# 2022 HiMCM
# Problem A: The Need for Bees (and not just for honey)

Team 12855

## SUMMARY

The shocking synergy of climate change and commercial pesticide use over the past few decades has hastened the phenomena of Colony Collapse Disorder: a widespread decimation of honeybee populations. Honeybees are one of the most prolific pollinators around the world, responsible for plant biodiversity and fertility in necessary crops and vegetation. Thus, it is imperative to effectively model the growth of a honeybee hive so as to better counter Colony Collapse Disorder, understand the ability of honeybees to sustain given areas of arable land, and predict which factors most adversely impact honeybee populations.

We develop and present a discrete-time model of a healthy honeybee hive, taking advantage of the highly seasonal population fluctuations that wild hive populations experience. Orienting our model around temperature fluctuations that are detrimental to a healthy hive, we observe that the growth and prosperity of the hive's surrounding flora is first to be impacted. We thus focus on modeling *both* the complex interactions within the hive and the hive's wildly interdependent dynamics with the surrounding environment. Forecasting how both plant and bee populations fluctuate, we aim to understand the fascinating relationship between plants and honeybee pollination. We make use of additional normalization and probability functions to ensure reliability in real-world applications. We find that 16 healthy hives can sustain a 20-acre field of clover and we provide a generalized equation to predict for any land area and crop.

After defining our model of a healthy hive and its surrounding environment, we consider how changes to in-hive factors like birthrate and caste imbalance impact the population of the colony. Introducing *in-hive stressors*, *environmental stressors*, and performing a sensitivity analysis, we find that the base survival rates and the dependence of brood on nursing workers are highly detrimental to overall population growth; this is corroborated by our observation that pathogens and pesticides turn out to be the leading causes of colony collapse within our model— two factors that directly influence the brood's development and forager survival. Using our model, we test and present how various stressors commonly suspected to cause colony collapse disorder influence fluctuations in population. We find stress significantly hampers pollination, with 34 stressed hives being required to sustain a 20-acre clover field.

We present and implement our model as a simple Python framework for modeling the impact of various environmental and in-hive stressors on a colony's population. As we strive to elucidate the murky causes of colony collapse in honeybee populations, we hope our forecasting can be a valuable tool for beekeepers and scientists alike trying to address these pressing population threats. As more unexpected stressors appear in a rapidly changing world, our expandable and simple approach allows for robust prediction strategies that can address changes in hive health.

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# I Blog

Team 12855

## TELEGRAM

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Credit: UNC Greensboro

## Modeling Honeybee Populations & Colony Collapse Disorder

Far more than just a source of honey, bees are responsible for pollination and plant reproduction in a myriad of species. That's why a recent phenomena is worrying scientists: the bees are disappearing. Colony Collapse Disorder (CCD) refers to the global exodus of honeybees from their hives, resulting in population declines and agricultural turmoil. Luckily, Team 12855 has designed mathematical models of CCD and population dynamics of the hive, providing an invaluable tool for the future study of these important insects.

Our models are designed with three cases in mind: healthy hives, stressed hives, and hives that must sustain a given land area. We consider the cyclical nature of both seasonal temperatures and bee reproduction in order to track insects through the year. We found that survival of a healthy hive is impacted by forager survival outside the hive, and reproduction. Stressed hives are most adversely affected by pathogens and pesticides.

Considering a 20-acre area of clover, 16 healthy hives are required to sustain it. The model indicates food supply as the key factor affecting pollination ability. Considering stressors, additional hives are required to support areas of land, due to population decline. We identify pathogens and pesticides as markers of CCD. In the future, changes to pest control procedures could aid bee population recovery.

### Takeaways

1. Colony Collapse Disorder (CCD) accelerates decline of bee populations
2. Forager survival, brood development, and food supply impacts hive survival and pollination potential
3. Pathogens and pesticides are the strongest stressors of CCD
4. Changes to pest control strategies could improve survival rates of bee populations

Credit: Jacek Nowak / Alamy Stock Photo

# II INTRODUCTION

## 2.1 Problem Interpretation

Problem A describes modeling a honeybee hive and its ability to pollinate a given area of arable land. Mathematical and computational models of this nature are becoming increasingly valuable tools for population biologists and environmental conservators who have witnessed unprecedented disappearance of large swaths of honeybees. Dubbed "Colony Collapse Disorder," (abbreviated as CCD), this growing phenomena destabilizes growth cycles for numerous plants and has caused great concern as to the future of our most prolific pollinators.

To understand the longitudinal population dynamics of a hive, we demarcate the problem into three distinct modeling challenges: a healthy honeybee hive, a hive with *stressors* (which we define as factors impacting reproduction, pollination, and population), and the potential of bees to pollinate given land areas.

## 2.2 Goals

In order to best understand how different environmental factors can affect a hive, we begin by modeling a healthy hive in an optimal environment. This allows us to then introduce various environmental stressors, including malnutrition, extreme temperatures, mites, and pesticides, to quantify their effects on a healthy hive. To predict how many honeybee hives one would need to support the pollination of a 20-acre (81,000 square meters) parcel of land containing crops that benefit from pollination, we use the models of a healthy hive and stressed hive to predict honeybee populations—and by extension, the number of foragers needed to pollinate the land.

## 2.3 Initial Questions

We formally begin the modeling process through the consideration of questions we find imperative to constructing models (and ultimately solutions):

1. How do environmental stressors impact an otherwise healthy hive? How do in-hive factors and stressors impact a healthy hive?
2. What stressors contribute most heavily to population decline associated with Colony Collapse Disorder?
3. How do growth rates differ between castes of bees?
4. How do seasonal changes, *especially* with regard to temperature, affect hive populations?

# III BACKGROUND

The fascinatingly complex world of honeybees (*Apis mellifera*) is one that spans various ecological domains, from wide-ranging flora to the small-scale interactions between bees and a web of other environmental factors. Honeybees find themselves in a unique role and position in their environments: they are natural symbiotes with many plants in their area. And although honeybees do have a few natural predators, the main success and survival of honeybees lies in this mutually-beneficial relationship with plants. Being just as critical to the ecosystem as the ecosystem is to them, honeybees maintain complex societies that are designed to maximize efficiency within this unique and ecologically invaluable niche.

## 3.1 Plants

The most important resources to honeybees are plants— they are the honeybee's main source of food, and therefore, and survival. There is a plethora of different plant species that exist in regions inhabited by honeybees, ranging from prickly pears to cashews. While these plants differ in their physical structure and evolutionary history, they all tend to share a set of clear characteristics and behaviors that make them suitable for honeybees to pollinate and feed off of. Among these commonalities are small variations in their properties, such as growth rate or optimal temperature. While these different plant species share some behaviors, they differ in the ways they are expressed and developed.

***Nectar.*** Many plant species depend on the spread of pollen by pollinators like honeybees to reproduce. Producing both pollen and nectar at a mature age, plants begin attracting honeybees with the sweet nectar and allow the honeybee to collect pollen at the same time. Honeybees then go on to spread this pollen to other plants of the same species, fertilizing their flowers and producing genetically diverse offspring. Bees, on the other hand, depend on nectar as a primary ingredient in their food source. This leads to an extremely interdependent relationship between pollinating plants and honeybees.

***Growth and Reproduction.*** In order to properly model the honeybee population, it is vital to understand how the growth patterns of their food sources affects their population. Different plant species experience varying patterns of growth and reproduction, accounting for the time it takes for the plant to flower (and thus produce nectar/pollen), the number of new plants created as a result of pollination, and the optimal growth temperature of the region.

## 3.2 Bees

The complex societies maintained within a colony of bees are organized primarily at the level of the *hive*— the central housing space of the colony, and their supply storage. Within the hive, bees are naturally delegated into castes based on their sex, age, and current hive dynamics. Each caste is responsible for certain specific tasks that they carry out until their death. Bees are not seen to interchange caste during adulthood [17]; once a bee attains a role, it keeps it forever. This makes the colony extremely interdependent and the success of the population entirely reliant on how efficiently each caste performs its tasks.

***Queen Bee.*** The Queen bee is the central caste of any hive. There is exactly one queen for any one hive and she is responsible for laying eggs for the entire colony. The queen does not leave the hive and instead mates with male drones, laying up to 2000 eggs in a single day [22].

***Forager Worker Bees.*** The caste of honeybee that is exclusively responsible for out-of-hive duties is the forager bee. This subclass of the worker bee is responsible for retrieving nectar, carrying and transporting pollen, and protecting the hive. Like all worker bees, foragers are female, have stingers, and typically dwindle in numbers when the hive must downsize (whether that be due to unexpected food shortages or other stressors). Foragers frequently wear out from the extreme metabolic stress that accompanies foraging vast distances and for long periods of time.

***Hive Worker Bees.*** Worker bees within the hive are female and are responsible for all of the critical duties that come with maintaining a large society. Specifically, they are responsible for nursing the young, maintaining the food supply, and protecting and caring for the queen and drones. Workers have also been seen to cannibalize other workers when the hive is at high population stress, in order to control the food supply and maintain enough space for the queen, drones, and eggs [21].

***Drone Bees.*** Drones are male bees that lack stingers and whose only job is to mate with the queen. They mate in groups of a couple dozen during the Queen's mating flights and do not directly fight for reproduction, but do compete for their chance. There is typically a relatively low number of drones in the hive at any given time.

***Eggs, Larvae, Pupae.*** Eggs, larvae, and pupae comprise the *brood*, a caste of bees in developmental stages. Eggs refer to unborn honeybees, larvae refer to immature honeybees yet to molt, and pupae refer to bees on the cusp of adulthood. Surviving members of the brood will eventually be promoted to other castes. The brood does not leave the hive.

## 3.3 Colony Collapse Disorder

Colony Collapse Disorder (CCD) occurs when over half of the worker bees in a hive disappear [12]. CCD can cause significant economic damages and devastating decreases in crop yield [12, 15]. With climate change resulting in more extreme weather patterns across the globe, the future of several agricultural sectors is uncertain. Removing significant populations of pollinators changes this uncertainty to profound instability. Especially in areas of the world lacking investments in advanced agricultural technology, CCD may cause significant decreases in food production. Research into the causes of CCD has leveraged statistical and mathematical methods, field data collection, and even assays assessing neurochemical impacts of pesticides on honeybees [1], but many past studies lack comprehensive tools for beekeepers and scientists to utilize for simulation—and crafting solutions to the causes of CCD. Although much about CCD remains a mystery, its cause can often be narrowed down to one of a few primary external stressors.

***Stressor 1: Pesticides.*** Many commercial beekeeping operations are mobile, which involve moving hives over vast geographic distances, exposing the colonies to a multitude of pesticides over the course of a season. This leads to an accumulation of pesticides in the hive, which can ultimately cause CCD [29].

***Stressor 2: Pathogens.*** Pathogens, which broadly include any organism that produces disease, are often to blame for CCD. Perhaps the most destructive pathogen is the Varroa mite. This deadly creature carries with it ailments such as deformed wing disease and acute bee paralysis virus, both of which are common culprits behind CCD [31].

***Stressor 3: Antibiotics and Miticides.*** Ironically, the antibiotics and Miticides beekeepers use to fight off pathogens might be the culprits behind some cases of CCD. Studies have shown that certain types of antibiotics and miticides are behind instances of CCD across the United States [10].

***Stressor 4: General Environmental Conditions.*** All other causes of CCD, known or unknown, may be grouped under General Environmental Conditions. These can include electromagnetic radiation and malnutrition [32].

## 3.4 Assumptions

We go on to outline the primary assumptions we employ for the development of our models.

| **Category** | **Assumptions** |
|---|---|
| Plants | **A.1** A plant takes $\mu$ days (see section 3.6) to reach maturity, at which point it can begin producing nectar and pollen, and can be pollinated. Once mature, a plant remains that way and always holds pollen and nectar.<br>**A.2** A plant that has nectar will always have pollen. The amount of pollen and nectar collected from a single plant does not change.<br>**A.3** The nectar collected from a plant is constant in quantity and is measured in "food" units ($\eta$ food per plant; see section 3.6)— a single serving size that a bee consumes in a day. All in-hive bees eat approximately the same amount per day. |
| General honeybee colony | **B.1** A bee's caste is determined at the point of egg formation. A bee cannot change its caste, but its tasks within the caste can (and frequently do) change.<br>**B.2** The hive cannot survive without a queen bee. If there is no queen, the hive will quickly die out. Similarly, if there are no drones remaining for the queen to mate with, colony collapse will ensue.<br>**B.3** The queen lays eggs at a constant rate, which we denote as $\beta$ (see section 3.6).<br>**B.4** The number of days between conception and adulthood for all castes is equal. We denote this value as $n$ (see section 3.6). |
| Forager Bees | **C.1** Forager bees do not travel farther than 6 km from the hive during a single foraging round-trip [3]. We assume a circular region around the hive that the foragers can reach.<br>**C.2** Forager bees travel in a uniformly random pattern around the surrounding crop. They visit plants completely randomly and on average visit a constant $\varphi$ plants (with a sufficiently large plant population). |

## 3.5 Variables

Prior to discussing and analyzing our models, we introduce a list of variables we refer to throughout.

| | |
|---|---|
| **Indices** | |
| $t$ | Index for the current day (i.e., $t$th day of hive) |
| $q$ | Index for queen bee |
| $f$ | Index for forager bee |
| $d$ | Index for drone bee |
| $w$ | Index for worker bee |
| $b$ | Index for brood (eggs, larvae, and pupae) |
| $\rho$ | Species of plant in region. We initially limit our model to one plant species. |
| **Populations** | |
| $P$ | Total number of honeybees in the hive. |
| $Q$ | Total number of queen bees in the hive. This number is always either 0 or 1. |
| $F$ | Total number of forager bees in the hive. |
| $D$ | Total number of drone bees in the hive. |
| $W$ | Total number of **in-hive** worker bees (not drones or foragers) |
| $B$ | Total number of brood in the hive (eggs, larvae, and pupae) |
| $\Delta_k^{(t)}$ | Number of bees demoted **from** caste $k$ at time $t$ |
| $p_k^{(t)}$ | Number of bees promoted **to** caste $k$ at time $t$ |
| **Environment** | |
| $\mathcal{P}_t$ | Total number of plants in the defined region at time $t$ |
| $\mathcal{P}_{pol}^{(t)}$ | Total number of plants in the region pollinated at time $t$ |
| $T$ | Ambient (environmental) temperature |
| **Hive** | |
| $\Phi_t$ | Total hive food supply on day $t$ |

## 3.6 Constants

In addition to the variables that fluctuate within our model, we hold a set of initial constants we adopt from real-life honeybee data and hyper-parameters that we tune in accordance with our model. We provide further sensitivity analysis in section 4.2.

| | |
|---|---|
| **Hyperparameters** | |
| $c_{temp}$ | Constant controlling relative impact of ambient temperature on the hive |
| $c_{food}$ | Constant controlling relative impact of food surplus/deficiency on the hive |
| $c_{forage}$ | Constant controlling relative impact of over/under working on foragers |
| $c_{nurse}$ | Constant controlling brood sensitivity to over/under-staffed nursing workers |
| $k$ | Constant controlling the plants' sensitivity to temperature deviations |
| **Constants** | |
| $T_{optimal}$ | Optimal operating ambient temperature of a beehive |
| $T_{optimal}^{(\rho)}$ | Optimal growth temperature of plant species $\rho$ |
| $\eta$ | Percentage of daily food collected by a single forager per visited plant |
| $\varphi$ | Average number of plants a forager visits in a day |
| $\beta$ | The egg laying rate of the queen |
| $\gamma$ | Number of new plants created per pollination of one plant |
| $n$ | Days spent as brood before adulthood |
| $\mu$ | Number of days a plant must mature before producing or taking pollen |

# IV MODELING THE HIVE

## 4.1 Isolated Hive-Crop Model

We first consider modeling a single hive in absence of external stressors and under a single crop region. In other words, we model the population of a hive with respect to time and for a region of finite crop availability. We additionally consider seasonal changes that may influence crop yield and thus change the foraging behaviors of the hive.

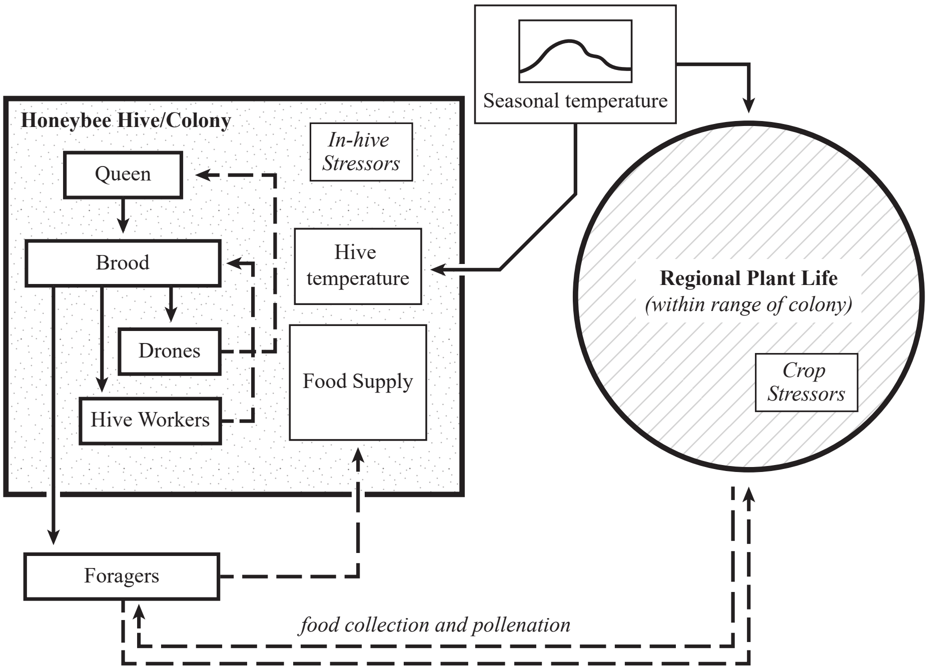

**Figure 1:** Overview of our honeybee colony model. We focus on isolating the behavior of the hive and environment towards understanding how environmental and in-hive stressors influence the population of an otherwise healthy hive.

***Goal and Structure.*** We base our model on the observation that the overall health of a honeybee hive is largely dependent on the surrounding temperature [20], which is seasonal. This temperature fluctuation controls much of the regional plant growth and thus keeps a population at a steady maximum in the summer months and at a low in the winter, when the bees have few plants to forage. Basing our model on this time-progression and seasonal temperature, we structure our analyses around a discrete-time model that aims to predict how the hive's different *castes* of honeybees fluctuate in population. We consider the interdependence of each caste and accordingly model how one their daily *survival rate* changes based on the health of the hive. We initially assume a fully healthy hive and go on to introduce stressors that may adversely affect the population of the hive. We outline an overview of our model in fig. 1.

***Population.*** We express the total population of the hive as the cumulative population of each caste and the brood

$$P = Q + F + D + W + B. \tag{4.1.1}$$

From one time-step (one day) to another, the relative population within each caste changes based on its current survival rate $s_{caste}^{(day)}$. For example, the total queen population that survives from day $t$

to day $t+1$ can be expressed by

$$Q_{t+1} = s_q^{(t)} Q_t.$$

More generally, we say for all caste populations $K \in \{Q, F, D, W, B\}$ and corresponding indices $k \in \{q, f, d, w, b\}$,

$$K_{t+1} = s_k^{(t)} K_t + p_k^{(t)} - \Delta_k^{(t)} \tag{4.1.2}$$

where $p_k^{(t)}$ indicates the number of bees *promoted* to caste $k$ at time $t$ and $\Delta_k^{(t)}$ indicates the number of bees *demoted* from the caste at that time. We explain the concepts of demotion and promotion in the following paragraphs.

***Caste demotion.*** The only caste that actively demotes bees from its population (loses bees due to non-fatal causes) is the brood. In other words, the only bees that lose caste are young bees that become adults. Thus, $\Delta_k$ is non-zero only for $k = b$ and we express this value more concretely as

$$\Delta_b^{(t)} = \beta \prod_{i=t-n}^{t-1} s_k^{(i)},$$

where $n$ is the number of days a bee spends as brood before reaching its adult caste and $\beta$ is the constant birthrate/egg laying rate, as outlined in assumption B.3.

***Caste promotion.*** Castes are able to gain new bees through *promotion*, whereby a brood grows old enough to perform hive duties and joins the caste. A brood's sex is determined at birth by the queen based on hive conditions and pheromones. As noted in assumption B.1, we assume this caste is decided at conception and will be delayed by $n$ days as the brood develops. We capture this relationship for caste $k$ as

$$p_k^{(t)} = r_k^{(t-n)} \Delta_b^{(t)} \tag{4.1.3}$$

where $r_k^{(t)}$ is the ratio of brood selected to promote to caste $k$. Note the $n$-day delay; it takes $n$ days since the queen's caste selection for the brood to become adults and go into their caste.

***Initial Survival Rate.*** Every caste of bee has its own respective daily survival rate $s_{caste}^{(day)}$ that is influenced by a slue of factors, not just limited to the relative danger of the caste's tasks. For our model, we consider a changing base-level survival rate $s_{caste}^{(0)}$ for the population of each caste as opposed to having a set life expectancy for each bee. This allows us to better model the natural fluctuations in population-level lifespan. In our sensitivity analysis we reference our initial (baseline) survival rates for each caste and the source of these data points.

***Survival rate.*** The survival rate of each caste is influenced by different factors, each having different levels of impact on the respective populations. For example, the amount of plants in the region will impact the survival of foragers differently than the queen and workers (who stay in the hive). We outline the specific factors we consider for each caste and how they influence the caste's daily survival rate in table 1.

***Dependence on Temperature.*** As noted previously, we extensively refer to the seasonal fluctuations in temperature that influence plant growth and overall hive health. In the winter seasons, the number of foragers decreases and in-hive workers remain huddled around the queen to keep her warm, steadily decreasing the population. During summer and peak flowering seasons there are more foragers in the wild gathering supplies to sustain the hive. We reflect these fluctuations in the castes' survival rates, as seen in table 1.

**Table 1:** Overview of how hive conditions influence the daily survival rates of the hive. We note that each caste's survival rate is governed by a weighted sum of factors that is normalized[1] according a normalization function $\phi_{s_k} : \mathbb{R} \to (0, 1)$ centered[2] on base-line survival rate $s_k$ (see section 4.2). We additionally use symmetric logarithmic scales when weighing certain factors and denote these with $\mathrm{symlog}(x)$.

| **Caste** | **Survival Rate ($s^{(t)}_{caste}$)** |
|---|---|
| **Queen** | The Queen bee's survival is dependent directly on its body temperature and the hive's food supply. She reproduces but doesn't forage and rarely leaves the hive, thus enjoying relative safety while under constant supervision.<br>$s_q^{(t)} = \phi_{s_q}\left(c_{food}(\Phi_t - \underbrace{(P_t - F_t)}_{\text{In-hive bees}}) + c_{temp}(T - T_{optimal})\right)$ |
| **Brood** | The brood's survival fully depends on the internal temperature of the hive, the amount of food available, and the number of workers able to nurse them to adulthood. They are not self-sufficient and must be raised in a healthy environment.<br>$s_b^{(t)} = \phi_{s_b}(c_{food}(\Phi_t - (P_t - F_t)) + c_{temp}(T - T_{optimal}) + c_{nurse} \cdot \mathrm{symlog}(W - B))$ |
| **Workers** | Workers in the hive depend on the overall hive temperature and the current food supply brought in by foragers. By nature of their slightly more intensive tasks, they may have a smaller baseline survival rate due to natural exhaustion.<br>$s_w^{(t)} = \phi_{s_w}(c_{temp}(T - T_{optimal}) + c_{food}(\Phi_t - (P_t - F_t)))$ |
| **Drones** | Drones, like workers, depend on the overall hive-health factors such as temperature and food supply. However, they have a naturally low survival rate as drones die immediately after mating.<br>$s_d^{(t)} = \phi_{s_d}(c_{temp}(T - T_{optimal}) + c_{food}(\Phi_t - P_t))$ |
| **Foragers** | Foragers have the most physically demanding jobs that depend on environmental temperature and the number of plants in the region they are able to visit; with more plants, foragers tend to die more frequently of exhaustion.<br>$s_f^{(t)} = \phi_{s_f}\left(c_{forage} \cdot \mathrm{symlog}\left(\frac{\mathcal{P}}{F} - \varphi\right) + c_{temp}(T - T_{optimal})\right)$ |

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[1] We describe our choice of normalization function in our sensitivity analysis.

[2] A normalization function is *centered* at a point $y$ if $\phi_y(0) = y$.

***Food supply.*** Up to this point, we have fully modelled the base survival capabilities of a single hive. What left is to include the influence of the environment and surrounding crops on the hive, which undeniably influence the food supply and the survival of forager bees. By assumption C.1, we consider a circular region of radius **6 km** (this is the maximal reachable environment by the colony's forager bee population). As foragers return, they bring back units of "food" (nectar) for the hive to feed on and cultivate. As per assumption A.3, we break food into units of serving sizes per bee (i.e., 1 "food" is how much a single in-hive bee eats per day); this is done for ease of notation. Every day, the total amount of food (nectar) within the hive can be expressed by,

$$\Phi_{t+1} = \Phi_t - (P - F) + \eta(\min\{\varphi F, \mathcal{P}\}) \tag{4.1.4}$$

where $\Phi$ is the total food supply, $(P - F)$ is the amount of food expended to feed all in-hive (non-forager) bees, and $\eta(\min\{\varphi F, \mathcal{P}\})$ expresses the amount of food brought in from foraging $\mathcal{P}$ plants with $F$ foragers that forage $\varphi$ plants per day and collect $\eta$ food per plant.

***Plants/crops.*** In the region surrounding the hive, the flora demands certain healthy temperatures to flourish. In addition, plants require the pollination of honeybees to reproduce and increase regional genetic diversity. For a plant species $\rho$ that takes $\mu$ days to be able to produce/take pollen, we model the total population $\mathcal{P}$ of plants as

$$\mathcal{P}_{t+1} = s_\rho^{(t)}\mathcal{P} + \gamma\mathcal{P}_{pol}^{(t)} \tag{4.1.5}$$

where $s_\rho^{(t)}$ is daily survival of plant species $\rho$, $\mathcal{P}_{pol}^{(t)}$ is the number of flowers pollinated at time $t$ with $\gamma$ expressing the number of new plants created by pollinating one plant. We more concretely express this survival rate as a function of the total forager bees and the previous population of plants,

$$s_\rho^{(t)} = \phi_{s_\rho}\Big(k(T - T_{optimal}^{(\rho)})\Big). \tag{4.1.6}$$

Recall $\phi_{s_\rho}$ is our normalization function centered at a baseline plant survival rate of $s_\rho$ and note that $k$ is a constant that controls the plant's sensitivity to temperature deviations.

***Maturing Plants.*** Note that plants are not able to reproduce with pollen until a certain age. Thus, certain plants in the population cannot yet be visited by bees until they are fully mature. We note that (of the total population of $\mathcal{P}$ plants) the number of *new* plants that are able to be pollinated can be expressed as

$$\gamma\mathcal{P}_{pol}^{(t-\mu)}\prod_{i=0}^{\mu-1} s_\rho^{(t-i)},$$

where $\gamma$ is the number of new plants created by pollinating one plant, $\mu$ is the number of days it takes a plant to produce pollen/nectar, and $s_\rho^{(t)}$ is the survival rate of plant species $\rho$ at time $t$. Thus, the number of plants that are pollinated per day is equal to

$$\mathcal{P}_{pol}^{(t+1)} = \mathbf{G}_F\left(s_\rho^{(t)}\mathcal{P}_{pol}^{(t)} + \gamma\mathcal{P}_{pol}^{(t-\mu)}\prod_{i=0}^{\mu-1} s_\rho^{(t-i)}\right) \tag{4.1.7}$$

where $\mathbf{G}_F(x)$ allows us to model the expected number of *unique plants* visited by $F$ foragers that have $x$ *mature* plants to choose from. We expand upon the assumed movement of bees in the following paragraph.

***Forager Pollination.*** By assumption C.2, we assume each forager visits plants completely randomly and independently of other bees (as long as the plants they visit can be pollinated). As noted in the previous paragraph, it is necessary to figure out exactly how many **unique** plants were visited (and pollinated) by the forager bees as they follow this random pattern of behavior. Note that since bees move randomly two bees may visit the same plant twice and thus can't pollinate it twice; we need to count *unique* plant visits. We express the number of unique random plant selections (out of a population of $x$ plants to choose from and $y$ foragers moving randomly, each visiting $\varphi$ plants) as

$$\mathbf{G}_y(x) = x - \mathbb{E}[\text{repeated pollinations}] = x - x\left(1 - \left(\frac{x-1}{x}\right)^{\varphi y}\right). \tag{4.1.8}$$

This follows from a simple probabilistic argument that assumes each plant can be chosen uniformly at random by a bee (see assumption C.2).

## 4.2 Parameter Selection & Sensitivity Analysis

We implement and analyze our model in Python against a recorded temperature dataset that reports daily temperatures of major cities across the world [23]. For initial testing purposes, we consider data collected from Jan. 1, 2019 to Dec 31, 2020 in Des Moines, Iowa, which is geographically representative of a farming region commonly inhabited by honeybees. We note that our model can be easily re-calibrated for any other region given adequate temperature data. Within this environment, we model how bees pollinate and influence a population of three common, high-impact plants that depend on honeybee pollination.

***Choice of Constants.*** In order to initialize our model, we must begin by defining a set of *hyperparameters* that have appeared throughout our model. These include the initial survival rates and sensitivities to changes in temperature and nursing. To establish a baseline, we begin by manually tweaking these hyperparameters until the model achieves a stable state; i.e., the bee population does not collapse immediately. We include this baseline configuration in table 3. We additionally have a set of constants that do not change throughout the simulation of our model. These constants account for factors like the optimal growth temperature of the plant species in question ($T^{(\rho)}_{optimal}$) or the number of eggs a queen lays in a single day ($\beta$). We describe these constants in table 2, where we provide cited justification for our choice of values.

***Initial Survival Rates.*** We additionally select a set of initial survival rates for each caste. These values were determined by a combination of hyperparameter selection and reference to previous research surrounding the population fluctuations of bees. We refer to our code where these constants can be found (see appendix A).

**Table 2:** Initial environmental and hive constants for radish, clover, and corn, along with cited sources of constant value selected.

| Constant | Radish | Source | Clover | Source | Corn | Source |
|---|---|---|---|---|---|---|
| $\gamma$ | 300 | [8] | 6 | [26] | 800 | [9] |
| $\mu$ | 22 days | [18] | 15 days | [30] | 60 days | [27] |
| $T^{(\rho)}_{optimal}$ | $65°F$ | [4] | $34.5°F$ | [5] | $77.5°F$ | [11] |
| $T_{optimal}$ | $74.5°F$ | | | | | [19] |
| $\eta$ | $\frac{6.46nl}{22\mu l} = 2.936 \times 10^{-4}$ | | | | | [16, 13] |
| $\varphi$ | 2000 plants | | | | | [14] |
| $\beta$ | 2000 eggs | | | | | [22] |
| $n$ | 21 days | | | | | [7] |

**Table 3:** Initial hyperparameters used to instantiate the model. We tune these parameters individually in accordance with our model.

| **Hyperparameter** | $c_{temp}$ | $c_{food}$ | $c_{forage}$ | $c_{nurse}$ | $k$ |
|---|---|---|---|---|---|
| **Initial config** | 0.170 | 0.093 | 0.150 | 0.130 | 0.280 |

***Maximal Crop Density.*** Within our model we implement a soft limit on the number of plants within the 6 km region we consider. Given that plants occupy finite space, for different sizes of plants we take relative densities per unit space (e.g., watermelons may take up more room than carrots). This allows us to max out the plant population at a certain value, indicating the region is at full density.

***Choice of Normalization $\phi$.*** Throughout our modeling of survival rate for both bees and plants, it was useful to consider an average value between 0 and 1 that encompasses the expected proportion of the population that persists after the time step. While there are many choices of normalization functions that allow us to map a weighted sum of factors to the interval $(0, 1)$, in our implementation we select a modified *sigmoid* curve. Our implementation can be found in appendix A.

## 4.3 Analysis and Takeaways

***Sensitivity Analysis & Takeaways.*** To analyze the impact of various factors on our model, we vary them incrementally and record the average honeybee population of a hive over one year in fig. 2. Figure 2 demonstrates the importance of various factors to the survival of the hive. We suggest that, of the factors analyzed, the survival rate of forager bees ($s_f$) and nursing dependence ($c_{nurse}$) are the most important; the average population of the hive appears to increase exponentially with $s_f$ and decrease exponentially with $c_{nurse}$. In section 5.2, we consider these factors in relation to relevant environmental factors that may impact honeybee populations in a natural setting.

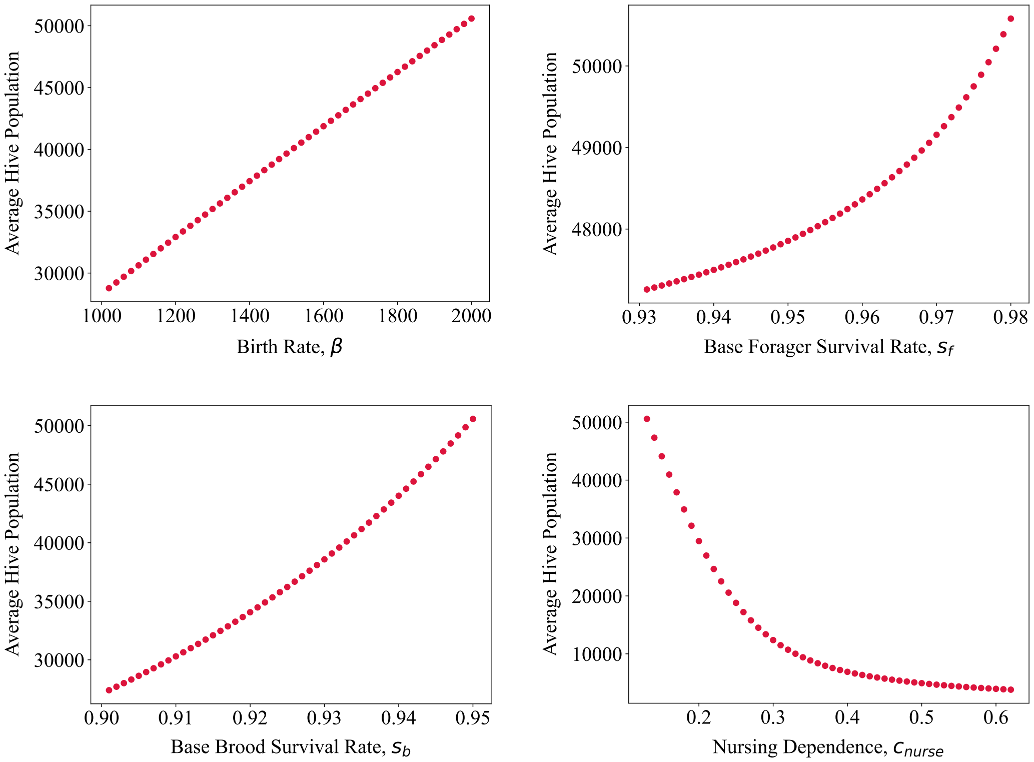


**Figure 2:** Sensitivity analysis over the births per day $\beta$, base survival rate of foragers $s_f$, base survival rate of brood $s_b$, and the nursing dependence $c_nurse$. We note that the survival rate of foragers and the dependence of brood on nursing are of the most important factors towards maintaining a healthy population.

## 4.4 Optimizing Crop Yield

We consider applying our model (which tells us how many plants are supported by a healthy hive) to optimize a crop yield. Considering a 20-acre yield of a crop (as opposed to 20-acres of land), we can easily apply our model to approximate the number of hives needed to support such a yield.

***Clover.*** For practicality we apply our model to a 20-acre (81000 sq. meter) field of clover plants. For an area $A$ (sq. meters), an area of a clover plant $C$ (sq. meters), and number of plants supported per hive $p$, we can compute the number of hives $h$ required to sustainably pollinate the area. Our computation for $h$ is then expressed as:

$$h = \frac{Ap}{C} \tag{4.4.1}$$

We are given $A = 81000$ sq. meters and set $p = 17000$ plants, obtained from running parameters from clover plants on our model. We set $C = 2916$ sq. centimeters [25]. Substituting in these values, we find $h = 16.33$ hives. We round this to $h = 16$ hives. Given assumption C.1, honeybees are able to travel over an area *greater* than that of the field we are modeling; exact space-filling is not a concern, and *generally* is unnecessary due to typical crop densities. We round down $h$ for optimization because rounding up could result in increased competition between hives and raise rates of malnutrition in bees unable to procure nectar.

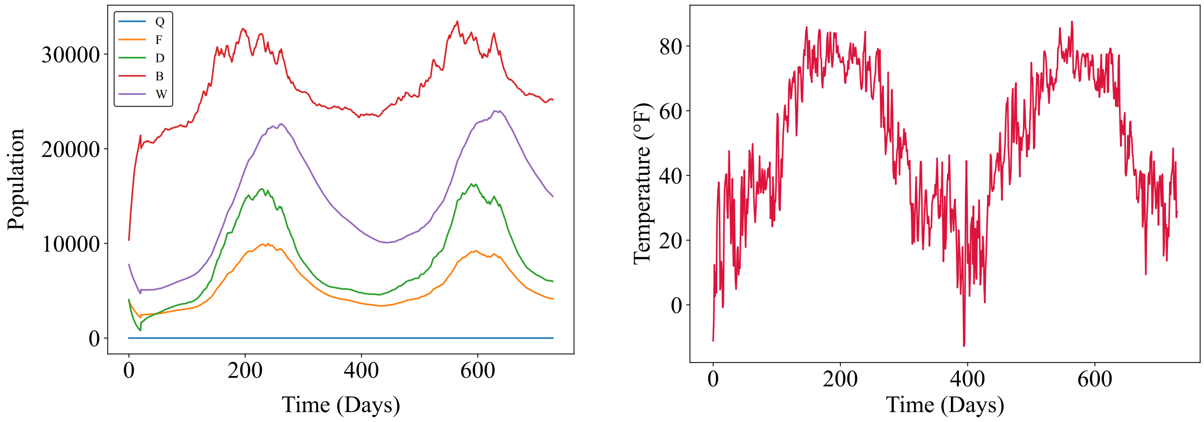


**Figure 3:** Our model's baseline population forecast for a healthy hive over the span of **two years** in a mid-west region of clover plants and its corresponding regional temperature temperature fluctuations.

# V MODELING THE IMPACT OF STRESSORS

## 5.1 Extending Our Model

Now that we are able to model the population fluctuations of a healthy honeybee colony, we turn to stressors that may cause collapse in the hive. In order to "introduce" a stressor to the hive, we modify relevant constants in a manner that may adversely affect the hive. We provide concrete justifications behind our choice of modification based on prior research on these stressors and their specific physiological and environmental impact on honeybee colonies. Our goal is to observe how different stressors accelerate the progression of colony collapse or permanently stunt the growth of a honeybee colony (and to what extent).

## 5.2 Modeling Stressors

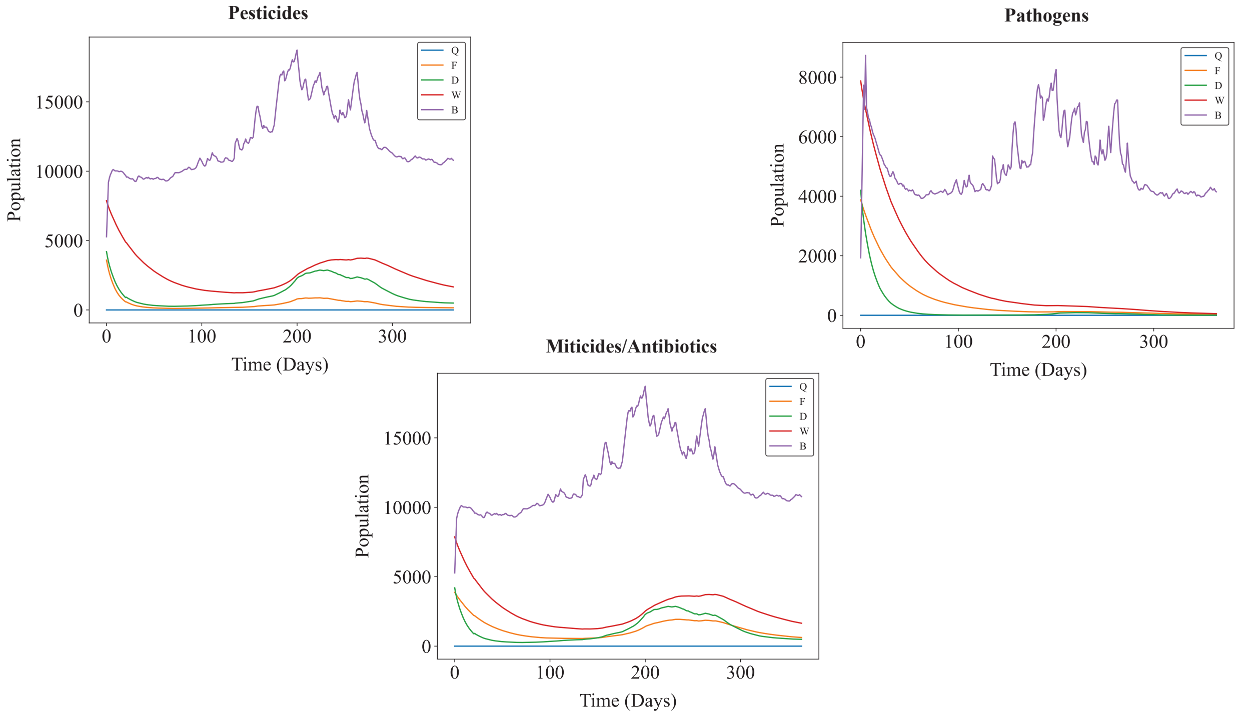
We categorize stressors into two distinct classes: in-hive and environmental stressors. Environmental stressors impact surrounding plant life and other regional patterns of hive behavior. In-hive stressors primarily target bees within the hive and consequently wreak havoc on the development and progression of in-hive tasks. We outline the main stressors we consider below and how we quantify their impact on the population.

***Stressor 1: Pesticides.*** The impact of pesticides on bee populations have been observed in the memory, genetic, and reproductive health of honeybees [29, 24]. We quantify pesticides as an in-hive stressor the decreases the birth rate $\beta$ and decrease the baseline survival of foragers $s_f$, whose impacted memory and behavioral health has been seen to cause higher rates of exhaustion and consequent death during foraging.

***Stressor 2: Pathogens.*** Pathogens, which broadly include any organism that produces disease, are often to blame for CCD. We consider the most destructive pathogen, the Varroa mite, and note that they primarily feed off the hive's brood. Varroa mites impact brood survival, forager flight endurance and wing strength, and deplete the food supply [31, 6]. Concretely, mites decrease the baseline brood survival rate $s_b$, increase the brood's dependence on nursing, $c_{nurse}$, and decrease the number of plants foragers can visit $\varphi$.

***Stressor 3: Antibiotics and Miticides.*** Antibiotics and miticides are critical environmental stressors that find their way into healthy hives. Primarily damaging the nutritional, physiological, and behavioral (and consequently developmental) stages of the brood's growth, we quantify the impact of these stressors as increasing the total time it takes brood to fully mature $n$ as well as increasing the dependence on nursing workers $c_{nurse}$ [2, 10].

***Stressor 4: General Environmental Conditions.*** All other causes of CCD, known or unknown, may be grouped under General Environmental Conditions. We quantify general environmental factors as primarily impacting plant prosperity and this observe how increased sensitivity to temperature influences plant's growth patterns and consequently honeybee populations.



Pesticides

Pathogens

Miticides/Antibiotics

**Figure 4:** Example of hive population forecasting with the introduction of the pathogens, miticides/antibiotics, and pesticides as stressor. We compare which stressors cause the most damage to population growth and aim to understand which causes of colony collapse are most detrimental to the colony. Notice that the introduction of these stressors drastically decreases total population and increases population fluctuation.

***Takeaways.*** As indicated in our sensitivity analysis (see section 4.2), the survival rate of foragers and the nursing of brood turn out to be extremely influential to the overall hive survival. It is thus not surprising that the results of our stressor analysis in fig. 4 revealed that pathogens and pesticides were the leading stressors involved in decreasing honeybee populations and leading to collapse. These two stressors are directly responsible for changes in brood development and forager survival out of the hive— the very two factors we found to be leading influences on hive prosperity.

## 5.3 Optimizing Crop Yield

We compute eq. (4.4.1) for a stressed hive, allowing us to model a real-world scenario where CCD would have negative impacts on pollination.

***Clover.*** We have already established $A = 81000$ sq. meters and $C = 2916$ sq. centimeters. We set $p = 8000$ plants, obtained from running parameters from clover plants on our model of a stressed hive. We obtain $h = 34.72$ hives. To optimize this, we round $h$ down, especially concerned here with adverse risks of increased competition and resulting food shortages. Thus, 34 **stressed** hives are needed to sustain a 20-acre field of clover, indicating the high impact of stressors on crop yield.

# VI DISCUSSION

## 6.1 Conclusion

In this paper, we developed a robust model for a honeybee colony operating in both healthy and *stressed* environments under a specified regional crop. To achieve refined population predictions that consider environmental, seasonal, and in-hive factors we use a discrete-time model and simple probabilistic arguments over larger populations. This allows us to model complex individual behaviors while accounting for finer-grain factors that may be influenced by sudden changes to the otherwise standardized work life of honeybees. Using this framework, we introduce various *stressors* that allow us to predict how honeybee populations are adversely impacted by various potential causes of Colony Collapse Disorder. We find stressors significantly impact Colony Collapse Disorder and pollination ability, raising the number of hives needed to pollinate a 20-acre clover field from 16 to 34.

We hope our model can be a meaningful first step towards understanding and addressing the puzzling causes behind the collapse of honeybee colonies worldwide. In the future, we aim to share our models with beekeepers, zoological population biologists, and entomologists. Open-sourcing our code on public repositories like GitHub—or even on a dedicated website—will allow for faster diffusion of our work so that it may be used to address the incredibly time-sensitive issue of CCD. A user could modify the parameters based on their temperature zone, local flora, and additional factors in order to pinpoint particularly virulent stressors.

Future iterations of our models may consider additional factors like rain patterns, human population density near the hive, and whether the bees live in the wild or captivity. We hope these added considerations will further increase precision and utility of our models.

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# A Hive-Crop Model Simulation Code

```python
# caste.py
from tools import normalize, symlog
import math


class Caste:
    def __init__(self, caste_data, name):
        """
        :param caste_data: a dictionary of variables to initialize a caste
        """
        self.hist_time = 0  # keeps track of oldest entry in population history
        self.history = [caste_data[f"{name}_initial_population"]]
        self.params = caste_data
        self.s = caste_data[f"{name}_base_survival"]

    def survival(self, factors):
        """
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        return normalize(self.params["base_survival"], 1)  # this will be normalized

    def get_population(self):
        return round(sum(self.history))

    def step(self, factors):
        """
        configures the population change in a caste after one time step.
        :param factors: dictionary of environmental/hive factors
        """
        s = self.survival(factors)
        self.history = [h * s for h in self.history]

    def promote(self, p):
        # print(p)
        self.history.append(p)

    def demote(self, factors):
        self.hist_time += 1
        return self.history.pop(0)


class Queen(Caste):
    def __init__(self, params, name):
        super().__init__(params, name)

    def produce(self, factors):
        """
        calculates the amount of eggs laid by the queen in a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors for the current time step
        :return: number of eggs laid in the time step
        """
        return self.params["birth_rate"]

    def survival(self, factors):
        """
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        x = factors["food_const"] * symlog(factors["food"]-factors["population"]+factors["num_foragers"]) + \
            factors["temp_const"] * (factors["temperature"] - factors["optimal_hive_temp"])
        return normalize(self.s, x)


class Forager(Caste):
    def __init__(self, params, name):
        super().__init__(params, name)

    def survival(self, factors):
        """
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        x = factors["temp_const"] * symlog(factors["temperature"] - factors["optimal_hive_temp"])
        x = x if factors["num_foragers"] == 0 \
            else x + factors["forage_const"] * symlog(factors["num_plants"]/factors["num_foragers"])
        return normalize(self.s, x)


class Drone(Caste):
    def __init__(self, params, name):
        super().__init__(params, name)

    def survival(self, factors):
        """
```

```
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        x = factors["food_const"] * symlog(factors["food"]-factors["population"]+factors["num_foragers"]) + \
            factors["temp_const"] * symlog(factors["temperature"] - factors["optimal_hive_temp"])
        return normalize(self.s, x)


class Worker(Caste):
    def __init__(self, params, name):
        super().__init__(params, name)

    def survival(self, factors):
        """
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        x = factors["food_const"] * symlog(factors["food"]-factors["population"]+factors["num_foragers"]) + \
            factors["temp_const"] * symlog(factors["temperature"] - factors["optimal_hive_temp"])

        return normalize(self.s, x)


class Brood(Caste):
    def __init__(self, params, name):
        super().__init__(params, name)

    def survival(self, factors):
        """
        calculates a caste's survival rate for a time step given environmental/hive factors
        :param factors: dictionary of environmental/hive factors
        :return: survival rate <= 1
        """
        x = factors["food_const"] * symlog(factors["food"]-factors["population"]+factors["num_foragers"]) + \
            factors["temp_const"] * symlog(factors["temperature"] - factors["optimal_hive_temp"]) + \
            factors["nurse_const"] * symlog((factors["num_workers"] - factors["num_brood"]))

        return normalize(self.s, x)

    def demote(self, factors):
        if factors["time"] - self.hist_time >= factors["brood_mature_age"]:
            return super().demote(factors)
        else:
            return 0
```

```
# environment.py
from tools import normalize, symlog


class Environment:
    def __init__(self, environment_data):
        self.temperature = None
        self.history = [environment_data["initial_plants"]]
        self.population = [environment_data["initial_plants"]]
        self.params = environment_data

    def step(self, factors):
        s = self.survival(factors)
        self.history = [h * s for h in self.history]
        p = round(sum(self.history))
        # add plants for the next time-step based on current data
        self.history.append(self.params["gamma"] * self.pollinate(self.get_mature_plants(), factors["num_foragers"]))
        self.population.append(sum(self.history))
        return p

    def survival(self, factors):
        """
        calculates the plant population change after one time step.
        :param factors: dictionary of environmental/hive factors. Must contain temperature parameter.
        """
        temp = self.params["temp_sensitivity"]*(factors["temperature"]-self.params["optimal_temp"])
        return normalize(self.params["plant_base_survival"], symlog(temp))

    def get_mature_plants(self):
        """
        calculates the number of mature plants available for pollination.
        :return: the number of mature plants available for pollination.
        """
        if len(self.history) < self.params["mu"]:
            return 0
        else:
            return round(sum(self.history[:-self.params["mu"]]))

    def pollinate(self, x, y):
        """
        :param x: number of mature plants
        :param y: number of foragers
        :return: number of plants pollinated
        """
        return 0 if x == 0 else x - x*(1-((x-1)/x)**(self.params["phi"]*y))
```

```python
# hive.py
import pandas as pd
from environment import Environment
from caste import Queen, Forager, Drone, Worker, Brood
import json
import os


class Hive:
    def __init__(self, config):
        # TODO: refactor this to config
        self.config = config
        headers = ["Q", "F", "D", "W", "B"]
        castes = [Queen, Forager, Drone, Worker, Brood]

        self.k = {h: c(config, h) for h, c in zip(headers, castes)}
        self.population = pd.DataFrame(columns=headers)
        self.environment = Environment(config)
        self.food = 10000  # TODO: configure this as a hyper-parameter?
        self.time = 0

    # TODO: get environmental factors
    def get_factors(self):
        factors = {
            **{"temperature": self.environment.temperature,
               "food": self.food,
               "time": self.time,
               "num_foragers": self.k["F"].get_population(),
               "num_workers": self.k["W"].get_population(),
               "num_brood": self.k["B"].get_population(),
               "population": round(sum(self.get_population())),
               "num_plants": sum(self.environment.history)
               },
            **self.config
        }
        return factors

    def get_population(self):
        return [caste.get_population() for caste in self.k.values()]

    def forage(self, factors):
        p = self.environment.step(factors)
        f = factors["num_foragers"]
        self.food = max(0,
                        self.food - (sum(self.get_population()) - f) +
                        self.config["eta"] *
                        min(self.config["phi"] * f, p))

    def step(self):
        # interact with environment
        # calculate survival and update caste states
        # increment time and store data

        factors = self.get_factors()  # get environmental/hive factors
        self.forage(factors)
        delta = self.k["Q"].produce(factors)  # queen lays eggs
        self.k["B"].promote(delta)  # add eggs to brood
        mature = self.k["B"].demote(factors)  # get number of brood that have matured

        # TODO: promotion/demotion between workers and foragers?

        for k in self.k.values():  # update caste states
            k.step(factors)

        for k, v in self.config["promotion_distribution"].items():  # promotion scheme is constant.
            self.k[k].promote(mature * v)

        self.population.loc[self.time] = self.get_population()
        self.time += 1
```

```python
# tools.py
import math
import numpy as np


def normalize(center, x):
    return sigmoid(logit(center) + x)


def sigmoid(x):
    if x >= 0:
        return 1. / (1. + np.exp(-x))
    else:
        return np.exp(x) / (1. + np.exp(x))


def logit(x):
    return math.log(x / (1 - x))


def symlog(x):
    if x == 0:
        return 0
    elif x < 0:
        return -np.log(-x)
    else:
        return np.log(x)
```

```python
# main.py
from hive import Hive
import matplotlib.pyplot as plt
import pandas as pd
import os
import json
from datetime import datetime


def main(global_config, plot=False):
    hive = Hive(global_config)
    temp_data1 = pd.read_csv("Data/DesMoines_2019.csv")
    temp_data2 = pd.read_csv("Data/DesMoines_2018.csv")
    temp_data = pd.concat([temp_data2, temp_data1], ignore_index=True)
    print(temp_data.size)

    time_window = 365 * 2
    for i in range(time_window):
        hive.environment.temperature = temp_data["AvgTemperature"].iloc[i]
        hive.step()

    df = hive.population
    if plot:
        # Saving data
        now = datetime.now().strftime("%H-%M-%S")

        df["Plant"] = hive.environment.population[:time_window]
        df["Temperature"] = temp_data
        df.to_csv(f"Out/Tables/{now}.csv")
        df[["Q", "F", "D", "W", "B", "Plant"]].plot()
        plt.legend(frameon=False)
        plt.savefig(f"Out/Images/{now}.svg")

        with open(f"Out/Params/{now}.json", "w") as f:
            json.dump(global_config, f)

    return round(df.mean().mean())


if __name__ == "__main__":
    with open("Config/global.json") as f:
        global_config = json.load(f)

    #for i in range(1000):
        #delta = -2

    main(global_config, True)
```

```json
// config file global.json
{
  "Q_initial_population": 1,
  "W_initial_population": 10000,
  "F_initial_population": 4000,
  "D_initial_population": 8000,
  "B_initial_population": 18000,
  "Q_base_survival": 0.99,
  "W_base_survival": 0.95,
  "F_base_survival": 0.98,
  "D_base_survival": 0.85,
  "B_base_survival": 0.95,
  "birth_rate": 2000,
  "brood_mature_age": 21,
  "promotion_distribution": {
    "D": 0.5,
    "F": 0.2,
    "W": 0.3
  },
  "optimal_hive_temp": 75,
  "gamma": 6,
  "mu": 15,
```

```
  "eta": 21,
  "phi": 2000,
  "optimal_temp": 34.5,
  "temp_sensitivity": 0.28,
  "initial_plants": 25000,
  "plant_base_survival": 0.999,
  "food_const": 0.093,
  "temp_const": 0.17,
  "nurse_const": 0.13,
  "forage_const": 0.15
}
```