Honeybee diet: individual forager decisions and colony health correlates

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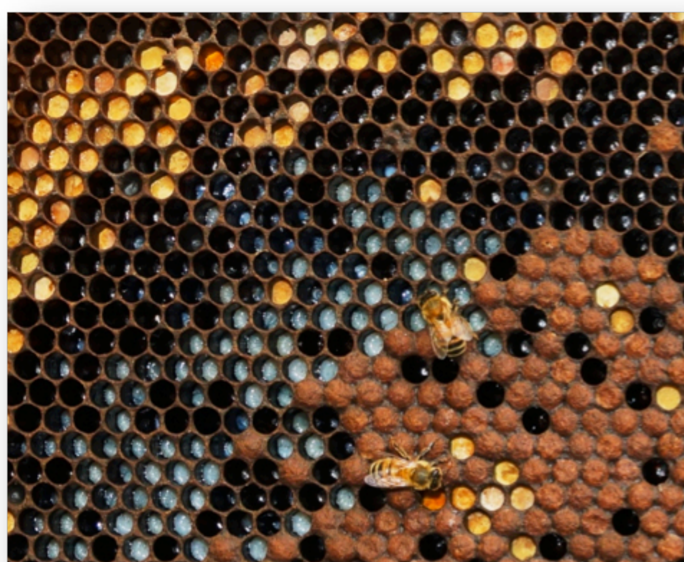
Pollination as an ecosystem service

Bees perform a very important service for farmers and backyard growers: they pollinate flowers, and thus contribute to crop production. This ecological service is not the result of a "selfless act" on the part of the bee, but in reality is driven by the demands of the voracious bee larvae that await food back in the hive, and by the flower's need for pollen exchange.

Pollen as bee food

Pollen is one of two rewards offered by flowers to insect visitors. Pollen is essential for brood rearing in solitary and social bees (Leonhardt and Blüthgen, 2012). Pollen provides the protein, lipids, and essential amino acids needed for the developing larvae (Seeley, 1995). In honeybees, pollen is collected by older foragers that are specializing in that task, the foragers return to the hive and empty the contents of their corbicula or "pollen basket" into pollen storage cells. Pollen brought to the hive and stored in these cells is called "bee bread"; its chemical nature having been slightly changed by the addition of salivary solutions. Younger workers, called nurse bees, consume the bee bread and manufacture larval food in their hypopharyngeal glands. Young developing larvae are fed "royal jelly" directly by the nurse bees, but larval diet changes as they get older. Larvae meant to develop into workers are switched to "worker jelly," a mixture of hypopharyingeal products, honey, and pollen, as they approach the pupation stage (Barchuk et al., 2007).



Pollen forager on a cucurbit plant (above left) and hive frame with pollen (right) showing stored pollen (top left corner of the image), open brood (bee larvae center), and capped brood (pupating brood), bottom right.

Possibly due to the global decline of pollinators, the effect of malnutrition on the health of social bees has been the focus of many recent studies. Vanderplanck et al (2014) showed that bumble bee workers that had access to high chemical quality pollen produced larger larvae, these larvae turn into more successful adults, that may be better at surviving the winter, and finding a mate. It is important to note that the role of larval food in social insects goes beyond providing the fuel for the larva to transform into an adult bee. Food quantity and quality in social bees also impacts the production of individuals in different castes, the immunocompetence of the individual worker bee, and the colony's ability to resist infection and survive periods of unsuitable foraging weather (Alaux et al., 2010). In honeybees, pollen quality impacts both the nurse bees, and the developing larvae that are being fed by those bees. The physiology of nurse bees is particularly relevant to colony health because they are in charge of processing pollen, and producing larval food from their hypoharyngeal glands, as such, they are a living link between food stored and food delivered to developing brood. In a laboratory setting Di Pasquale et al (2013), compared the health and physiology of nurse bees that were fed monofloral pollen diets to those fed multifloral diets. The results showed that the nurse bees fed multifloral pollens were more competent at dealing with disease, in particular, the gut parasite, *Nosema ceranae*. Pollen consumption has also been shown to strengthen metabolic pathways that are important in promoting adult bee longevity and the production of antimicrobial peptides which provide protection to the colony (Alaux et al., 2011). In addition, Alaux, et al (2010) also showed that production of glucose oxidase (GOX), an enzyme that contributes to sterilizing the food and the colony, is enhanced by diverse pollen diets.

What the colony wants

Social bees are strongly polylectic, visiting a variety of flowers to provide for their young. Among the possible reasons for a wide diet breadth is that single pollen sources may be deficient in one or more nutrients, or may not provide adequate protein levels needed for larval development. Consequently, variety is, literally, the spice of life for colonial bees. In practice however, managed honeybee colonies are often used to pollinate large scale field of monocrop plantings. How colonies respond to this reduction on pollen diversity reflects the internal tension between individuals and colony goals. Although honeybees and other social bees show a high degree of polylecty at a colony level, individual forager bees tend to respond to available resources, and utilize the common species more intensively, at least temporarily.

This tendency to use common flowering plants that occur near the nest allows the individual bee to reduce foraging costs in time and energy and allows the colony as a whole, to track and exploit effectively different plant species as they come into bloom in a natural ecosystem. In large scale agriculture we exploit the tendency of individual bees to prefer "the abundant and the nearby" by placing them in a blooming field. The large numbers of workers in each colony, and the colony internal need for pollen makes them ideal for agricultural use. However, crop pollination exposes bees to a large number of pesticides in the nectar and pollen they collect from the fields, adding yet another layer to diet quality.

Pesticides are used worldwide to protect important crops from insect pests and diseases, unfortunately some of these chemicals can be problematic for pollinators. Research has shown that some chemicals have neurological effects in bees leading to disorientation and navigation problems, as well interfering with the learning behavior of bees (Belzunces et al., 2012; Schenider et al, 2012, Henry et al., 2012). Intact cognitive and flying abilities are indispensable for individual workers to successfully seek food and return to the hive. Farm and garden owners can help by selecting "softer" chemicals, and/or reducing the use of pesticides, and in this way improving the micro-habitat from which bees collect food.

What we are studying and how

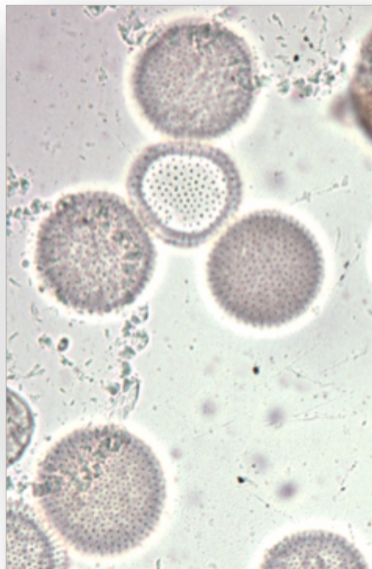
We have begun to look at what plants bees are utilizing in Hawaii by sampling the pollen being brought to the hive by the bees themselves. This can be done by placing a "pollen trap" at the front of the hive entrance. A pollen trap is a plastic "grid" that allows the worker bees to enter the hive through small holes, as the bees squeeze to get in, they may lose one or both pollen loads that were carrying. The pollen pellets fall into a tray and can then be collected. Looking at pollen pellets under the microscope gives you an idea of what individual bees are bringing, as well as what the colony as a whole is receiving.

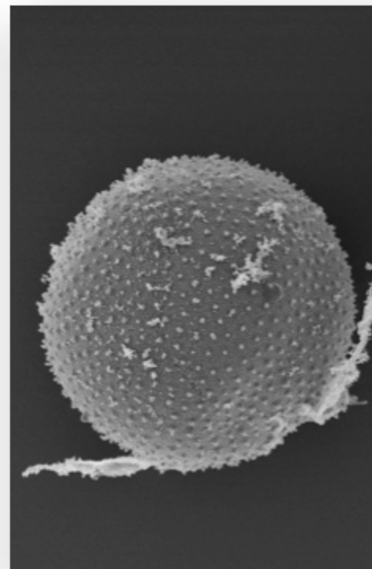
Pollen trap and returning foragers (left). Red arrows point to pollen loads on the bees' legs. Blue arrow points to the openings through which the workers will have to squeeze in to get inside the hive. A colorized pollen grain (right) under the Scanning Electron Microscope (above right) Pollen grains have unique and sometimes spectacular protective outer walls.

What information are we obtaining?

Preliminary work suggests that bees are using a variety of resources, from fruit trees, such as avocado (see below), to weedy species, such as haole koa. Based on our preliminary results a colony may be using over 10 species of plants on a single day. The long term goal of the project is to compare the diversity of the pollen sources at different landscapes (urban, agricultural, etc) and to examine the fluctuations of pollen quality and quantity over time at each site. Sampling pollen pellets also allow us to examine more than just the diversity of plants being used, but also the abundance of each resource. By counting how many pollen pellets of each type it is possible to determine relative importance of each pollen source, and track which kinds of pollen are dominant at each site, and when the peak use during the year. It can also help us quantify the importance of companion or border crops, such as buckwheat, and sunnhemp, which are frequently used to enhance crop fields.

Avocado flowers are often visited by pollinating flies, but honeybees also visit the flowers.





Avocado pollen grains seen through a light microscope (middle) notice how the pollen grains can appear different depending on the depth of focus, and the lighting. Far left: Scanning Electron Microscope image of an avocado pollen grain collected from a bee. The avocado pollen grain is about 30µ (0.03 mm) in diameter.

Why is this important?

Understanding the types of plants that bees are using and the relative contribution of each plant to the bee's diet is crucial to help us make management decisions for our gardens and farms. We know that we can "please" bees by planting many types of herbs such as basil, mint, oregano, etc, and letting the plants go to flower. A little "benign neglect" is also beneficial in the garden. We know that some native Hawaiian plants make good bee forage; options to consider include, Ohia, Naupaka, some of the native "ice plants" such as Akulikuli, and other indigenous ground covers such as Akia and Eluehe.

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