



Effects of vitellogenin in age polyethism and population dynamics of honeybees



Marisabel Rodriguez Messan^{a,b}, Robert E. Page Jr.^{c,d}, Yun Kang^{e,*}

^a Department of Mathematics, Dartmouth College, Hanover, NH 03755, USA

^b School of Mathematical and Statistical Sciences, Arizona State University, Tempe, AZ 85287, USA

^c School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

^d Department of Entomology and Nematology, University of California Davis, Davis, CA 95616, USA

^e Science and Mathematics Faculty, College of Integrative Sciences and Arts, Arizona State University, Simon A. Levin Mathematical, Computational, and Modeling Sciences Center, Mesa, AZ 85212, USA

ARTICLE INFO

Keywords:

Honeybees
Division of labor
Vitellogenin
Nutrition
Mathematical model
Seasonal changes
Pollen-derived proteins

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 macronutrients (i.e. proteins, carbohydrates, and fats) and 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

* Corresponding author.

E-mail addresses: marisabel@dartmouth.edu (M. Rodriguez Messan), robert.page@asu.edu (R.E. Page), yun.kang@asu.edu (Y. Kang).

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 (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

Download English Version:

<https://daneshyari.com/en/article/11021796>

Download Persian Version:

<https://daneshyari.com/article/11021796>

[Daneshyari.com](https://daneshyari.com)