

Modeling Bumble Bee Population Dynamics with Delay Differential Equations

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June 30, 2016

Abstract

Bumble bees are ubiquitous creatures and crucial pollinators to a vast assortment of crops worldwide. Bumble bee populations have been decreasing in recent decades, with demise of flower resources and pesticide exposure being two of several suggested pressures causing declines. Many empirical investigations have been performed on bumble bees and their natural history is well documented, but the understanding of their population dynamics over time, causes for observed declines, and potential benefits of management actions is poor. To provide a tool for projecting and testing sensitivity of growth of populations under contrasting and combined pressures, we propose a delay differential equation model that describes multi-colony bumble bee population dynamics. We explain the usefulness of delay equations over ordinary differential equations, particularly for bumble bee modeling. We then describe a particular numerical method that approximates the solution of the delay model. Next, we provide simulations of seasonal population dynamics in the absence of pressures. We conclude by describing ways in which resource limitation, pesticide exposure and other pressures can be reflected in the model.

Key words: population models, delay differential equations, non-linear, non-autonomous, spline approximations, *Bombus terrestris*, reproduction, neonicotinoids

1 Introduction

The protection of bumble bee populations, among other pollinators, is vital to sustain global agricultural food production [29, 44], biodiversity and ecosystem functioning [28, 53]. It is now widely accepted that bumble bee diversity has dramatically declined in the past several decades [10, 13, 14]. Diminishing populations have been ascribed to habitat loss, resulting in loss of nest and flower resources, pathogens, climate change and exposure to chemical insecticides [57, 71]. The buff-tailed bumble bee *Bombus terrestris* has been the subject of much study (see for example, [1, 21, 22, 54, 68]), as it is abundant in Europe and known to be an important pollinator [43]. Much effort has been devoted to mapping its biology and natural history, statistical analysis, and experimentation

[12,36]. However, much less is understood about its population *dynamics* over time and the growth of bumble bee populations subjected to pressures and limitations of resources (see [18]).

Mathematical modeling based on empirical information on life history parameters can be a strong tool to project population dynamics and identify vulnerable traits and life stages, e.g., through sensitivity analysis [9, 19, 51]. With a realistic time-dependent model, it is possible to implement and study many suggested single and combined pressures that may affect bumble bees. Empirical research has concluded that forage resources (pollen and nectar) in the landscape affect overall bumblebee abundance. Furthermore, explicit modeling of resource dynamics over time bears potential to elucidate the mechanisms underlying these patterns and explain observed discrepancies (e.g., [17, 61, 70, 72]) in which life stages (of queens, workers, males, and gynes) are supported under contrasting timing, amount, type and quality of food resources.

Recently, and adding to the list of pressures, the exposure of nontarget organisms, especially economically important arthropods that provide ecosystem services such as biological control and pollination, to insecticides, designed to control insect pests in agricultural crops, has received increasing attention [16, 27, 30, 48, 52]. One recently much debated scenario is that of exposure of bumble bees from insecticides used to control insect pests in agricultural crops. In particular, neonicotinoids, a class of insecticides introduced to the market in the 1990s [25] have been under intense scrutiny for their suspected negative effects on bees [34, 37, 47]. Neonicotinoids are systemic; i.e., they are absorbed into plant tissues, rather than sticking to the surface of plants [25]. Consequently, although often applied to seeds, they can be present in pollen and nectar, and negative effects on bumblebee colony growth and reproduction have been detected in both laboratory [26, 27, 31] and field experiments [62]. However, more can be learned about long term consequences on population dynamics of pesticide exposure of the entire life cycle, something that is logistically extremely difficult to assess empirically, but lends itself to dynamic modeling.

We are motivated by the desire to understand the various ways in which *B. terrestris* populations are dynamically affected by environmental pressures, including pesticide exposure and resource limitation. Mathematical modeling, especially in an iterative approach [9], can be used for projecting population abundance and understanding the importance of key life traits, such as survival, reproduction and seasonal reproductive switch times under contrasting scenarios. Mathematical modeling, particularly when paired with rich empirical data, provides analytic tools that experimentation alone cannot offer [7]. In this paper, we present a delay differential equation (DDE) model to simulate the abundance of different bumble bee casts and in-nest resources over time, with dynamics including colony establishment, mortality, colony growth, reproduction, and queen hibernation. Delay equations have been used in various applications, including biology, ecology, engineering (see [2, 20, 35, 39] for examples) and even honeybee population modeling [42]. We refer the reader to [64] for an introduction to DDEs and applications, as well as [45] for DDEs in ecology.

We first introduce the class of DDEs and provide a brief overview for the reader. We motivate why a DDE model may be preferable over the more commonly used ordinary differential equation (ODE) system for describing bumble bee and other population dynamics. Next, we present our model with the underlying assumptions, including a description of the literature references which provided us either direct or indirect estimates of some model parameters. We describe a linear spline approximation method for obtaining a numerical solution to our model. Subsequently, we provide model simulations in the absence of pressures. Lastly, we propose ways in which pressures such as resource limitation and insecticide exposure can be reflected in the model.

2 Methods

2.1 Delay differential equations

We explain the key features of a DDE system by comparing it with a more well-known class of equations: the ODE. Let's first consider the ODE model in the context of an n -dimensional initial value problem

$$\dot{\mathbf{x}}(t) = \mathbf{f}(t, \mathbf{x}(t), \mathbf{q}), \quad \mathbf{x}(t_0) = \mathbf{x}_0, \quad (1)$$

where \mathbf{x} is the vector of state variables, whose derivative is a function of time t , \mathbf{x} at time t and some vector of parameters \mathbf{q} . In order to find a unique solution to this ODE, a corresponding n -vector \mathbf{x}_0 of the state variable

at some initial time t_0 is required. For simplicity, let $t_0 = 0$. Next consider the DDE model, presented here as the n -dimensional vector system

$$\begin{aligned}\dot{\mathbf{x}}(t) &= \mathbf{f}(t, \mathbf{x}(t), \mathbf{q}, \mathbf{x}_t), \quad t \geq 0 \\ \mathbf{x}(0) &= \eta \in \mathbb{R}^n, \mathbf{x}(s) = \phi \text{ on } [-r, 0)\end{aligned}\tag{2}$$

where $\mathbf{x}_t \equiv \mathbf{x}(t + s)$ for $s \in [-r, 0)$ for some finite $r > 0$. In other words, the change in \mathbf{x} at time t is a function of time, parameters \mathbf{q} and the state at time t as well as the state at prior discrete and/or continuous times $t - s$ with the above restrictions on s . This direct dependence of the solution on the solution at prior time(s) is one fundamental difference between ODEs and DDEs. In addition, we see that we need not only the initial conditions of the states at time t_0 , but also a n -vector function ϕ describing the state at previous time $t \in [-r, 0)$. The combined information η and ϕ is known as the *history* of the system. For our methodology, it is not required that $\lim_{s \rightarrow 0^-} \phi(s) = \eta$. This additional requirement of a history function ϕ is another fundamental difference between ODEs and DDEs. Lastly, we point out that the solution of a DDE at time \bar{t} is not simply $\mathbf{x}(\bar{t})$, but also must include the history $\mathbf{x}(\bar{t} + s)$ for all $s \in [\bar{t} - r, \bar{t})$. This leads us to a further distinction between ODEs and DDEs: the solution to a n -dimensional ODE is finite-dimensional, whereas the solution to an n -dimensional DDE is infinite-dimensional. We propose that DDEs offer an advantage over ODEs when modeling bumble bee populations as well as other populations exhibiting hysteresis effects. Included in these is the incubation time of all colony offspring, which is described in detail in the next section.

2.2 Our Proposed Model

Our system of DDEs describes six state variables in a collection of bumble bee colonies: in-nest nectar abundance $A(t)$, in-nest pollen abundance $B(t)$, queens $Q(t)$, workers $W(t)$, males $M(t)$ and gynes (daughter queens) $G(t)$. While our model certainly allows for multiple year projections, we consider a time span of less than one year here. We define the first day of spring $T_S := 0$, which denotes the day on which all hibernating gynes emerge from hibernation to become queens and found new colonies. The independent variable t measures time in days. We use exposure to neonicotinoid insecticides to exemplify how the impact of a pressure can be modeled and projected. We denote the environmental neonicotinoid level as \hat{n} . While many variables and parameters are functions of \hat{n} , we will only consider $\hat{n} = 0$ for our first simulation, to present projections free of neonicotinoid exposure.

We consider the following assumptions and basic seasonal timeline [12, 22, 36, 52]. Hibernating gynes emerge and become queens that found new colonies at $t = T_S$. These queens immediately begin foraging for and storing resources (nectar and pollen) inside the nest, as well as producing worker eggs. Assuming a 22-day worker incubation time (from an egg laid to the emergence of an adult worker) [22, 36], the first workers emerge at $t = T_S + 22$. At this time, the workers take over resource foraging and tending to new eggs, while the queens devote all energy to production of worker eggs [36]. The authors of [12, 36] discuss in detail the somewhat mysterious process of bumble bee reproduction. There are varying theories on what factors contribute to the switch from worker to male and queen offspring production; these factors include, but are not limited to, queen condition during the season or during hibernation, queen pheromones, and worker abundance [12, 22, 23, 36, 38, 46, 52, 60]. Environmental conditions can also cause nests to have either early or late season switch times [22]. In our model, we assume at time $t = T^*(W)$, i.e., some time which is dependent on the number of workers present, the queen begins to lay sexual (male and gyne) eggs while continuing to produce worker eggs. At time $t = T^{**}(W)$, the queen stops producing worker eggs and devotes all energy to sexual egg production. At time $t = T^{**}(W) + 22$, the last new worker emerges. At times $t = T^*(W) + 26$, and $t = T^*(W) + 30$, respectively, the first males and gynes emerge (assuming respective 26 and 30 day incubation periods [22]). Because of these important incubation times, we define $\tau_1(t) := t - 22$, $\tau_2(t) := t - 26$, and $\tau_3(t) := t - 30$, which are seen in the model. Sexu- als continue to emerge until time $t = T_W$, at which point workers, queens and males die, and gynes go into hibernation and prepare to become queens in the following year [12, 36]. The exact values of these timeline points depend greatly on geography, environment and weather. Furthermore, we believe that allowing T^* and T^{**} to be functions of the worker population will allow us, in future work, to explore whether environmental changes and pressures such as insecticide exposure can have an indirect effect on reproductive switch times. A timeline of the bumble bee's

seasonal life cycle is depicted in Figure 1. To first demonstrate the usefulness of the DDE model, we fix timeline values T^* , T^{**} , T_S and T_W at constant values estimated by [52], which are given in Table 1 and described in Section 2.3 below.

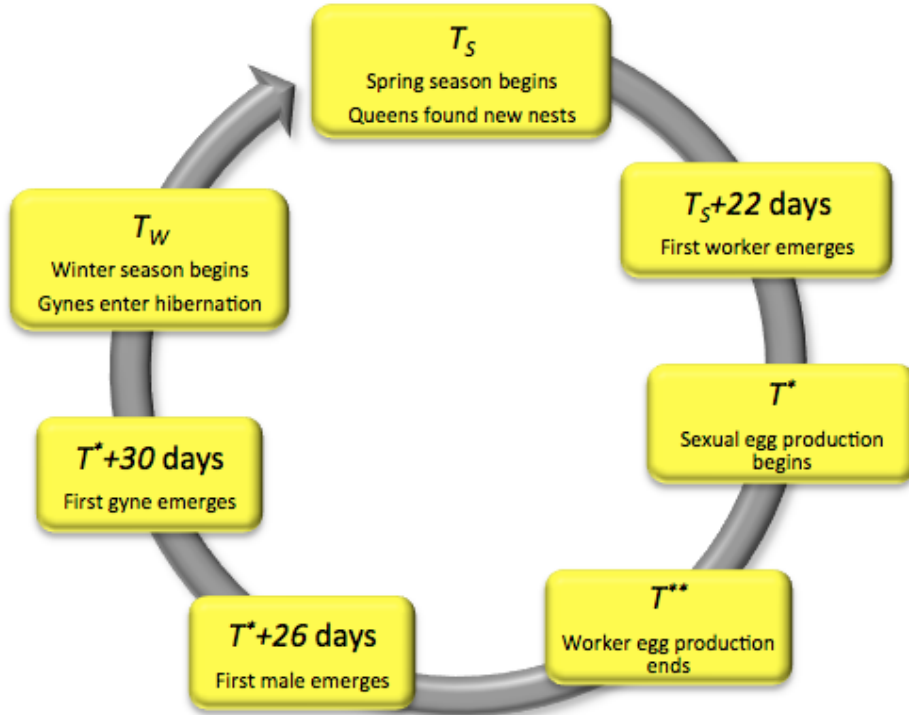


Figure 1: Timeline of bumble bee seasonal dynamics

We assume that the founding queen, workers, and worker, male and gyne larvae consume both nectar and pollen [22]. We also assume that all colony members have a mortality rate, which encompasses mortality by aging and mortality during foraging trips. We now present the mathematical model as well as the pre-spring history information in (3) and (4). Because of the previously described changes in seasonal dynamics, all differential equations are piecewise defined. All model variables, switch times, and parameters are described in Table 1. In addition, to elucidate the definitions of $\frac{dA}{dt}$ and $\frac{dB}{dt}$, we have included a description of seasonal resource (nectar and pollen) consumption and collection changes in Table 2. Resource consumption will be described later in more detail.

$$\begin{aligned}
\frac{dA}{dt} &= \begin{cases} b_A Q - \mu_{AQ} Q - 2l_W(t, Q) & T_S \leq t < T_S + 22; \\ b_{AW} W - \mu_{AQ} Q - \mu_{AW} W - 2l_W(t, Q) & T_S + 22 \leq t < T^*; \\ b_{AW} W - \mu_{AQ} Q - \mu_{AW} W - 2(l_W(t, Q) + l_M(t, Q) + l_G(t, Q)) & T^* \leq t < T^{**} + 22; \\ B_{AW} W - \mu_{AQ} Q - \mu_{AW} W - 2(l_M(t, Q) + l_G(t, Q)) & T^{**} + 22 \leq t < T_W; \end{cases} \\
\frac{dB}{dt} &= \begin{cases} b_B Q - \mu_{BQ} Q - l_W(t, Q) & T_S \leq t < T_S + 22; \\ b_{BW} W - \mu_{BQ} Q - \mu_{BW} W - l_W(t, Q) & T_S + 22 \leq t < T^*; \\ b_{BW} W - \mu_{BQ} Q - \mu_{BW} W - (l_W(t, Q) + l_M(t, Q) + l_G(t, Q)) & T^* \leq t < T^{**} + 22; \\ b_{BW} W - \mu_{BQ} Q - \mu_{BW} W - (l_M(t, Q) + l_G(t, Q)) & T^{**} + 22 \leq t < T_W; \end{cases} \\
\frac{dQ}{dt} &= \begin{cases} -\mu_Q Q & T_S \leq t < T_W; \\ 0 & \text{else;} \end{cases} \\
\frac{dW}{dt} &= \begin{cases} b_W(t, \hat{n}) Q(\tau_1, \hat{n}) \int_{\tau_1(t)}^t \gamma_W W(s) (A(s) + \frac{B(s)}{d_B}) (1 - \frac{A(s) + \frac{B(s)}{d_B}}{Q(s)(A_{max} + \frac{B_{max}}{d_B})}) ds - \mu_W W & T_S + 22 \leq t < T^{**} + 22; \\ -\mu_W W & T^{**} + 22 \leq t < T_W; \\ 0 & \text{else;} \end{cases} \\
\frac{dM}{dt} &= \begin{cases} b_M(t, \hat{n}) Q(\tau_2, \hat{n}) \int_{\tau_2(t)}^t \gamma_M W(s) (A(s) + \frac{B(s)}{d_B}) (1 - \frac{A(s) + \frac{B(s)}{d_B}}{Q(s)(A_{max} + \frac{B_{max}}{d_B})}) ds - \mu_M M & T^* + 26 \leq t < T_W; \\ 0 & \text{else;} \end{cases} \\
\frac{dG}{dt} &= \begin{cases} -\mu_{G_w} G & t < T_S; \\ 0 & T_S \leq t < T^* + 30; \\ b_G(t, \hat{n}) Q(\tau_3, \hat{n}) \int_{\tau_3(t)}^t \gamma_G W(s) (A(s) + \frac{B(s)}{d_B}) (1 - \frac{A(s) + \frac{B(s)}{d_B}}{Q(s)(A_{max} + \frac{B_{max}}{d_B})}) ds - \mu_G G & T^* + 30 \leq t < T_W; \\ -\mu_{G_w} G & t \geq T_W. \end{cases} \tag{3}
\end{aligned}$$

$$\begin{aligned}
A(t, \hat{n}) &= \begin{cases} 0 & t < T_S; \\ A_0 & t = T_S; \\ 0 & t \geq T_W; \end{cases} & W(t, \hat{n}) &= \begin{cases} 0 & t < T_S + 22; \\ W_0 & t = T_S + 22; \\ 0 & t \geq T_W; \end{cases} \\
B(t, \hat{n}) &= \begin{cases} 0 & t < T_S; \\ B_0 & t = T_S; \\ 0 & t \geq T_W; \end{cases} & M(t, \hat{n}) &= \begin{cases} 0 & t < T^*; \\ M_0 & t = T^* + 26; \\ 0 & t \geq T_W; \end{cases} \tag{4} \\
Q(t, \hat{n}) &= \begin{cases} 0 & t < T_S; \\ G(T_S - 1, \hat{n}) & t = T_S; \\ 0 & t \geq T_W; \end{cases} & G(T_S, \hat{n}) &= \begin{cases} G_0 e^{-\mu_{G_w} t} & t < T_S; \\ 0 & t = T_S; \\ G_1 & t = T^* + 30; \end{cases}
\end{aligned}$$

Variable	Description	Units	Estimate
t	time	days	
\hat{n}	neonicotinoid level	currently n/a	
$A(t)$	amount of nectar in colonies	ml	
$B(t)$	amount of pollen in colonies	g	
$Q(t)$	number of queens	individuals (queens)	
$W(t)$	number of workers	individuals (workers)	
$M(t)$	number of males	individuals (males)	
$G(t)$	number of gynes	individuals (gynes)	
Timeline			
T_S	first day of spring		$T_S := 0$
$T^*(W)$	first day male/gyne eggs laid		40 [52]
$T^{**}(W)$	end of worker eggs laid		44 [52]
T_W	beginning of winter		
Parameters			
b_A	queen nectar collection rate	$\frac{\text{ml}}{\text{day} \cdot \text{individual}(Q)}$	1.37 [32, 54]
μ_{AQ}	queen nectar consumption rate	$\frac{\text{ml}}{\text{day} \cdot \text{individual}(Q)}$	
b_{AW}	worker nectar collection rate	$\frac{\text{ml}}{\text{day} \cdot \text{individual}(W)}$	
μ_{AW}	worker nectar consumption rate	$\frac{\text{ml}}{\text{day} \cdot \text{individual}(W)}$	
b_B	queen pollen collection rate	$\frac{\text{g}}{\text{day} \cdot \text{individual}(Q)}$	1.146 [27]
μ_{BQ}	queen pollen consumption rate	$\frac{\text{g}}{\text{day} \cdot \text{individual}(Q)}$	
b_{BW}	worker pollen collection rate	$\frac{\text{g}}{\text{day} \cdot \text{individual}(W)}$	
μ_{BW}	worker pollen consumption rate	$\frac{\text{g}}{\text{day} \cdot \text{individual}(W)}$	
μ_Q	queen death rate	$\frac{1}{\text{day}}$	0.0154 [31]
$b_W(t, \hat{n})$	worker birth rate	$\frac{\text{workers}}{\text{queen} \cdot \text{day}}$	
μ_W	worker death rate	$\frac{1}{\text{day}}$	
γ_M	worker-male conversion coefficient	$\frac{1}{\text{individual}(W) \cdot \text{ml} \cdot \text{day}}$	
$b_M(t, \hat{n})$	male birth rate	$\frac{\text{males}}{\text{queen} \cdot \text{day}}$	
μ_M	male death rate	$\frac{1}{\text{day}}$	
γ_W	worker-worker conversion coefficient	$\frac{1}{\text{individual}(W) \cdot \text{ml} \cdot \text{day}}$	
μ_{G_W}	hibernation gyne death rate	$\frac{1}{\text{day}}$	
γ_G	worker-gyne conversion coefficient	$\frac{1}{\text{individual}(W) \cdot \text{ml} \cdot \text{day}}$	
$b_G(t, \hat{n})$	gyne birth rate	$\frac{\text{gynes}}{\text{queen} \cdot \text{day}}$	
μ_G	in-season gyne death rate	$\frac{1}{\text{day}}$	
A_{max}	in-nest nectar maximum (per nest)	$\frac{\text{ml}}{\text{individual}(Q)}$	
B_{max}	in-nest pollen maximum (per nest)	$\frac{\text{g}}{\text{individual}(Q)}$	
d_B	pollen grain density	$\frac{\text{g}}{\text{ml}}$	
P_0	initial larval pollen consumption	$\frac{\text{g}}{\text{individual}(W) \cdot \text{day}}$	0.001 [58]
\bar{r}	larval pollen consumption growth rate	$\frac{1}{\text{day}}$	0.25 [58]

Table 1: Model variables and parameters; the corresponding parameter estimate, if available, is given along with its respective source reference in the last column.

Time interval	Resource collection and consumption
$[T_S, T_S + 22)$	queen collecting and consuming resources worker larvae consuming resources
$[T_S + 22, T^*)$	workers collecting and consuming resources queen consuming resources worker larvae consuming resources
$[T^*, T^{**} + 22)$	workers collecting and consuming resources queen consuming resources worker larvae consuming resources male and gyne larvae consuming resources
$[T^{**} + 22, T^* + 30)$	workers collecting and consuming resources queen consuming resources male and gyne larvae consuming resources
$[T^* + 30, T_W)$	workers collecting and consuming resources queen consuming resources male and gyne larvae consuming resources

Table 2: Seasonal time intervals and corresponding effects of colony members on resources, nectar and pollen.

We now add some assumptions to the model:

- For these preliminary simulations, we simplify the model by letting the worker, male and gyne birth rates $b_W(t, \hat{n})$, $b_M(t, \hat{n})$, and $b_G(t, \hat{n})$ respectively, be constants.
- In our model equations for workers, males and gynes, we see the term $A(s) + d_B^{-1}B(s)$, quantifying the net resources at time s , which we shall call $R(s)$. Because A is measured in milliliters, and B is measured in grams, it is reasonable to give R a unit of either ml or g, so without loss of generality, we let R have the unit ml. We can convert the mass of pollen B into volume using the density of pollen. In other words,

$$B_V(t) = d_B^{-1}B(t),$$

where $B_V(t)$ denotes the volume of pollen and d_B denotes its density (a constant). There are various species of pollen, each with different specific material densities. According to [15], an estimated value for pollen grain density is 1g/ml. Using this value, we have the following formulation for net resources

$$R(t) = A(t) + B_V(t) = A(t) + d_B^{-1}B(t) = A(t) + B(t) = A(t) + B(t),$$

if we choose $d_B = 1$.

- In the equations for $\frac{dW}{dt}$, $\frac{dM}{dt}$, and $\frac{dG}{dt}$, we see three parameters γ_W , γ_M and γ_G . As seen in Table 1, these are conversion coefficients for the production of workers, males, and gynes respectively. In reality, one can think of each as the product of multiple conversion parameters, i.e.,

$$\gamma_k = \gamma_{kW}\gamma_{kR}$$

for $k = W, M$, or G , where γ_{kW} and γ_{kR} have units $\frac{1}{\text{individual}(k)\cdot\text{day}}$ and $\frac{1}{\text{ml}}$ respectively. It is unreasonable to expect to estimate each of these parameters individually, thus we simply consider each product γ_k (for $k = W, M$, and G).

- Before becoming an adult, a bumble bee goes through three sequential stages: egg, larval, and pupal. Larvae consume resources but eggs and pupa do not. Larval stage length can be modified based on food availability [67] or in-nest temperature. For simplicity, we assume that bumble bees have constant incubation schedules, seen in Table 3 [22].

Caste	Total no. incubation days	Egg (days)	Larva (days)	Pupa (days)
Workers	22	4	9	9
Males	26	4	11	11
Gynes	30	4	13	13

Table 3: Bumble bee incubation breakdown by caste

Our model tracks resources (pollen and nectar) and adult colony members (i.e., queens and non-egg,-larval, or -pupal workers, males and gynes). However, because larvae contribute to resource consumption, we must be clear that we are accurately modeling this. In Table 2, we summarize the effects of all colony members on resources (nectar and pollen) at all phases of the season. We tentatively assume, for sake of simplicity, that the last worker emerges when the first male emerges (because of our knowledge of incubation times of 22 and 26 days for workers and males, respectively, and our estimate that $T^* = 40$ and $T^{**} = 44$, as seen in Table 1). With these assumptions, we have three functions in (3), $l_W(t, Q)$, $l_M(t, Q)$ and $l_G(t, Q)$, which reflect larval pollen consumption, which require definition.

According to [56, 58, 59] daily pollen intake (measured in mass of pollen per larvae per day) increases exponentially as age increases. Therefore, we can model daily pollen intake per worker larvae by $P_0 e^{\bar{r}a}$ where a measures age with unit [day], for some positive constants P_0 and \bar{r} . The number of worker larvae of age a produced per day at time t is given by $b_W Q(t - a)$, for $4 \leq a \leq 13$. Therefore, we can model pollen consumption per day by worker larvae by

$$l_W(t, Q) = \int_4^{13} b_W Q(t - a) P_0 e^{\bar{r}a} da. \quad (5)$$

Similarly, we have

$$l_M(t, Q) = \int_4^{15} b_M Q(t - a) P_0 e^{\bar{r}a} da, \quad (6)$$

for pollen consumption by male larvae and

$$l_G(t, Q) = \int_4^{17} b_G Q(t - a) P_0 e^{\bar{r}a} da, \quad (7)$$

for pollen consumption by gyne larvae. By examining data in [58], we assume that initial larval consumption (per larva) P_0 is constant across castes, along with exponential consumption rate \bar{r} . In addition, according to [55], larval diet consists of approximately 34% pollen, and the rest is a combination of nectar and a trivial amount of digestive enzymes. Consequently, we can assume an approximate 2:1 ratio of nectar to pollen for larval consumption, which explains the larval consumption terms in the model for $\frac{dA}{dt}$.

We will refer to the state variables as components of the 6×1 -vector \mathbf{x} . As described earlier, delay equations require not only the initial values, η of the states at time 0 ($t \equiv T_S$), but also the history information, ϕ for all $t \in [-r, 0)$, for r defined by the model (in this case, $r = 30$). For now, we further simplify the model by changing the history information for the gyne population, G . Instead of the exponential decay we see above for $t < T_S$, we will first assume that G remains non-zero, but some constant value G_0 , for $t < T_S$. Initially, we made these choices of history information, letting ϕ be constant:

$$\eta = [A_0, B_0, Q_0, 0, 0, 0]^T$$

where $Q_0 = G(T_S - 1, \hat{n}) = G_0$ (i.e., the number of queens when spring begins is the number of gynes at $t = -1$), and

$$\phi = [0, 0, 0, 0, 0, G_0]^T,$$

for some constants A_0 , B_0 , and G_0 . With these choices of history information, all history functions are continuous except at $t = 0$ where there is a jump discontinuity in four of the six variables. While this is theoretically acceptable for our numerical solution method of using spline approximations, in practice this jump discontinuity created a computational error in our model that was propagated over time (because solving delay equations requires

iteratively solving large linear systems, which we shall describe in Section 3). To remediate this, we instead choose a continuous history function by incorporating a “ramp” function for nectar, pollen, queens, and gynes. For example, let $\phi_A(t)$ and η_A denote the history function on $t \in [-r, 0)$ for nectar and $A(0)$, respectively. Then we have

$$\phi_A(t) = \begin{cases} 0 & -r < t < -2; \\ \eta_A(\frac{t}{-2} + 1) & -2 \leq t < 0; \end{cases}.$$

Defining similar ramp functions and incorporating them into our history for pollen, gynes and queens alleviated the computational error faced with the jump discontinuities at $t = 0$.

2.3 Literature search for parameter values

We searched the literature to determine reasonable values for various model parameters. For now, we tentatively fix several parameters at values that produce reasonable colony populations, and aim to estimate these more confidently with experimental data in future work. In Table 1 all model variables, time points, parameters and initial conditions are reported with corresponding units and literature comments. We now comment further on these choices.

In order to quantify queen nectar collection b_A using ml rather than mg, we used the conversion rate that 1166 mg = 1 ml of 40% sucrose solution, which was used to assimilate nectar in [31, 32].

In order to estimate the queen death rate μ_Q , we used the information that 14 out of 40 total colonies saw mother queen loss (hence 26 queens survived) in a given experiment lasting 28 days ([31]). We performed a simple inverse problem for the model

$$\frac{dQ}{dt} = -\mu_Q Q, \quad Q(0) = 40$$

with the sole data point $Q(28) = 26$. This returns the best fitting estimate $\mu_Q = 0.0154$. The authors of [31] found that there was no difference in queen loss between control groups and various pesticide treatment groups. Therefore, this should be a reasonable estimate regardless of neonicotinoid exposure.

For the purposes of the first simulation, we use the following information taken from [52] to determine seasonal switch times. Let the term “first egg” denote the first egg laid in the colony, regardless of caste determination. In the experiments conducted in [52], the average time from first egg to last worker emergence was approximately 66 days; assuming a 22 day incubation time, this implies that $T^{**} = 44$. The average time from first egg to first emergence of gynes and males was 70 and 65 days respectively. Assuming 30 and 26 day incubation periods for gynes and males, respectively, this provides two estimates for T^* : $T^* = 40$ or $T^* = 39$. Because these values are so similar, we assume $T^* = 40$ for these simulations. Lastly, [52] gives an estimate for the average number of workers produced per day in a given colony, which gives us a direct estimate: $b_W = 2.4$. We initially use this value.

3 Numerical methods

Here we provide a brief summary of the numerical methods used to approximate the solution to (3)-(4), with all further simplifications as detailed in Section 2.2. As mentioned previously, DDEs (sometimes called functional differential equations) differ from ODEs in many ways, including the dimension of the solution. Because (3)-(4) cannot be solved analytically using tools such as the method of steps [11], we must use some type of numerical method to find a finite dimensional approximation to the infinite dimensional solution. Matlab’s built-in DDE solver, `dde23`, which uses a multi-step method to approximate the solution to a simple DDE with constant delays, is convenient and useful, but limited in scope. One main limitation is the solver’s inability to handle continuum hysteresis terms, which are seen throughout our model, in functions l_W, l_M , and l_G as well as the integral terms seen in equations for $\frac{dW}{dt}$, $\frac{dM}{dt}$ and $\frac{dG}{dt}$. In addition, our model is piecewise defined, and using the solution (output) of one DDE as the history “function” for a future DDE becomes quite clumsy with `dde23`. Therefore, it becomes useful to consider an approximation in some finite dimensional solution subspace, similar to the method of finite elements for partial differential equations.

There are many possible choices of solution spaces, one of which is some space of spline functions [2, 4, 8, 40, 41]. While the use of cubic and other higher order spline methods can be considered, the authors of [8] found that piecewise linear splines, when implemented with a fairly fine mesh, produced excellent results. Therefore, we explore the use of linear spline functions to approximate the solution to our nonlinear, non-autonomous DDE, the theory of which is partially developed in [4]. In [5], we complete this theory and show that our model satisfies the necessary conditions upon which the theory is based. Here, we summarize this method of approximating the DDE solution.

Consider the following DDE form:

$$\frac{dx}{dt} = f(t, x(t), x_t, x(t - \tau_1), \dots, x(t - \tau_\nu)) + g(t), \quad (8)$$

for $0 \leq t \leq T$, $x_0 = \phi$, where $f = f(\eta, \psi, y_1, \dots, y_\nu) : Z \times \mathbb{R}^{n\nu} \rightarrow \mathbb{R}^n$. We define $Z = \mathbb{R}^n \times L_2(-r, 0; \mathbb{R}^n)$, $0 < \tau_1 < \dots < \tau_\nu = r$, $x_t(\theta) = x(t + \theta)$ for $-r \leq \theta \leq 0$ and $\phi \in H^1(-r, 0)$. The function $g(t)$ can be understood as some control function (in the case of our initial model, $g(t) \equiv 0$). The Banach space $L^2[a, b]$ is the space of all continuous, real-valued square integrable functions. The notation H^j or $H^j(a, b)$ denotes the Sobolev space $W^{j,2}(a, b, \mathbb{R}^n)$ of \mathbb{R}^n -valued functions f such that $f \in L_2[a, b]$ and $\partial^j f \in L_2[a, b]$. Specifically, H^1 is the space of absolutely continuous functions $f : [a, b] \rightarrow \mathbb{R}^n$ such that $\partial f = \dot{f} \in L_2[a, b]$.

In [5], we prove Theorem 1 in [4]; i.e., under certain conditions of f , let $y(t; \phi, g) = (x(t; \phi, g), x_t(\phi, g))$ where x is the solution of (8) corresponding to $\phi \in H^1, g \in L_2$. Then for $\zeta = (\phi(0), \phi)$, $y(\phi, g)$ is the unique solution on $[0, T]$ of

$$z(t) = \zeta + \int_0^t (Az(\sigma) + (g(\sigma), 0)) d\sigma. \quad (9)$$

where A is a nonlinear operator defined in [4]. This equivalent form of the solution to (8) is some function in the infinite-dimensional solution space Z . Therefore, we must choose an appropriate finite dimensional subspace Z^N containing the solution approximation. As previously mentioned, our choice for this problem is a space of linear splines. Let P^N be the orthogonal projection of Z onto Z^N (see [4] for details). Then, defining the approximating operator $A^N = P^N A P^N$, the approximating solution in Z^N is defined as

$$z^N(t) = P^N \zeta + \int_0^t (A^N z^N(\sigma) + P^N(g(\sigma), 0)) d\sigma. \quad (10)$$

Therefore, we must simply solve this large, but finite-dimensional linear system to approximate the solution to the DDE. As the dimension N of Z^N , increases, the solution (10) becomes more accurate, and converges to the solution of (8). See [5] and [3, 4] for details. Because Z^N is finite dimensional, (10) is equivalent to the ODE system

$$\dot{z}^N(t) = A^N z^N(t) + P^N(g(t), 0), z^N(t) = P^N \zeta. \quad (11)$$

In summary, we have taken an infinite dimensional solution to a DDE and approximated it with a solution to a finite dimensional ODE system. To solve this system over a finite time span, this large matrix system is solved using some method of choice for solving ODEs. In our case, we chose to use Matlab's stiff ODE solver `ode15s` as it excelled in both accuracy and speed for (3)-(4).

In addition to the linear spline approximation method, we also had to consider how to approximate the numerous integral terms in the model. We chose to use the trapezoidal method, specifically the `trapz` function given by Matlab. Although the error for this method is higher than that of more refined quadrature methods, this method allowed us to have solutions at all nodal values, without requiring interpolation.

Lastly, because our model is piecewise defined as reproduction and other dynamics change, we used the linear spline approximation method over each phase and then solved the subsequent phases using approximate solutions of previous phases (i.e., using past phases as part of the DDE's required history over the interval $[t - r, t]$). We found that a mesh size of $1/8$ (i.e. $N = 8r = 240$) produced a sufficient approximation, the simulations of which are seen in Section 4.

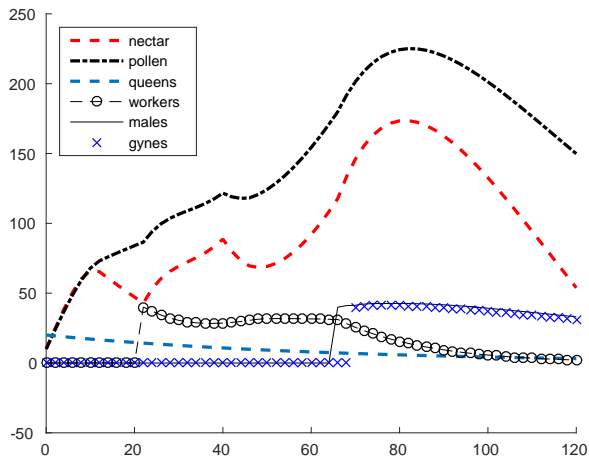
4 Results

With nearly 30 parameters and initial conditions, there are a plethora of combinations we could exhaust in presenting population simulations. Using the fixed values as seen in Table 1, we choose to vary a subset of the remaining unknown parameters and initial conditions to explore a small collection of parameter sets and subsequent population projections. For these simulations we mainly explore worker traits, such as resource collection and consumption and initial worker hatches at time $t = T_S + 22$ (W_0). In one simulation we also vary sexual (male and gyne) birth rates. We choose to present these simulations to demonstrate examples of the changes in population projections due to perturbations in key colony traits. We present four model simulations in Figure 2, each created using parameter sets with slight variations (see Table 4). In all four simulations, we see a slow exponential decay of queen bees and a jump discontinuity in workers, males and gynes at times $t = T_S + 22$, $t = T^* + 26$ and $t = T^* + 30$ respectively. Although end-of-season timing depends on weather and geography, we choose $T_W = T_S + 120$ for these preliminary simulations. We arbitrarily choose Sim 1 as the “baseline” projection seen in Figure 2a, against which we can compare other simulations.

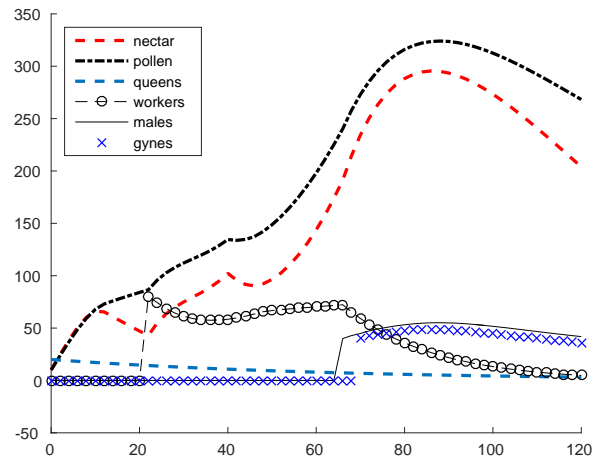
In Sim 2, we change certain worker-related parameters and examine the change in results. As seen in Table 4, we decreased worker nectar and pollen collection, increased worker nectar and pollen consumption, and doubled the initial population of workers, W_0 . In Figure 2b, we observe very similar dynamics, although higher resource storage is attained. In both simulations, the workers almost die out by winter’s start, and the number of males and gynes surviving by winter’s start are similar.

In Sim 3, we again implement change in worker-related parameters. We decrease worker pollen collection as in Sim 2, and to a lesser degree, decrease worker nectar collection. We again double the initial worker population W_0 at time $t = T_S + 22$, but do not increase worker resource consumption. Comparing Figure 2c to 2a, we see a much higher nectar storage, and all other dynamics stay quite consistent, including end-of-season worker, male and gyne populations.

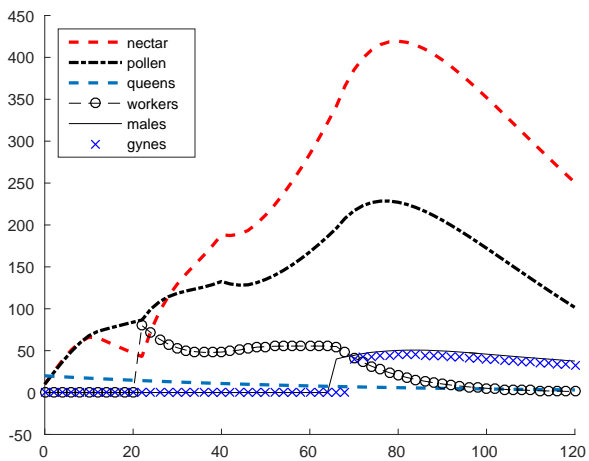
Lastly, in Sim 4, we implement all changes seen in Sim 2, but also increase both sexual birth rates, with a substantial increase in the male birth rate b_M (see Table 4). Consequently, in Figure 2d, we see similar worker dynamics, increased male and gyne populations by the end of the season, and a greater usage of resources, with nectar storage almost diminished by the end of the season.



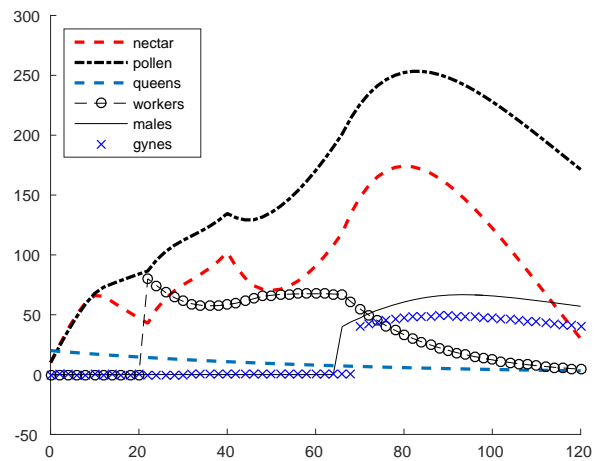
(a) Sim 1



(b) Sim 2



(c) Sim 3



(d) Sim 4

Figure 2: Four simulations of bumble bee populations over the interval $[T_S, T_W]$ using different parameters presented in Table 4.

Parameter/I.C.	Sim 1	Sim 2	Sim 3	Sim 4
b_A	1.37	1.37	1.37	1.37
b_{AW}	0.8	0.5	0.6	0.5
μ_{AQ}	1	1	1	1
b_B	1.146	1.146	1.146	1.146
b_{BW}	0.6	0.4	0.4	0.4
μ_{BQ}	0.8	0.8	0.8	0.8
μ_Q	0.0154	0.0154	0.0154	0.0154
b_W	2.4	2.4	2.4	2.4
μ_W	0.05	0.05	0.05	0.05
γ_M	5×10^{-7}	5×10^{-7}	5×10^{-7}	5×10^{-7}
b_M	0.7	0.7	0.7	1.2
μ_M	0.01	0.01	0.01	0.01
γ_W	5×10^{-7}	5×10^{-7}	5×10^{-7}	5×10^{-7}
μ_{G_W}	n/a	n/a	n/a	n/a
γ_G	5×10^{-7}	5×10^{-7}	5×10^{-7}	5×10^{-7}
b_G	0.7	0.7	0.7	0.8
μ_G	0.01	0.01	0.01	0.01
A_{max}	60	60	60	60
B_{max}	60	60	60	60
d_B	1	1	1	1
μ_{AW}	0.12	0.15	0.12	0.15
μ_{BW}	0.12	0.15	0.12	0.15
P_0	0.001	0.001	0.001	0.001
\bar{r}	0.25	0.25	0.25	0.25
A_0	10	10	10	10
B_0	10	10	10	10
Q_0	20	20	20	20
W_0	40	80	80	80
M_0	40	40	40	40
G_1	40	40	40	40

Table 4: Parameter values and initial conditions (I.C.) used to simulate bumble bee population on the interval $[T_S, T_W]$. Any value listed as “n/a” refers to a parameter which is not used in the simulation over the time period $[T_S, T_W]$. Parameters $b_A, b_B, \mu_Q, P_0, \bar{r}$ and b_W are fixed at literature values (see Table 1). The remaining parameters are currently fixed at values that produce reasonable population projections. Q_0 represents the number of queens at the beginning of the season, which is equivalent to the number of nests. Any circled parameter value represents one that was changed for the purpose of exploring its effect on the ensuing model projections seen in Figure 2.

5 Discussion

In this paper we presented a delay differential equation model to describe population dynamics of a collection of bumble bee colonies. We chose to use a DDE model over an ODE model because of the incubation times inherent

in bumble bee reproduction. Although the use of delay terms produced a more complex mathematical problem, we suggested that an ODE model is insufficient to describe bumble bee population dynamics. We presented the population projections in the absence of environmental pressures over one season with four different parameter sets. We saw subsequent changes in the population dynamics, particularly at the beginning of winter.

We chose these four parameter sets to explore life history differences. For instance, Sim 2 represented a decline in worker foraging productivity. This reflected recent studies that have demonstrated that bees exposed to neonicotinoids collected less pollen and returned to the nest less frequently than bees not exposed to neonicotinoids [27, 33, 65], though effects may have varied with particular pesticide configurations [50]. Sim 2 also incorporated greater worker resource consumption, which allowed us to explore different rates of toxin exposure and uptake. Sim 3 explored similar effects without the increase in worker resource consumption. Sim 4 increased sexual birth rates which resulted in a greater male and gyne populations, which in turn will produce more colonies beyond the first season. These simulations hardly exhausted the possible scenarios and outcomes of varying life history traits. However, they provided examples of the ways in which this model can represent bumble bee populations in many environments. In addition, these simulations demonstrated the utility of a DDE model for general population modeling.

Although we have yet to corroborate these simulations with experimental data, the model depicted reasonable seasonal bumble bee dynamics. The authors of [18] also advocated for better understanding of colony growth mechanism in order to more accurately predict queen production and direct efforts to conserve bumblebee populations. In [18], total colony weight was expected to increase exponentially and subsequently decrease once workers begin to die and sexuals begin to leave the nests. As in our model, colony growth was related to resources by modeling colony weight gain as a function of cumulative floral resources. Furthermore, queen production in [18], as in our model, was driven by multiple mechanisms, including floral resources. The authors of [18] found that defining colony growth as a function of floral resources was the best of the models they considered. This supported our proposed model. Lastly, the general trend of increased total population until worker death and sexual dispersal seen in the model and experimental data of [18] lended further support to our proposed model.

As mentioned repeatedly, it is important to understand bumble bee population dynamics in the presence of various environmental pressures, including resource scarcity and insecticide exposure. There are multiple ways to incorporate both lethal and sub-lethal effects of insecticide-exposure, including changes in worker death rate, worker collection rate, worker productivity rates, queen death rate, and queen reproduction rates. One can also define the above parameters as functions of insecticide exposure, rather than as constants. In addition, one can implement changes due to environmental effects by exploring variable reproductive switch times, maximum resource availability, etc. By comparing model results to experimental data in the absence and presence of these pressures, one can test the model's accuracy. Lastly, the linear spline approximation method, with a mesh size of $1/8$, was both accurate and efficient. We took advantage of Matlab's excellent ODE solvers to solve the approximating ODE system (11). With the model and techniques and outlined here, it is also feasible to approximate multi-year projections.

6 Conclusion

A great challenge is the accurate estimation of multiple unknown parameter values. For parameter estimation and subsequent model validation, we intend in our future work to use experimental longitudinal data tracking colony fitness, worker production, mother queen survival, and worker resource collection which are experimentally impacted by a particular pressure, such as both unexposed and neonicotinoid-exposed colonies, e.g., as in [26]. After using this data to estimate more parameters with a reasonable level of confidence [7], we will move to a motivating problem of understanding how pressures such as neonicotinoid exposure may have lethal and/or sublethal effects on bumble bee colonies. Some effects to be explored may include birth rates, resource consumption, worker productivity (efficient care of eggs/larvae), death rates, and season switch times. In addition, we would like to extend our simulations to include multi-seasonal projections to better understand long term effects of single and combined pressures such as habitat loss, resource limitations and pesticides.

7 Acknowledgements

We thank Oliver Schweiger for assisting with parameter values collected from the literature. This research was supported by the Air Force Office of Scientific Research under grant numbers AFOSR FA9550-12-1-0188 and AFOSR FA9550-15-1-0298, by a CRSC/Lord Fellowship, by the August T Larson guest researchers programme at the Swedish University of Agricultural Sciences, and by the Swedish research council FORMAS.

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