

STUDENT VERSION

INSECT COLONY SURVIVAL OPTIMIZATION

STATEMENT

We model insect colony propagation or survival from nature using differential equations. We ask you to analyze and report on what is going on and develop an optimal strategy for success of a natural phenomena.

Your responses are to contain traditional elements of good reporting, complete statement of the problem - copied from the problem or reformulated in your own words, your analysis and results, and discussion of issues relevant to the analyses and results.

In considering the life cycle of colonies of insects it is believed that the colony appears to maximize the number of reproducer insects at the end of its season. This enables the colony to spread its genes and thus propagate its own kind in an optimal fashion. But how does the colony do this? One could consider different models for hibernating (e.g., wasp) and non-hibernating (e.g., honey bees) insects. The non-hibernating case is more complex due to the need to build up substantial resources and hives to survive the winter.

We consider an energy model for the colony in which we discuss two kinds of insects in the colony, workers and reproducers (or queens).

Let $W(t)$ be the number of worker insects in the colony at time t (usually measuring days into the season) and let $Q(t)$ be the number of reproducer insects or queens in the colony at time t . We will not presume any age-class distinctions.

A proposed model [1] for rates of growth of each species is (can we defend/explain this model?):

$$\begin{aligned}\frac{dW(t)}{dt} &= b * u(t) * R(t) * W(t) - \mu * W(t) \\ \frac{dQ(t)}{dt} &= b * c * (1 - u(t)) * R(t) * W(t) - \nu * Q(t)\end{aligned}\tag{1}$$

Here we start with $W(0) = 1$ and $Q(0) = 0$ as we are counting the founding queen as a worker, since she forages to feed the first brood.

Another possible population to consider is drones. One needs them to fertilize the queens and they typically come from other hives. A good hive during the mating season may have 1-10 percent drones that gather daily in clouds that queens seek out to be fertilized. Queens mate with 5-20 drones and each drone dies after mating. Unfortunately drones do nothing else but eat honey. They don't gather resources, defend, make wax, take care of brood, etc. Typically, all the drones are chased out of the hive at the end of the season. In (1) we do not consider drones.

- $R(t)$ is the return function (per unit member of the colony) which stands for the resource abundance and the foraging capability of the colony at time t . Resource abundance is very important for honey bees and is not a constant at all. So this is a first approximation. This may be a measure of the floral diversity in the case of a colony of bees. Often it can be assumed to be constant, but the models are quite robust and apply when $R(t)$ is more reflective of broader changes in the ecosystem.
- $-\mu W(t)$ is an exponential decay term which says, in the absence of any energy input ($R(t)$) the worker population will die off.
- $u(t)$ is that utilization percentage (between 0 and 1) which the colony applies to worker production. Turning to the equation for $Q(t)$ we see that $(1 - u(t))$ then represents that portion (between 0 and 1) of the resource which the colony applies to reproducer or queen production.
- b stands for a biomass conversion factor - i.e. from the resource energy, how much actually becomes worker insects per unit time.
- c stands for a differential conversion factor, i.e. if $c > 1$ it takes more energy to produce a reproducer insect than to produce a worker insect. If $c = 1$ energy needed to produce worker and reproducer are the same. Often this latter case is assumed. While it does take more energy to make a queen, e.g., more wax for the cell (larger) and more royal jelly (probably twice as much) for a queen is larger - as much as twice as large as a worker insect. But the energy is not a lot in either case.
- $-\nu Q(t)$ represents exponential decay of the reproducer population in the absence of any further energy inputs. NB: For honey bees the reproducer population is basically 1 or 2. They do produce several queens at the same time (2 to 8 about) when they get ready to swarm. But the Queens "fight" and only one survives. It is not known why they do this but it is believed that it is to manage risk for they must have one (but not more) survive or the hive will die. This is because the mother of these queens typically took off in a swarm a week or so before this event. Hence you have 2 surviving queens - one home and one gone to start a new hive. This can repeat several times in a season so there might be up to 4 surviving queens (3 swarms) at season end.

Another factor is honey inventory. When there is a lot then the bees begin to change behavior. They get ready for a swarm and raise more bees. So maybe one could also include an "Inventory" of resources that is added to with available resources from outside the colony. Perhaps there is an

inventory threshold above which behavior changes. One other factor is that a swarm needs enough bees and honey to take with them to start a successful new colony and leave behind enough bees (and brood) to be viable. A rough estimate is 50% of the bees go in a swarm and good colony size before a swarm is about 50,000 bees. There is a LOT of variation here.

Now the question is this,

“What $u(t)$ should the colony use so that the number of reproducers, $Q(T)$, at season’s end (when $t = T$) is maximum?”

Determining this function $u(t)$ is in the province of a discipline known as *optimal control theory*. This is one of a class of problems which seeks to find the value of T so that some functional value, in this case $Q(T)$, is optimized subject to some dynamic system, in this case differential equations (1) with initial conditions.

Consider these values of the parameters, $b = 0.0013$, $c = 1$, $\mu = 0.022$, $\nu = 0.005$, $T = 205$ - days, and $R(t) = 50$. Recall $u(t)$ is a function (in this case, called an *admissible control function*, actually) that is between 0 and 1, where $u(t) = 0$, means at time t the colony puts 0% of its energies into worker production; $u(t) = 1$, means at time t the colony puts 100% of its energies into worker production; and, for example, $u(140) = 0.31$, means at time $t = 140$ the colony puts 31% of its energies into worker production.

1. Model - try outs!

For each model below, i.e. $u(t) = u_1(t)$, $u(t) = u_2(t)$, and $u(t) = u_3(t)$:

- a) plot $u(t)$ in the time interval $[0, 205]$;
- b) describe what the colony is doing;
- c) compute the number of Queen insects at the end of the season, i.e. $Q(205)$; and
- d) plot both $Q(t)$ and $W(t)$ in the time interval $[0, 205]$ - with variables identified.

$$u_1(t) = 0.5 + 0.5 \sin\left(\frac{\pi}{205}t\right)$$

$$u_2(t) = \frac{1}{205}t$$

$$u_3(t) = 1 - \frac{1}{205}t$$

2. Now pick one **strategy of your own** - different in form and substance from those offered in (1) - and model it with a function $u(t)$. Proceed to analyze it in the same manner as (a) - (d) in (1) above. Explain what you were trying to model in your selection of $u(t)$.
3. **Bang-Bang Solution** Quite often the optimal solution for $u(t)$ is called a Bang-Bang Theory, because $u(t)$ is all or nothing, (on or off) in this case 1 or 0, respectively.

There is a switching that occurs from not raising any queens to raising a few queens. However, there are way too many bees to have them devote all their energy to raising queens. You

only need a few bees to raise queens, say 5 to 100 out of 50,000. It is probably driven by the rate a worker can produce royal jelly and how much a queen needs. The remainder of the bees deal with gathering more nectar, making wax cells, fending off intruders, gathering pollen, cleaning out the hive, etc. Thus another model might consider that there are two levels of $u(t)$: low ($u(t) = 0$) and high ($u(t) \approx 0.0001 * W(t)$). It may be that the energy to make a queen is not a big issue. It is more about number of bees, honey inventory, brood inventory, natural resource levels, season (you need lots of drones out there from other hives), temperature, etc. Now can we determine an optimal switching time t_s when the colony should go from producing all worker insects ($u(t) = 1$ for $t < t_s$, so $u(t) = 1 - \text{UnitStep}[t - t_s]$) to producing all reproducers (queens) ($u(t) = 0$ for $t > t_s$)?

- a) Show what the curve of $Q(T = 205)$ vs. t_s looks like, i.e. try out a number of switching times, t_s in the time interval $[0, 205]$ (over a broad range and over a narrow range about your optimal value, collect the resulting $(t_s, Q(205))$ data points into a set, `data`, and plot these points to see what an optimal switching time might be.
 - b) Using the colony's optimal switching time you have discovered in (3), show how this compares to all the results from the Model - try outs! section above and your own strategy in (2).
4. Explore the effect on our optimization strategy from (3) if we change our c value - recall what the significance of c is - see above. For instance, suppose we alter our problem from $c = 1$ to, say, $c = 2$, or $c = \frac{1}{2}$ (be sure to explain what each of these means in terms of the colony and the model) then what effect do such changes have on our optimal switching time?
 5. Explore the effect on our optimization strategy from (3) if we change our $R(t)$ function to more closely model the availability of resources as modeled by the seasonal (in this case 205 days from early spring to late fall) return function. Propose a function for $R(t)$ which is different from $R(t) = 50$ which you believe might be one seasonal resources model. Then compare your model results with those of (3). Explain any differences or similarities.
 6. Some species (e.g., bees) are known to swarm or get up and leave the hive, as the reproducers start new colonies in the middle of the season. Model this behavior with the parameters, $b = 0.0013, c = 1, \mu = 0.022, \nu = 0.005, T = 205$ - days, and $R(t) = 50$. Then compare this with your results (i.e. number of reproducers available at end of the season) in your optimal switching time discovered in the bang-bang Solution section above. Make any additional assumptions you need.

REFERENCES

- [1] Macevicz, S. and G. Oster. 1976. Modeling Social Insect Populations II: Optimal Reproductive Strategies in Annual Eusocial Insect Colonies. *Behavioral Ecology and Sociobiology*. 1: 265-282.