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How regulation based on a common stomach leads to economic optimization of honeybee foraging

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HIGHLIGHTS

- Task regulation of collective behavior is modeled by individual ODE based approach.
- The colony uses 'common stomachs' that buffer and regulate foraging.
- The colony dynamically adapts to perturbations and changes in nutrition quality.
- The model predicts an adaptive strategy for both bees and plants.
- The mechanisms explain the self-regulating behavior of the collective.

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ABSTRACT

Simple regulatory mechanisms based on the idea of the saturable 'common stomach' can control the regulation of protein foraging and protein allocation in honeybee colonies and colony-level responses to environmental changes. To study the economic benefits of pollen and nectar foraging strategies of honeybees to both plants and honeybees under different environmental conditions, a model was developed and analyzed. Reallocation of the foraging workforce according to the quality and availability of resources (an 'adaptive' strategy used by honeybees) is not only a successful strategy for the bees but also for plants, because intensified pollen foraging after rain periods (when nectar quality is low) compensates a major fraction of the pollination flights lost during the rain. The 'adaptive' strategy performed better than the'fixed' (steady, minimalistic, and non-adaptive foraging without feedback) or the 'proactive' (stockpiling in anticipation of rain) strategies in brood survival and or in nectar/sugar economics. The time pattern of rain periods has profound effect on the supply-and-demand of proteins. A tropical rain pattern leads to a shortage of the influx of pollen and nectar, but it has a less profound impact on brood mortality than a typical continental rainfall pattern. Allocating more bees for pollen foraging has a detrimental effect on the nectar stores, therefore while saving larvae from starvation the 'proactive' strategy could fail to collect enough nectar for surviving winter.

1. Introduction

Parallel processing generally increases the reliability of biological systems and if it is paired with division of labor and task partitioning, remarkably successful biological super-organisms such as insect societies emerge (Beshers and Fewell, 2001). Honeybees (*Apis mellifer*a L.) have coevolved with flowering plants and honeybee colonies have developed complex collective behaviors allowing them to flourish in a wide range of climatic and ecological conditions. The strong mutualistic relationship between honeybees and flowering plants is basically built on a significantly more effective pollination service (compared to wind-pollination) which is provided by bees in exchange for proteins (pollen) and sugars (nectar) offered by plants. This rich supply of nutrients is used for massive brood production and colony growth, that in turn leads to an extended pollination capacity of honeybee colonies. Having a higher number of pollinators provides an evolutionary advantage for plants, thus any adaptations that may attract more pollinators is assumed beneficial (Darwin, 1862). For this mutualistic relationship to work well in a wide range of conditions, plants and bees require regulation of behaviors to adapt to climate, to weather, to internal physiological changes and to external perturbations.

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Bee colonies have only finite workforce thus efficient allocation of workers to different tasks can significantly affect costs and gains on multiple timescales. For example, employing more pollen foragers increases the influx of proteinaceous pollen, leading to lower larval mortality and less starvation. This keeps the number of brood high and allows frequent nursing of brood (Schmickl and Crailsheim, 2001, 2002; Schmickl et al., 2003). With a time-delay, high brood production increases the future workforce for foraging and nursing. However, due to the finite workforce these extra pollen foragers will be recruited from bees that could have become nectar foragers otherwise, therefore the nectar input will decrease. In turn, this will affect the survivability of the colony in the long run (overwintering), thus regulation of population dynamics (Schmickl and Crailsheim, 2007) and homeostatic regulation mechanisms of protein collection and protein allocation are crucial for successful survival and reproduction of colonies (Schmickl and Crailsheim, 2004).

Recent studies have shown (Greco et al., 2013) that the sugar concentration brought back in the crops of foraging bees, is very close to the sugar concentration of the nectar offered by plants. The sugar concentration of the nectar also governs the optimality of nectar storage, processing and allocation of nectar in the honeybee colony. Therefore regulation of work governed by the sugar concentration of nectar offered by plants seems to be an important factor for colony-level fitness of a honeybee colony.

The regulation of collective behaviors in a honeybee colony often happens in a decentralized manner via simple worker-worker interactions. The core of the behavior regulation in honeybees, as it is proposed in literature, spans from fixed programs, pheromone-based, dance-based to threshold-based mechanisms (Beshers and Fewell, 2001). Recently, several novel models based on information-exchange have also been proposed (Johnson and Linksvayer, 2010). Several recent models for decentralized regulation of work focus on material exchange of workers via a common stomach (Karsai and Wenzel, 2000; Karsai and Schmickl, 2011; Karsai and Phillips, 2012; Karsai and Runciman, 2011; Hamann et al., 2013), which builds upon the idea of an 'information center', as it was proposed by Seeley (1985,1995). The common stomach is a community material storage with which the individuals are interacting. This storage can be a composite storage consisting of the crops of many individuals, such as the way the wasps store water or it could be an external storage area such as the comb where individuals can deposit or acquire materials. These concepts assume a network of material/information-exchange among workers through the common stomach and this in turn is accessible by the individuals to adjust their own behaviors according to the needs of the collective. Based on this paradigm we present here a model of a honeybee colony to test how nutrient and workforce allocation is influenced by different weather regimes (rainy weather, continental versus tropical climates). We use this model to study how time patterns in rain period and corresponding nectar constitutions offered by plants affect the sugar and protein harvest of bees, which in turn determines the brood status in the colony and the pollination service received by plants.

Our goal is to construct a mathematical model to draw predictions on the expected nutrient economics and pollination services in various weather conditions. Our main hypothesis is that the time pattern of rainy weather, which prevents foraging, as well as the dynamics of sugar concentration of nectar offered by plants have a significant impact on pollination service and nutrient economics. We furthermore hypothesize that different foraging strategies performed by a honeybee colony (adaptive recruitment versus fixed foraging levels) affect important colony-level and fitness-relevant factors: brood survival and nectar/sugar accumulation in the hive.

Finally, we test whether or not plants could significantly affect the economics of honeybees' collective foraging strategies by secreting different nectar qualities and nectar volumes in relation to current and past weather conditions. After extensive rain periods, plants have to cope with an over-abundance of water, leading to higher surrounding air humidity and reduced photosynthetic activity during the rain. Thus, production of high-sugar nectar is costly just after such rain periods. After rainy weather, nectar is present in higher volumes in individual plants (Bertsch, 1983; Carrión-Tacuri et al., 2012), but has lower sugar concentration (Kenoyer, 1917; Bertsch, 1983). Our study investigates how such weather-dependent nectar dynamics can affect the economics of the division of labor observed in honeybee colonies and also investigates the impact of the time pattern of rain on these economics.

2. Model

2.1. Basic assumptions and bee demography

In a honeybee colony, a single queen lays worker-producing eggs (1000–2000 per day (Bodenheimer, 1937). The egg stage lasts 3 days and is followed by an actively feeding larva (uncapped) stage (4.5–5.5 days) and a subsequent capped non feeding pupa stage (12 days) followed by the emergence of the new bee (Fukuda and Sakagami, 1968; Sakagami and Fukuda, 1968). Larvae are fed by a group of young bees (nurse bees) with nectar, pollen and a proteinaceous jelly, derived from pollen (Haydak, 1963; Lindauer, 1952; Sakagami, 1953). In addition, adult bees spend nectar-derived carbohydrates on thermo-regulating the brood region to steady it at 36–38 °C. Older bees generally carry out foraging for water, resin, nectar and pollen – in this paper we focus on only the last two foraged resources. Honeybees regulate their pollen foraging activity on the ratio of supply-to-demand (see (Schmickl and Crailsheim, 2004) for a detailed review). Blaschon et al. (1999) reports that during adverse weather conditions (such as rain) pollen stores and the number of brood show strong negative correlation with duration of rainy weather. Rainy weather prevents foraging for both nectar and pollen, but by using a 'pollen trap' at the hive entrance the success of pollen foraging can be decreased experimentally without impairing nectar foraging. Several studies (Schmickl and Crailsheim 2001, 2002; Schmickl et al., 2003) show that both-rainy weather and pollen trap-significantly affect brood survival, brood care of surviving brood and general activity of the queen. However, egg laying of the queen was found to stay almost constant (Schmickl et al., 2003), thus producing a constant inflow of demanding brood to feed. In adverse weather conditions, the bees employ counter measures such as reallocation of foragers, cannibalism of brood and feeding parts of the remaining brood less during such food-shortages (Schmickl and Crailsheim, 2001, 2002) to compensate quickly for the pollen losses. Lindauer (1952) observed that several days of rain or application of a 'pollen trap' at the hive entrance leads to a significant increase in the ratio of pollen foragers to nectar foragers. In times of high pollen need, the colony responds with a high number of pollen foragers without changing the total flight activity or the total number of all foragers (Weidenmuller and Tautz, 2002). Two mechanisms have been suggested to explain the dynamic supply-to-demand regulation of pollen foraging. Pankiw et al. (1998) suggest that pollen foraging activity is regulated by brood pheromones, while Camazine (1993) and Camazine et al. (1998) suggest a food-sharing-based mechanism. Both mechanisms have in common that substances are diffusing within the worker community, converting the collective of nest-workers into an "information center" (Seeley, 1985). While the first study