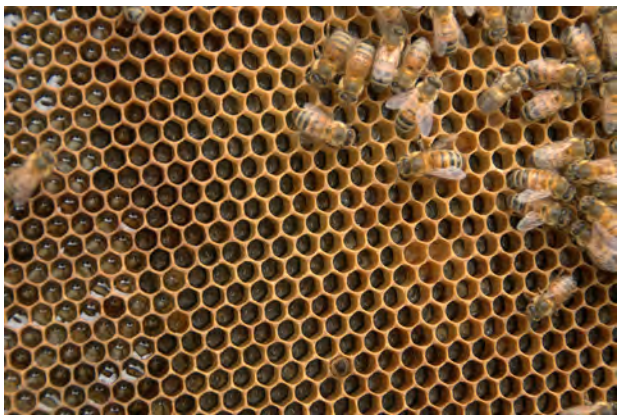
Calculus of Bees

There's a calculus of bees in the springtime hive. It's a dynamic that escapes notice because of the unobtrusive way in which individual bees die and are removed from the colony and because the foragers that are continually recruited to replace their fallen sisters look pretty much the same to the human eye **–** we just don't notice what's going on.

As biologists learn, mathematical descriptions of life processes can be *approximated* using simple algebra, but to convey the crisp reality of the *constant changes that occur in living systems*, the equations of differential calculus are required. Of course, engineers are the only ones not frightened at once by the terms *differential equation* and *calculus*. For the rest of us, it's like green kryptonite to Superman**:** we become weak and confused. No need for that, however. It's the simple problem of a tank being filled at a certain rate with *marbles of one color* while *marbles of another color* leak out at a different rate. How quickly does the content of the tank change **…** that is, what is the *turnover*?

That's the case in the spring and summer hive of honeybees. If we could see it, we would be astounded that *only one* of the vast colony (perhaps 30,000 bees) working the comb and filling the air in late April would be there in late June (colony of 40,000+ by then) **…** only the queen **–** all the rest outworn, gone, replaced. It's a story of perpetual youth, the cruel beauty of the mortal state of being.


One simplification of the life of the bee is this: 3 weeks to develop from an egg to an adult bee, 3 weeks to work the hive, 3 weeks to forage the fields.

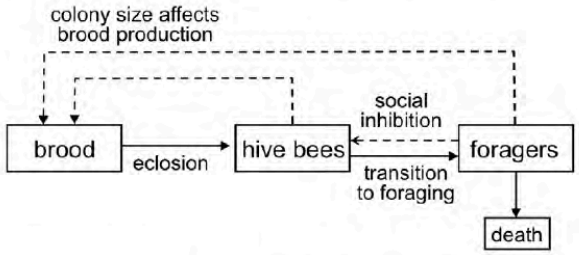


Figure 1. Elements of honey bee social dynamics considered by our model. Eggs laid by the queen are reared as brood that eclose three weeks later as adult bees. Adult bees work in the hive initially before becoming foragers. Our model considers the death rate of adult bees within the hive to be negligible, but forager death rate is a parameter varied in our simulations. We assume the amount of brood reared is influenced by the size of the colony (number of hive and forager bees) and that the rate at which bees transition from hive bees to forager bees is influenced by the number of foragers to represent the effect of social inhibition.

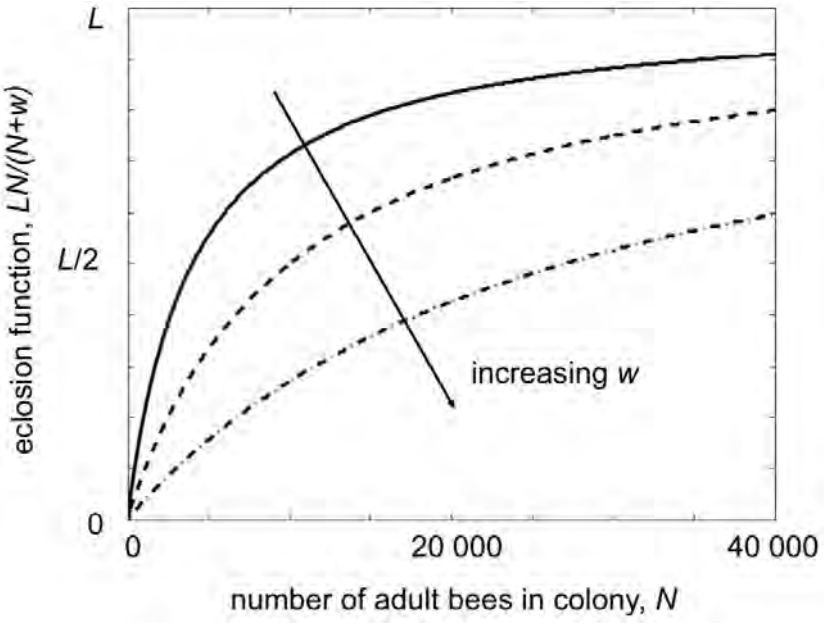
Here's the mathematical analysis**:** Let the rate of honeybee death in the springtime colony be represented by **m** and the rate of egg laying be represented by **L**. [For simplicity, we'll assume that all eggs laid by the queen hatch (after 3 days), feed as larvae (for 6 days), pupate as sealed brood (for 12 days), and then emerge as adults bees, joining the foraging workforce some days later. We will not consider here the small losses that inevitably occur along the pathway of development.]

Let **H** be the number of inside-the-hive workers
Let **F** be the number of foragers.
So, **N = H + F** is the total number of bees in the colony.
Let **L** be egg-laying *rate* of the queen
Let **R** be the *rate* at which bees are recruited to the forager ranks
E is a *function* that increases in proportion to **L** (and is influenced by **N** and by a variable, **w**) : **E = (L)(N) / (N + w)**

[Note that the "***d***" in the equations below simply stands for "*delta*", meaning "*change*", and "***t***" means "*time*". That's all that's going on with these math terms.]

Then, **dH/dt = E - HR** … that is, the **rate of increase in inside-the-hive workers** (**H**) equals **E** *minus* the number of inside-the-hive workers *times* their rate of recruitment to become foragers.

… and **dF/dt = HR – mF** … that is, the **rate of increase in foraging bees** *equals* the number of hive bees *times* the rate of recruitment of hive bees to become foragers *minus* the death *rate* of foragers *times* the number of foragers [note that the death rate of inside-the-hive workers is negligible and assumed to be zero]



(“eclosion function” is **E**)

Here are a couple of references for those who want more**:**

1) http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0018491

2) http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0059084

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