

QUEEN ESSENTIALS

*'The colony's nerve center doesn't control egg laying, swarming or other behaviors.
But without her, there is no colony*

Larry Connor

Egg Laying by the queen bee

The exact number of eggs a queen lays each day is difficult to quantify, but we can put together numbers that will start our discussion. Most references suggest that during the active brood rearing season (roughly a four-five month period from February through June, depending upon where you are in North America), a queen lays between 1,200 and 1,500 eggs per day, as based on the amount of brood present in a colony.

If a single queen is laying 1,500 eggs per day for 21 days – the length of development of worker bees – there should be 1,500 divided by 25 cells per square inch, or 60 square inches of eggs each day. When we multiply 60 square inches by 21 days we get 1260 square inches of brood in the colony.

A standard deep Langstroth frame holds foundation measuring roughly 17 x 9 inches or a bit more than 150 square inches of brood per side, or about 300 square inches per frame. When we divide 1260 square inches of brood by 300 square inches per frame, the result is that there are a little more than four frames of brood produced in this colony.

Experienced beekeepers know that it's a rare queen that fills *every* cell in a comb with eggs, so the 1260 square inches of brood may be present on six to nine frames in a colony. For example, if the colony leaves a one-inch border around the brood, the brood area would be reduced to 15 x 7 inches, or 105 square inches/side for x two sides, or 210 square inches of brood on one frame. Dividing that into 1560, we get 7.5 frames of brood. This more realistically reflects what you might see in a 'normal' colony.

My point is this: a vigorous queen laying 1,500 eggs per day will generate brood on six to nine frames yielding about 31,500 bees emerging over the next 21 days. The weight of these bees, at 3,500 bees per pound (average) gives us nine pounds of bees produced in 21 days.

Number of bees in a hive

If we project these numbers forward, we can predict the number of bees in a colony. Conveniently for us in our computations, some scientists estimate that worker bees live about six weeks post emergence,¹ pro-

viding an adult population of about 31,500 bees x two brood cycles, or 63,000 worker bees in a colony. That is 18 pounds of bees – the equivalent of six three-pound packages of bees in one hive. This is an impressive number of bees to observe.

There are reports of colonies where queens produce 3,000 eggs per day over an extended period. If true, this would provide a colony of 126,000 worker bees, with a weight of 36 pounds, with a brood area covering 12 to 18 frames, depending on brood pattern. This is impossible, right?

Not if there are two queens in one colony. I have routinely seen two queens during the Spring build-up period, when 10 to 20 percent of all the overwintered colonies I inspected held multiple queens.² In almost all cases, these were mother and daughter queens laying eggs in the same hive, and sometimes on the same side of the same comb. Did they ignore the memo about queens fighting to the death? Didn't they watch the special on the Nature Channel? Or did they simply agree to forego unpleasantness and decide to set examples for mothers and daughters everywhere?

Worker bees and queens continue to exist without replacement queen production until the queen is producing about half the number of eggs she did as a matter of routine. Even after such a dramatic decline in brood rearing, the old queen is allowed to exist in the colony for as long as possible. The workers may desire to produce more reproductive bees from their mother's eggs for as long as possible, and do not kill her, rather than use eggs from their mother's replacement queen. This is one aspect to a genetic advantage to keeping the old queen around.

There is also a second very strong evolutionary advantage allowing the old queen to continue to live and laying eggs at a reduced rate. In an effort to produce a huge population of bees to generate multiple large swarms from the parent hive, keeping two queens helps insure survival of the 'daughter' swarms. This is maternal sexual reproduction at a different level: rather than reproduction of the individual queen, we are concerned with the biological process involved in reproducing an entire colony. The simple natural reality is

¹ I think that six weeks must be a seasonal average, because during the rapid build-up period of the season and during periods of intensive forage, the adult life of the bee lasts only three or four weeks. Of course, during the winter months, worker bees live from September to February or March; it is brood rearing which depletes their food reserves and causes aging. All parents raising children know this.

² I learned this the hard way when I was trying to raise queen cells. It was quite easy to open a colony, find a queen, remove her, and assume the colony was queenless for cell producing reasons. When all the cells were destroyed by the remaining queen I went searching and found the second queen. Some stocks tolerate mother-daughter queens, and these are sometimes called "Supercedure" strains. A Supercedure strain was selected in England some years ago, but I am not aware of such a stock in North America.

this: the largest and earliest swarms enjoy the highest rate of building a colony, having success in overwintering, and reaching their first birthday alive. The opposite is just as instructive: late and small swarms suffer the highest failure rate of all swarms.

Nest Size, Colony Expansion & Colony Survival

Bee nests in hollow trees are between 15 to 80 liters (one liter = 1.0567 liquid quart) in volume, anything smaller would not be large enough to hold the stored honey needed (about 15 kg) to survive the Winter.³ A contemporary single deep hive body contains about 42 liters and a double deep hive body contains 84 liters. Thus beekeeper-managed colonies are almost always in boxes similar to the largest nest volume found in nature.

During Winter, New Haven, Connecticut based colonies lost between 20 and 26 kg in weight, most of which was due to the consumption of stored pollen and honey. This agrees with beekeeper practices of leaving a minimum 60 pounds (27 kg) (a deep hive body) of stored honey in the hive for Winter stores.

Such colonies experience a very rapid buildup in the Spring, with colony mass (weight) – as expressed as brood, bees, stored honey and stored pollen – rapidly increasing from about 15 to 20 kg in April to 65 to 75 kg in July. During this time the colony may swarm once or even twice. Any further swarming may result in too much of a decline in the colony's population and reserves, making it less likely to survive the Winter.

Swarms vary in size, but the average prime swarm is about 16,000 worker bees, the mother queen or several daughter queens, and a few drones (the drones produced during swarming season visit drone congregation areas, and do not need to travel with the swarm). In seven colonies monitored by Winston, prime swarms ranged from 11,676 to 21,818 bees while 1st afterswarms ranged from 6,091 to 14,625 bees. Two colonies produced 2nd afterswarms that were 3,765 and 4,086 bees, and one colony produced a 3rd afterswarm of 4,296 bees. It does not take much imagination or beekeeping experience to know that the 3rd afterswarm has a much reduced chance of survival. That is why I recommend to beekeepers that they add such small swarms to colo-

nies that will benefit from additional bees.

This brings us back to the first part of this article, about egg-laying rates. At 1,500 eggs per day, a loss of 16,000 worker bees represents a little over half of one brood cycle's worth of worker bees. When you consider that half the colonies issued a second swarm (1st afterswarm), some of which were nearly as large as the first, then you realize that swarming represents about a month's worth of labor and resources invested by the bees during the critical three-month buildup period, so important is this reproductive swarming. For beekeepers, it represents a month or more effort by the bees lost in terms of buildup, pollination services, and honey production. Remember that during swarming, foraging slows, and more bees are 'hanging out' in the hive. Also, keep in mind that this is not a lost month out of the 12-month calendar, but one month lost out of three months of the very critical buildup period in the annual cycle of the hive.

Before I move on, I don't mean to suggest that many

natural colonies reach the 3,000 eggs-per-day yield of 126,000 bees (36 pounds). I just don't see this happening. Beekeepers can come close by using a two-queen system of management, a highly desirable management system I hope to discuss in a later article.

Who's in Charge?

We often speak glibly that "the queen did this, the queen did that" but when we do we are not accurately



describing what is actually happening. The queen does what she is allowed, encouraged, and stimulated to do by the worker bees from the moment they determine – when the future queen is a tiny larva – that she will become a queen rather than a worker bee. The workers also control her confinement to a cell at emergence, keep her separated from other new queens during swarming, and make sure she's 'kept around' by genetically loyal daughters who tolerate a 50% drop in egg laying to keep "mom" in the hive. During the day-to-day life in a hive, workers control the rate of the queens feeding and the number of queen cells prepared for her to lay into, thus determining the rate of egg laying of the queen. This is why stock evaluation tests should allow for the replacement of old bees when a queen is introduced into a colony. Not only do you need to evaluate the queen, but you must also evaluate all behaviors of the worker bees she produces!

Just about the only independent act where workers do not assist the queen is in mating itself: that is solely the business of the virgin queen and the hundred or more drones chasing her in a drone congregation area. She mates drone after drone, sending them falling to the ground paralyzed and unable to fly, their reproductive guts spilled out of their abdomens. The

³ Seeley, Thomas D., 1985. Honeybee Ecology, A study of adaptation in social life. Princeton University Press. Out of print, but available as a Print on Demand text via Amazon.com. Many of the additional facts about bee nests, swarming and related issues are from this very useful reference.

next drone mounts the queen in the air and pushes aside the endophallis of his predecessor. When she returns to the hive she's carrying the last drone's endophallis (the mating sign) in her reproductive tract. Immediately the worker bees attend to her, removing the male remains, and massaging her body to help the sperm migrate into her spermatheca.

Queen Development

As I just mentioned, worker bees decide which young larvae will become

queens, and there is competition between workers with different drone fathers as to which larvae are selected and which queen cells will be finished. Queens also lay into the queen cups during swarming season.

Since queens develop from fertilized eggs identical to the worker bees, all worker and queen eggs hatch in three days. For five days the queen larva is fed food produced by the worker bees known as royal jelly, which they provide in surplus for the last-stage larva. Then the cell is sealed by the workers and the queen larva spins a cocoon inside and undergoes her complex metamorphosis to an adult queen. She emerges from the cell seven days later.

When sexually mature, about 10 to 12 days after emergence, the queen leaves the colony to mate with drones from many colonies found in drone congregation areas. On average, she receives about 85 million sperm during mating. There may be one or more mating flights, and she mates with upwards to 20 drones. When she returns to the hive, her median oviduct is filled with all these sperm, and she rests on the comb and moves her body in such a way as to encourage sperm migration. Worker bees also massage her body during this period.

The final result is that between five and eight million sperm enter the spermatheca. The rest of the sperm are expelled from the queen's body as thin, brown strands of dry semen. Worker bees help remove this material. If the queen is unable to remove the sperm from the median oviduct, the queen will not be able to lay eggs properly. This sometimes happens in natural mating, but is a tremendous concern in the instrumental insemination process. If the sperm do not migrate to the spermatheca within 24 to 48 hours, there will be a mass of sperm that blocks eggs from passing through the median oviduct; this sometimes results in the queen's death.

Inside the queen's abdomen we find a pair of ovaries, each holding about 360 ovarioles, or egg tubes. They are joined by the lateral oviducts connecting to the median common oviduct (where the sperm are tem-



porarily stored during mating). The vaginal orifice enlarges to form a vaginal chamber which has a finger-like, ribbed structure called the vaginal valvifold. The

valvifold opens and closes passage to the oviduct by muscle action. This valvifold makes instrumental insemination difficult, since it must be moved out of the way in order for the syringe to enter the median oviduct, before sperm may be released. If the queen is

not open, the semen will leak out into the sting chamber; none of the spermatozoa will enter the spermatheca.

The spermatheca holds about one microliter of fluid, and is connected to the oviduct by the spermathecal duct. This duct has muscles attached to it and is involved in pumping sperm into the spermatheca after mating, and releasing sperm during egg-laying.

The spermathecal gland is attached to the spermathecal duct; it covers the spermatheca like a wig. This gland secretes and activates substances that contain nutrients to waken the sperm after their long rest in the spermatheca. The median oviduct is 0.33 mm in diameter, and eggs are 0.39 - 0.42 mm in diameter. This means that the egg must be compressed, squeezed out of shape, as it passes through this structure. Sperm stored in the queen will remain alive for many years, at least five years in the literature. And, since queens do not mate again this is understood to be the longest period of sperm storage reported in any animal. And yet we poorly understand the mechanism of storage: what nutrient solutions are being provided to the sperm to keep them in a state of suspension?

Queen Chemicals

Chemicals associated with queens include hormones that are present in - and regulate - her body, and pheromones produced by her body that influence other bees. There is a rapid increase of the hormone vitellogenin in the blood of a queen as she starts to lay eggs. We know that a newly-emerged queen has a very low level, about seven micrograms, of 9-O-decenoic acid (a primary component of queen substance), while a 10 day old queen will produce about 133 micrograms of the pheromone. In a future article I will review our knowledge of queen chemicals. **BC**

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