Modeling bumble bee population dynamics with delay differential equations

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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 as a natural modeling formulation, particularly for bumble bee modeling. We then introduce 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.

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1. Introduction

The protection of bumble bee populations, among other pollinators, is vital to sustain global agricultural food production (Klein et al., 2007; Garibaldi et al., 2013), biodiversity and ecosystem functioning (Fontaine et al., 2005; Ollerton et al., 2011). It is now widely accepted that bumble bee diversity has dramatically declined in the past several decades (Bartomeus et al., 2013; Biesmeijer et al., 2006; Bommarco et al., 2012). Diminishing populations have been ascribed to habitat loss, resulting in loss of nest and flower resources, pathogens, climate change and exposure to chemical insecticides (Potts et al., 2010; Winfree et al., 2011). The buff-tailed bumble bee *Bombus terrestris* has been the subject of much study (see for example, Duchateau and Velthuis, 1988, 1988; Peat and Goulson, 2005; Duchateau, 1989; Baer and Schmid-Hempel, 2005), as it is abundant in Europe and known to be an important pollinator (Kleijn et al., 2015). Much experimental and analytic effort has been devoted to mapping its biology and natural

history (Benton, 2006; Goulson, 2010). 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 Crone and Williams, 2016).

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 (Crouse et al., 1987; Banks and Tran, 2009; Morris and Doak, 2002). 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 has the potential to elucidate the mechanisms underlying these patterns and explain observed discrepancies (e.g., Williams et al., 2012; Rundlöf et al., 2014; Carvell et al., 2015; Wood et al., 2015) in which life stages (of queens, workers, males, and gynes) are supported under contrasting timing, amount, type and quality of food resources. Previous theoretical (Oster, 1976) and empirical (Beekman et al., 1998) work has focused on the influence of particular aspects of foraging behavior and queen survival on colony growth. Special

attention in particular has been given to modeling the allocation of resources among workers and sexual offspring and its implications for colony growth (Oster, 1976), with some evidence that optimal tradeoffs are a function of colony size as well as queen egg-laying rates (Poitrineau et al., 2009; Beekman et al., 1998). We take a broader approach here, developing a population model in which we can explicitly test hypotheses about how landscape use and exposure to environmental toxins affect bumblebee populations.

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 (Godfray et al., 1818; Goulson and Velthuis, 2013; Lundin et al., 2015). Mathematical modeling, especially in an iterative approach (Banks and Tran, 2009), can be used for projecting population abundance and understanding the importance of life history 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 (Banks et al., 2014). In this paper, we present a delay differential equation (DDE) model to simulate the abundance of different bumble bee castes 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 Banks, 1977; Cushing, 2013; Gopalsamy, 2013; Hutchinson, 1948 for examples) and even honeybee population modeling (Khoury et al., 2013). We refer the reader to Smith (2011) for an introduction to DDEs and applications, as well as Kot (2001) for DDEs in ecology.

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 naturally introduce the class of DDEs and provide a brief overview for the reader. We introduce a linear spline approximation method for obtaining a numerical solution to our model. Next 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. Model

2.1. Our proposed model

As we shall further develop below, our model is naturally a nonlinear system of delay differential equations (DDE) which describe 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) $G(t)$. According to Gill et al. (2012), only 70% of foragers return to their own colony after a foraging trip; we therefore assume that there is not-insignificant interaction between colonies and model a collection of bumblebee colonies which share a common pool of resources. 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 consider the following assumptions and basic seasonal timeline (Goulson, 2010; Duchateau and Velthuis, 1988; Müller et al., 1992; Benton, 2006). 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. In the absence of information about queen foraging efficacy, we assume that the queen accumulates a negligible store of resources during this time,
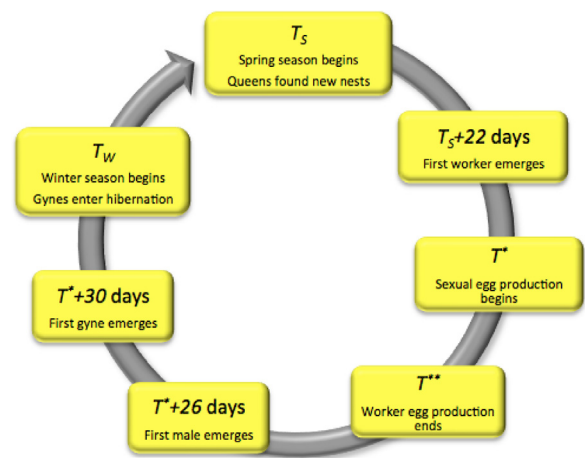

Fig. 1. Timeline of bumble bee seasonal dynamics.

primarily providing for herself and the initial brood of workers. Assuming a 22-day worker incubation time (from an egg laid to the emergence of an adult worker) (Goulson, 2010; Duchateau and Velthuis, 1988), the first workers emerge at $t = T_S + 22$. At this time, the workers take over resource foraging to develop a store of in-nest resources and tending to new eggs, while the queens devote all energy to production of worker eggs (Goulson, 2010). The authors of Goulson (2010) and Benton (2006) 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 (Goulson, 2010; Benton, 2006; Holland et al., 2013; Röseler, 1970; Duchateau et al., 2004; Duchateau and Velthuis, 1988; Lopez-Vaamonde et al., 2009; Müller et al., 1992). Environmental conditions can also cause nests to have either early or late season switch times (Duchateau and Velthuis, 1988). In our model, we assume at some time $t = T^*$, the queen begins to lay sexual (male and gyne) eggs while continuing to produce worker eggs (Benton, 2006). At time $t = T^{**}$, the queen stops producing worker eggs and devotes all energy to sexual egg production. At time $t = T^{**} + 22$, the last new worker emerges. At times $t = T^* + 26$, and $t = T^* + 30$, respectively, the first males and gynes emerge (assuming respective 26 and 30 day incubation periods (Duchateau and Velthuis, 1988)). Sexuals 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 (Goulson, 2010; Benton, 2006). 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 Fig. 1. To demonstrate the usefulness of the DDE model, we fix timeline values T^*, T^{**}, T_S and T_W at the values estimated by Müller et al. (1992) as given in Table 1 and described in Section 2.2.

We assume that the founding queen, workers, as well as worker, male and gyne larvae consume both nectar and pollen (Duchateau and Velthuis, 1988). We explicitly assume that nectar and pollen consumption in the nest is negligible for adult males and adult gynes; Goulson (2010) notes that males leave the colony a few days after reaching adulthood and that gynes may stay in the nest and forage for some time before finding a place to hibernate. In the absence of estimations for the resource consumption by emerging males and gynes in a colony, we assume that this short period