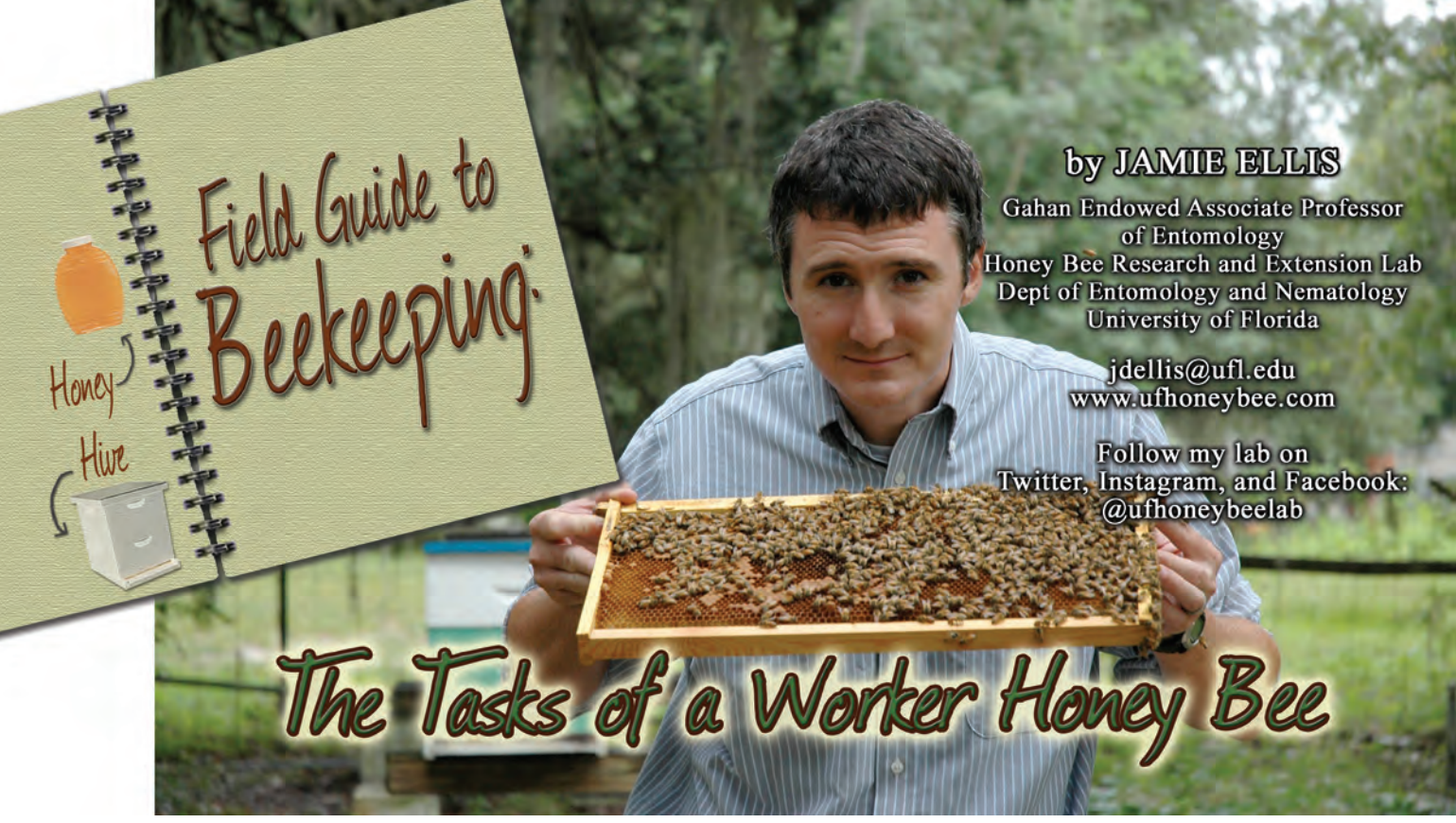

Worker honey bees are marvelous creatures. These females could have been queens, had their older sisters simply fed them more food while they were developing as larvae. The amount and quality of diet they were fed while young were the only things separating them from royalty. If they had been a queen, they could have laid eggs, maintained the colony's homeostasis, and lived up to a few years. Yet, they were born workers, destined to work their lives away in just a few short weeks.

Many worker bee equals in other social insect colonies, such as ants or termites, are born into a caste system, with a designated task that they perform their entire lives. Not so for worker honey bees. Worker honey bees subscribe to temporal polyethism, or "time related" (temporal) "many" (poly) "behaviors" (ethism). This simply means that worker honey bees perform a number of tasks over time and the performance of these tasks is age dependent. Beekeepers called this phenomenon age-related division of labor. The end result is simple: worker honey bees are not born into a task in which they remain their entire lives. Instead, they progress through a somewhat predictable series of tasks as they march toward the day that they can work no longer.

Interestingly enough, not all workers perform all tasks. Some workers may skip certain tasks altogether as they mature. Furthermore, the task system is not rigid. Old bees can perform young bee tasks and *vice versa*. This can be exacerbated further given the fact that a worker bee usually performs multiple tasks at any one age. Regardless, enough of a pattern exists in worker task performance that we can discuss these tasks in somewhat of a chronological order, as long as one remembers (1) workers may skip tasks, (2) workers perform many tasks at each age, and (3) workers spend more time resting and patrolling the nest than they do anything else.

Emphasizing point 3 above, I find it quite interesting that workers bees are even called *worker* bees at all. They spend the vast majority of their lives resting in the nest. Resting, of course, grants a worker needed respite. After all, who does not benefit from a little R&R? Things are not always as they seem, though, as bees are not always resting when they appear to be. Workers may remain immobile while secreting wax, producing brood food, etc. Thus, the period of immobility may simply be times of preparation to perform a given task. Worker bees also spend quite a lot of time patrolling the nest. The performance of this behavior seems to be a worker's attempt to find out what needs to be done in a colony, with the idea that they are looking for something to do.

Though there is considerable overlap in the tasks that workers perform, there is an overall pattern to where and when they perform the tasks. Young worker bees engage in nest-based tasks while older worker bees perform tasks near the colony entrance or outside of the colony. Generally speaking, the tasks follow this natural progression: (1) cell cleaning and capping, (2) brood and queen tending, (3) comb building, cleaning and food handling, and (4) outside tasks.

Worker progression through their tasks probably is regulated physiologically, hormonally and by colony need. For example, certain glands in workers must develop before the workers are able to perform a given task – after all, they cannot feed larvae without being able to produce brood food. Given that worker honey bees perform the vast majority of essential tasks in the colony, their activity ensures that the colony has all of its needs met. The local environment around the colony also likely plays a role in worker task allocation, given that colony requirements vary based on a variety of environmental conditions and that workers respond to colony needs by doing jobs that must be done to ensure colony homeostasis.

I am going to spend the rest of the article introducing you to the tasks performed by worker honey bees. I will do my best to present the tasks to you in the order that they typically are performed, though admittedly I found this really hard to do given the massive variation in the timing and duration of tasks that workers perform. Keep in mind, bee progression through these tasks varies; only very loose conclusions can be drawn about the order and performance of worker tasks. Much of what I share will be based on the information provided by Winston (1980) and Seeley (1982). The books they wrote are masterpieces of bee biology and ecology. They are worth being in every beekeeper's library. I provide full citations in the reference section of this manuscript in the event that you wish to explore these books further. The order that I discuss the tasks are the approximate order in which they are preformed, as noted by Winston (1980). I list the common age ranges and the mean age of workers performing each task.

AGE-RELATED TASKS

Cell preparation (about 2-16 days of age, mean age about 8 days old) – This

is the first task that workers perform when they emerge from their cells as adult bees. This task can be split into two subtasks: polishing cells and cleaning cells, with the latter happening later in the bee's life. For the former, the workers begin cleaning a cell from the back of the cell, working their way up the walls of the cell and to the entrance of the cell (Figure 1). They will remove the remains of cocoons and excreta left by previous cell occupants. They will cover any remaining adulteration in the cell with a thin layer of wax.

Figure 1 – Two worker bees cleaning cells shortly after their emergence as adults. *Photograph by Mike Bentley.*

Capping brood (about 3-10 days of age, mean age about 8 days old) – Young worker bees are able to secrete wax in small amounts. This allows them to cap the cells of larvae that are ready to begin transforming into pupae (Figure 2). They also may seal cells of ripe honey while at this age. A cell can take 20 minutes to 6 hours to cap.

Figure 2 – A worker capping a brood cell. Notice that the cell the worker's head is over is partially capped. *Photograph by Mike Bentley.*

Feeding larvae (about 3-15 days of age, mean age about 10 days old) – Worker bees performing this task are called nurse bees and often are said to be tending brood. Worker bees need well developed hypopharyngeal and mandibular glands (see my article in the September 2015 article for a discussion of both sets of glands) in order to create the food they use to feed larvae. Workers must consume pollen so that these glands can mature.

Brood tending peaks when bees are about 10 days old. Nurse bees will look into cells containing young larvae and decide whether or not to feed the larvae (Figure 3). Not all cell inspections lead a worker to feed the developing larvae. A cell may be visited many thousands (5000+) of times while the larvae grows, with less than half of those visits (1,000 – 2,000) resulting in larval feeding events. Interestingly, workers bees may be able to determine the age of the developing larvae because they are able to adjust the proportion of glandular secretions in the diet in response to the age of the immature bee (different age larvae eat slightly different mixtures of brood food). A single nurse bee rears the equivalent of 2-3 larvae during its life.

Figure 3 – A worker bee feeding a larva. *Photograph by Mike Bentley.*

Tending the queen (about 3-14 days of age, mean age about 11 days old) – Worker bees tend the queen about the same time period that they perform nurse bee tasks. Workers tending the queen lick her, examine her with their antennae and forelegs, groom her and feed her with glandular secretions and honey (Figure 4). The queen may be fed by workers every 20-30 minutes for about 2-3 minutes per feeding. Worker bees performing this task often form a circle around the queen, with the circling bees being referred to as the queen's attendants or retinue. The licking behavior is quite important. Licking the queen is how the workers acquire and distribute the queen's pheromones around the nest. This spreading of her pheromones maintains nest homeostasis. It lets all workers know she is present.

Figure 4 – The retinue of a queen. At least 19 bees can be seen attending the queen in this picture. *Photograph by Mike Bentley.*

Receiving, ripening and depositing nectar (about 10-20 days of age, mean age about 13 days old) – It may be reasonable to believe that worker bees returning from their work in the field deposit the nectar they collect directly in cells in the nest. However, this is not the case. There is a cohort of workers whose job it is to receive the nectar from returning foragers and process it for conversion into honey. These bees typically wait close to the nest entrance, ready for nectar-laden foragers to return. The nectar receivers are quick to unload the incoming foragers so that the foragers can return to the field. A single returning forager may regurgitate her crop contents to 2-3 receiver bees. The receiver bees, in turn, transport the nectar into the nest as they search for a cell in which they can deposit their nectar load.

Before they deposit the load, workers will spit out the nectar and suck it back into their mouths over and over. This behavior helps start the process of nectar dehydration and conversion into honey. After blowing nectar bubbles, the worker bees deposit the nectar into available cells (Figure 5).

Figure 5 – A worker depositing nectar into a cell. *Photograph by Mike Bentley.*

Cleaning debris (11-15 days of age, mean age about 14 days old) – Workers performing this task are the waste management force of the hive. They will remove debris from the nest. This debris includes moldy pollen, old cell cappings, wax debris, dead brood or adult bees, etc. The removal of dead or diseased brood is called hygienic behavior and is a special type of cleaning behavior that helps the colony battle pests and diseases. With this behavior, the workers can detect dead or diseased brood in cells, even capped cells, uncap the cells, and remove the dead or sick bees from the nest. This behavior is the subject of bee selection programs aimed at reducing disease and pest pressures in the nest.

Handling pollen (about 10-19 days of age, mean age about 15 days old) – Unlike nectar foragers, pollen foragers deposit their pollen loads directly into cells (Figure 6). At this point, a cohort of worker bees who handle pollen mix the pollen with nectar, pack the pollen into the cell using their head and mandibles, and cover the pollen with a thin layer of honey. This starts the conversion of pollen into bee bread (Figure 7).

Figure 7 – Bee bread packed neatly in cells. *Photograph by Mike Bentley.*

Figure 6 – A worker bee depositing pollen into a cell. The image on the left shows the worker on a comb and laden with pollen. In the middle image, the worker is inspecting a cell to determine if it can receive pollen. The worker decides that it can and positions her hind legs over the cell (right). Using her other legs, she rakes the pollen balls from her legs and into the cell. *Photograph by Mike Bentley.*

Comb building (about 12–23 days of age, mean age about 16 days old) – Workers engaged in this behavior secrete wax scales from the wax plates underneath their abdomens. They grab the wax with their mandibles, shape it, and add it to existing cells or use it to develop new comb in the nest.

Cell cleaning (about 11-15 days of age, mean age about 17 days old) – This is the second time in a worker's life that she cleans cells; though this time they use their mandibles to restore cell walls, smooth cell edges, and remove cell cappings (Figure 8). They do this to prepare a cell for use. A cell can take around 41 minutes to prepare, with anywhere between 5-30 workers taking part in the cell-cleaning process.

Figure 8 – Workers mending wax. *Photograph by Mike Bentley.*

Ventilating the nest (about 2-25 days of age, mean age about 18 days old) – This often is the first task that workers do outside the nest. Ventilating bees face the nest entrance with their abdomen pointing down (Figure 9). Next, they fan their wings away from the nest entrance, thus cooling the hive, evaporating honey, or decreasing the carbon dioxide levels in the nest. Hundreds of bees can perform this task at the nest entrance at any given time.

Guard duty (about 15-28 days of age, mean age about 19 days old) – Not all worker bees are destined to become guard bees, but many are. Guard bees guard the nest entrance, usually for only a few hours or days before they ultimately progress to foraging-based tasks. Guard bees have a characteristic stance at the nest entrance.

Figure 9 – Workers ventilating at the nest entrance. *Photograph by Mike Bentley.*

They stand on their back 4 legs with their front legs up in the air and their antennae forward (Figure 10). They employ this behavior in an attempt to keep foreign invaders out of the nest. They smell and touch many of the bees returning from the field, thus deciding who is a nest mate and who should be attacked.

Figure 10 – A worker bee guarding the nest entrance. Notice how the worker's front two legs are in the air and its mandibles are open. *Photograph by Mike Bentley.*

First orientation flight (about 17-27 days of age, mean age about 23 days old) – Orientation flights are common among workers who are about to begin a life as foragers. Essentially, workers transitioning to foraging will spend a great deal of time outside of the nest. Consequently, it is important for these workers to know where the nest is located. They do this by leaving the nest and taking short flights to determine where their nest is in relation to the surrounding landmarks (Figure 11). The latter could be trees, bushes, etc. Orientation flights tend to occur on warm, windless, sunny afternoons with the flights lasting about 5 minutes, lengthening in duration and distance from the nest as the number of flights increases. Orienting workers may use these first few flights as opportunities to defecate.

Figure 11 – Worker bees on their orientation flight. *Photograph by Mike Bentley.*

First foraging flight (about 18-28 days of age, mean age about 24 days old) – Worker bees begin to forage when they are about 3 weeks old. This is the task that the worker bee will die doing. Workers leave the nest to collect water (to cool the nest – Figure 12), pollen (to eat – see Figure 6), nectar (to convert to honey and use as fuel – Figure 13), and plant resins (for propolis). The average worker bee forages only about 4-5 days before dying. They take multiple foraging trips per day and usually die after flying around 500 total miles.

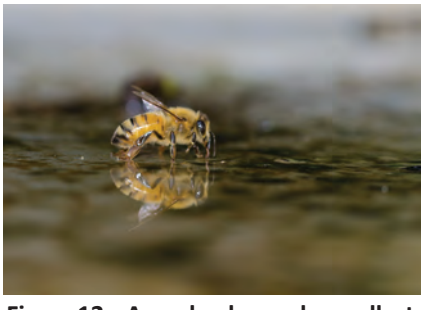

Figure 12 – A worker honey bee collecting water. Notice her reflection in the water. *Photograph by Mike Bentley.*

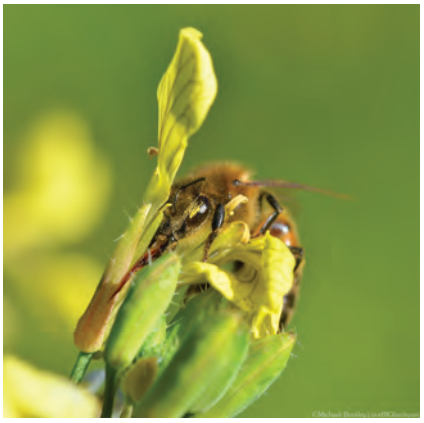

Figure 13 – A worker bee collecting nectar from a flower. *Photograph by Mike Bentley.*

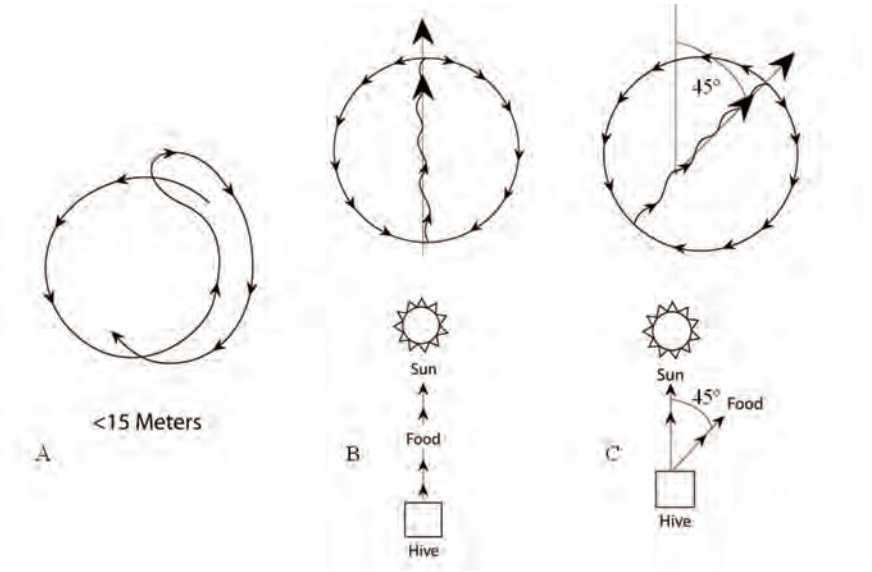

Figure 15 - The dance language of the honey bee. A – The round dance communicates the food resources are <50 feet from the nest. The figure 8 or "waggle" dance communicates food sources >300 feet from the nest. B - When the returning forager bee dances a straight run point up on the face of the comb, the food source is in the direction of the sun. C – When the returning forager bee dances 45º to the right of up on the face of the comb, the food source is 45º to the right of the sun. Drawing by Kay Weigel, University of Florida. Published in Ellis, J.D., Atkinson, E.B., Graham, J.G. 2014. Honey bee biology. In: W. Ritter (ed) Bee Health and Veterinarians. OIE World Organization for Animal Health, Paris, France. pp. 15-28.

OTHER TASKS PERFORMED BY WORKERS

Workers display a host of other behaviors, behaviors that are not as time dependent as those discussed already. A non-exhaustive list of these behaviors follows.

Bearding – Worker bees often coalesce on the outside of a colony in mid-to-late afternoon and early evening. If enough workers do this, large clusters of bees can be seen around the hive entrance (Figure 14). This cluster of bees can grow from the entrance toward the ground. This phenomenon is called "bearding" because it looks like a beard of bees growing on the face of the colony. This behavior does not indicate any problem with the colony. In fact, it is quite normal. It happens most during summer evenings when it is hot outside, thus causing many workers to vacate the nest and cluster outside rather than risk overheating the brood.

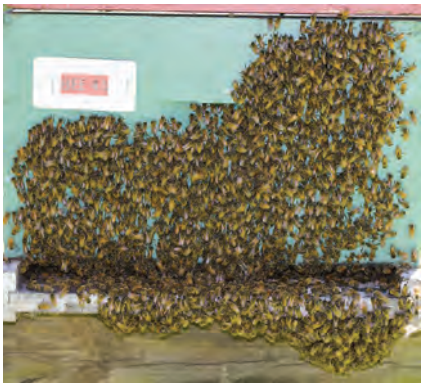

Figure 14 – A colony with a small bee beard. Bee beards can get much larger, with considerably more workers contributing to the formation of the beard. *Photograph by Mike Bentley.*

Dancing – Probably the most famous behavior exhibited by worker bees is the dance language they employ to communicate information to other workers concerning the location/quality of foodstuffs/possible nesting sites. There are three basic dances: (1) the round dance (communicates that food is within about 50 feet from the nest – Figure 15), (2) the transition dance (communicates that food is between 50 and 300 feet from the nest) and (3) the waggle or figure 8 dance (communicates that food is over 300 feet from the nest – Figure 15).

Defensive response – All worker bees possess the ability to sting nest intruders

Figure 16 – A worker honey bee stinging the photographer. *Photograph by Mike Bentley.*

Figure 17 – Workers fighting on the face of a comb. One worker is trying to fly away while another worker grasps its leg. *Photograph by Mike Bentley.*

(Figure 16). Bees respond to nest invasion and disturbances by releasing alarm pheromone. Older bees tend to be more sensitive to alarm pheromone than are younger bees. Thus, they tend to respond in greater numbers than do young bees. Bees often attack other bees when they determine them not to be members of the colony (Figure 17)

Grooming behavior – Bees lick, comb (with their legs), and otherwise groom themselves and their sisters, brothers and queen throughout the day as needed. Grooming helps remove debris and/or pests from the groomed bee's body.

Laying workers – Workers inhabiting colonies that have gone hopelessly queenless can begin to lay eggs. They can do this even though they cannot mate. Beekeepers call these workers *laying workers*. Given that workers cannot mate, they only can lay unfertilized eggs. The simple application from this is that workers can produce only drone offspring. Though workers can lay many eggs, and usually more than one egg per cell, colonies headed by laying workers are doomed since no worker bees are being produced (except for *capensis*).

Patrolling – Workers walk around the nest, looking for tasks that can be done.

Resting – At any given time, many workers in the nest simply are resting (Figure 18). Resting bees remain motionless on the combs for some time.

Robbing - During certain times of the year, colonies are prone to being robbed by workers from other colonies. Workers exhibiting this behavior are called robbers. Robber bees can be seen trying to get into the hive through cracks between the supers, under

Figure 18 – A resting worker bee. *Photograph by Mike Bentley.*

the lid, in the hive entrance, etc. (Figure 19). This behavior appears quite costly to the robbing worker as she often loses all of her hair, develops tattered wings, etc. Regardless, it must be worth doing given how common the behavior is and how it can escalate quickly during periods of nectar dearth.

Figure 19 – Worker honey bees robbing the sugar water from a hive top feeder. *Photograph by Mike Bentley.*

Thermoregulation – Most adult worker bees contribute to nest thermoregulation during winter. Temperatures in the low 60's and below cause the worker bees in a colony to cluster to keep warm. This behavior is exhibited mostly in fall and winter.

Trophallaxis – This is feeding behavior between two adult bees. A hungry bee (receiver) approaches a bee containing food (donor) and requests some of the food by antennating (rubbing antennae) with the donor bees. This causes the donor bee to regurgitate a droplet of honey that the receiver bee consumes (Figure 20).

Figure 20 – Two worker honey bees engaged in trophallaxis. The bee on the right is the receiver (hungry) bee, this being evident because of her extended tongue to suck honey from the donor bee's (left) mouth. *Photograph by Mike Bentley.*

In this month's article, I briefly described the many tasks that worker bees perform and behaviors that they exhibit over their 3-6 week life. The behavioral repertoire of worker bees is remarkably diverse and absolutely essential to colony survival. Worker honey bees are altruistic in the purest sense – they do what helps the colony and put the colony's needs over those of their own. I hope you have enjoyed this brief overview of worker bee behavior and that you have a deeper appreciation of the bee that was starved into a life of servitude; after all, with just a little bit more and different food, they could have been queens.

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