Aims & Objectives

Aims
1. To describe experiments showing how honey bee colonies exploit the better nectar sources in their environment.
2. To describe how information flow within an insect colony consists of both signals and cues.

Objectives
1. Understand how the experiments were carried out and what their results show.
2. Understand the difference between cues and signals and learn some examples.

Basic Ecology of Nectar Foraging in the Honey Bee

A honey bee colony in a temperate-climate location (here New York State) can only collect nectar during part of the year. During the warm months most of the nectar is collected during relatively brief nectar flows of common plants. Nectar collection can be monitored by weighing a hive daily. A colony has an essentially unlimited appetite for nectar. It does collect nectar both to fuel its current activities, and to build up a large honey store for winter.

Honey Bee Waggle Dance

Dancer (forager)

Dance Followers
(unemployed foragers)

Waggle Dance: Angle of Flowers to Sun
Waggle Dance: Angle of Dancing Bee to Vertical

Dance Duration Encodes Distance

Foraging Map, 16 August 1996

Peak District: Patch of Heather

Foraging Map, 1 May 1997

Summary of Distances Foraged

- Schneider 1989
- Visscher & Seeley 1982
- Beekman & Ratnieks 2000, August data
- Beekman & Ratnieks 2000, May data
Basic Ecology of Nectar Foraging in the Honey Bee

Honey bee colonies live all year round. They balance their energy budget by storing large amounts of honey during periods of nectar abundance. Honey is a stable product that does not easily ferment or decompose and can be stored for later use, even months later. By contrast, honey bee colonies store only modest amounts of pollen, and collect water only when it is needed.

Forager workers communicate the location of flowers to their nestmates using the waggle dance, which is carried out inside the nest on the vertical combs. The duration of the waggle run gives the distance. The angle of the dancing bee’s body to vertical gives the angle of the flowers relative to the sun.

Decoding of dances is one way to investigate honey bee foraging. Dance decoding shows that honey bees normally forage within a few kilometers of their nest, but can forage as far as approximately 12km. The fact that honey bees can communicate the locations of flowers means that not all bees need scout. In fact, only about 10% of foragers find flower patches by scouting. The rest do so by following dances. In bumble bees, which do not have the waggle dance, every forager must scout for herself.

Dancing also means that more costly scouting will be profitable. Scouting in the honey bee is similar to prospecting in an oil company. If a new resource is found, the bees from the same hive can be recruited to work it.

Honey Bee Colonies Are Good at Finding & Recruiting to Patches of Flowers

Ability of Colonies to Locate Flowers

Tom Seeley planted small patches of buckwheat, 100m², at various distances from a group of hives within a forest in Connecticut, USA. (There are relatively few flowers in forest.) Foragers seen on the flowers were marked with paint dots. To determine if a colony had located the patch, the hives were opened to see if any bees inside had paint dots. This method may underestimate the probability that colonies detect flowers. Foragers that were not marked may have found the flower patch.

Ability of Colonies to Locate Flowers

Table 3.1. Results of the experiment analyzing the ability of honey bee colonies to discover 100 m² patches of buckwheat flowers planted at various distances from their hives. “X/4” denotes that X out of the 4 test colonies discovered the patch in this trial of the experiment. The totals indicate the probability that a colony will discover a particular patch of flowers located at the distance shown. After Seeley 1987.

<table>
<thead>
<tr>
<th>Trial date</th>
<th>1000</th>
<th>1000</th>
<th>1900</th>
<th>2000</th>
<th>3200</th>
<th>3600</th>
</tr>
</thead>
<tbody>
<tr>
<td>August 1984</td>
<td>2/4</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>June 1985</td>
<td>3/4</td>
<td>3/4</td>
<td>1/4</td>
<td>2/4</td>
<td>0/4</td>
<td>0/4</td>
</tr>
<tr>
<td>August 1985</td>
<td>4/4</td>
<td>2/4</td>
<td>1/4</td>
<td>4/4</td>
<td>—</td>
<td>0/4</td>
</tr>
<tr>
<td>Totals</td>
<td>14/20 = 0.70</td>
<td>8/16 = 0.50</td>
<td>—</td>
<td>0/12 = 0.00</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Rapid Recruitment to a Patch of Flowers

Once a honey bee has found a patch of flowers, it can rapidly recruit nestmates.

In this experiment 14 potted borage plants in bloom were set out at various distances from a bee hive. It took 1-3 hours for the first forager to land on the flowers. But from then in took about 15 minutes to recruit another forager and less than an hour to recruit 10-20 more foragers.

The bee hive was located on Appledore island, a small island off the coast of New Hampshire, USA. It was the only honey bee colony on the island.

How Do Honey Bee Colonies Recruit Foragers to the More Rewarding Patches of Flowers?
Variation in Flower Patches

Honey bee colonies have vast foraging ranges. Forage at up to c. 14km from hive: c. 600km²

There is a constantly changing mosaic of flowers, variation in locations over time, species coming in and out of bloom, many species, patches or areas within a species.

Variation in quality, less and more rewarding flowers, more rewarding: closer, higher conc., quicker to collect.

More Efficient Colony Foraging

To gather nectar more efficiently, a colony should send foragers to the better patches. This is achieved by:

- Abandonment of less-rewarding patches
- Recruitment to more-rewarding patches
- Searching for new patches (scout bees)

Approximately 10% of the foragers are scouts. Most foragers find flowers by following dances. Following dances does not help a recruit find a patch of flowers more quickly. In fact, only about 25% of foragers who have followed a dance find the advertised location. But following dances helps recruits to locate more rewarding patches.

Relative Recruitment to Two Syrup Feeders

In this study a single colony was trained to two syrup feeders in opposite directions each 500m from the hive. Therefore, the feeders did not vary in quality due to distance. But they did vary in quality due to sucrose concentration. One was a reference feeder which had 2.25 molar sucrose (= very strong nectar). At different times, the test feeder syrup was 2.25, 2.125, 2.0, 1.5, 1.0 molar.

30 marked foragers were allowed to forage at each feeder. On returning to the hive some of them would make waggle dances, leading to more bees being recruited to the feeder. These could be recognized as they were unmarked, and because there was no other hive nearby to send foragers. The recruits were captured and stored to prevent them from dancing.

The relative numbers of recruits was greatly affected by the sucrose concentration in the test feeder. Only 50% as many came when it was 2.0 molar, and only 25% when it was 1.5 molar. This shows that a colony can direct more recruits to a better source.

More Concentrated Nectar Results in More Dancing

This study measured dancing by 30 foragers trained to a syrup feeder and the number of new foragers they recruited to the feeder.

Two hives were studied, each 420m from its own feeder. One was a control. Its feeder always had 1.5m sucrose. The syrup in the experimental hive’s feeder varied from 0.5 (very weak) to 2.5 (very strong).

As the syrup in the experimental hive’s feeder was made more concentrated during the day, the amount of dancing increased and the number of recruits increased. Dancing increased both as the probability that a returning forager would dance, and the number of waggle runs made.

Studying Foraging Using Feeders

When the weather is warm and there are few natural sources of nectar, honey bee colonies can easily be trained to collect syrup to a syrup feeder. The feeder is first placed right beside the hive and then gradually moved further away.

It is possible to mark the foragers with paint dots or numbered tags and to stick with a certain number of them. Recruits (unmarked bees) can be captured and stored in a jar before being returned to the hive.

Foragers can be observed dancing and unloading nectar to receivers when they return to their nest if an observation hive is used. The feeder can be at any distance or direction to the hive, and the concentration of syrup can be whatever the experimenter wants. Normal table sugar, sucrose, is normally used as this is the main sugar found in nectar.

Depending on the needs of the experiment one hive can be trained to one feeder or several feeders. Or two hives can be trained to their own separate feeders, or even to the same feeder.

Interference from bees from other hives can be a problem. Seeley did many of his studies on a small island off the coast of New Hampshire with no bee hives or in a coniferous forest at Cranberry Lake, in the Adirondack mountains of New York where there are very few flowers and very few honey bees.
In this study a single colony was trained to two syrup feeders in opposite directions each 400m from the hive.

The number of recruits was in exact proportion to the number of waggle runs made. Foragers from the 2.0 molar feeder danced more (5190 waggle runs, 75%) than those from the 1.75 molar feeder (1695, 25%). The numbers of recruits were 122 (76%) and 38 (24%).

These results indicate that the effectiveness of dancing in recruiting foragers can be explained by the total amount of dancing. There is probably no “dance liveliness” effect. Von Frisch thought that there was a liveliness effect, but this study indicates that no such effect exists, at least for differences between 2 molar and 1.75 molar.

In another study at Cranberry Lake, an observation hive was given two feeders each of 1.5 molar sucrose. There were very few flowers and about 50% of the foraging was from these two feeders. One feeder had 30 marked foragers and the other 90. Only about 3% of the foragers danced and the average time delay in being served by a receiver bee was about 25 seconds.

60 foragers were then removed from the 90 forager feeder. Immediately, the bees from the other feeder increased their dancing to about 40% of foragers. The average delay in being served decreased to about 10 seconds.

This study shows that it was not the quality of the nectar that affected the probability of dancing, because the quality never changed. It suggests that it was the delay in being served.

In the study on the previous slide, also carried out at Cranberry Lake, two observation hives (control hive and experimental hive) were set up each with their own feeder. The experimental hive had the glass over the dance floor area replaced with mesh. The nectar storer (= receiver) bees were marked with paint dots as they received nectar. (Receiver bees cannot be identified except by their behaviour.) In the evening they were removed.

In the experimental hive there was an increase in the search time (= delay in being served) and a great reduction in the proportion of foragers that danced and number of recruits to the feeder. There was no effect on the control hive. The receivers were then replaced in the evening and things returned to normal. The removal and replacement of the receivers was then repeated on two more days.

The results show that honey bee colonies use the unloading delay to modulate dancing. A combination of nectar quality and the overall influx of nectar into the nest combine to determine if a bee will dance or not. In this way, the colony can recruit appropriately when nectar is abundant or not.
Information

Signals & Cues

Within an insect society, the individuals deliberately send information “signals” to one another. This information helps to coordinate the activities of the colony members. The honey bee has several dozen known communication signals, which are either pheromones or various types of dance or other tactile communication. Below are some of them. They are mainly produced by the workers, but also by the queen and even by larvae.

- Waggle dance
- Tremble dance
- Shaking signal or dance
- Alarm pheromone
- Attractant (Nasanov) pheromone
- Queen pheromone

Shaking Signal

The shaking signal or dance (sometimes known as the dorso-ventral abdominal vibration) is also part of the foraging system. A forager bee may literally shake another forager bee so that it moves into the dance floor area where it may follow waggle dances. The signal is often made when foraging resumes after several days of inclement weather. It upregulates foraging.

Attractant (Nasanov) Pheromone

If a forager takes a long time to find the nest entrance, it will often “scent fan”. It faces the entrance, lifts its abdomen and kinks the tip to expose the Nasanov gland which is located in the intersegmental membrane, and fans its wings to send out a jet of pheromone (which smells of citrus). In this way it will help guide nestmate bees, who may also be confused, to the entrance. Other bees who are confused do the same thing leading to chains of scent fanning bees.

Cues

Not all useful information is in the form of deliberate signals. Workers can also acquire information that is incidentally produced. These are known as cues. Both cues and signals are important in organizing the colony. For example, in nectar collection several signals, in particular the waggle dance and the tremble dance, and one cue, the delay experienced by nectar foragers in being unloaded, help maintain balance in the work capacities of the foragers and the receivers.

- Delay to forager in being unloaded by a nectar receiver
- Carbon dioxide level in the nest
  - high levels cause increased ventilating behaviour
- Level of amino acids in trophallactic secretions
  - low levels cause greater collection of pollen
- Brood nest temperature
  - low temperature will result in heating
  - high temperature in ventilating

Information Flow

Information can either flow directly between bees, or indirectly via effects on the shared nest environment. Most cues act indirectly and most signals directly. Some signals are one bee to another bee (e.g., the vibratory signal), some are one bee to several bees (e.g., waggle dance, Nasanov attraction pheromone), and some one bee to the whole colony (e.g, the queen pheromone).