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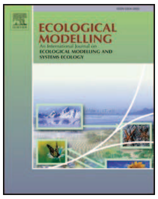

Effects of vitellogenin in age polyethism and population dynamics of honeybees

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ABSTRACT

The complexity of honeybees provides systems to study mechanisms affecting their population dynamics. An essential environmental variable influencing the age-based division of labor of worker honeybees is their nutritional status. We present basic but important assumptions that can help us understand the complexity of honeybee population dynamics given their nutritional status. We propose a non-linear differential equation system that models the population dynamics of brood and worker bees (nurses and foragers) within a colony. The dynamics of these populations are influenced by the available stored pollen in cells and the current levels of vitellogenin (VG), a major storage protein, in the fat body of nurse bees. Our model shows: (a) the importance of pollen collection and consumption rates, adequate feeding rates to the queen, and the impact of good nutrition during the larvae stage for future foraging activity; (b) the size of both the brood and worker populations at equilibrium are directly dependent upon the increase of levels of VG titers in nurse bees; (c) division of labor regulatory effects determined by the VG titers in nurse bees are important for balancing nurse bee and forager populations; (d) coexistence of both brood and worker populations is dependent upon available food for the brood (i.e. pollen collected and converted to VG and available foragers); (e) taking into account seasonal changes in pollen collection improves the prediction of long term consequences.

1. Introduction

Honeybees (*Apis mellifera*) are social and have a high structured division of labor. A typical colony of honeybees is composed of 10–20 thousand eggs, larvae, and pupae, up to 30,000 adult workers (all females), zero to several hundred drones (males), and a single female queen. In general, the queen bee is the only egg-laying member, while worker bees perform a number of tasks including feeding the queen, colony maintenance, colony defense against honey robbers, but most importantly, rearing the brood and maintaining the required nutritional demands of the colony such as pollen, nectar, propolis and water (Robinson, 1992; Seeley, 2009; Calderone, 1998; Johnson, 2010). Behavioral task distribution of bees can be influenced by aging, genes, and environment (Wright et al., 2018). For instance, in the spring and summer, division of labor is shaped to maximize the accumulation of resources (e.g. honey) and growth rate, while in the winter, worker bees become less differentiated in task performance because the primary goal is to maintain worker survivorship through this season (Johnson, 2010).

The growth, development, productivity, and health of a honeybee colony is dependent upon fulfilling the nutritional demands of larvae and adult workers (Brodschneider and Crailsheim, 2010). Survival and quality of larvae and adult workers are of prime importance for the productivity and health of a colony. In general, a honeybee colony requires of macronutrients (i.e. proteins, carbohydrates, and fats) and of micronutrients (i.e. vitamins and minerals) for growth and development of healthy larvae and adults (Brodschneider and Crailsheim, 2010; Winston, 1992; Crailsheim et al., 1992). The colony, having specific needs, monitors foraging efforts to collect nectar, pollen, water and tree resin (Wright et al., 2018). However, the nutritional needs at the individual bee level are mostly determined by somatic demands arising with age and behavioral role in the colony (Paoli et al., 2014). For instance, findings in (Paoli et al., 2014), show that young bees require higher protein intake than older adult workers prioritizing their dietary

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intake of carbohydrates over protein as they age.

For honeybees, the main source of carbohydrates is floral nectar, while pollen satisfies the nutritional requirements for protein, lipids, sterols, and micronutrients (Winston, 1992; Wright et al., 2018; Vaudo et al., 2015). Several studies have shown that honeybees regulate the intake of macronutrients around specific proportions (Wright et al., 2018; Schmickl and Crailsheim, 2004). Nectar is collected in excess according to floral nectar availability (Wright et al., 2018; Schmickl and Crailsheim, 2004; Vaudo et al., 2015), transformed gradually to honey during the returning flight and within the nest (Nicolson and Human, 2008), stored in sealed cells as honey (Brodschneider and Crailsheim, 2010), and reserved for overwintering needs (Khoury et al., 2013). Honey, stored in tens of kilograms (Seeley, 2009), is used as fuel for energy-intensive flights, colony thermoregulation and wax production (Wheeler and Robinson, 2014; Wright et al., 2018). On the other hand, pollen is collected as a reserve for only a few days depending on the ratio of pollen supply to pollen demand (Dreller et al., 1999; Camazine, 1993), maintaining in storage about 1 kg on average (Wright et al., 2018). Pollen foragers make decisions based on the pollen available in cells acting as a negative stimulus (i.e. decreasing pollen-foraging), and on chemical pheromones from the existing larvae acting as a positive stimulus (i.e. increasing pollen-foraging) (Dreller et al., 1999; Schmickl and Crailsheim, 2004; Pankiw and Page, 2001a; Fewell and Winston, 1992; Page, 2013).

Bees hoard food in the form of honey (nectar) and bee bread (pollen) (Wright et al., 2018). The pollen stored and processed by young hive bees (bee bread) differs in its nutritional value from floral pollen (Wright et al., 2018). The protein and lipid content in bee bread is found to be in smaller ranges than floral pollen (Wright et al., 2018; Herbert and Shimanuki, 1978). However, the quantity of protein in pollen is of less significance than the amount of essential amino acids proportional to bee requirements (Wright et al., 2018; Groot and d., 1953). Pollen is the only source of the ten essential amino acids (i.e. protein) required by honeybees (Bitondi and Simoes, 1996; Brodschneider and Crailsheim, 2010; Huang et al., 2010). In fact, some studies have suggested a link between foraging behavior and amino acid nutrition (Hendriksma and Shafir, 2016). Therefore, consumption of pollen is evidence of high protein levels in the haemolymph, which is usually accompanied by high levels of storage proteins, such as vitellogenin (Frias et al., 2016).

In this study, we want to focus our attention to a glycolipoprotein, vitellogenin. Vitellogenin (VG) is an egg yolk protein which is the primary source of amino acids (Hughes, 2015), and it appears to be one of the most important regulators of immunity and longevity of honeybees (Amdam et al., 2009; Amdam and Omholt, 2002; Glavinic et al., 2017). Worker bees begin the synthesis of vitellogenin 2–3 days later after emerging as an adult (Amdam et al., 2010, 2003). VG is synthesized primarily in the fat body cells of the abdomen, released into the haemolymph, and incorporated into the hypopharyngeal glands (HPGs) where it is used to make royal jelly proteins (Amdam and Omholt, 2002; Hölldobler and Wilson, 2009). These glands provide secretions rich in protein, which are fed by nurse bees to larvae and adults of all three castes (Ahn et al., 2012; Crailsheim et al., 1992; Paoli et al., 2014). A wide range of proteins are stored in the fat body and haemolymph, but vitellogenin is the most dominant in both queens and workers (Amdam and Omholt, 2002; Brodschneider and Crailsheim, 2010). Studies have shown that vitellogenin is dependent on the availability and quality of pollen (Amdam et al., 2010). It has several functions in worker bees such as adult bee physiological development, immune responses such as reducing susceptibility to parasites and pathogens (Amdam et al., 2004, 2009; Alaux et al., 2011; Page et al., 2012), and oxidative stress resistance (Seehuus et al., 2006; Amdam and Omholt, 2002). Also, vitellogenin is utilized for various metabolic purposes in addition to brood food production (Amdam and Omholt, 2002; Oliver, 2007; Guidugli et al., 2005), such as acting as an antioxidant to prolong queen bee and forager lifespans as well as acting as a hormone that affects future foraging behavior (Amdam et al., 2010; Oliver, 2007; Page et al., 2012; Ihle et al., 2010).

Vitellogenin levels are important during the nest stage and thus influence honeybee worker division of labor. The relationship between vitellogenin and their pronounced division of labor can be seen by comparing the levels of vitellogenin in the fat body or by comparing the size of the HPG. For instance, in nurse bees, vitellogenin titer levels in the fat body are high allowing them to transfer protein to larvae and other colony members (Amdam and Omholt, 2003; Tsuruda and Page, 2009), while in foragers are low (Ahn et al., 2012; Crailsheim, 1992). On the other hand, the size of HPG is an indicator of protein nutrition prior to becoming a nurse and affects their ability to care for larvae (Ahn et al., 2012; Huang and Otis, 1989; Hrassnigg and Crailsheim, 1998). Two to three weeks after emergence as an adult, vitellogenin synthesis declines in workers, inducing a transition from nursing to foraging behavior (Amdam and Omholt, 2002; Tsuruda and Page, 2009; Amdam et al., 2010; Guidugli et al., 2005). Individual foragers may concentrate more on collecting either pollen or nectar due to variation in the life history, anatomy, physiology, and genotypes of individuals that are linked to the titers of vitellogenin and juvenile hormone (Amdam et al., 2010; Tsuruda and Page, 2009).

The consequences of protein shortage could be tremendous. It could affect brood production, the quality or the number of larvae reared to adulthood, and colony nutritional state towards future brood rearing (Brodschneider and Crailsheim, 2010). This does not only have an effect on the size of the population but also on the age demography which then affects the division of labor (Schmickl and Crailsheim, 2007). Also, when pollen is unavailable due to bad weather or other adverse environmental conditions, bees will engage in brood cannibalism to obtain the protein necessary to feed other larvae (Brodschneider and Crailsheim, 2010; Carroll et al., 2017; Haydak, 1970; Schmickl and Crailsheim, 2004; Khoury et al., 2013). Several studies show that poor pollen nutrition can have an impact on different causes leading to colony collapse disorder, such causes include resistance to infections and viruses such as *Nosema* and *Varroa* in addition to sensitivity to pesticides (DeGrandi-Hoffman et al., 2010; Huang, 2012; Wahl and Ulm, 1983).

Change of season, weather, and temperature have huge impacts on the population dynamics of a honeybee colony, but also on social regulation (Johnson, 2003). They can affect the amount of proteins in the fat body of a worker bee (Amdam and Omholt, 2002; Brodschneider and Crailsheim, 2010). For instance, wintering workers have, in general, a high haemolymph vitellogenin titer (higher in late autumn than at the end of winter). However, the titer of brood-less worker bees in the summer may be higher than in the winter bees probably due to the absence of food transmission to brood (Amdam and Omholt, 2002). Climate variability has an effect on nutritional factors related to the quality and the quantity of nectar and pollen resources (Switanek et al., 2017). Intensity of temperature, rain or solar radiation have been connected with the foraging activity of honeybees (Switanek et al., 2017; Vicens and Bosch, 2000; Szabo, 1980; Abou-Shaara, 2014), which induces an effect on the egg-laying rate of the queen bee (Torres et al., 2015). There are studies showing that rainy periods can cease foraging activities (Switanek et al., 2017; Riessberger and Crailsheim, 1997; Schmickl and Crailsheim, 2007; Amdam et al., 2010). Availability of nectar and pollen in the field affected by environmental factors that change seasonally also influence foraging activity (Amdam et al., 2009). Therefore, summer time is when bees foraging rate is the highest along with mortality rate (Amdam and Omholt, 2002), and during fall foraging is almost ceased.

Mathematical models have been developed to study honeybee colony population dynamics (Schmickl and Crailsheim, 2007; Becher et al., 2014; Perry et al., 2015; Kang et al., 2016; Messan et al., 2017; Khoury et al., 2011, 2013; Schmickl and Karsai, 2017). The most relevant studies to our work are those of Schmickl and Crailsheim (2007), Khoury et al. (2013), Becher et al. (2014), Perry et al. (2015), and

Schmickl and Karsai (2017), which all modeled the population dynamics of honeybees and nutrient stores. The approach of these studies differs from each other but have primarily focused on specific factors affecting the dynamics of brood and worker population. For instance, Schmickl and Crailsheim (2007) created a difference equation model to study the population and resource dynamics of a honeybee colony by focusing on the importance of pollen supply and of brood cannibalism. They also provided an extensive review about other mathematical models and their purpose. Several of these models have focused on behavioral aspects of foraging, food processing, spatial organization, and processes associated with division of labor. In Khoury et al. (2013), they presented a theoretical framework to explore how the dynamics of food flow through a colony might interact with population dynamics to determine colony growth and development. More recently, Becher et al. (2014) developed BEEHAVE, which integrates honeybee colony dynamics and population dynamics of the varroa mite and transmitted viruses with and explicit foraging model. Later, Becher et al. (2016) developed another software tool, BEESCOUT, which can simulate bee search patterns in any mapped landscape aiding the explanation of how landscape configurations and parameters describing searching behavior affect detection probability of food sources. In addition, seasonal nectar and pollen availability in realistic landscapes is also implemented in BEESCOUT. This software tool can also be used as an input for BEEHAVE to predict the overall impact of multiple stressors that can affect colony growth and death. Perry et al. (2015) developed a model to explore possible impacts of age-dependent foraging performance on a colony affected by different stressors including nutritional. Schmickl and Karsai (2017) developed a mathematical model that links age polyethism by predicting the dynamics of brood population and it links colony-level fitness by predicting the dynamics of adult forager populations and nutrient stores. Another relevant study to our work is that of Amdam and Omholt (2002) developing a nonlinear differential equation model to predict the vitellogenin dynamics in the fat body, the haemolymph, and the HPGs of an individual bee that is exposed to various task scenarios in different seasons. The results of this model show consistency with empirical data and serve as a starting point to the assumptions of our model.

We investigate the implications of the information stated above by developing a honeybee population model using nonlinear differential equations. This model will allow us to investigate how the dynamics of vitellogenin titers might interact with population dynamics to influence colony growth. We will be looking at the vitellogenin dynamics of the adult worker population influencing the distribution of adult worker bees to tasks such as brood nursing and food collection. Specifically, we focus on the importance of pollen-derived proteins and the impacts on the division of labor. Our goal is to propose a starting point of modeling techniques that can allow us to study present problems leading to colony collapses, such as nutritional stress (Naug, 2009), scarcity of food sources (Naug, 2009), and climate change.

2. Model development

We propose a nonlinear ordinary differential equations model with the following state variables: $B(t)$ represents the brood population size consisting of eggs and larvae, and $N(t) + F(t)$ represents the worker population size of the two main task groups in a colony, i.e. nurses and foragers, respectively, at time t. In addition, we consider the current pollen storage in the colony $P(t)$, and the available vitellogenin titers in nurse bees $V(t)$, at time t, respectively.

Our five compartment model is derived following specific details found in the literature and assumptions from empirical findings:

1. The rate of change of brood population, $B'(t) = \frac{\mathrm{d}B}{\mathrm{d}t}$ is determined by:
   Input: The egg laying rate by the queen is related to the amount of royal jelly fed by nurse bees and each egg contains certain amount of VG to start developing (Allen, 1960; Moore et al., 2015; Amdam and Omholt, 2002), i.e., $\frac{c_q \alpha_q V}{e_g}$, where e_g is the average content of VG in one egg, and $c_q \in (0, 1)$ is the conversion efficiency of queen transfer of VG into egg-laying production, i.e., $(1 - c_q)\alpha_q V$ can be considered as the metabolic cost of queen for egg-laying production.
   Output: transition rate from brood to nurse bee: $\beta_{\mathrm{bh}} = \frac{1}{\tau_{\mathrm{bf}}}$ where τ_{bf} is the developmental time from brood to nurse bee. Here, we assume that there is no additional brood death.
   Thus, the dynamics of the brood can be described by the following equation:

   $$B' = \underbrace{\frac{c_q \alpha_q V}{e_g}}_{\text{queen's egg}-\text{laying rate}} - \underbrace{\beta_{\mathrm{bf}} B}_{\text{transition rate to nurse}} . \tag{1}$$

2. Nurse bees are a temporal worker sub-caste that specializes in brood rearing (Dreller et al., 1999; Münch and Amdam, 2010). The rate of change of the nursing worker population, $N'(t) = \frac{\mathrm{dN}}{\mathrm{dt}}$, is determined by:
   Input: transition rate from brood $\beta_{\mathrm{bh}} B$.
   Outputs:
   - Transition rate to forager, $\beta_{\mathrm{hf}} = \frac{1}{\tau_{\mathrm{hf}}}$, where τ_{hf} is the developmental time from nurse to forager bee. After nursing, bees transition to foraging tasks outside the colony due at least in part to low levels of vitellogenin titers (Amdam et al., 2010; Amdam and Omholt, 2003; Huang et al., 1994; Goblirsch et al., 2013). The transition rate to forager increases when nurse bees have low levels of vitellogenin at time t. This implies that the transition rate $\beta_{\mathrm{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)$ from nurse to forager is a decreasing function of the average of VG per nurse bee. An example of this transition rate can be $\beta_{\mathrm{hf}} = \frac{\beta_{\mathrm{hf}}^m N}{1 + \alpha_v \left(\frac{V}{N}\right)^{-1}}$ where β_{hf}^m is the maximum transition rate from nurse bee to forager when the average of VG per nurse bee $\frac{V}{N}$ is very low, and α_v regulates the effects of the VG per nurse bee on the transitional rate from nurse bee to forager when $\frac{V}{N}$ is high, i.e. if $\frac{V}{N}$ is high, then the transition rate from nurse to forager bee will be very small.
   - Mortality rate d_h is a nonlinear function of VG contained in nurse bees and its population size N, and foragers F (Seehuus et al., 2006). We assume that d_h is decreasing with respect to the average VG per nurse bee $\frac{V}{N}$, and increasing with respect to N and foragers F, i.e., $d_h\left(\frac{V}{N}, N\right)$. For simplification, we can just take d_h as a constant that is smaller than the death rate of forager.
     Thus, the dynamics of the hive can be described by the following equation:

   $$N' = \underbrace{\beta_{\mathrm{bh}}}_{\text{transition from brood}} B - \underbrace{\beta_{\mathrm{hf}}((\frac{V}{N})^{-1})}_{\text{transition to forager decreasing with V}} N - \underbrace{d_h(\frac{V}{N}, N)}_{\text{nurse mortality rate dependent on VG and N}} N \tag{2}$$

3. The rate of change of foraging worker population, $F'(t) = \frac{\mathrm{d}F}{\mathrm{dt}}$, is determined by:
   Input: transition rate from nurse $\beta_{\mathrm{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)N$.
   Output: mortality rate $d_f F$ should be a nonlinear function of VG contained in forager bees and its population size F. For simplicity, we assume that $d_f > d_h$ is constant (Münch and Amdam, 2010). Thus, the dynamics of the foragers can be described by the following equation:

$$F' = \underbrace{\beta_{\text{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)N}_{\text{transition from nurse bee to forager, decreasing with V}} - \underbrace{d_f F}_{\text{forager mortality rate}} \tag{3}$$

4. The rate of change of pollen storage $P'(t) = \frac{\text{d P}}{\text{dt}}$ is determined by:
   Input: The parameter r is the maximum pollen collection rate by foragers. The pollen collection rate is regulated by the foraging worker population F and brood population B, and the available pollen stored P in the colony (Tsuruda and Page, 2009; Fewell and Page, 1993; Pankiw and Page, 1999, 2001b), described by $\frac{\text{rBF}}{1+\text{aB}+\text{b P}}$ which implies: (a) more larvae results in more brood pheromone that stimulates pollen foraging behavior; and (b) more stored pollen reduces pollen foraging activity (Traynor et al., 2014; Camazine, 1993). The parameters a and b represent the regulation effects of brood and pollen storage, respectively.
   Output: On average, each nurse bee removes pollen at the rate of αP, i.e., more pollen, faster removing rate. The total removing rate of pollen by all nurse bees is αP N. In addition, we assume that the pollen has a deterioration rate of d_p due to the lack of attending or consumption. It is known that nurse bees prefer to consume fresh pollen (Wright et al., 2018) stored less than 72 h (Anderson et al., 2014).
   Thus, the dynamics of the pollen storage can be described by the following equation:

$$P' = \underbrace{\frac{\text{rB}}{1+\text{aB}+\text{bP}}}_{\text{regulated pollen collection rate}} F - \underbrace{\alpha\text{NP}}_{\text{removing rate of pollen by nurse bee for VG production}} - \underbrace{d_p P}_{\text{deterioration rate of pollen}} \tag{4}$$

5. The rate of change of VG in nurse bees, $V'(t) = \frac{\text{d V}}{\text{dt}}$, is determined by:
   Inputs: production rate of VG from pollen by nurses and the total VG contained in newly emerged adult bees.
   - Nurse bees deplete pollen reserves for the synthesis of vitellogenin (Dreller et al., 1999; Münch and Amdam, 2010). The conversion rate of pollen per gram to VG is represented by c. Thus the consumed pollen αP H would be converted to VG with the amount of $c\alpha$P H.
   - There are $\beta_{\text{bh}}B(t) = \frac{1}{\tau_{\text{bf}}}B(t)$ newly emerged adult bees whose content of VG could be estimated as follows:

$$\beta_{\text{bh}}\left[c_q\alpha_q V(t-\tau_{\text{bf}}) + \frac{c_q\alpha_q V(t-\tau_{\text{bf}})}{e_g}\int_{t-\tau_{\text{bf}}}^{t} V(\tau)d\tau\right].$$

   Outputs: nurse bee's distribution rate of VG, removal rate of VG due to death of nurse bee, and transition rate to foraging. The nurse bees:
   - administer VG to the queen to regulate egg-laying production and longevity (Haydak, 1970; Wang et al., 2014), and to the brood to regulate growth and development (Traynor et al., 2014; Crailsheim et al., 1992). The portion of VG distributed to brood is measured by the product of the brood population B and the average brood's consumption rate $\alpha_b V$. Similarly, feeding rate to queen is measured by $\alpha_q V$.
   - use VG for their own metabolism, which is described by α_hNV.
   - dying during the nursing stage is described by $d_h V$.
   - surviving and transitioning into foragers can be described by $\beta_{\text{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)V$.

   Thus, the dynamics of the VG in nurses can be described by the following equation:

$$\begin{aligned} V' = {} & \underbrace{c\alpha\text{NP}}_{\text{VG production by nurse bee with available pollen}} - \underbrace{\alpha_b\text{B V}}_{\text{brood consumption rate of VG}} \\ & - \underbrace{\alpha_q V}_{\text{VG allocation to queen}} - \underbrace{\alpha_h\text{N V}}_{\text{metabolic use of VG by nurse bee}} - \underbrace{\beta_{\text{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)}_{\text{transition to forager}} V \\ & - \underbrace{d_h\left(\frac{V}{N}, N\right)}_{\text{removal rate due to nurse bee death}} V \\ & + \underbrace{\beta_{\text{bh}}\left[c_q\alpha_q V(t-\tau_{\text{bf}}) + \frac{c_q\alpha_q V(t-\tau_{\text{bf}})}{e_g}\int_{t-\tau_{\text{bf}}}^{t} V(\tau)d\tau\right]}_{\text{VG of newly emerged adult bees}} \end{aligned} \tag{5}$$

A simplified version of (5) can be described as follows:

$$\begin{aligned} V' = {} & \underbrace{c\alpha\text{NP}}_{\text{VG production by nurse bee with available pollen}} - \underbrace{\alpha_b\text{B V}}_{\text{brood consumption rate of VG}} \\ & - \underbrace{(1-c_q)\alpha_q V}_{\text{Queen's metabolic costs}} \\ & - \underbrace{\alpha_h\text{N V}}_{\text{metabolic use of VG by nurse bee}} - \underbrace{\beta_{\text{hf}}\left(\left(\frac{V}{N}\right)^{-1}\right)}_{\text{transition to forager}} V \\ & - \underbrace{d_h\left(\frac{V}{N}, N\right)}_{\text{removal rate due to nurse bee death}} V \end{aligned} \tag{6}$$

The assumptions with detailed derivations above give us the following nonlinear model:

$$\begin{aligned} B' &= \frac{c_q\alpha_q}{e_g}V - \beta_{\text{bh}}B \\ N' &= \beta_{\text{bh}}B - \frac{\beta_{\text{hf}}^m N}{1+\alpha_v\frac{N}{V}} - d_h N \\ F' &= \frac{\beta_{\text{hf}}^m N}{1+\alpha_v\frac{N}{V}} - d_f F \\ P' &= \frac{\text{r BF}}{1+\text{aB}+\text{bP}} - \alpha\text{NP} - d_p P \\ V' &= c\alpha\text{NP} - (1-c_q)\alpha_q V - \alpha_h\text{NV} - \alpha_b\text{B V} - d_h V - \frac{\beta_{\text{hf}}^m V}{1+\alpha_v\frac{N}{V}} \end{aligned} \tag{7}$$

where we take $\beta_{\text{hf}}^m\left(\frac{N}{V}\right) = \frac{\beta_{\text{hf}}^m}{1+\alpha_v\frac{N}{V}}$, $d_h\left(\frac{V}{N}, N\right) = d_h$, and the simplified version of V in Eq. (6). When $V = 0$, we define $\frac{\beta_{\text{hf}}^m}{1+\alpha_v\frac{N}{V}} = 0$. We provide a state diagram in Fig. 1 to aid visualize the relationships of the state variables in our model.

3. Results

In this section, we explore the dynamics of Model (7) analytically and provide biological implications. Note that an interior equilibria of Model (7) can be expressed in the following form:

$$\begin{aligned} &(P^*, V^*, B^*, N^*, F^*) \\ &= \left(\Phi(\xi) + \frac{N^*}{c\alpha\xi}\left(\alpha_h + \frac{c_q\alpha_b\alpha_q}{e_g\beta_{\text{bh}}\xi}\right), \frac{N^*}{\xi}, \frac{c_q\alpha_q}{e_g\beta_{\text{bh}}\xi}N^*, N^*, \frac{\beta_{\text{hf}}^m N^*}{d_f(1+\alpha_v\xi)}\right), \end{aligned} \tag{8}$$

where

$$\Phi(\xi) = \frac{\alpha_q}{c\alpha\xi}\left[1 - c_q\left(1 - \frac{1}{e_g\xi}\right)\right]$$

and N^* is a positive solution of the polynomial: $f(N) = c_3N^3 + c_2N^2 + c_1N + c_0$, where c_i, $i = 0, a, b, 3$ are

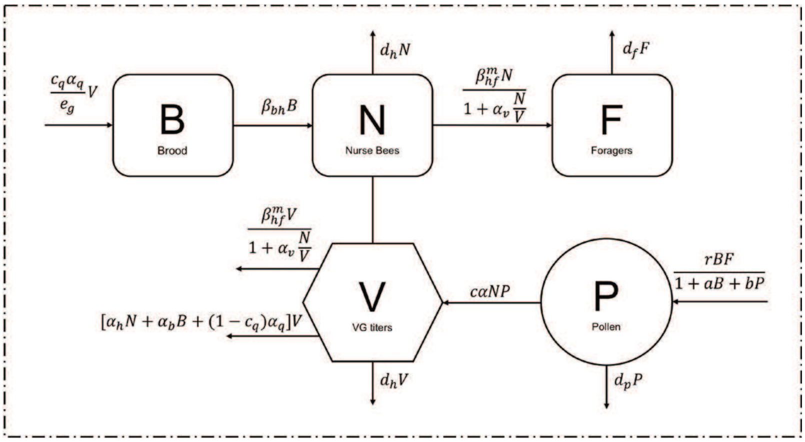


Fig. 1. State diagram of proposed model.

polynomials of ξ (see details in (B.5)). The parameter ξ measures nurse bees' nutritional status and can be expressed as follows:

$$\xi = \frac{c_q\alpha_q\alpha_v - d_h e_g - \beta_{\mathrm{hf}}^m e_g + \sqrt{(c_q\alpha_q\alpha_v - e_g d_h - e_g\beta_{\mathrm{hf}}^m)^2 + 4c_q\alpha_q\alpha_v d_h e_g}}{2\alpha_v d_h e_g} \tag{9}$$

Note that $\xi^{-1} = \frac{V}{N}$ is the VG content per nurse bee. From simple analysis (see Appendix A), we can conclude that the level of VG per nurse bee decreases when the feeding rate to queen and the efficiency of converting VG for egg-laying production (α_q and c_q, respectively) increases. Also, since α_v is a parameter that regulates the effects of the levels of VG per nurse bee that have on the transition rate from nurse to forager, if α_v is too small this can void this regulation effect, but 'too large' can enhance it and possibly lose tractability of this effect. Moreover, the levels of VG per nurse bee show an increase when there is an increase of the average content of VG per egg, the mortality rate of bees during the nursing stage, and the maximum transition rate from nurse to forager, i.e. e_g, d_h, and β_{hf}^m.

Let a, b, c, c_q, d_f, d_h, d_p, e_g, α, α_b, α_q, α_v, β_{hf}^m, β_{bh} be positive parameters. More details regarding the derivation of (8) can be found in Appendix B and the number of interior equilibria the model (7) have is determined with the following theorem.

Theorem 3.1. *[Existence of interior equilibria] System (7) is positive invariant in* $\mathbb{R}_+^5$. *Model (7) always has the extinction equilibrium* $\mathbf{E_0}$ *which is always asymptotically stable, and can have none or two interior equilibria under the following conditions:*

1. *No interior equilibria if* $\alpha_b > \mathrm{cr}\xi\frac{\beta_{\mathrm{hf}}^m}{d_f(1+\alpha_v\xi)}$.
2. *Two interior equilibria if* $\alpha_b < \mathrm{cr}\xi\frac{\beta_{\mathrm{hf}}^m}{d_f(1+\alpha_v\xi)}$

Biological implication: Our model can have up to two interior equilibria, i.e., two possible points of the form (P^*, V^*, B^*, N^*, F^*), where all the components are greater than zero and have the potential to become stable. If an interior equilibrium point becomes stable, it means that depending on parameter values and initial conditions, both the brood and worker populations, and quantities of stored pollen and vitellogenin in nurse bees will reach a specific size determined by (8) and stay stable at that point in the long term. Note that, $\alpha_b < \mathrm{cr}\xi\frac{\beta_{\mathrm{hf}}^m}{d_f(1+\alpha_v\xi)} = \mathrm{cr}\frac{N}{V}\frac{\beta_{\mathrm{hf}}^m}{d_f(1+\alpha_v\xi)} = \frac{\mathrm{cr}}{V}F$, which can be simplified as $\frac{\mathrm{cr}}{\alpha_b} > \frac{V}{F}$. This is interpreted as follows: if the colony's nutritional status is good, i.e., pollen collection, processing and consumption are suitable for colony's needs then both brood and worker populations are able to coexist, i.e., both populations can reach one of the two interior equilibria, otherwise, the colony may die out. Also, from (8), we can conclude that the components P^*, V^*, B^*, F^* increase when ξ decreases or levels of vitellogenin per nurse bee (i.e., $\frac{1}{\xi}$) increases.

Next, we analyze the synergetic effects in a numerical fashion over the population size of brood and worker bees given by parameters affecting the levels of vitellogenin per nurse bee.

The levels of vitellogenin per nurse bee (i.e., $\frac{1}{\xi}$) increase as the transition rate from nurse to forager β_{hf}^m increases (see Appendix A). In Fig. 2, we can see that as V/N increases the brood population and forager task group's size increase in a similar fashion until they both reach a maximum while the nurse task group's size decreases when $\beta_{\mathrm{hf}}^m \approx \frac{1}{7}$. Both brood and foragers follow a similar shape because in our model brood population is mostly dependent by the amount of pollen collected by foragers which then will be converted to nutritious jelly. Another explanation to this observation in our model is that recruiting more pollen foragers increases the inflow of proteinaceous pollen, prompting to lower larval mortality and less starvation (Schmickl and Karsai, 2016). Also, forager task group's size display a maximum when $V/N = 0.0058$ g which corresponds to 7 days old after emerging from cell. This level of VG at 7 days old may represent a minimum time for nurse bees to initiate foraging activity at a faster rate. Also, we can see that the left end to mid-range of the V/N-axis corresponding to the low-mid levels of VG per nurse bee coincide with the transition rate of $\beta_{\mathrm{hf}}^m = (\frac{1}{21}, \frac{1}{7})$. This range is consistent with empirical findings in (Tsuruda and Page, 2009) where the bees start foraging 2–3 weeks after emerging.

Fig. 3 help us understand the impact of α_v, which measures the regulation of VG per nurse bee affecting the developmental time from nursing to foraging, on the dynamics of V/N in our model. For instance, if α_v is too large, then the levels of V/N become very small having no impact on the transition rate from nurse to forager. However, if α_v is too small, it can diminish the tractability of the effects of the levels of VG towards the task switching from nurse to forager. In this figure we can see that as the levels of V/N increase, the task group's size of nurses decreases while the foragers' one increases. This is not true from our assumptions where transition rate from nurses to foragers increases if the VG levels per nurse bee decreases. This is an example in which if α_v is too large, it can overemphasize the regulation effects of levels of VG. However, medium ranges for α_v could be most optimal in our model. Hence, α_v seems to be a sensitive parameter that strongly determines the effects of the levels of V/N on task switching rates and should be chosen very carefully in order to capture more realistic effects.

In Fig. 4 we observe the importance of the rate at which the queen is fed by the nurses given that it can determine the future of the colony since it affects the colony as a whole in the same way. For instance, the highest values of V/N displayed in these figures are given by a small α_q. This means that if very low amount of VG is fed to the queen, the nurse bees will have more VG stored in their body fats. Also, we observe that a decreasing feeding rate to the queen negatively affects the colony no matter if other mechanisms such as feeding the brood, collection rate of

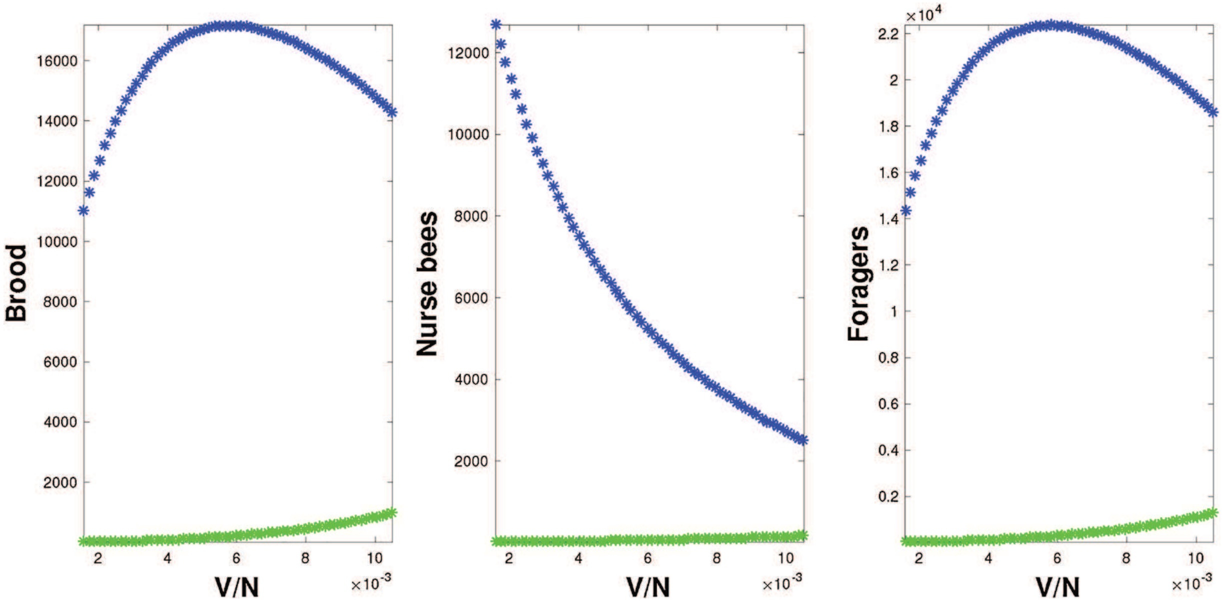


Fig. 2. ($1/\xi$ varying with respect to β_{hf}^m) Effects of the levels of VG per nurse bee with respect to the maximum transition rate from nurse bee to forager β_{hf}^m across all populations. $r = 1$; $a = 0.3$; $b = 2$; $e_g = 3.82{*}10^{-6}$; $\alpha_q = 0.0007$; $\alpha_b = 5{*}10^{-5}$; $c_q = 0.124$; $d_h = .00001$; $d_f = 0.032$; $d_p = 1$; $c = 0.003$; $\alpha = 0.00688$; $\alpha_h = 0.0001$; $\alpha_v = .0005$; $\beta_{bh} = 1/24$ (Stability of equilibria: Stable (blue) and Unstable (green)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pollen, or synthesis of VG are in place.

Decreasing parameters such as α_v, α_q and c_q can increase the VG content per nurse bee, i.e., decreasing the regulation effects of the amount of VG per nurse on the transition rate from nurse bee to forager, feeding rate to the queen, and efficiency of converting the VG for egg-laying by the queen, respectively. Low conversion rate of VG from pollen can cause the colony to collapse (see white region in Fig. 5a–c). Note that these three parameters act in a synergistic manner creating a chain of events starting from the fact that if α_v is reasonably small, then there is an increase amount of foragers more likely bringing back pollen. Then, if the conversion rate from pollen to VG by nurse bees is low, there is not enough VG per nurse bee produced to feed the queen, i.e., small α_q (lower right-end white region in Fig. 5b) and therefore the queen cannot use stored VG for egg-laying production (lower right-end white region in Fig. 5c). All these synergetic effects can cause colony's death. Increasing parameters such as e_g, β_{hf}^m, and d_h can increase VG content per nurse bee, i.e., increasing the average amount of VG per egg laid, the maximum transition rate from nurse bee to forager, and mortality rate of nurse bee, respectively. Large parameter values of e_g and β_{hf}^m and low to medium conversion rate of VG from pollen, c, can cause death of populations within the colony (see Fig. 5d and e). However, if the mortality rate of nurse bees increases or is too large,

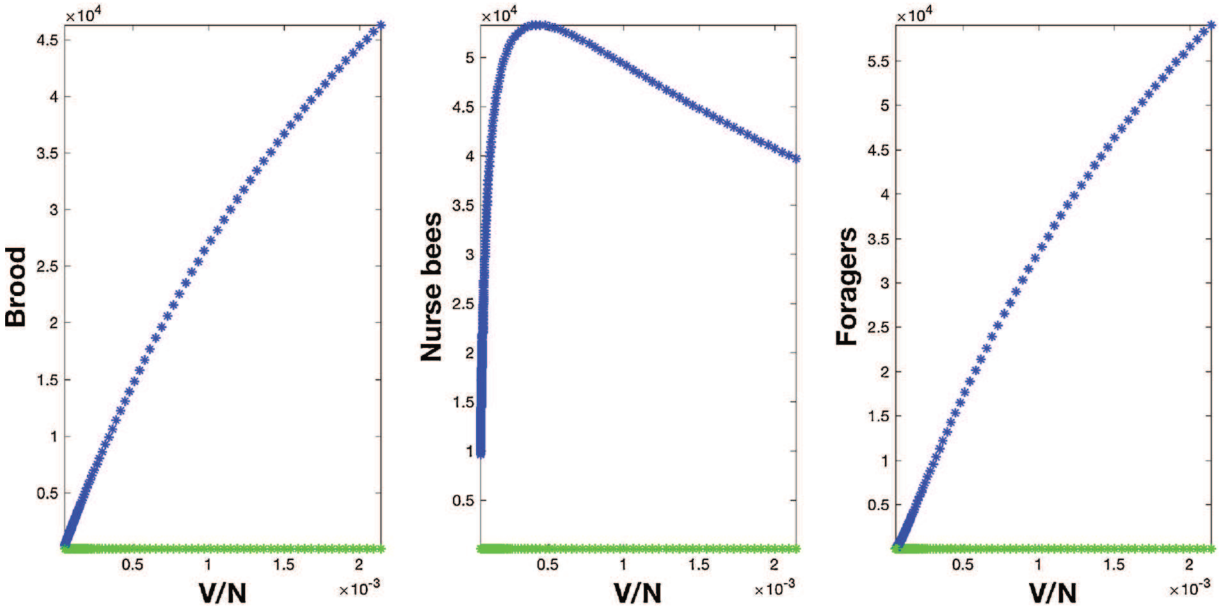


Fig. 3. ($1/\xi$ varying with respect to α_v) Effects of the levels of VG per nurse bee with respect to the effect it has on the developmental rate of transitioning from nurse bee to forager over all populations. $r = 1$; $a = 0.3$; $b = 2$; $e_g = 0.00000382$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_q = 0.0007$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable (blue) and Unstable (green)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

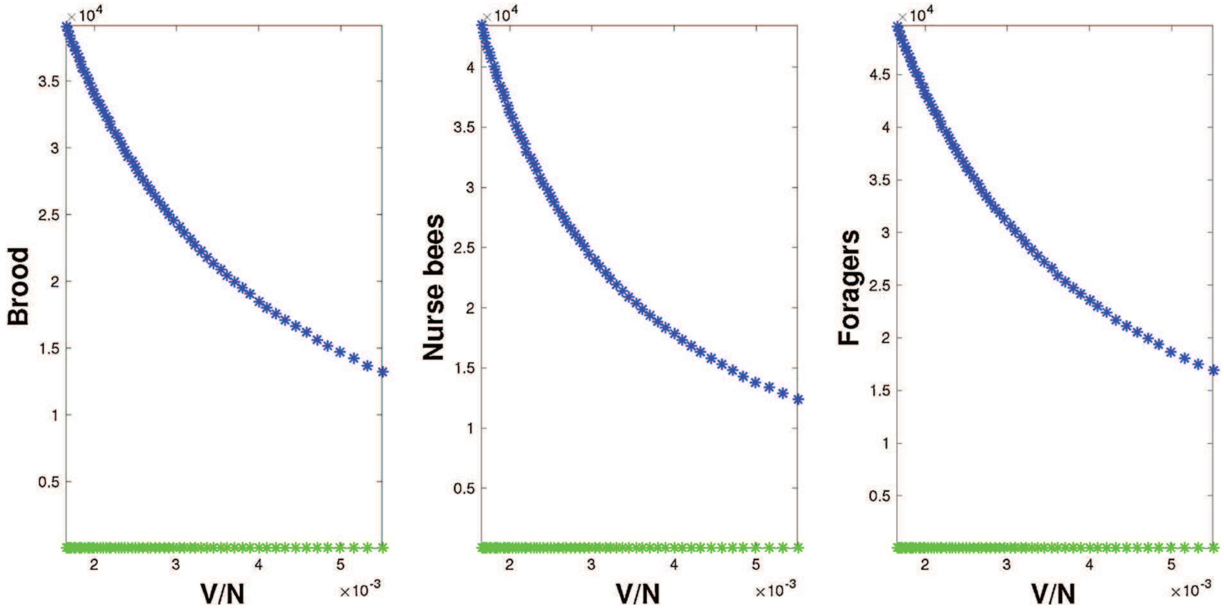
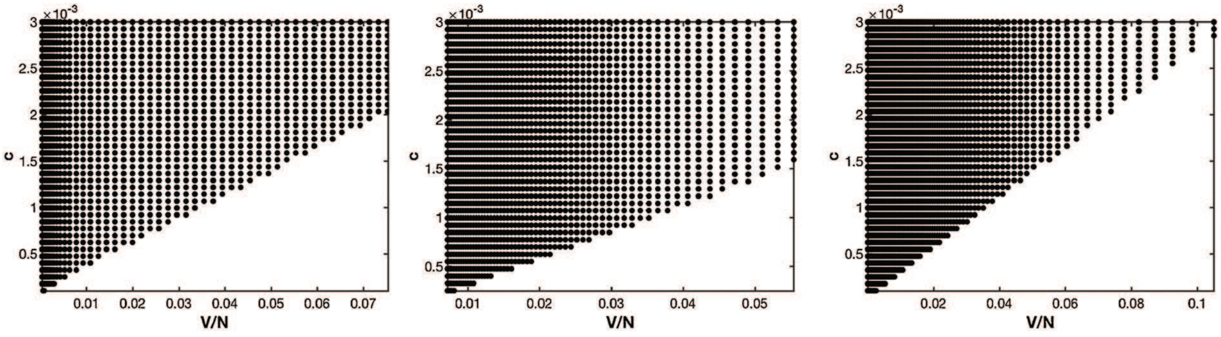


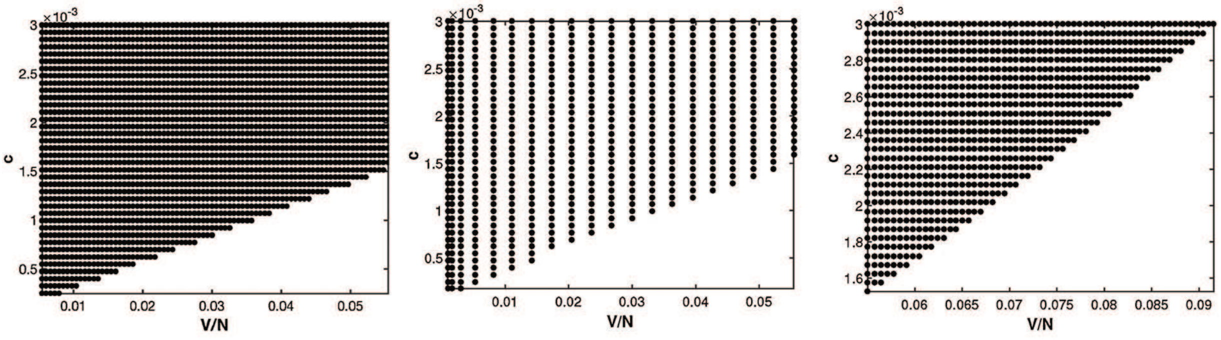
Fig. 4. ($1/\xi$ varying with respect to α_q) Effects of the levels of VG per nurse bee over all populations with respect to the feeding rate to queen. $r = 1$; $a = 0.3$; $b = 2$; $e_g = 0.00000382$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable (blue) and Unstable (green)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

then our results show that the conversion rate of VG to pollen must be high in order to keep the colony alive (see Fig. 5f).

From a simple analysis (see Appendix A), we know that the content of VG per nurse increases with the decrease of c_q which measures the efficiency of using VG for egg-laying production by the queen. Results in Fig. 6a and b suggest that low collection rate of pollen r and low consumption rate of pollen by nurses α, together with low c_q can drive the colony to die out. Similarly, medium to low c_q and low to high values of average feeding rate of VG to brood can cause colony's death (see Fig. 6c). It is clear, from these simulations, that the efficiency of converting VG for egg-laying production by the queen plays an important role for colony survival. In addition, a rapid depletion of food stores for brood feeding can cause the colony to die of starvation (Le Conte and Navajas, 2008).

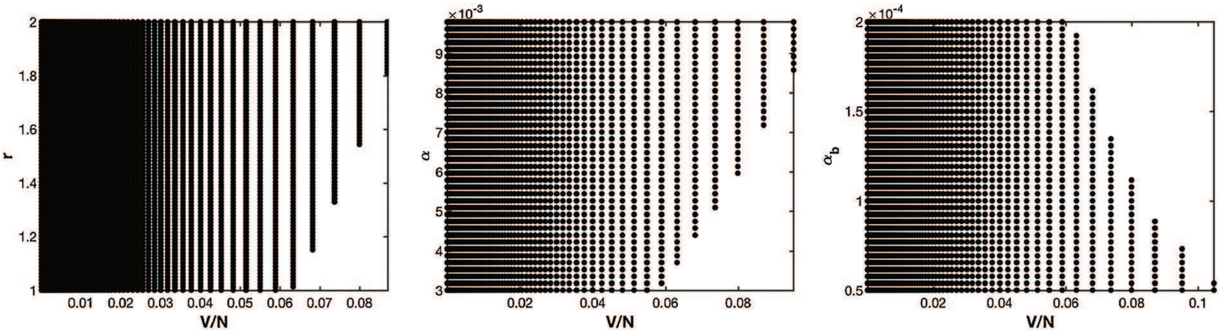


(a) $V/N(\alpha_v)$. (b) $V/N(\alpha_q)$. (c) $V/N(c_q)$.



(d) $V/N(e_g)$. (e) $V/N(\beta^m_{hf})$. (f) $V/N(d_h)$.

Fig. 5. Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta^m_{hf} = .25$;.



(a) $V/N(c_q)$. (b) $V/N(c_q)$. (c) $V/N(c_q)$.

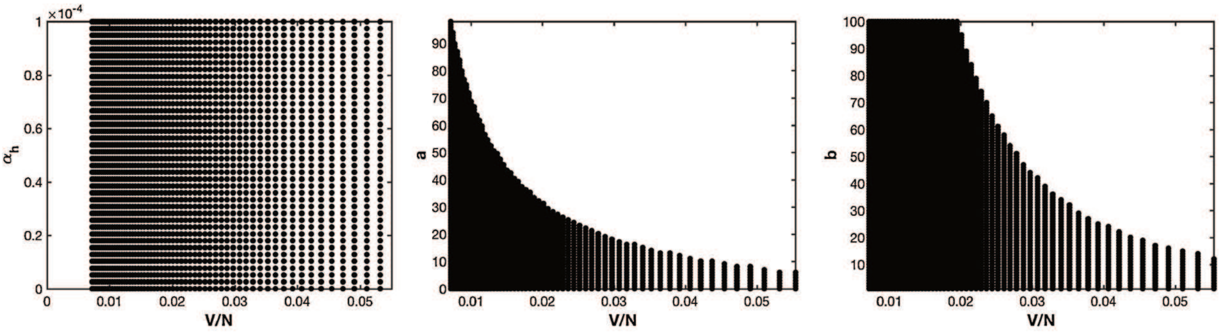
Fig. 6. Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;.

High feeding rate to queen, α_q, prompts a decrease of VG per nurse bee since the queen is usually fed with larger quantities than brood. If this is the case, the nurse bees will not have enough VG to feed brood and for their own metabolic use. Therefore, this extreme situation can cause colony's death (see Fig. 7a). Moreover, if α_q is low, then the regulation effects of current brood in the colony, a, and the regulation effects of stored pollen, b, are high (see white region on right-end of Fig. 7b and b) it will prompt a smaller overall pollen collection rate. However, a small overall pollen collection rate will cause a decrease and limited availability of pollen for consumption by nurse bees and feeding to brood and queen. This scenario will be critical on the survivability of the colony and according to our numerical results in Fig. 7b and c, respectively, shows that nurse bees will invest more on the queen by feeding it at higher rates (reducing available VG per nurse bee) in order to lay more eggs and maintain the colony alive. Also, an increase or decrease of α_q has no influence with respect to the maximum pollen collection rate, r, on determining coexistence of populations within the colony.

In Fig. 8a–c, we vary the parameter a_v which regulates the effects of the levels of VG per nurse that have over the transition rate from nurse to forager. In order to have a clear understanding of these simulations, it is necessary to have in mind that when α_v is very small (close to zero), the effects of the level of VG per nurse on task switching rates from nurse to bee are almost null. Also, 'too large' α_v may have a negative impact in the assumptions made for our model. With this in mind, we proceed to the explanations of each scenario. In Fig. 8a and b, we can see that low collection and consumption rate of pollen, r and α respectively, can cause the colony to die when the levels of VG per nurse bee have no effect on task switching rates, α_v. Further implications can be made about these results. For instance, for our choice of $\beta_{\text{hf}}^m = 0.25$ (fast transition rate from nurse to forager) in these simulations given that r is relatively low (white region in Fig. 8a), it could suggest that foragers are collecting other nutrients such as nectar instead of pollen. Hence, remaining nurse bees may not be able to rear brood due to lack of pollen which may also influence low consumption rate of pollen, α, for VG synthesis (white region in Fig. 8b). Moreover, if the feeding rate to brood, α_b, is high and α_v low (see white region in Fig. 8c), i.e. there is no significant effect of the level of VG per nurse on task switching rates, then the colony may not survive. In general, for any of these cases, we can conclude that regulating the transition rate from nurse to forager by considering levels of VG per nurse bee is of great importance and significant in our modeling.

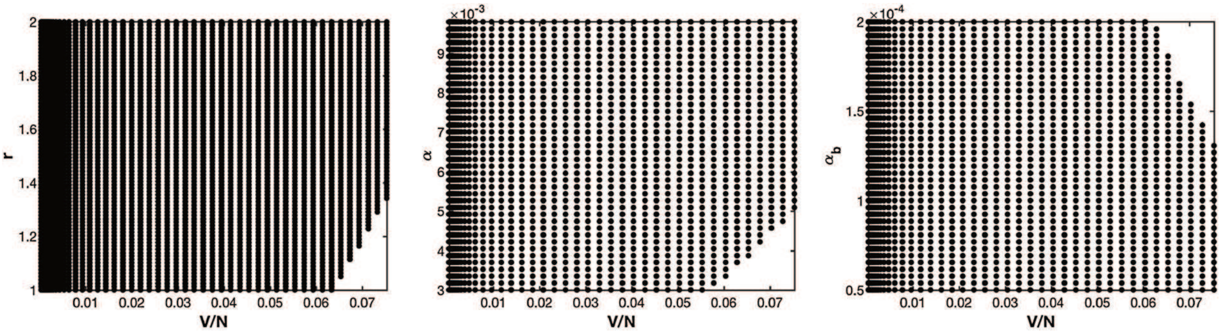
In the following 2D bifurcation we can see the synergistic effects of different parameters. For instance, if the transition rate from nurse bee to forager β_{hf}^m is large (inducing less nurse bees rearing brood) and the conversion rate from pollen to VG by nurse bees c is very small (i.e. levels of VG per nurse bee decreases and it is limited), this will cause the collapse of the colony (see white region of Fig. 9a). In addition, if the consumption and conversion rate of pollen, α and c, respectively, the colony cannot survive due to insufficient levels of VG necessary for the different mechanisms in the colony (see white region of Fig. 9a). Moreover, if we do not consider the regulation effects of available brood and stored pollen in the colony, i.e., $a = b = 0$, our model has a unique interior equilibrium (red point in Fig. 9c). However, if we consider large values of a and b, which produces a very low overall collection rate of pollen, then the colony cannot survive due to insufficient pollen in the colony.

Lastly, we found that variation of V/N (or $\frac{1}{\xi}$) with respect to α_v, c_q, e_g, β_{hf}^m have no effect on the metabolic use of VG in nurse bees, α_h,



(a) $V/N(\alpha_q)$. (b) $V/N(\alpha_q)$. (c) $V/N(\alpha_q)$.

Fig. 7. Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;.



(a) $V/N(\alpha_v)$.

(b) $V/N(\alpha_v)$.

(c) $V/N(\alpha_v)$.

Fig. 8. Area of coexistence and extinction of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;.

on determining the survival of the colony, i.e., decreasing or increasing these parameters with respect to α_h do not cause the colony to die out. Similarly, the variation of V/N with respect to α_q, e_g, β_{hf}^m have no effect on the consumption rate of pollen to VG, α.

3.1. Seasonality effects

First we perform a validity check by including the influence of environmental factors such as change of season affecting pollen collection, which has effects on variation of population sizes within a honeybee colony. Our simulations compare results with empirical data from Harrís (1980). In order to include seasonality in our model we assume that the pollen collection rate has annual periodicity and can be approximated by the first order harmonic:

$$s(t) = r\left(1 + \cos\left(\frac{3\pi(t-\phi)}{365}\right)\right)$$

where r is the baseline collection rate and ϕ is the day of the year when the collection rate is maximal (Fig. 10).

The regulated pollen collection rate in Eq. (4) is then modified as follows:

$$\frac{s(t)B}{1 + \mathrm{aB} + \mathrm{b\,P}}$$

The values of r and ϕ were chosen to fit best to our choice of empirical data. The rest of the parameters from model (7) were chosen by following the ranges in Table 1.

Fig. 11 shows the population dynamics of brood and workers (nurses and foragers) for approximately one year.

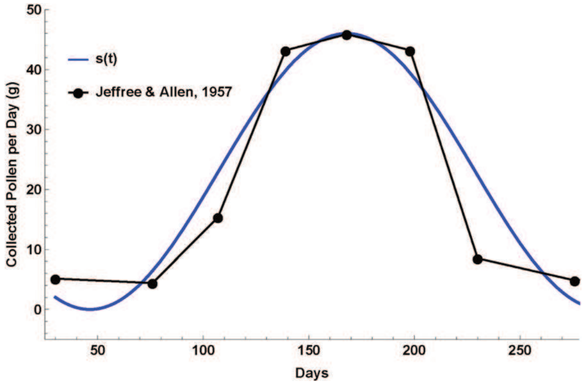
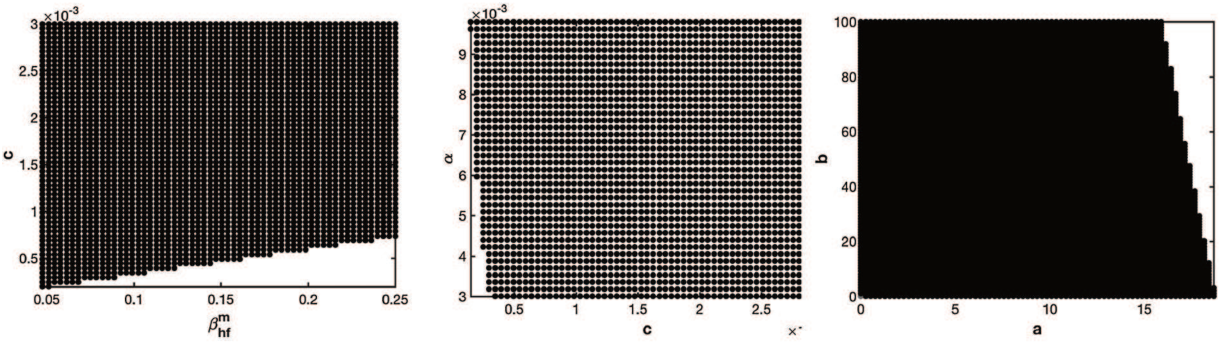


Fig. 10. Data from Allen and Jeffree (1956) was normalized using the information provided in (Camazine et al., 1990) where one full cell can contain 0.27 g of pollen (see also Schmickl and Crailsheim, 2007).

Exploring the long term dynamics of both models considered with and without seasonality we can obtain the following case when the original model without seasonality produces coexistence, meaning both brood and worker populations reach a stable equilibrium, while the model with seasonality produces an output such that the colony die out. Both cases were obtained by lowering simultaneously the parameter value c_q which determines the efficiency of using vitellogenin for egg-laying production by the queen. In this case, the model with seasonality could give us a more realistic intuition of what could happen in the long term, since reducing the efficiency of using the nutrient vitellogenin for



(a)

(b)

(c)

Fig. 9. Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 1$; $a = 0.3$; $b = 2$; $e_g = 3.82{*}10^{-6}$; $\alpha_q = 0.0007$; $\alpha_b = 5{*}10^{-5}$; $c_q = 0.124$; $d_h = .00001$; $d_f = 0.032$; $d_p = 1$; $c = 0.003$; $\alpha = 0.00688$; $\alpha_h = 0.0001$; $\alpha_v = .0005$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = 1/21$.

Table 1
Parameters description and values for VG model.

Parameter	Description	Value	Reference
r	Maximum collecting rate of pollen	average of [1,2] g/day per bee	Percival (1950)
a	Regulation effects of brood towards pollen collection	(0,10)	est. from simulation
b	Regulation effect of stored pollen towards pollen collection	(0,10)	est. from simulation
e_g	Average content of VG in one egg	[0.0000025–0.0000075] g/egg	Amdam and Omholt (2002)
c_q	Efficiency of converting VG into egg production by the queen	(0, 1) Per gram	assumption
c	Conversion rate of pollen per gram to VG	[0,0.003] per gram of pollen (summer &autumn), [0,0.00012] per gram in winter	Amdam and Omholt (2002)
α	Consumption rate of pollen by nurses	0.055 g/day	Camazine et al. (1990)
α_b	Average consumption of VG by brood	[0.00005,0.0002] g/day	Amdam and Omholt (2002)
α_h	Metabolic use of VG by nurse bee	$\leq$ 0.0001 g/day	Amdam and Omholt (2002)
α_q	Feeding rate to queen	[0.00025,0.0007] g/day	est. from simulations
α_v	Regulation of VG per nurse bee affects the developmental time from nurse bee to forager	(0,1) g/unit	est. from simulations
$\beta_{bh} = \frac{1}{\tau_{bh}}$	Transition rate from brood to nurse bee	$\frac{1}{24}$ per day	Winston (1992)
$\beta_{hf}^{m} = \frac{1}{\tau_{hf}}$	Maximum transition rate from nurse bee to forager (2–3 weeks old as an adult bee)	$(\frac{1}{3}, \frac{1}{21})$ per day	Winston (1992)
d_h	Mortality rate of nurse bees	(0,0.17) per day	Rueppell et al. (2007)
d_f	Mortality rate of forager	(0,0.8) per day	Rueppell et al. (2007)
d_p	Deterioration rate of pollen (1–8 days) per day	(0.125, 1) per day	Winston (1992)

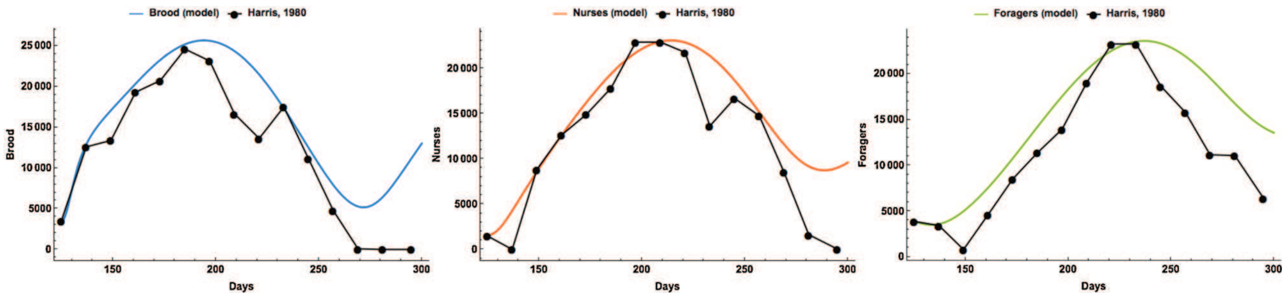
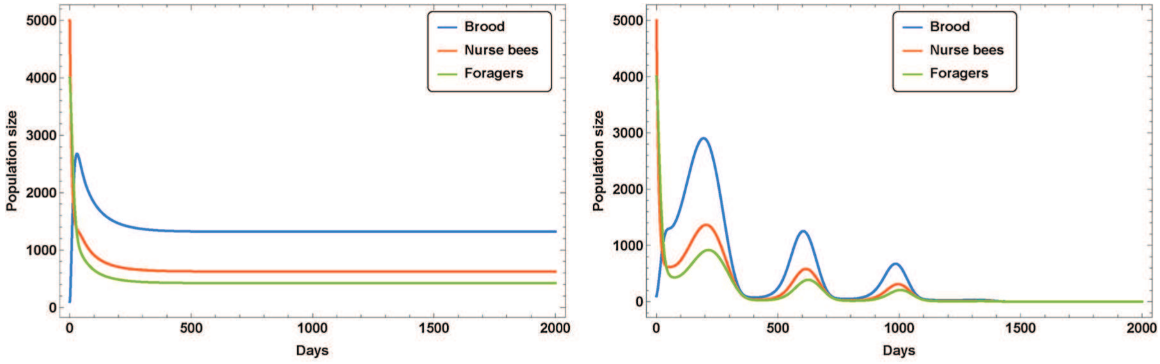


Fig. 11. Empirical data from Harrís (1980); $\phi = 135$; $r = 1.3$; $a = 0.3$; $b = 5$; $e_g = 7.32{*}10^{-6}$; $\alpha_q = 0.000688$; $\alpha_b = 5.48{*}10^{-5}$; $c_q = 0.125$; $d_h = .0008$; $d_f = 0.036$; $d_p = 1$; $c = 0.003$; $\alpha = 0.06$; $\alpha_h = 0.000046$; $\alpha_v = .00055$; $\beta_{bh} = 1/24$; $\beta_{hf}^{m} = 1/21$; Initial conditions at $t = 125$ days: $P(t) = 17$; $V(t) = 2$; $B(t) = 3539$; $H(t) = 1487$; $F(t) = 3875$.



(a) Model without seasonality showing colony survival.

(b) Model with seasonality showing colony collapse.

Fig. 12. Time series of original model and model with seasonality showing different long term dynamics using parameter values: $r = 1$; $a = 0.95$; $b = 4$; $e_g = 4.88{*}10^{-6}$; $\alpha_q = 0.0007$; $\alpha_b = 5{*}10^{-5}$; $c_q = 0.4$; $d_h = .02$; $d_f = 0.1$; $d_p = 1$; $c = 0.003$; $\alpha = 0.006$; $\alpha_h = 0.0001$; $\alpha_v = 5{*}10^{-5}$; $\beta_{bh} = 1/24$; $\beta_{hf}^{m} = 1/21$; $\phi = 165$; Initial conditions at $t = 0$ days: $P(t) = 20$; $V(t) = 2$; $B(t) = 100$; $H(t) = 5000$; $F(t) = 4000$.

egg-laying by the queen could cause a decrease of new brood produced and therefore a decrease of future adult workers until the colony dies out (see Fig. 12).

3.2. Sensitivity analysis

Up until this point, our model simulations, including bifurcations and time series, rely on parameter values (see Table 1) that have been collected from numerous empirical studies, while some are yet unknown. In many of these studies, the precision at which this values were measured is uncertain. However, these parameters can be considered a good baseline to study our model and make predictions. Nevertheless, we consider sensitivity analysis techniques such as Partial Rank Correlation Coefficient (PRCC) by using an appropriate sampling technique such as Latin Hypercube Sampling (LHS) in order to determine which parameters are important in contributing to the variability of outcomes. In this case, we the outcomes of interest are the population size of brood B, and workers of both task groups, i.e., nurse bees N, and foragers F, but also the nutritional content of VG per nurse given by $\text{NV}^{-1} = \frac{1}{\xi}$.

This sensitivity analysis method can quantify the impact of model outcomes given the uncertainty of parameters and initial conditions (input) (Marino et al., 2008). In this case, our model outcomes will be the size of each of the populations considered in our model and the nutritional content of VG per nurse at a given time-point. The LHS method assumes a uniform distribution to create ranges of parameters with their respective baseline values (Marino et al., 2008). We perform multiple runs ($N = 500$) of the sampled values for the response output. Here, we use the best-fit parameter values as the baseline values to compute LHS PRCC values with ± 15% to create the ranges.

In order to quantify the impact of seasonality in our model, we asses the sensitivity on the size of populations considered in our model (i.e. brood and adult worker bees) and the vitellogenin content per nurse bee to each of the parameters at a given time point. We explore the sensitivity of parameters on these population sizes for our model (7) with and without seasonality. The results for each model, respectively, are depicted in blue (no seasonality) and purple (with seasonality). The time-points considered at each outcome are the highest and lowest point for each population in Fig. C.19.

In Figs. 13–16, we observe that the sensitivity of parameters in the model without seasonality (in blue) at $t = 185$, 360, and 380 have no difference, but also in the model with seasonality (in purple) at time $t = 185$ (when both brood and worker populations are at the highest). However, we can determine that the parameters having a positive impact on these population sizes for these cases are the collection rate of pollen, conversion rate of pollen to VG, the queen's feeding rate, the efficiency of converting VG for egg production by the queen, and the maximum transition rate from nurse bee to forager (r, c, α_q, c_q, and β_{hf}^m, respectively). The parameters having a negative impact on the brood population size are the brood's regulation effects on pollen collection, the brood's feeding rate, the average content of VG in one egg, the metabolic use of VG by nurse bee, forager's mortality rate, and the transition rate from brood to nurse bee (a, α_b, e_g, α_h, d_f, and β_{bh}, respectively).

Furthermore, in Fig. 13, sensitivity analysis of parameters at time $t = 360$, when population size is the lowest (Fig. C.19) in the model with seasonality (in purple), shows a different outcome than at $t = 185$ (in purple). Here we observe that, when population is at the lowest, the parameters having a positive impact on the population size are r, c, β_{hf}^m, and ϕ; and the parameters having a negative impact are a, d_f, α_h, and β_{bh}. In comparison, at the time-point when brood population is at the highest, parameters such as α_q and c_q had a positive impact on the population size but not at the lowest point. In terms of seasonality, when the brood population is at the highest, it represents the period of time when queen's nutritional status is of utmost important for egg-laying production.

In Fig. 14, we observe that the parameters having a positive impact on the nurse task group size (outcome) at the time-point $t = 185$ and at $t = 360$ (both in purple) are r, α_q, c_q, and c. In addition to the previous parameters listed, at the time-point when the size of the nurse task group is the highest, β_{bh} shows a positive impact on the population size. This makes sense since transition rate from brood to adult bee as a nurse determines nurse task group size. Also, at time $t = 360$ (in purple), when the size of the nurse task group is the lowest, we observe that instead β_{bh} has a significant negative impact on this task group size and α_v, which regulates the transition rate from nurse bee to forager given levels of VG titers in their body fat, has a positive impact on the outcome. This suggests that regulation effects on task switching has an important impact on maintaining nurse bees in colony's low season.

In general, the parameters having a positive impact on brood population and nurse task group sizes across all times (higher and lowest points) are the collection rate of pollen, the conversion rate of pollen to VG, and the maximum transition rate from nurse to forager (r, c, β_{hf}^m). Notice that these parameters are linked to each other representing the availability of food source for the brood (available pollen foragers bringing back pollen to the hive for VG production).

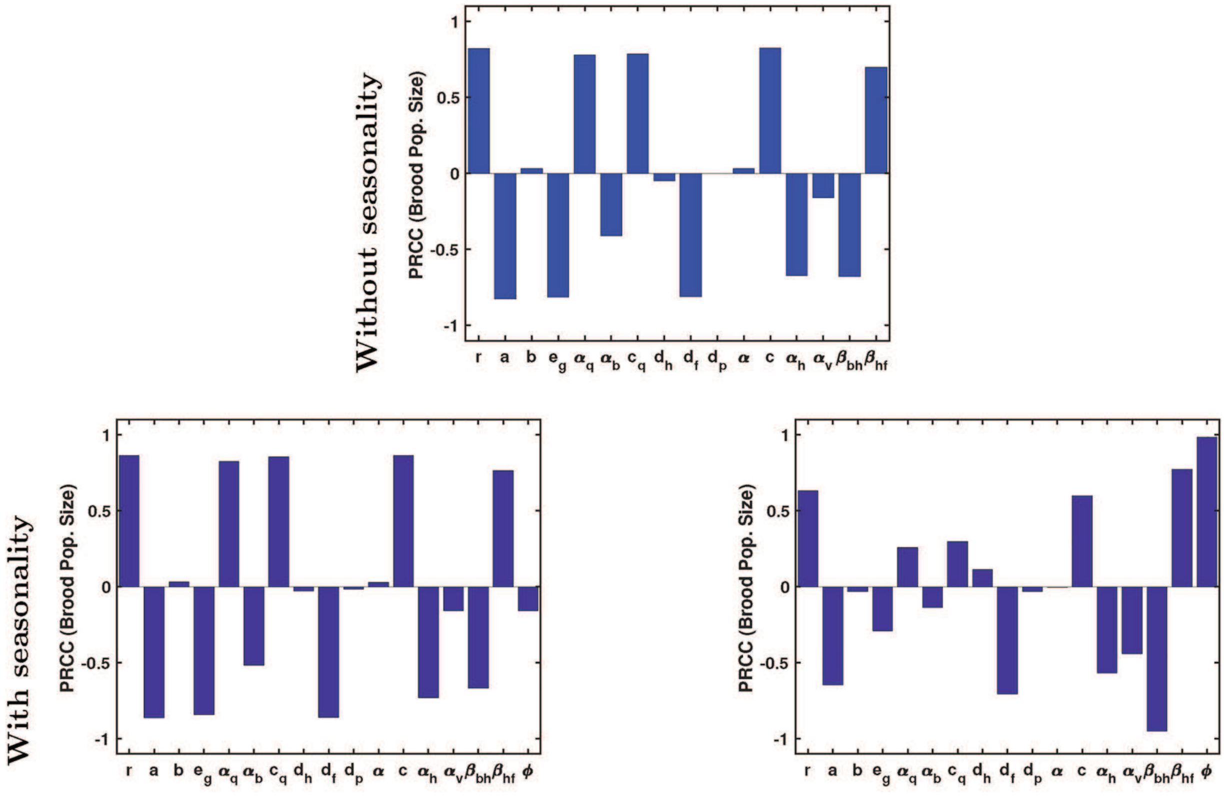
In Fig. 15, the sensitivity of parameters at time $t = 370$, when population size is the lowest in the model with seasonality (in purple), shows a different outcome than at $t = 200$ (in purple). Here we observe that when forager task group size is at the lowest, the parameters having a positive impact on the size of this task group are e_g and β_{hf}^m; and the parameters having a negative impact are α_q, c_q, d_f, and α_v. In comparison, at the two different time-points, we conclude that the parameter describing the maximum transition rate from nurse to forager β_{hf}^m has a positive impact on the forager task group size across all time and not seasonal-sensitive. Also, we observe that parameters such as e_g, α_q, and c_q have opposite impact at the highest point versus at the lowest point, changing from positive to negative, respectively. This suggest that if more VG is spent towards queen's feeding for egg-laying production during low season (i.e. winter, cold temperatures, rainy), the forager task group size can be negatively affected due to an increase of foraging behavior to satisfy colony needs. In reality, this is unlikely to occur since bees have the ability to determine when to forage under good weather conditions. However, it is known that the colony prepares for overwintering season and a decrease number of foragers is needed which it is reflected in these results. Also, another result implying this, is that the parameter α_v describing the regulation effects of amount of VG per nurse bee on the transition time from nurse to forager has a higher and more significant negative impact on the forager task group size. This implies that the parameter α_v strongly regulate the transition time from nurse to forager given that more VG titers are in the fat body of nurse bees since less is used towards brood and queen feeding.

In Fig. 16, we observe that parameters in the model with seasonality (in purple) at time $t = 185$ having a positive impact on the outcome: amount of vitellogein per nurse bee, are e_g, β_{hf}^m, and ϕ, and similarly for the time-point $t = 360$, except for ϕ which is having a negative impact on the outcome. This is explained by the fact that at $t = 185$ corresponds to the high foraging and brood production season, whereas at $t = 360$ corresponds when pollen collection and brood production is low, thus showing a negative impact on the outcome. Moreover, parameters having a significantly negative impact on the amount of VG per nurse bee are α_q, and c_q at $t = 185$ (when brood population size is at the highest), and, in addition, d_f at $t = 360$ (when brood population size is at the lowest). This suggests that efficiency of feeding the queen for brood production has a significant negative impact on the amount of VG per nurse bee, and in any case, it shows the importance to the colony. On the other hand, at time-point $t = 360$, forager death rate d_f is negatively affecting the amount of VG per nurse bee and this can be explained by the fact that this time-point corresponds to colony's low season when weather is not optimal for foraging and pollen collection rate r is minimal (see positive to negative impact switch in Fig. 16a and b in purple).

4. Discussion

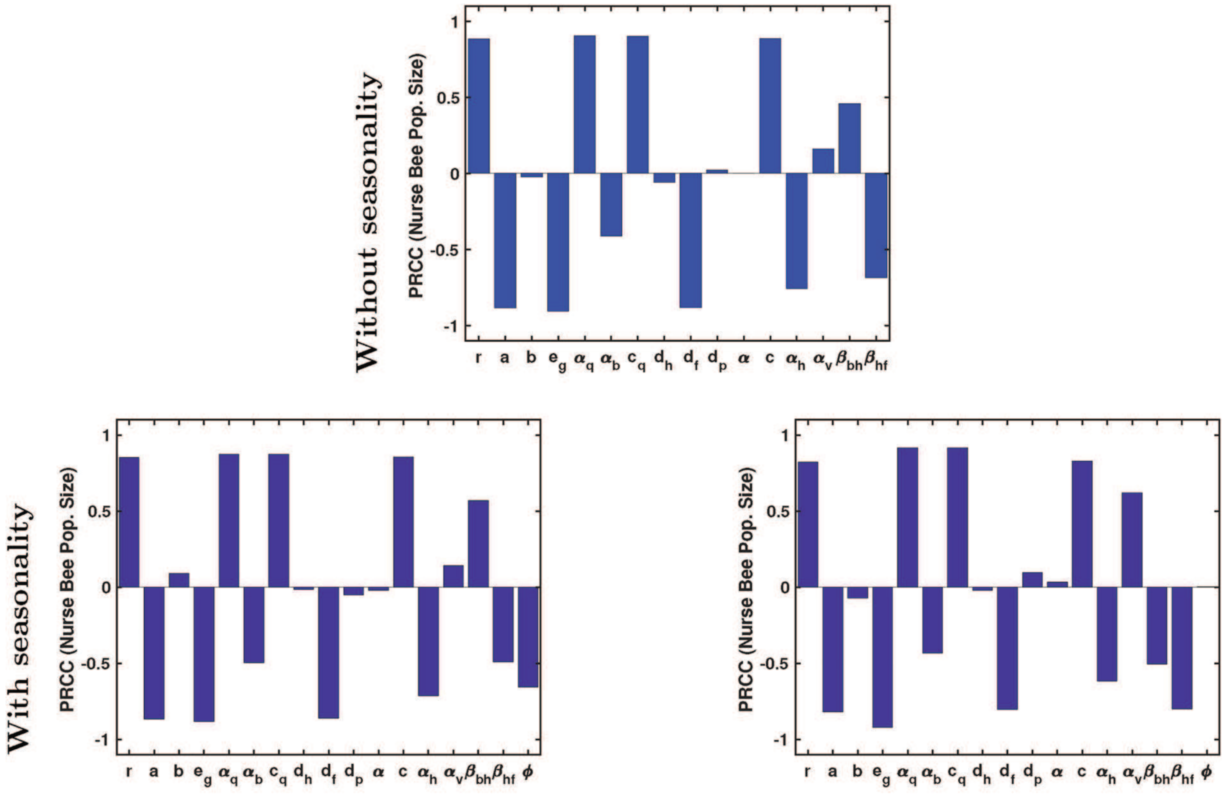
The population dynamics of honeybees has been studied for decades now (Hölldobler and Wilson, 2009; Ament et al., 2010) by looking at different aspects and mechanisms that regulate and influence sudden or gradual changes of the brood and worker populations within a colony. The study of the mechanisms that enable or restrict changes in behavior of honeybees in response to changes in the environment is an active area of research (Ament et al., 2010; Schulz et al., 1998; Toth et al., 2005; Toth and Robinson, 2005; Robinson, 1992).

The intention of the model presented here is not an attempt to simulate reality but to provide a modeling framework that considers factors influencing colony dynamics (i.e., growth or decrease of population). In this work, we explore the effects of an essential



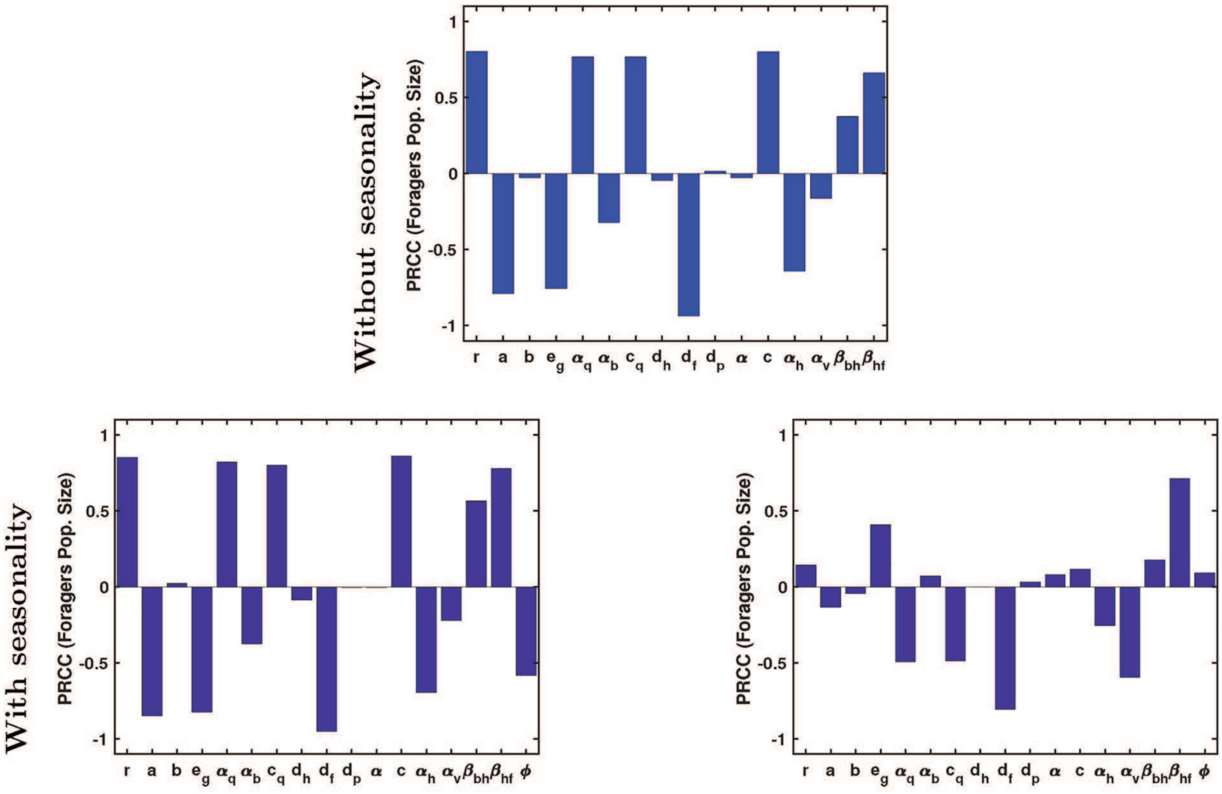
(a) $t = 185$ days (b) $t = 360$ days

Fig. 13. PRCC values for the parameters of model (7) using the population size of brood as the output of interest.



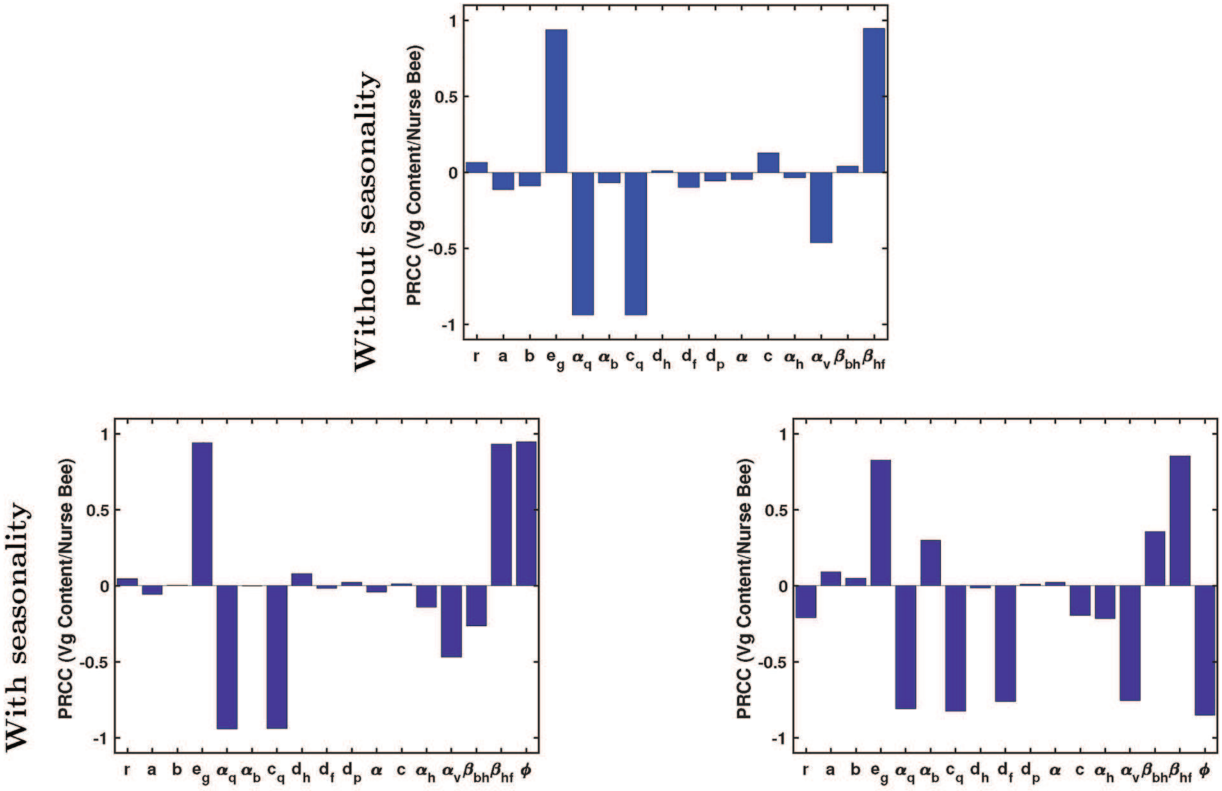
(a) $t = 200$ days (b) $t = 380$ days

Fig. 14. PRCC values for the parameters of model (7) using the population size of nurse bees as the output of interest.



(a) $t = 200$ days (b) $t = 370$ days

Fig. 15. PRCC values for the parameters of model (7) using the population size of forager bees as the output of interest.



(a) $t = 185$ days (b) $t = 360$ days

Fig. 16. PRCC values for the parameters of model (7) using the level of vitellogenin per nurse bee as the output of interest.

environmental variable influencing the age-based division of labor of worker honeybees is their nutritional status (Ament et al., 2010; Avni et al., 2014). For instance, in the work of (Avni et al., 2014), important understanding of the temporal and spatial fluctuations of pollen-derived nutrients for honeybees were provided. However, their findings do not support the hypothesis of colony growth affected by pollen quantity and nutritional quality. Specifically, we focused on the effects of vitellogenin content per nurse bee and how it interacts with the essential demographic and allocation processes within the colony to influence colony growth.

We presented a non-linear differential equation system that models the population dynamics of a honeybee colony. This model considers the population of brood and adult workers divided in two task groups (nurses and foragers), stored pollen in the hive and vitellogenin content in nurse bees. Analytical results of model (7) provide the existence of up to two interior equilibria, i.e., two possible points where all the components of our model B, N, F, P, V are greater than zero and have the potential to become stable. The size of both the brood and worker populations within the colony at a stable point are directly dependent upon the increase of VG levels per nurse bee, i.e., increase of $\frac{1}{\xi}$. Also, coexistence of both brood and worker populations is dependent upon enough food to feed the brood (pollen collected and converted to VG and available foragers). For example, among African races of *A. mellifera*, starvation is more frequent because they store low honey reserves (Toth et al., 2005; Winston, 1991).

From the numerical simulations, we learned that the parameter α_v, which describes the regulation effects that the levels of VG per nurse bee have on the transition rate from nurse to forager, seems to be very sensitive. For instance, too small α_v can neutralize the regulation effects of task switching, but too large can overemphasize these effects. Therefore, a good value choice for α_v in our model is critical to capture true regulation effects of levels of VG per nurse bee on the transition rate form nurse to forager. In addition, the regulation effects of current brood in the colony and stored pollen, a and b, respectively, are very important in our model. These parameters give a certain sensitivity that respond to brood pheromone and current levels of stored pollen in cells. In our model, when these parameters are ‘too large’, it means that there is enough pollen to feed current brood and foragers must decrease foraging for pollen. Under this scenario, low pollen collection rate and low queen feeding rate can cause colony's death. The only way a colony can survive is if feeding rate of the queen is high enough, since it will prompt production of new brood to preserve the colony. In Fig. 4 we can see that a decreasing rate of α_q decreases both brood and worker population sizes.

Several scenarios in our numerical simulations provide conditions at which the colony is prone to die. For instance, low collection rate of pollen by foragers leads to low pollen consumption rate by nurse bees, which promotes colony's death (see white region in Fig. 6). This implication has been explored in the work of Naug (2009) stating that scarce food resources lead to low pollen consumption rates, which then affects the ability to improve worker longevity (Huang, 2012). Our results also confirmed that survival of the colony is dependent on worker longevity. For instance, as the mortality rate of nurse bees increases, it is necessary to maintain a high conversion rate of pollen to VG in order to provide enough food for new brood (see Fig. 5f). However, rapid depletion of food stores for brood feeding can cause the colony die of starvation (Le Conte and Navajas, 2008). Also, our results indicate that medium to large conversion rate of pollen to VG by nurse bees is necessary for colony survival providing enough VG available to feed the queen for egg-laying production (see Fig. 5a–c). In general, the rates of food collection and consumption are essential elements of food storage inside the hive (Anderson et al., 2014).

Further results indicate that fast transition rate from nurse bee to forager can cause the colony to die out (see Fig. 5d and e). In the long run, if the transition rate from nurse to forager is high it may not be sustainable for the colony because there will be fewer available nurse bees synthesizing VG and rearing brood while foragers have higher mortality rates during high foraging season. Gordon (1996) states that rapid changes in tasks are caused as a result of a response to environmental stimuli. Other results show that when the efficiency of using vitellogenin for egg-laying production by the queen is decreased (or low), the levels of vitellogenin per nurse bee increases. An explanation of this could be that the queen is not been fed enough and therefore not able to produce eggs. For instance, depending on food conditions, some species of ants control the composition of eggs and nutritional quality (Wheeler, 1986).

The sensitivity analysis performed in this study helped us quantify the impact of model outcomes given the uncertainty of parameters and initial conditions. We used PRCC sensitivity analysis with LHS as the sampling technique in order to determine which parameters are more influential on the different outcomes of interest. We found that the parameters having a positive impact on brood population and nurse task group sizes across all time are the pollen collection rate, pollen conversion rate to vitellogenin, and the maximum transition rate from nurse to forager. These parameters show that the availability of food resources, specifically pollen (Huang, 2012), mainly for brood survival and brood production, are of vital importance for the success of the colony, which has been confirmed in the work of Naug (2009). Also, results showed that the amount of VG titers per nurse bee is significantly positively influenced by the amount of VG deposited in an egg and the period of time corresponding to the colony's high season, but also the transition rate from nurse bee to foraging. However, the amount of VG titers per nurse bee is significantly negatively influenced by queen's feeding rate and the efficiency of converting VG for egg production. Overall, the sensitivity analysis provided further confirmation that food source for queen, egg production, and developing brood are of vital importance for colony's success.

Lastly, we considered seasonality for the collection rate of pollen since, in reality, pollen collection rate is not constant due to changes in weather conditions (Synge, 1947; Thorp, 1979). In order to perform a validity check of our model with seasonality, we compared time series simulations generated by our model with empirical data from Harrís (1980). Comparing the effects of seasonality model (7), we learned that seasonality can provide a more realistic intuition of long term consequences. For instance, when the efficiency of converting VG for egg-laying production is decreased, the model without seasonality does not show catastrophic events such as colony's death, however, the model with seasonality showed a periodic decrease of population size until the colony collapsed (see Fig. 12).

Several studies with mathematical models for honeybee colonies are existent (Schmickl and Crailsheim, 2007; Khoury et al., 2013; Becher et al., 2014; Perry et al., 2015; Schmickl and Karsai, 2017). Most of these have modeled the population dynamics of honeybees and nutrient stores. For example, Schmickl and Crailsheim (2007) created a model to study the population and resource dynamics of a honeybee colony and including the effect of division of labor in the hive. However, the modeling approach is complicated and since it is well known that bees have a strong age-based division of labor, the theory used to model task allocation is more relevant in ants. The model presented in Khoury et al. (2013) has similar assumptions to ours. However, one of the main differences from our model is the assumption of the transition from nurse bee to forager. In our model, we assume that the transition from nurse bee to foragers increases by a transition rate that depends on the levels of vitellogenin in the nurse bee and not only by the absence of stored food and reduced social inhibition. Also, we enhanced their simple assumption of food collection rate by including the regulation effects of brood pheromone and stored pollen. In BEEHAVE by Becher et al. (2014), although they take into considerations many aspects affecting colony dynamics, they assume that the level of pollen and nectar stores in the colony affects the age at which workers initiate foraging activities. They do not take into account other mechanisms changing at the molecular (Guidugli et al., 2005; Amdam et al., 2010; Amdam and Omholt, 2002, 2003) and physiological level (Johnson, 2005; Amdam and Omholt, 2002). In our model, we attempt to incorporate in a general manner those mechanisms within a bee that affect the initiation of foraging. The model of Perry et al. (2015) proposes an ODE model that captures the impacts of precocious foraging induced by different stressors. The model suggests that food limitation set by inefficiency of a young foraging force would hasten colony terminal decline. Results from our model also suggest that high transition rate to foraging (i.e. precocious bees) can cause a decline of brood and forager population. These implications have also been reviewed by (Klein et al., 2017; Scofield and Mattila, 2015) stating that early foraging and for a short period is due to shortage of pollen, and thus vitellogenin, during development. In any case, these models are useful in their own way and have been designed to address specific questions.

The analytical and numerical results presented here are unique and simple in the sense that we incorporate mechanisms that affect the age-based division of labor and implications that can have on the change of brood and worker population sizes over time. We presented basic but important assumptions that can help us understand and have greater insight in the complexity of honeybee population dynamics given their nutritional status and(or) needs. This model can be extended by including other scenarios such as limiting the pollen influx in the late summer and study how it can affect the lifespan of bees and possibly lead to colony collapse, or when bees opt to engage in brood cannibalism as a natural strategy to recycle protein. Other mechanism to be included is the transition back from forager to nurse bee under certain environmental conditions (Oettler et al., 2015), and the interplay of diseases or infections, such as *Nosema ceranae* which is known to alter vitellogenin levels, and therefore alter normal age polyethism causing colony imbalance (BenVau and Nieh, 2017; Goblirsch et al., 2013).

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Appendix A. Effects of parameters on ξ which measures nurse bees' nutritional status

- ξ is always increasing with α_q:

$$\frac{\partial \xi}{\partial \alpha_q} = \frac{c_q}{2d_h e_g}\left(1 + \frac{e_g(d_h - \beta_{\mathrm{hf}}^m) + c_q\alpha_q\alpha_v}{\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}}\right) > 0$$

- ξ is always increasing with c_q:

$$\frac{\partial \xi}{\partial c_q} = \frac{\alpha_q}{2d_h e_g}\left(1 + \frac{e_g(d_h - \beta_{\mathrm{hf}}^m) + c_q\alpha_q\alpha_v}{\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}}\right) > 0$$

- ξ increases with α_v as long as the maximum transition rate from nurse to forager is greater than the nurse bee death rate:

$$\frac{\partial \xi}{\partial \alpha_v} = \frac{-c_q\alpha_q\alpha_v(d_h - \beta_{\mathrm{hf}}^m) - e_g(d_h + \beta_{\mathrm{hf}}^m)^2 + (d_h + \beta_{\mathrm{hf}}^m)\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}}{2d_h \alpha_v^2\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}} > 0$$

  if $c_q\alpha_q\alpha_v(\beta_{\mathrm{hf}}^m - d_h) > e_g(d_h + \beta_{\mathrm{hf}}^m)^2$ when $\beta_{\mathrm{hf}}^m > d_h$.
- ξ always decreases with e_g:

$$\frac{\partial \xi}{\partial e_g} = -\frac{c_q\alpha_q\left(d_h e_g + c_q\alpha_q\alpha_v - e_g\beta_{\mathrm{hf}}^m + \sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}\right)}{2d_h e_g^2\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^m))^2}} < 0,$$

  because simplifying this inequality we obtain the following true inequality: Fig. A.17

  $d_h e_g^2 \beta_{\mathrm{hf}}^m > 0$

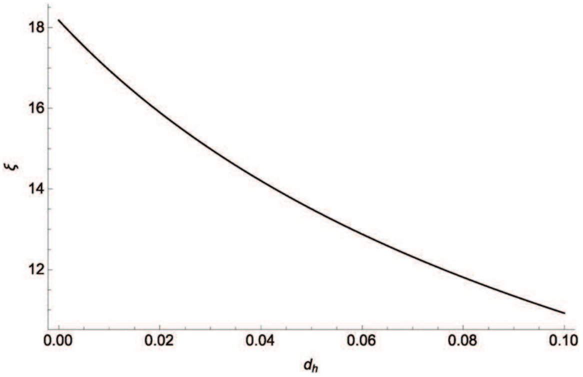


Fig. A.17. Effects on ξ as d_h increases.

- ξ always decreases with β_{hf}^{m}:

$$\frac{\partial \xi}{\partial \beta_{\mathrm{hf}}^{m}} = \frac{\frac{-c_q\alpha_q\alpha_v + e_g(d_h + \beta_{\mathrm{hf}}^{m})}{\sqrt{4c_q d_h e_g \alpha_q \alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^{m}))^2}} - 1}{2d_h\alpha_v} < 0,$$

because simplifying this inequality we obtain the following true inequality: $4c_q d_h e_g \alpha_q \alpha_v > 0$

- ξ always decreases with d_h:

$$\frac{\partial \xi}{\partial d_h} = c_q\alpha_q\alpha_v + e_g\beta_{\mathrm{hf}} + \frac{d_h e_g(d_h e_g + c_q\alpha_q\alpha_v + e_g\beta_{\mathrm{hf}}}{\sqrt{4c_q d_h e_g\alpha_q\alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^{m}))^2}} - \sqrt{4c_q d_h e_g\alpha_q\alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^{m}))^2} < 0,$$

because simplifying this inequality we obtain the following inequality:

$$(c_q\alpha_q\alpha_v - e_g\beta_{\mathrm{hf}}^{m})^2 + (c_q\alpha_q\alpha_v + e_g\beta_{\mathrm{hf}}^{m})(d_h e_g + \sqrt{4c_q d_h e_g\alpha_q\alpha_v + (c_q\alpha_q\alpha_v - e_g(d_h + \beta_{\mathrm{hf}}^{m}))^2}) > 0$$

Appendix B. Proofs and mathematical analysis

Equilibria derivation

Assume that (P^*, V^*, B^*, N^*, F^*) is an interior equilibrium of Model (7), then it satisfies the following five equations:

From $B' = 0$,

$$\frac{c_q\alpha_q}{e_g}V - \beta_{\mathrm{bh}}B = 0 \quad \Leftrightarrow \quad B^* = \frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}}V^*$$

From $N' = 0$,

$$\beta_{\mathrm{bh}}B - \frac{\beta_{\mathrm{hf}}^{m}N}{1 + \alpha_h\frac{N}{V}} - d_hN = 0 \quad \Leftrightarrow \quad \frac{c_q\alpha_q}{e_g}V - \frac{\beta_{\mathrm{hf}}^{m}N}{1 + \alpha_v\frac{N}{V}} - d_hN = 0 \quad \Leftrightarrow \quad N^* = \xi V^*$$

$$\Leftrightarrow \frac{N}{\xi}\left(\frac{c_q\alpha_q}{e_g}\right) = N\left(d_h + \frac{\beta_{\mathrm{hf}}^{m}}{1 + \alpha_v\xi}\right) \quad \Leftrightarrow \quad \frac{c_q\alpha_q}{\xi e_g} = d_h + \frac{\beta_{\mathrm{hf}}^{m}}{1 + \alpha_v\xi}$$

From $F' = 0$,

$$\frac{\beta_{\mathrm{hf}}^{m}N}{1 + \alpha_v\frac{N}{V}} - d_fF = 0 \quad \Leftrightarrow \quad F^* = \frac{\beta_{\mathrm{hf}}^{m}N^*}{d_f\left(1 + \alpha_v\frac{N^*}{V^*}\right)} = \frac{\beta_{\mathrm{hf}}^{m}N^*}{d_f(1 + \alpha_v\xi)} \tag{B.1}$$

From $V' = 0$,

$$c\alpha \mathrm{NP} - (1 - c_q)\alpha_qV - \alpha_h\mathrm{NV} - \alpha_b\mathrm{B\,V} = d_hV + \frac{\beta_{\mathrm{hf}}^{m}V}{1 + \alpha_v\frac{N}{V}}$$

$$c\alpha\mathrm{NP} - \left((1 - c_q)\alpha_q + \alpha_hN + \alpha_b\frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}}V\right)V = \left(d_h + \frac{\beta_{\mathrm{hf}}^{m}}{1 + \alpha_v\frac{N}{V}}\right)V$$

$$c\alpha\mathrm{NP} = \left((1 - c_q)\alpha_q + \alpha_hN + \alpha_b\frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}}V\right)V + \frac{c_q\alpha_q}{\xi e_g}V$$

$$\Leftrightarrow P^* = \frac{(1 - c_q)\alpha_q + \frac{c_q\alpha_q}{\xi e_g}}{c\alpha}\frac{V^*}{N^*} + \frac{\alpha_hV^*}{c\alpha} + \frac{c_q\alpha_b\alpha_qV^*}{c\alpha e_g\beta_{\mathrm{bh}}}\frac{V^*}{N^*} = \frac{(1 - c_q)\alpha_q + \frac{c_q\alpha_q}{\xi e_g}}{c\alpha\xi} + \frac{\alpha_hV^*}{c\alpha} + \frac{c_q\alpha_b\alpha_qV^*}{c\alpha e_g\beta_{\mathrm{bh}}\xi}$$

$$\Leftrightarrow \quad \frac{(1 - c_q)\alpha_q + \frac{c_q\alpha_q}{\xi e_g}}{c\alpha\xi} + \frac{\alpha_hN^*}{c\alpha\xi} + \frac{c_q\alpha_b\alpha_qN^*}{c\alpha\xi e_g\beta_{\mathrm{bh}}\xi} = \frac{\alpha_q}{c\alpha\xi}\left((1 - c_q) + \frac{c_q}{\xi e_g}\right) + \frac{N^*}{c\alpha\xi}\left(\alpha_h + \frac{c_q\alpha_b\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}\right)$$

$$P^* = \Phi(\xi) + \frac{N^*}{c\alpha\xi}\left(\alpha_h + \frac{c_q\alpha_b\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}\right)$$

From $P' = 0$ and substituting B^*, F^*, P^*,

$$\frac{rB^*F^*}{1 + \mathrm{a}B^* + \mathrm{b}P^*} - \alpha N^*P^* - d_pP^* = 0 \quad \Leftrightarrow \quad \frac{r\frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}N^*\frac{\beta_{\mathrm{hf}}^{m}N^*}{d_f(1 + \alpha_v\xi)}}{1 + a\frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}N^* + \mathrm{b}P^*} = P^*(\alpha N^* + d_p)$$

$$r\frac{c_q\alpha_qN^{*2}}{\xi e_g\beta_{\mathrm{bh}}d_f}\left(\frac{c_q\alpha_q}{e_g\xi} - d_h\right) = \left(\Phi(\xi) + \frac{N^*}{c\alpha\xi}\left(\alpha_h + \frac{c_q\alpha_b\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}\right)\right)(1 + a\frac{c_q\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}N^* + b\Phi(\xi) + \frac{\mathrm{b}N^*}{c\alpha\xi}\left(\alpha_h + \frac{c_q\alpha_b\alpha_q}{e_g\beta_{\mathrm{bh}}\xi}\right))(\alpha N^* + d_p) \tag{B.2}$$

where

$$\begin{aligned}
\xi &= \frac{c_q\alpha_q\alpha_v - d_h e_g - \beta_{\text{hf}} e_g + \sqrt{(c_q\alpha_q\alpha_v - e_g d_h - e_g\beta_{\text{hf}})^2 + 4c_q\alpha_q\alpha_v d_h e_g}}{2\alpha_v d_h e_g}\\
&= \frac{\frac{c_q\alpha_q\alpha_v - \beta_{\text{hf}} e_g}{d_h e_g} - 1 + \sqrt{(\frac{c_q\alpha_q\alpha_v - \beta_{\text{hf}} e_g}{d_h e_g} - 1)^2 + \frac{4c_q\alpha_q\alpha_v}{d_h e_g}}}{2\alpha_v}\\
\Phi(\xi) &= \frac{[(1-c_q)\alpha_q + d_h]}{c\alpha\xi} + \frac{\beta_{\text{hf}}^m}{c\alpha\xi(1+\alpha_v\xi)} = \frac{(1-c_q)\alpha_q}{c\alpha\xi} + \frac{c_q\alpha_q}{c\alpha e_g\xi^2} = \frac{\alpha_q}{c\alpha\xi}\left[1 - c_q\left(1 - \frac{1}{e_g\xi}\right)\right].
\end{aligned} \tag{B.3}$$

Jacobian

The stability of the equilibria of Model (7) is determined using the following Jacobian matrix evaluated at each of the $\mathbf{E_i}$.

$$\begin{aligned}
J &= \begin{pmatrix}
-d_p - \frac{\text{brBF}}{(1+\text{aB}+\text{bP})^2} - \alpha N & 0 & \frac{\text{Fr}}{1+\text{aB}+\text{bP}}\left(1 - \frac{\text{aB}}{1+\text{aB}+\text{bP}}\right) & -\alpha P & \frac{\text{rB}}{1+\text{aB}+\text{bP}}\\
\alpha\text{c N} & -d_h - \alpha_h N - (1-c_q)\alpha_q - \frac{\beta_{\text{hf}}^m}{1+\alpha_v\frac{N}{V}}\Psi_2 & 0 & \alpha\text{cP} - \alpha_h V - \frac{\alpha_v\beta_{\text{hf}}^m}{\left(1+\alpha_v\frac{N}{V}\right)^2} & 0\\
0 & \frac{\alpha_q c_q}{e_g} & -\beta_{\text{bh}} & 0 & 0\\
0 & \frac{N^2\alpha_v\beta_{\text{hf}}^m}{V^2\left(1+\alpha_v\frac{N}{V}\right)^2} & \beta_{\text{bh}} & -d_h - \frac{\beta_{\text{hf}}^m}{1+\alpha_v\frac{N}{V}}\Psi_1 & 0\\
0 & -\frac{N^2\alpha_v\beta_{\text{hf}}^m}{V^2\left(1+\alpha_v\frac{N}{V}\right)^2} & 0 & \frac{\beta_{\text{hf}}^m}{1+\alpha_v\frac{N}{V}}\Psi_1 & -d_f
\end{pmatrix}\\
&= \begin{pmatrix}
-d_p - \frac{\text{brBF}}{(1+\text{aB}+\text{bP})^2} - \alpha N & 0 & \frac{\text{Fr}}{1+\text{aB}+\text{bP}}\left(1 - \frac{\text{aB}}{1+\text{aB}+\text{bP}}\right) & -\alpha P & \frac{\text{rB}}{1+\text{aB}+\text{bP}}\\
\alpha\text{c N} & -d_h - \alpha_h N - (1-c_q)\alpha_q - \frac{\beta_{\text{hf}}^m}{1+\alpha_v\xi}\Psi_2 & 0 & \alpha\text{cP} - \alpha_h V - \frac{\alpha_v\beta_{\text{hf}}^m}{(1+\alpha_v\xi)^2} & 0\\
0 & \frac{\alpha_q c_q}{e_g} & -\beta_{\text{bh}} & 0 & 0\\
0 & \frac{\xi^2\alpha_v\beta_{\text{hf}}^m}{(1+\alpha_v\xi)^2} & \beta_{\text{bh}} & -d_h - \frac{\beta_{\text{hf}}^m}{1+\alpha_v\xi}\Psi_1 & 0\\
0 & -\frac{\xi^2\alpha_v\beta_{\text{hf}}^m}{(1+\alpha_v\xi)^2} & 0 & \frac{\beta_{\text{hf}}^m}{1+\alpha_v\xi}\Psi_1 & -d_f
\end{pmatrix}
\end{aligned} \tag{B.4}$$

where $\Psi_1 = 1 - \frac{\alpha_v N}{V\left(1+\alpha_v\frac{N}{V}\right)} = 1 - \frac{\alpha_v\xi}{(1+\alpha_v\xi)}$ and $\Psi_2 = 1 + \frac{\alpha_v N}{V\left(1+\alpha_v\frac{N}{V}\right)} = 1 + \frac{\alpha_v\xi}{(1+\alpha_v\xi)}$.

Proof of Theorem 3.1

Proof. We start by showing positivity of Model (7) as follows: Note that

$$P'|_{P=0} = \frac{\text{rBF}}{1+\text{aB}} \geq 0, \qquad V'|_{V=0} = c\alpha\text{NP}$$

$$B'|_{B=0} = \frac{c_q\alpha_q}{e_g}V \geq 0, \qquad N'|_{N=0} = \beta_{\text{bh}}B \geq 0, \qquad F'|_{F=0} = \frac{\beta_{\text{hf}}^m N}{1+\alpha_v\frac{N}{V}} \geq 0$$

hence according to Theorem A.4 (p.423) in Thieme (2003), we can conclude that the system (7) is positively invariant in $\mathbb{R}_+^5$. To show existence of equilibria, notice that from Eq. (B.2), we can obtain the following polynomial, which is the nullcline of our model:

$$f(N) = c_3N^3 + c_2N^2 + c_1N + c_0, \tag{B.5}$$

where c_i, $i = 0, 1, 2, 3$ are polynomial of ξ:

$$\begin{aligned}
c_3 &= d_f\alpha(1+\alpha_v\xi)(c_q\alpha_b\alpha_q + e_g\alpha_h\beta_{\text{bh}}\xi)(c_q\alpha_q(b\alpha_b + \text{ac}\alpha\xi) + \text{be}_g\alpha_h\beta_{\text{bh}}\xi) > 0\\
c_2 &= \text{bd}_f(1+\alpha_v\xi)(c_q\alpha_b\alpha_q + e_g\alpha_h\beta_{\text{bh}}\xi)(c_q d_p\alpha_b\alpha_q + e_g\beta_{\text{bh}}\xi(d_p\alpha_h + 2c\alpha^2\xi\Phi(\xi)))\\
&\quad + c\alpha\xi(e_g\alpha\beta_{\text{bh}}\xi(d_f e_g\alpha_h\beta_{\text{bh}}\xi(1+\alpha_v\xi) + c_q\alpha_q(d_f\alpha_b(1+\alpha_v\xi) - \text{cr}\beta_{\text{hf}}^m\xi))\\
&\quad + \text{ac}_q d_f\alpha_q(1+\alpha_v\xi)(c_q d_p\alpha_b\alpha_q + e_g\beta_{\text{bh}}\xi(d_p\alpha_h + c\alpha^2\xi\Phi(\xi))))\\
c_1 &= \text{cd}_f e_g\alpha\beta_{\text{bh}}\xi^2(1+\alpha_v\xi)\\
&\quad (c_q d_p\alpha_q(\alpha_b + 2b\alpha_b\Phi(\xi) + \text{ac}\alpha\xi\Phi(\xi)) + e_g\beta_{\text{bh}}\xi(c\alpha^2\xi\Phi(\xi)(1+b\Phi(\xi)) + d_p(\alpha_h(1+2b\Phi(\xi)))))) > 0\\
c_0 &= c^2 d_f d_p e_g^2\alpha^2\beta_{\text{bh}}^2\xi^4\Phi(\xi)(1+\alpha_v\xi)(1+b\Phi(\xi)) > 0
\end{aligned}$$

$$N_1^c = \frac{-d_1 - \sqrt{d_1^2 - 2d_0}}{3} < 0 \quad \text{and} \quad N_2^c = \frac{-d_1 + \sqrt{d_1^2 - 2d_0}}{3} > 0$$

This indicates $f(N)$ has no positive roots. If $\alpha_b < \text{cr}\xi\frac{\beta_{\text{hf}}}{d_f(1+\alpha_v\xi)}$, i.e. $d_1 < 0$, then $f(N)$ has two critical points such that $0 < N_1^c < N_2^c$. Hence since

$f'(0) = d_0 > 0$, $f(N)$ has a local maximum at N_1^c since

$$f(N_1^c) = \frac{27c_3^2(c_0 + c_2) - 9c_1c_3X_1 + 3c_3X_1^2 - X_1^3}{27c_3^3} > 0,$$

where $X_1 = \left(\frac{c_2}{c_3} + \sqrt{\left(\frac{c_2}{c_3}\right)^2 - 2\frac{c_0}{c_3^2}}\right) < 0$. Also, $f(N)$ has a local minimum at N_2^c. since

$$f(N_2^c) = \frac{27c_3^2(c_0 + c_2) + 9c_1c_3X_2 + 3c_3X_2^2 - X_2^3}{27c_3^3} < 0,$$

where $X_2 = \left(-\frac{c_2}{c_3} + \sqrt{\left(\frac{c_2}{c_3}\right)^2 - 2\frac{c_0}{c_3^2}}\right) > 0$, given that $\frac{c_2}{c_3} = d_1 < 0$. This implies that $f(N)$ has two positive roots, i.e. Model (7) has two interior equilibria.

$$J(0, 0, 0, 0, 0) = \begin{pmatrix} -d_p & 0 & 0 & 0 & 0 \\ 0 & -d_h - (1 - c_q)\alpha_q & 0 & 0 & 0 \\ 0 & \frac{\alpha_q c_q}{e_g} & -\beta_{\text{bh}} & 0 & 0 \\ 0 & 0 & \beta_{\text{bh}} & -d_h & 0 \\ 0 & 0 & 0 & 0 & -d_f \end{pmatrix},$$

which eigenvalues are:

$$\lambda_1 = -d_f, \quad \lambda_2 = -d_h, \quad \lambda_3 = -d_p, \quad \lambda_4 = -d_h - \alpha_q(1 - c_q), \quad \lambda_5 = -\beta_{\text{bh}}.$$

Hence, the extinction equilibrium is always locally asymptotically stable as long as $c_q < 1$.

Appendix C. Supplemental Material

Additional numerical results.

In Fig. C.18 we observe the effects of the average amount of VG that a laid egg by the queen can contain. In our model, increasing e_g increases levels of VG per nurse bee ($1/\xi$), thus, if the queen deposits large amounts of VG into an egg, then VG is recycled back into the available VG in the colony. However, it seems that depositing ‘large’ amounts of VG into eggs can have a negative effect on both the brood and worker populations size since as e_g increases these population sizes decrease.

The following figure aids the set up for sensitivity analysis results.

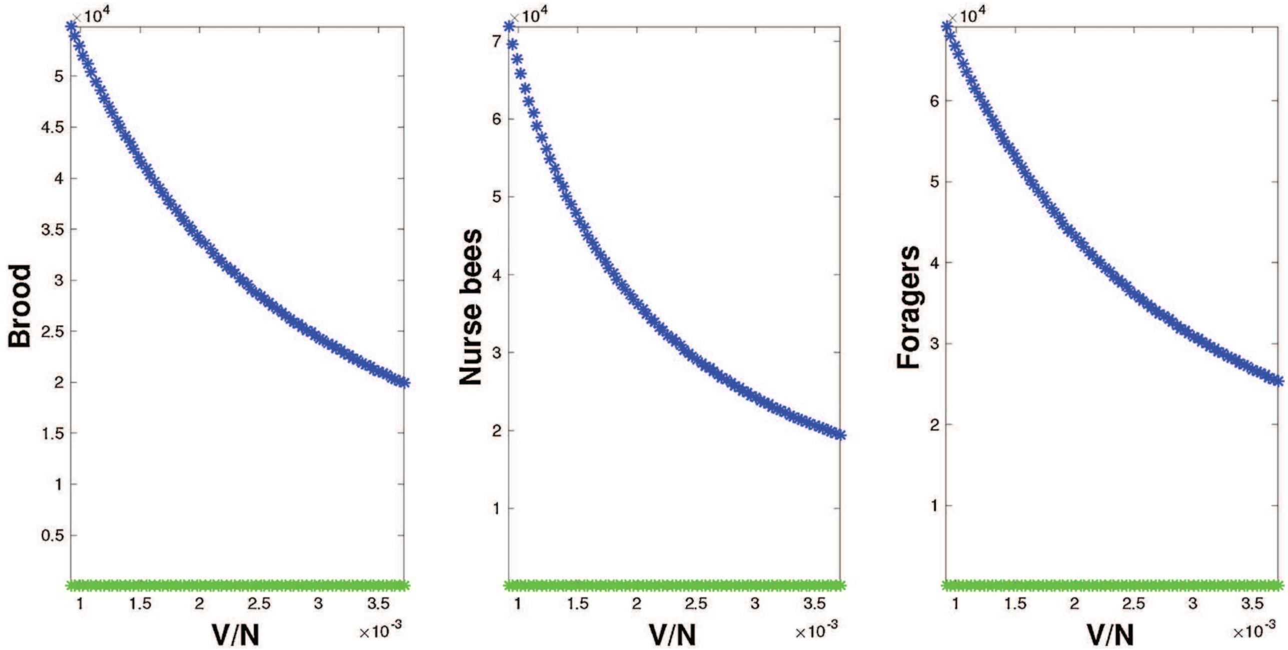
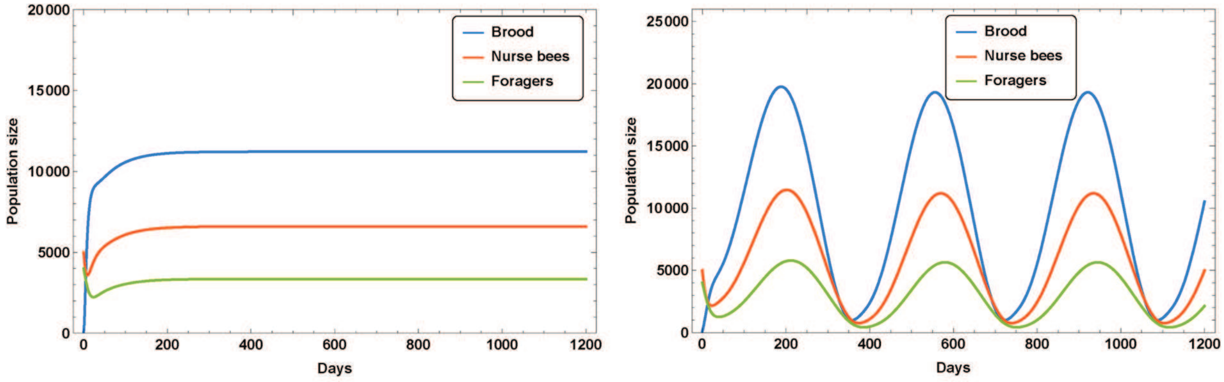


Fig. C.18. ($1/\xi$ varying with respect to e_g) Effects of the levels of VG per nurse bee over all populations with respect to the average levels of VG in one egg. $r = 1$; $a = 0.3$; $b = 2$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_q = 0.0007$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable (blue) and Unstable (green)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



(a) Model with no seasonality

(b) Model with seasonality

Fig. C.19. Time series of original model and model with seasonality showing different long term dynamics using parameter values: $r = 1$; $a = 0.95$; $b = 4$; $e_g = 4.88*10^{-6}$; $\alpha_q = 0.0007$; $\alpha_b = 5*10^{-5}$; $c_q = 0.4$; $d_h = .02$; $d_f = 0.1$; $d_p = 1$; $c = 0.003$; $\alpha = 0.006$; $\alpha_h = 0.0001$; $\alpha_v = 5*10^{-5}$; $\beta_{bh} = 1/24$; $\beta_{hf}^{m} = 1/21$; $\phi = 150$; Initial conditions at $t = 0$ days: $P(t) = 20$; $V(t) = 2$; $B(t) = 100$; $H(t) = 5000$; $F(t) = 4000$.

References

Abou-Shaara, H., 2014. The foraging behaviour of honey bees, *Apis mellifera*: a review. Vet. Med. 59 (1).

Ahn, K., Xie, X., Riddle, J., Pettis, J., Huang, Z.Y., 2012. Effects of long distance transportation on honey bee physiology. Psyche: J. Entomol. 2012.

Alaux, C., Dantec, C., Parrinello, H., Le Conte, Y., 2011. Nutrigenomics in honey bees: digital gene expression analysis of pollen's nutritive effects on healthy and varroa-parasitized bees. BMC Genomics 12 (1), 496.

Allen, M.D., Jeffree, E.P., 1956. The influence of stored pollen and of colony size on brood rearing of honeybees. Ann. Appl. Biol. 44 (4), 649–656.

Allen, M.D., 1960. The honeybee queen and her attendants. Anim. Behav. 8 (3), 201–208.

Amdam, G.V., Omholt, S.W., 2002. The regulatory anatomy of honeybee lifespan. J. Theor. Biol. 216 (2), 209–228.

Amdam, G.V., Omholt, S.W., 2003. The hive bee to forager transition in honeybee colonies: the double repressor hypothesis. J. Theor. Biol. 223 (4), 451–464.

Amdam, G.V., Norberg, K., Hagen, A., Omholt, S.W., 2003. Social exploitation of vitellogenin. Proc. Natl. Acad. Sci. U. S. A. 100 (4), 1799–1802.

Amdam, G.V., Simões, Z.L., Hagen, A., Norberg, K., Schrøder, K., Mikkelsen, Ø., Kirkwood, T.B., Omholt, S.W., 2004. Hormonal control of the yolk precursor vitellogenin regulates immune function and longevity in honeybees. Exp. Gerontol. 39 (5), 767–773.

Amdam, G.V., Rueppell, O., Fondrk, M.K., Page, R.E., Nelson, C.M., 2009. The nurse's load: early-life exposure to brood-rearing affects behavior and lifespan in honey bees (*Apis mellifera*). Exp. Gerontol. 44 (6), 467–471.

Amdam, G., Ihle, K., Page, R., 2010. Regulation of honeybee worker (*Apis mellifera*) life histories by vitellogenin. Hormones, Brain and Behavior Online. Elsevier Inc.

Ament, S.A., Wang, Y., Robinson, G.E., 2010. Nutritional regulation of division of labor in honey bees: toward a systems biology perspective. Wiley Interdiscipl. Rev.: Syst. Biol. Med. 2 (5), 566–576.

Anderson, K.E., Carroll, M.J., Sheehan, T., Mott, B.M., Maes, P., Corby-Harris, V., 2014. Hive-stored pollen of honey bees: many lines of evidence are consistent with pollen preservation, not nutrient conversion. Mol. Ecol. 23 (23), 5904–5917.

Avni, D., Hendriksma, H.P., Dag, A., Uni, Z., Shafir, S., 2014. Nutritional aspects of honey bee-collected pollen and constraints on colony development in the eastern Mediterranean. J. Insect Physiol. 69, 65–73.

Becher, M.A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P.J., Osborne, J.L., 2014. Beehave: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. J. Appl. Ecol. 51 (2), 470–482.

Becher, M., Grimm, V., Knapp, J., Horn, J., Twiston-Davies, G., Osborne, J., 2016. Beescout: a model of bee scouting behaviour and a software tool for characterizing nectar/pollen landscapes for beehave. Ecol. Model. 340, 126–133.

BenVau, L.R., Nieh, J.C., 2017. Larval honey bees infected with *Nosema ceranae* have increased vitellogenin titers as young adults. Sci. Rep. 7 (1), 14144.

Bitondi, M., Simoes, Z.P., 1996. The relationship between level of pollen in the diet, vitellogenin and juvenile hormone titres in africanized *Apis mellifera* workers. J. Apicult. Res. 35 (1), 27–36.

Brodschneider, R., Crailsheim, K., 2010. Nutrition and health in honey bees. Apidologie 41 (3), 278–294.

Calderone, N.W., 1998. Proximate mechanisms of age polyethism in the honey bee, *Apis mellifera* L. Apidologie 29 (1–2), 127–158.

Camazine, S., Sneyd, J., Jenkins, M.J., Murray, J., 1990. A mathematical model of self-organized pattern formation on the combs of honeybee colonies. J. Theor. Biol. 147 (4), 553–571.

Camazine, S., 1993. The regulation of pollen foraging by honey bees: how foragers assess the colony's need for pollen. Behav. Ecol. Sociobiol. 32 (4), 265–272.

Carroll, M.J., Brown, N., Goodall, C., Downs, A.M., Sheenan, T.H., Anderson, K.E., 2017. Honey bees preferentially consume freshly-stored pollen. PLoS ONE 12 (4), e0175933.

Crailsheim, K., Schneider, L., Hrassnigg, N., Bühlmann, G., Brosch, U., Gmeinbauer, R., Schöffmann, B., 1992. Pollen consumption and utilization in worker honeybees (*Apis mellifera* carnica): dependence on individual age and function. J. Insect Physiol. 38 (6), 409–419.

Crailsheim, K., 1992. The flow of jelly within a honeybee colony. J. Compar. Physiol. B 162 (8), 681–689.

DeGrandi-Hoffman, G., Chen, Y., Huang, E., Huang, M.H., 2010. The effect of diet on protein concentration, hypopharyngeal gland development and virus load in worker honey bees (*Apis mellifera* L.). J. Insect Physiol. 56 (9), 1184–1191.

Dreller, C., Page, R.E., Fondrk, M.K., 1999. Regulation of pollen foraging in honeybee colonies: effects of young brood, stored pollen, and empty space. Behav. Ecol. Sociobiol. 45 (3–4), 227–233.

Fewell, J., Page, R., 1993. Genotypic variation in foraging responses to environmental stimuli by honey bees, *Apis mellifera*. Cell. Mol. Life Sci. 49 (12), 1106–1112.

Fewell, J.H., Winston, M.L., 1992. Colony state and regulation of pollen foraging in the honey bee, *Apis mellifera* L. Behav. Ecol. Sociobiol. 30 (6), 387–393.

Frias, B.E.D., Barbosa, C.D., Lourenço, A.P., 2016. Pollen nutrition in honey bees (*Apis mellifera*): impact on adult health. Apidologie 47 (1), 15–25.

Glavinic, U., Stankovic, B., Draskovic, V., Stevanovic, J., Petrovic, T., Lakic, N., Stanimirovic, Z., 2017. Dietary amino acid and vitamin complex protects honey bee from immunosuppression caused by *Nosema ceranae*. PLoS ONE 12 (11), e0187726.

Goblirsch, M., Huang, Z.Y., Spivak, M., 2013. Physiological and behavioral changes in honey bees (*Apis mellifera*) induced by *Nosema ceranae* infection. PLOS ONE 8 (3), e58165.

Gordon, D.M., 1996. The organization of work in social insect colonies. Nature 380 (6570), 121–124.

Groot, A.P.d., 1953. Protein and Amino Acid Requirements of the Honeybee (*Apis mellifica* L.).

Guidugli, K.R., Nascimento, A.M., Amdam, G.V., Barchuk, A.R., Omholt, S., Sim oes, Z.L., Hartfelder, K., 2005. Vitellogenin regulates hormonal dynamics in the worker caste of a eusocial insect. FEBS Lett. 579 (22), 4961–4965.

Hölldobler, B., Wilson, E.O., 2009. The Superorganism: The Beauty, Elegance, and Strangeness of Insect Societies. WW Norton & Company.

Harrís, J.L., 1980. A population model and its application to the study of honey bee colonies (master's thesis).

Haydak, M.H., 1970. Honey bee nutrition. Annu. Rev. Entomol. 15 (1), 143–156.

Hendriksma, H.P., Shafir, S., 2016. Honey bee foragers balance colony nutritional deficiencies. Behav. Ecol. Sociobiol. 70 (4), 509–517.

Herbert Jr., E.W., Shimanuki, H., 1978. Chemical composition and nutritive value of bee-collected and bee-stored pollen. Apidologie 9 (1), 33–40.

Hrassnigg, N., Crailsheim, K., 1998. Adaptation of hypopharyngeal gland development to the brood status of honeybee (*Apis mellifera* L.) colonies. J. Insect Physiol. 44 (10), 929–939.

Huang, Z.-Y., Otis, G., 1989. Factors determining hypopharyngeal gland activity of worker honey bees (*Apis mellifera* L.). Insect. Soc. 36 (4), 264–276.

Huang, Z.-Y., Robinson, G., Borst, D., 1994. Physiological correlates of division of labor among similarly aged honey bees. J. Compar. Physiol. A 174 (6), 731–739.

Huang, Z., et al., 2010. Honey bee nutrition. Am. Bee J. 150 (8), 773–776.

Huang, Z., 2012. Pollen nutrition affects honey bee stress resistance. Terrest. Arthropod Rev. 5 (2), 175–189.

Hughes, A.L., 2015. Life-history evolution at the molecular level: adaptive amino acid composition of avian vitellogenins. Proc. R. Soc. B 282 (1812), 20151105.

Ihle, K.E., Page, R.E., Frederick, K., Fondrk, M.K., Amdam, G.V., 2010. Genotype effect on regulation of behaviour by vitellogenin supports reproductive origin of honeybee foraging bias. Anim. Behav. 79 (5), 1001–1006.

Johnson, B.R., 2003. Organization of work in the honeybee: a compromise between division of labour and behavioural flexibility. Proc. R. Soc. Lond. B: Biol. Sci. 270 (1511), 147–152.

Johnson, B.R., 2005. Limited flexibility in the temporal caste system of the honey bee. Behav. Ecol. Sociobiol. 58 (3), 219–226.

Johnson, B.R., 2010. Division of labor in honeybees: form, function, and proximate mechanisms. Behav. Ecol. Sociobiol. 64 (3), 305–316.

Kang, Y., Blanco, K., Davis, T., Wang, Y., DeGrandi-Hoffman, G., 2016. Disease dynamics of honeybees with varroa destructor as parasite and virus vector. Math. Biosci. 275, 71–92.

Khoury, D.S., Myerscough, M.R., Barron, A.B., 2011. A quantitative model of honey bee colony population dynamics. PLOS ONE 6 (4), e18491.

Khoury, D.S., Barron, A.B., Myerscough, M.R., 2013. Modelling food and population dynamics in honey bee colonies. PLoS ONE 8 (5), e59084.

Klein, S., Cabirol, A., Devaud, J.-M., Barron, A.B., Lihoreau, M., 2017. Why bees are so vulnerable to environmental stressors. Trends Ecol. Evol. 32 (4), 268–278.

Le Conte, Y., Navajas, M., 2008. Climate change: impact on honey bee populations and diseases. Revue Scientifique et Technique-Office International des Epizooties 27 (2), 499–510.

Münch, D., Amdam, G.V., 2010. The curious case of aging plasticity in honey bees. FEBS Lett. 584 (12), 2496–2503.

Marino, S., Hogue, I.B., Ray, C.J., Kirschner, D.E., 2008. A methodology for performing global uncertainty and sensitivity analysis in systems biology. J. Theor. Biol. 254 (1), 178–196.

Messan, K., DeGrandi-Hoffman, G., Castillo-Chavez, C., Kang, Y., 2017. Migration effects on population dynamics of the honeybee-mite interactions. Math. Model. Nat. Phenom. 12 (2), 84–115.

Moore, P.A., Wilson, M.E., Skinner, J.A., 2015. Honey bee queens: evaluating the most important colony member. Bee Health 7 (10).

Naug, D., 2009. Nutritional stress due to habitat loss may explain recent honeybee colony collapses. Biol. Conserv. 142 (10), 2369–2372.

Nicolson, S.W., Human, H., 2008. Bees get a head start on honey production. Biol. Lett. 4 (3), 299–301.

Oettler, J., Nachtigal, A.-L., Schrader, L., 2015. Expression of the foraging gene is associated with age polyethism, not task preference, in the ant cardiocondyla obscurior. PLoS ONE 10 (12), e0144699.

Oliver, R., 2007. Fat bees. Part 1. Am. Bee J.

Page Jr., R.E., Rueppell, O., Amdam, G.V., 2012. Genetics of reproduction and regulation of honey bee (*Apis mellifera* L.) social behavior. Annu. Rev. Genet. 46, 97.

Page Jr., R.E., 2013. The Spirit of the Hive. Harvard University Press.

Pankiw, T., Page Jr., R.E., 1999. The effect of genotype, age, sex, and caste on response thresholds to sucrose and foraging behavior of honey bees (*Apis mellifera* L.). J. Compar. Physiol. A 185 (2), 207–213.

Pankiw, T., Page, R.E., 2001a. Genotype and colony environment affect honeybee (*Apis mellifera* L.) development and foraging behavior. Behav. Ecol. Sociobiol. 51 (1), 87–94.

Pankiw, T., Page Jr., R.E., 2001b. Brood pheromone modulates honeybee (*Apis mellifera* L.) sucrose response thresholds. Behav. Ecol. Sociobiol. 49 (2–3), 206–213.

Paoli, P.P., Donley, D., Stabler, D., Saseendranath, A., Nicolson, S.W., Simpson, S.J., Wright, G.A., 2014. Nutritional balance of essential amino acids and carbohydrates of the adult worker honeybee depends on age. Amino Acids 46 (6), 1449–1458.

Percival, M., 1950. Pollen presentation and pollen collection. New Phytol. 49 (1), 40–63.

Perry, C.J., Søvik, E., Myerscough, M.R., Barron, A.B., 2015. Rapid behavioral maturation accelerates failure of stressed honey bee colonies. Proc. Natl. Acad. Sci. U. S. A. 112 (11), 3427–3432.

Riessberger, U., Crailsheim, K., 1997. Short-term effect of different weather conditions upon the behaviour of forager and nurse honey bees. *Apis mellifera* carnica 411–426.

Robinson, G.E., 1992. Regulation of division of labor in insect societies. Annu. Rev. Entomol. 37 (1), 637–665.

Rueppell, O., Bachelier, C., Fondrk, M.K., Page, R.E., 2007. Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). Exp. Gerontol. 42 (10), 1020–1032.

Schmickl, T., Crailsheim, K., 2004. Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply. Apidologie 35 (3), 249–263.

Schmickl, T., Crailsheim, K., 2007. Hopomo: A model of honeybee intracolonial population dynamics and resource management. Ecol. Model. 204 (1), 219–245.

Schmickl, T., Karsai, I., 2016. How regulation based on a common stomach leads to economic optimization of honeybee foraging. J. Theor. Biol. 389, 274–286.

Schmickl, T., Karsai, I., 2017. Resilience of honeybee colonies via common stomach: A model of self-regulation of foraging. PLOS ONE 12 (11), e0188004.

Schulz, D.J., Huang, Z.-Y., Robinson, G.E., 1998. Effects of colony food shortage on behavioral development in honey bees. Behav. Ecol. Sociobiol. 42 (5), 295–303.

Scofield, H.N., Mattila, H.R., 2015. Honey bee workers that are pollen stressed as larvae become poor foragers and waggle dancers as adults. PLOS ONE 10 (4), e0121731.

Seehuus, S.-C., Norberg, K., Gimsa, U., Krekling, T., Amdam, G.V., 2006. Reproductive protein protects functionally sterile honey bee workers from oxidative stress. Proc. Natl. Acad. Sci. U. S. A. 103 (4), 962–967.

Seeley, T.D., 2009. The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies. Harvard University Press.

Switanek, M., Crailsheim, K., Truhetz, H., Brodschneider, R., 2017. Modelling seasonal effects of temperature and precipitation on honey bee winter mortality in a temperate climate. Sci. Total Environ. 579, 1581–1587.

Synge, A.D., 1947. Pollen collection by honeybees (*Apis mellifera*). J. Anim. Ecol. 122–138.

Szabo, T.I., 1980. Effect of weather factors on honeybee flight activity and colony weight gain. J. Apicult. Res. 19 (3), 164–171.

Thieme, H.R., 2003. Mathematics in Population Biology. Princeton University Press.

Thorp, R.W., 1979. Structural, behavioral, and physiological adaptations of bees (apoidea) for collecting pollen. Ann. Missouri Botan. Garden 788–812.

Torres, D.J., Ricoy, U.M., Roybal, S., 2015. Modeling honey bee populations. PLOS ONE 10 (7), e0130966.

Toth, A.L., Robinson, G.E., 2005. Worker nutrition and division of labour in honeybees. Anim. Behav. 69 (2), 427–435.

Toth, A.L., Kantarovich, S., Meisel, A.F., Robinson, G.E., 2005. Nutritional status influences socially regulated foraging ontogeny in honey bees. J. Exp. Biol. 208 (24), 4641–4649.

Traynor, K.S., Le Conte, Y., Page, R.E., 2014. Queen and young larval pheromones impact nursing and reproductive physiology of honey bee (*Apis mellifera*) workers. Behav. Ecol. Sociobiol. 68 (12), 2059–2073.

Tsuruda, J.M., Page, R.E., 2009. The effects of young brood on the foraging behavior of two strains of honey bees (*Apis mellifera*). Behav. Ecol. Sociobiol. 64 (2), 161–167.

Vaudo, A.D., Tooker, J.F., Grozinger, C.M., Patch, H.M., 2015. Bee nutrition and floral resource restoration. Curr. Opin. Insect Sci. 10, 133–141.

Vicens, N., Bosch, J., 2000. Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (hymenoptera: Megachilidae and apidae). Environ. Entomol. 29 (3), 413–420.

Wahl, O., Ulm, K., 1983. Influence of pollen feeding and physiological condition on pesticide sensitivity of the honey bee *Apis mellifera* carnica. Oecologia 59 (1), 106–128.

Wang, Y., Kaftanoglu, O., Fondrk, M.K., Page, R.E., 2014. Nurse bee behaviour manipulates worker honeybee (*Apis mellifera* L.) reproductive development. Anim. Behav. 92, 253–261.

Wheeler, M.M., Robinson, G.E., 2014. Diet-dependent gene expression in honey bees: honey vs. sucrose or high fructose corn syrup. Sci. Rep. 4.

Wheeler, D.E., 1986. Developmental and physiological determinants of caste in social hymenoptera: evolutionary implications. Am. Nat. 128 (1), 13–34.

Winston, M.L., 1991. The Biology of the Honey Bee. Harvard University Press.

Winston, M., 1992. The honey bee colony: life history. The Hive and the Honey Bee. pp. 197–234.

Wright, G.A., Nicolson, S.W., Shafir, S., 2018. Nutritional physiology and ecology of honey bees. Annu. Rev. Entomol. 63.