.23
(120)

Nectar Distribution

Constant *
2.73
(60)

Variable
1.73
(60)

Flower Color

Blue *
2.97
(60)

Yellow
1.50
(60)

* Statistically significant preference.

Appendix B. (continued)Experiment III (N = 120) D = 44 meters, September 1982

<u>Source of Variation</u>	<u>Sum of Squares</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>P</u>
Main Effects					
Nectar Distribution	57.408	1	57.408	20.891	<0.001
Flower Color	12.675	1	12.675	4.613	0.034
Day	180.075	1	180.075	65.530	<0.001
Error Within	318.764	116	2.748		

Cell MeansTotal population

2.77
(120)

Nectar Distribution

Constant *

3.47
(60)

Variable

2.08
(60)

Flower Color

Blue *

3.10
(60)

Yellow

2.45
(60)

* Statistically significant preference.

Appendix B. (continued)Experiment V (N = 80) D = 26 meters, September 1982

<u>Source of Variation</u>	<u>Sum of Squares</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>P</u>
Main Effects					
Nectar Distribution	441.800	1	441.800	32.476	<0.001
Flower Color	273.800	1	273.800	20.127	<0.001
Day	266.450	1	266.450	19.586	<0.001
Error Within	1033.892	76	13.604		

Cell MeansTotal population

8.02
(80)

Nectar Distribution

Constant *
10.38
(40)

Variable
5.67
(40)

Flower Color

Blue *
9.88
(40)

Yellow
6.17
(40)

* Statistically significant preference.

Appendix C. Analysis of variance of numbers of foraging bees on separated artificial flower patches. Experiments II and IV.

Experiment II (N = 240) D = 83 and 158 meters, June-July 1982

<u>Source of Variation</u>	<u>Sum of Squares</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>P</u>
Main Effects					
Nectar Distribution	40.017	1	40.017	10.662	0.001
Flower Color	72.600	1	72.600	19.343	<0.001
Distance	11.267	1	11.267	3.002	0.084
Day	532.750	3	177.583	47.313	<0.001
Error Within	874.531	233	3.753		

Cell Means

Total population

2.94
(240)

Nectar Distribution

Constant *

3.35
(120)

Variable

2.53
(120)

Flower Color

Blue *

3.49
(120)

Yellow

2.39
(120)

Distance

83 meters

3.16
(120)

158 meters

2.72
(120)

* Statistically significant preference.

Appendix C. (continued)Experiment IV (N = 240) D = 44 and 87 meters, September-October 1982

<u>Source of Variation</u>	<u>Sum of Squares</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>P</u>
Main Effects					
Nectar Distribution	50.417	1	50.417	8.754	0.003
Flower Color	41.667	1	41.667	7.235	0.008
Distance	5.400	1	5.400	0.938	0.334
Day	1421.859	6	236.976	41.148	<0.001
Error Within	1324.606	230	5.759		

Cell MeansTotal population

2.84

(240)

Nectar Distribution

Constant

2.38

(120)

Variable *

3.30

(120)

Flower Color

Blue *

3.26

(120)

Yellow

2.42

(120)

Distance

44 meters

2.99

(120)

87 meters

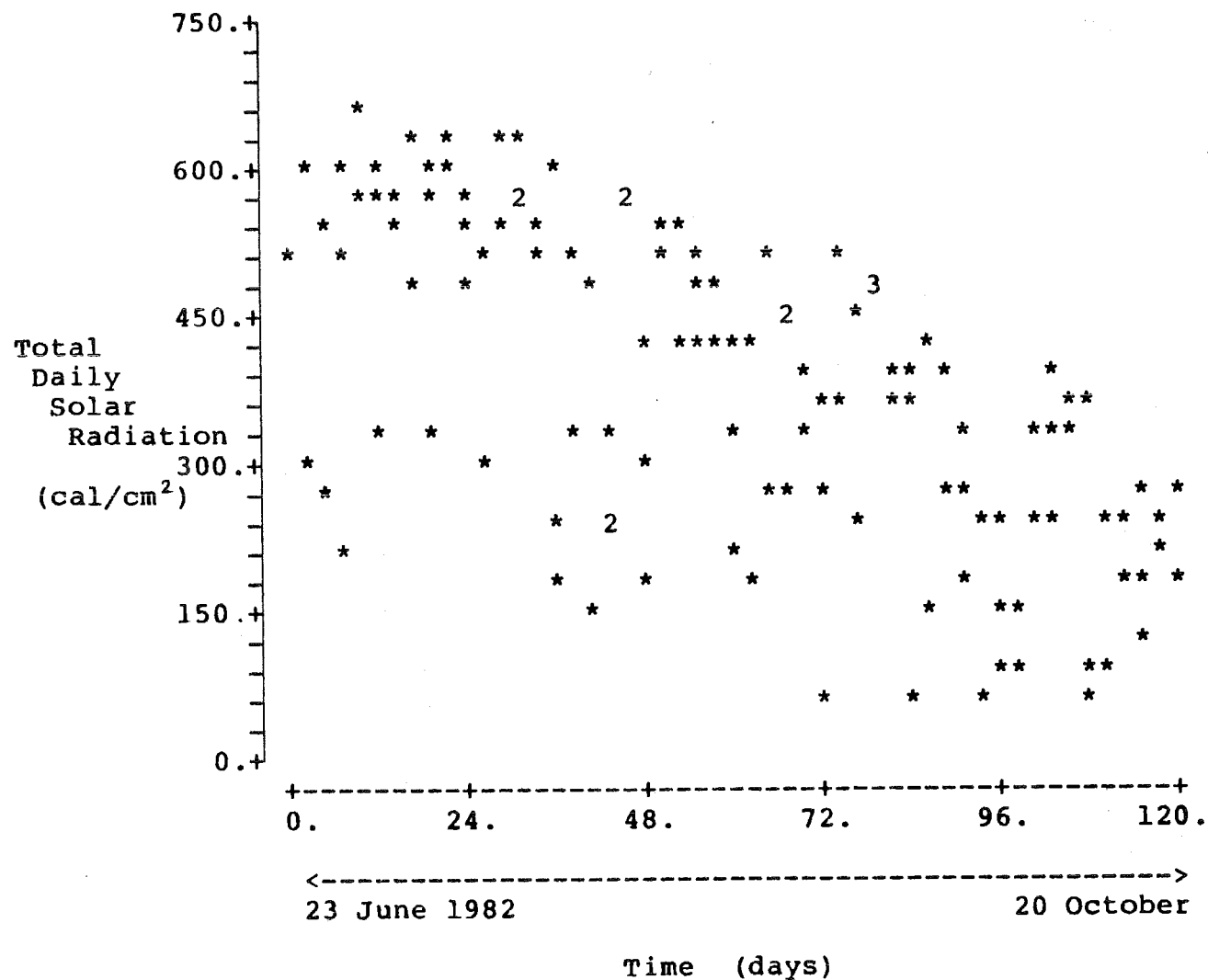
2.69

(120)

* Statistically significant preference.

Appendix D.

Relationship between solar radiation and season.

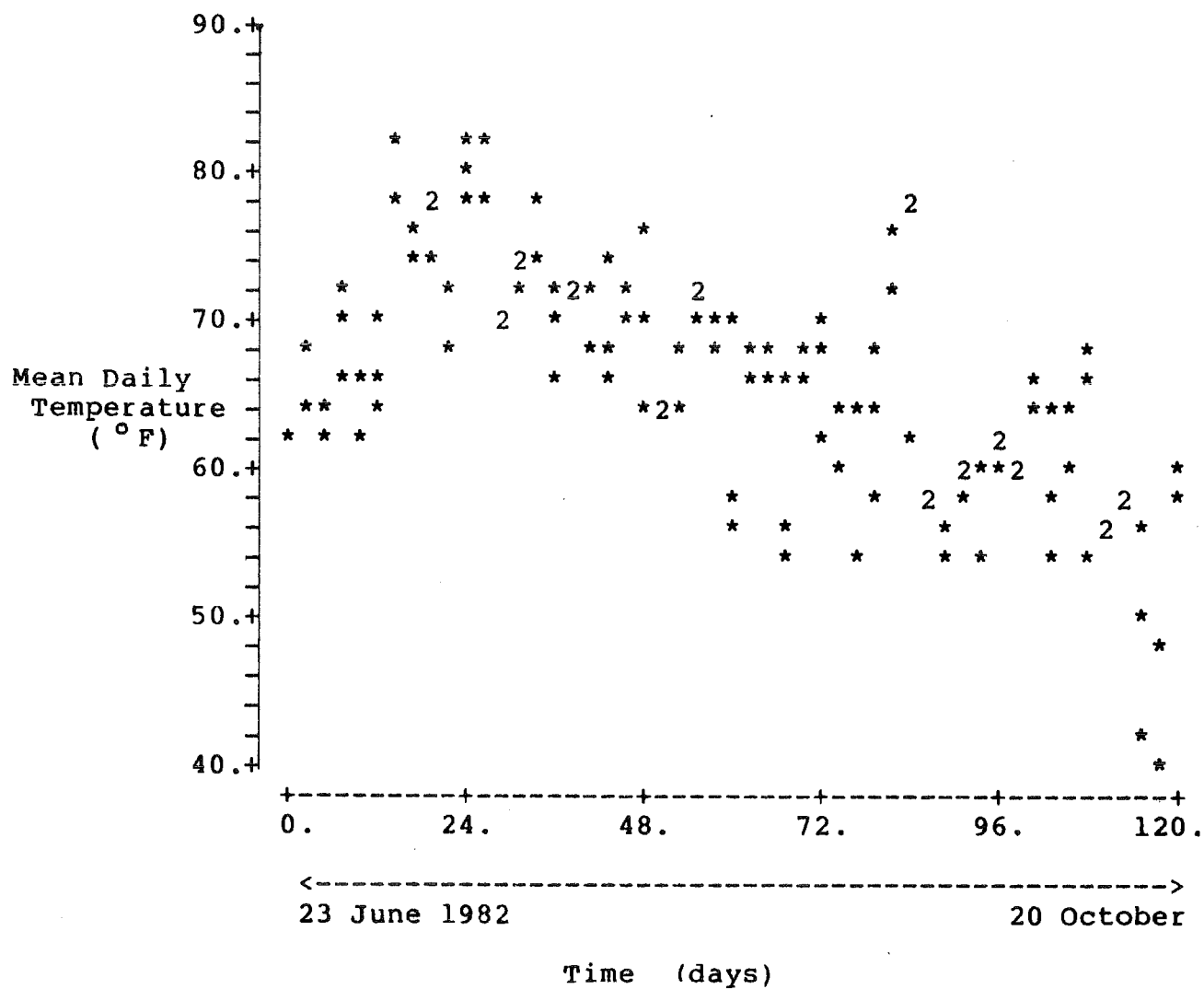


The regression equation is

$$Y = 555 - 3.0 X \quad r = -0.64$$

Appendix D. (continued)

Relationship between temperature and season.



The regression equation is

$$Y = 74 - 0.15 X \quad r = -0.64$$

Appendix E. Experimental set-ups; dates of testing and combinations of independent factors used.

Experiment I

Nectar Distribution	Flower Color	Distance (m)	Number of Observations	Date
Constant	Yellow	83	30	23 June
Variable	Blue	83	30	23 June
Variable	Yellow	83	30	15 July
Constant	Blue	83	30	15 July

Experiment II.

Nectar Distribution	Flower Color	Distance (m)	Number of Observations	Date
Constant	Yellow	158	30	13 July
Variable	Blue	83	30	13 July
Constant	Yellow	83	30	14 July
Variable	Blue	158	30	14 July
Variable	Yellow	83	30	19 July
Constant	Blue	158	30	19 July
Variable	Yellow	158	30	20 July
Constant	Blue	83	30	20 July

Experiment III.

Nectar Distribution	Flower Color	Distance (m)	Number of Observations	Date
Variable	Yellow	44	30	17 September
Constant	Blue	44	30	17 September
Constant	Yellow	44	30	18 September
Variable	Blue	44	30	18 September

Appendix E. (continued)

Experiment IV.

Nectar Distribution	Flower Color	Distance (m)	Number of Observations	Date
Variable	Yellow	87	20	30 September
Constant	Blue	44	20	30 September
Variable	Yellow	87	10	1 October
Constant	Blue	44	10	1 October
Constant	Yellow	44	10	8 October
Variable	Blue	87	10	8 October
Variable	Yellow	44	30	9 October
Constant	Blue	87	30	9 October
Constant	Yellow	44	20	14 October
Variable	Blue	87	20	14 October
Constant	Yellow	87	10	15 October
Variable	Blue	44	10	15 October
Constant	Yellow	87	20	20 October
Variable	Blue	44	20	20 October

Experiment V.

Nectar Distribution	Flower Color	Distance (m)	Number of Observations	Date
Constant	Yellow	26	20	22 September
Variable	Blue	26	20	22 September
Variable	Yellow	26	20	24 September
Constant	Blue	26	20	24 September