Understanding the Emerging Behaviors and Demands for the Colony Success of

Social Insects: A Mathematical Approach

by

Marisabel Rodríguez Messan

A Dissertation Presented in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Approved May 2018 by the
Graduate Supervisory Committee:

Yun Kang, Co-Chair
Carlos Castillo-Chavez, Co-Chair
Robert E. Page Jr.
Yang Kuang
Carl Gardner

ARIZONA STATE UNIVERSITY

August 2018

ABSTRACT

The most advanced social insects, the eusocial insects, form often large societies in which there is reproductive division of labor, queens and workers, have overlapping generations, and cooperative brood care where daughter workers remain in the nest with their queen mother and care for their siblings. The eusocial insects are composed of representative species of bees and wasps, and all species of ants and termites. Much is known about their organizational structure, but remains to be discovered.

The success of social insects is dependent upon cooperative behavior and adaptive strategies shaped by natural selection that respond to internal or external conditions. The objective of my research was to investigate specific mechanisms that have helped shaped the structure of division of labor observed in social insect colonies, including age polyethism and nutrition, and phenomena known to increase colony survival such as egg cannibalism. I developed various Ordinary Differential Equation (ODE) models in which I applied dynamical, bifurcation, and sensitivity analysis to carefully study and visualize biological outcomes in social organisms to answer questions regarding the conditions under which a colony can survive. First, I investigated how the population and evolutionary dynamics of egg cannibalism and division of labor can promote colony survival. I then introduced a model of social conflict behavior to study the inclusion of different response functions that explore the benefits of cannibalistic behavior and how it contributes to age polyethism, the change in behavior of workers as they age, and its biological relevance. Finally, I introduced a model to investigate the importance of pollen nutritional status in a honeybee colony, how it affects population growth and influences division of labor within the worker caste. My results first reveal that both cannibalism and division of labor are adaptive strategies that increase the size of the worker population, and therefore, the persistence of the colony. I show the importance of food collection, consumption, and processing rates

to promote good colony nutrition leading to the coexistence of brood and adult workers. Lastly, I show how taking into account seasonality for pollen collection improves the prediction of long term consequences.

To my parents Isabel and Benito Rodríguez for their love, teachings, and incessant support.

A mis padres Isabel y Benito Rodríguez por su amor enseñanzas y constante apoyo.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

x

Chapter 1

INTRODUCTION

Social insects, including ants, bees, wasps, and termites, which are classified as eusocial, represent some of the most advanced social systems and are among the most diverse and ecologically important organisms on Earth [Koenig and Dickinson, 2017]. These societies are characterized by their social behavior composed of complex interactions of groups of organisms. Eusocial colonies display the highest levels of organization found in the Animal Kingdom, and are distinguished by their cooperative division of labor, reproductive division of labor, and overlap of at least two generations in the same colony [Hölldobler and Wilson, 2010, Koenig and Dickinson, 2017]. In addition, they frequently display a division of labor among members of the non-reproductive caste (workers) where different workers specialize on performing different tasks. Often task specialization is age-dependent (temporal polyethism) [Beshers and Fewell, 2001].

The study of social insect behavior, its adaptive value and underlying mechanisms are of great interest to animal behavior and the social sciences and has advanced our understanding of behavioral ecology and human social behavior [Koenig and Dickinson, 2017]. For instance, the collective behavior of social insects can influence novel and effective solutions to human design challenges [Holbrook *et al.*, 2010] such as robot coordination [Krieger *et al.*, 2000] and flow shop scheduling [Cicirello and Smith, 2004], which application have derived from models studying the task distribution among groups of insects responding to a specific stimuli based individual thresholds [Holbrook *et al.*, 2010]. Therefore, social insects have provided the best models for studying the evolution and maintenance of cooperative behavior. Despite the impact

that social insect cooperation theories have made on our understanding of cooperation at large, mechanisms influencing their colony success such as cannibalism, nutritional demands of the colony, and multi-species interactions has mostly been overlooked.

Social interactions represent not only a benefit to the success of the colony but also a cost. For instance, due to close contact with conspecifics, there is an increased risk of parasitism, disease, and cannibalism. Although parasitism and disease can cause a decrease of the colony's fitness, cannibalistic interactions have been demonstrated across several field and laboratory studies as well as in model analysis to be an important mechanism that can benefit the colony fitness by improving growth rate, survivorship, vigor, longevity, and fecundity [Richardson *et al.*, 2010].

Cannibalistic interactions between different developmental stages in a population are prevalent among many groups of animals and social insects [Elgar and Crespi, 1992, Polis, 1981, Stenseth, 1985, Richardson *et al.*, 2010]. It has been regularly observed in social insect colonies, including leafcutter ants and honeybees [Schmickl and Crailsheim, 2001, Monnin and Peeters, 1997], and is suggested to be a selfish behavior influenced by environmental factors such as shortage of food resources [Matthews and Matthews, 2009, Richardson *et al.*, 2010], and individual traits such as sex [Schultner, 2014], but are also often part of typical intraspecies interactions [Fox, 1975]. A common form of cannibalism among social insects is the consumption of conspecific eggs by larvae or higher developmental stages. Egg cannibalism is a recycling process of energetic investments in social insects known to increase growth and developmental rates [Osawa, 1992, Roy *et al.*, 2007, Schultner *et al.*, 2013] and adult body size [Osawa, 2002, Schultner *et al.*, 2013], decrease competition of resources [Roy *et al.*, 2007, Schultner *et al.*, 2013, Wise, 2006], and improve survival [Roy *et al.*, 2007, Schultner *et al.*, 2013].

Cooperative behavior of social insects increases colony's fitness at the cost of

decreasing the fitness of individual colony members. Many social insects exhibit a complex system of division of labor by which task allocation depends on the age of the individual or on distinct anatomical features, or both [Hölldobler and Wilson, 2010]. Division of labor is an important factor for the evolutionary success of social insects because different activities are performed simultaneously by groups of specialized individuals [Robinson, 1992]. It facilitates the optimization of energy investment by the group workforce by 1) allocating optimal numbers of individuals, or work group effort, to different sets of tasks associated with nest construction, defense, food collection, colony growth, and reproduction, 2) decreasing the chances of social system failure by having tasks performed in parallel, and 3) increasing individual task performance efficiency through experience gained by repeated activity.

Mechanisms of division of labor include size polymorphism, age polyethism, variation in response thresholds, and learning [Beshers and Fewell, 2001]. For instance, age polyethism is a phenomenon observed in many social insects in which individuals perform different tasks as they grow older. [Oster and Wilson, 1978, Wilson *et al.*, 1971]. In leafcutter ants, including *Atta* and *Acromyrmex*, workers in the smallest physical class take care of brood and the fungus inside the nest when they are young [Camargo *et al.*, 2007, Van Bael *et al.*, 2011], while older workers from all size classes are more likely to participate in dangerous activities such as defending the nest [Hölldobler and Wilson, 2010].

Another mechanism regulating worker age-based division of labor involves the nutritional status of the colony and nutritional variation of the individual [Ament *et al.*, 2010, Avni *et al.*, 2014]. Colonies of social insects require protein, carbohydrates, minerals, and water. However, protein and carbohydrates are critical nutrients that influence growth, development, and foraging behavior. At the individual level, brood require more protein to aid in their development, while older workers require more

carbohydrates for energy to carry out tasks showing variation in nutritional needs. Worker fat and protein content are different from the queen's due to its reproductive task. Queens demand large quantities of protein and fat for making eggs while workers show gradual depletion of stored fat and protein associated with switching tasks from nest work to foraging [Smith *et al.*, 2011, Toth and Robinson, 2005]. Nutritional needs affect worker behavior. Pollen provides protein for vitellogenin, an important lipoprotein necessary for queen egg laying, food for larvae, youth and maturing adult workers, as well as resistance to diseases and environmental toxins [Alaux *et al.*, 2011, Page *et al.*, 2012]. Shortage of protein could affect brood production, the quality or the number of larvae reared to adulthood, worker longevity, and colony survival [Brodschneider and Crailsheim, 2010].

Although several models have addressed the dynamics of cannibalistic behavior in age-structure models (see Kang *et al.* [2015], Cushing [1991]), the dynamics of both egg cannibalism and division of labor together has not yet been studied. Therefore, the work in Chapter 2 aims to provide a study of both of these mechanisms through mathematical modeling. Specifically, I present a compartmental two-stage ODE model to study the ecological and evolutionary effects of both cannibalism and the invested energy on cooperative brood care and foraging that measure the efficacy of division of labor. The corresponding evolutionary model follows the evolutionary game theory framework used by [Cushing, 1991, Cushing and Hudson, 2012, Kang *et al.*, 2015, Kang and Udiani, 2014, Vincent and Brown, 2005]. Hence, the main purpose of this project is to investigate how egg cannibalism and division of labor can promote colony survival in both the ecological and evolutionary context.

In Chapter 3, using two sets of ODE models, I explore how division of labor (DOL), age polyethism, and egg cannibalism behavior interact to affect the colony population dynamics of leafcutter ants and their fungus garden in a two-fold manner.

First, to address how age polyethism affects the worker population dynamics when the leafcutter ants and fungus garden interaction model incorporates other mechanisms of DOL, I compare the dynamical outcomes of an interacting species model with and without age polyethism. The second part explores the effects of egg cannibalism in the population dynamics of a colony. In order to understand how to model such social conflict behavior realistically, I propose and study a leafcutter ant and fungus garden interaction model that uses different functional responses to incorporate benefits of egg cannibalism behavior.

In Chapter 4, I introduce a model to investigate the importance of pollen nutritional status in a honeybee colony affecting population growth and having impacts on division of labor among individuals. As for modeling techniques, I explore the inclusion of seasonal pollen collection improving forecasting. The proposed model serves as a starting point of modeling techniques that can allow us to study present factors leading to colony collapse, such as nutritional stress [Naug, 2009], scarcity of food sources [Naug, 2009], and climate change.

Chapter 2

COLONY AND EVOLUTIONARY DYNAMICS OF A TWO-STAGE MODEL WITH BROOD CANNIBALISM AND DIVISION OF LABOR IN SOCIAL INSECTS

Abstract

Division of labor (DOL) is a major factor for the great success of social insects because it increases the efficiency of a social group where different individuals perform different tasks repeatedly and presumably with increased performance. Cannibalism plays an important role in regulating colony growth and development by regulating the number of individuals in a colony and increasing survival by providing access to essential nutrients and minimizing competition among colony mates. To understand the synergy effects of DOL and cannibalistic behavior on colony dynamic outcomes, we propose and study a compartmental two-stage model using ecological and evolutionary game theory settings. Our analytical results of the ecological and evolutionary models suggest that: (1) A noncannibalistic colony can survive if the efficiency of energy investment reflecting the DOL is greater than the relative death rate of the older population. (2) A cannibalistic colony can die out if both the efficiency of energy investment and the relative cannibalism rate (where each is also reflecting the DOL) are too large; or if the relative cannibalism rate alone is too small. (3) From our numerical analysis, cannibalism can increase or reduce the colony?s total population size, which greatly depends on the benefit of egg cannibalism increasing or decreasing of adult?s lifespan. (4) A cannibalistic and noncannibalistic colony can experience bistability due to cooperative behavior. (5) In the evolutionary settings, DOL can pre-

vent colony death and natural selection can preserve strong Allee effects by selecting the traits with the largest investment on brood care and the lowest cannibalism rate. (6) Evolutionary dynamics may increase the fitness of the colony, i.e., the successful production of workforce which results in the increase of total worker population size, colony survival, and reproduction. Our results suggest both cannibalism and DOL are adaptive strategies that increase the size of the worker population, and therefore, persistence of the colony.

Introduction

Division of labor (DOL) is an important factor for the evolutionary success of social insects [Robinson, 1992]. It facilitates the optimization of energy investment by the group workforce by allocating optimal numbers of individuals, or work group effort, to different sets of tasks associated with nest construction, defense, food collection, colony growth, and reproduction. Individuals in a nest perform tasks in parallel, rather than serially, and DOL allows the optimization of the total effort of the worker population within the nest [Jeanne, 1986]. The structure of division of labor in colonies is, therefore, optimized by natural selection to produce a worker population that is demographically adapted to its environment. The honey bee is an exemplar of social evolution with both a distinct reproductive division of labor with a single reproductive female, the queen, and thousands of workers that are facultatively sterile [Wilson *et al.*, 1971]. Workers demonstrate a further division of labor that is age related where individuals change the sets of tasks they perform as they age. These tasks are associated with the construction and maintenance of the nest, honey processing, colony defense, brood rearing, and foraging for food resources [Winston, 1991]. Other social insects such as ants [Bonabeau *et al.*, 1998], termites [Korb *et al.*, 2012], and wasps [Arathi and Gadagkar, 1998] perform similar tasks such as cooperative brood

care, construction and maintenance of the nest, and foraging for food resources which have an energetic cost. We can therefore think of natural selection working to optimize the ergonomic efficiency of a colony by adapting its social structure associated with division of labor. Moreover, egg cannibalism, a recycling process of energetic investments in social insects is known to increase growth and developmental rates [Osawa, 1992, Roy *et al.*, 2007, Schultner *et al.*, 2013], and adult body size [Osawa, 2002, Schultner *et al.*, 2013], decrease competition for resources [Roy *et al.*, 2007, Schultner *et al.*, 2013, Wise, 2006] and improve survival [Roy *et al.*, 2007, Schultner *et al.*, 2013]. For example, the wood ant *Formica aquilonia* is known to compete by eating eggs and therefore increase their survival [Schultner *et al.*, 2013]. Other social insects presenting cannibalistic behaviors with these benefits are termites, wasps, and social bees [Polis, 1981]. In honeybees, foraging behavior is known to be driven by total number of brood in the colony [Al-Tikrity *et al.*, 1972, Filmer, 1932, Winston and Fergusson, 1986], and as described by Schmickl and Crailsheim [2001], when harsh environmental conditions prevent honeybees from collecting pollen, workers then use brood cannibalism to reduce larval protein demand. Both of these social behaviors, egg cannibalism and division of labor, illustrate individual and colony level selection in a social environment, respectively. Studies have shown that egg cannibalism is particularly a general way in social Hymenoptera to increase individual fitness (see Schultner [2014]). On the other hand, caring for the queen, foraging for food, tending the larvae, and other tasks related with the success of a colony are known as altruistic behaviors which are believed to be advantageous at the group level [Okasha, 2008, Schultner, 2014]. Although this behavior could represent a selective disadvantage at the individual level, the fitness of the colony as a whole will be intensified [Okasha, 2008].

Mathematical models help us understand the ecological as well as the evolutionary

effects of egg cannibalism and division of labor. Since both cannibalism and division of labor are observed at different developmental stages, age-structured population models have been used to study these behaviors. In 2015, Kang *et al.* [2015] proposed a compartmental two-stage model with egg cannibalism providing important analytical results such as forward transcritical bifurcation due to a large egg cannibalism rate, while a small egg cannibalism rate could lead to a backward subcritical bifurcation generating strong Allee effects meaning that a population, in this case worker force, could stabilize at the carrying capacity of population growth, or at the extinction level [Courchamp *et al.*, 2008]. The ecological model suggested that in fact cannibalistic behavior can regulate the worker population size and promote colony survival, while the worker population within a nest can die out without cannibalistic behavior. In 1998, Wakano *et al.* [1998] proposed an age-structured population model with division of labor between tasks inside and outside the nest and foraging mortality effects that can determine the most favorable task allocation demography that maximizes worker production. Tofilski [2006] used a model of integral equations with two sets of tasks and associated mortality rates suggesting that in most cases, caste polyethism reduces the expected life span of workers. Although, Tofilski's model lacks age-structure, his results explain the evolution of division of labor in social insects by showing that different ways of division of labor can prolong worker's longevity.

The evolutionary dynamic effects on worker population have not been well studied. Few mathematical models have addressed the evolutionary outcomes of age-structure models with cannibalism or division of labor (see the work of Dercole and Rinaldi [2002], Nishimura and Hoshino [1999], Nishimura and Isoda [2004], Rudolf [2007], Stenseth [1985], Wakano *et al.* [2002]). In some of these studies, we can encounter results such as evolutionary scenarios with evolutionary stable strategies [Dercole and Rinaldi, 2002, Stenseth, 1985], evolutionary dynamics of cannibalism using a

9

predator-prey interaction among conspecifics [Nishimura and Isoda, 2004], and effects of stage-structured cannibalism and behavioral avoidance of cannibalism that result in an indirect positive link between the prey and predator stages [Rudolf, 2007]. Kang *et al.* [2015] developed an evolutionary model using an evolutionary game theory framework showing that by choosing the trait with a small cannibalism rate, natural selection preserves strong Allee effects. Also, fitness of a colony may decrease or increase by decreasing or increasing the total worker population size, and the choice of the trait function can affect the permanence of the system, i.e. the long-term survival of the colony.

Although several models have addressed the dynamics of cannibalistic behavior in age-structure models, the dynamics of both egg cannibalism and division of labor together has not yet been studied. Therefore, we present a compartmental two-stage model to study the ecological and evolutionary effects of both cannibalism and the invested energy on cooperative brood care and foraging that measure the efficacy of division of labor. This model consists of eggs and mature stages, in which the population of eggs is cannibalized by mature stages and individuals in the mature stages invest energy to rear the brood. The corresponding evolutionary version presented model follows the evolutionary game theory framework used by others [Cushing, 1991, Cushing and Hudson, 2012, Kang *et al.*, 2015, Kang and Udiani, 2014, Vincent and Brown, 2005]. Therefore, the main purpose of this paper is to investigate how egg cannibalism and division of labor can promote colony survival in both the ecological and evolutionary settings.

A Mathematical Model with Division of Labor and Cannibalism

Model Derivation

We develop a two compartmental model of a social insect population consisting of stage-structure cannibalism and division of labor implicitly where each worker is performing a specific task such as brood care or foraging that contributes to the colony growth. The model's state variables are defined as follows: Let $x(t) + y(t)$ denote the total population of a focal colony at time t, where $x(t)$ denotes egg population that can be cannibalized by others (larvae, queens and adult workers) at time t, and $y(t)$ denotes the population of the older ones that may have cannibalistic behavior at time t. We propose the following set of nonlinear equations describing a two-stage population model of social insects with division of labor implicitly and egg cannibalism:

$$x' = \frac{ry}{1 + ax + \hat{c}y} - \hat{\alpha}xy - \beta x,$$

$$y' = \beta x \cdot \frac{\hat{c}y}{1 + ax + \hat{c}y} - \frac{1}{1 + c_a\hat{\alpha}x},$$

(2.1)

The ecological assumptions of the colony's population dynamics (2.1) above are summarized as follows:

1. **Egg population** $x(t)$: The egg population $x(t)$ that can be cannibalized by others at time t is determined by one inflow rate and two outflow rates:

    (i) *The inflow rate* is modeled by $\frac{ry}{1+ax+\hat{c}y}$ which gives the net egg production rate by queen(s). The term $\frac{ry}{1+ax+\hat{c}y}$ is modified from the recent work of Kang *et al.* [2015] where r could be considered as a baseline egg production from the work effort by workers; a is a coefficient measuring the combination effects of crowding effects and the resource allocation to egg population; and $\hat{c}$ is the brood care effort from the workers. The detailed

11

biological assumptions of $\frac{ry}{1+ax+\hat{c}y}$ are stated as follow. We assume that there is a p proportion of the adult workers performing the foraging task which provides food resource for the whole colony, and the rest $1-p$ proportion of workers performing brood care. Let the parameter $\hat{\gamma}$ be the average work effort of a worker that could either obtain food resource to contribute to egg production or perform brood care. Thus, the foraging task group can obtain food resource $\hat{\gamma}py = ry$ with a ratio of $\frac{1}{1+ax+\hat{\gamma}(1-p)y} = \frac{1}{1+ax+\hat{c}y}$ devoted for reproduction since the colony invests ax energy to the egg class and $\hat{c}y = \hat{\gamma}(1-p)y$ energy for the brood care including the effort of taking care of larvae, queens, and themselves. As a consequence, the ratio $\frac{1}{1+ax+\hat{c}y}$ also implies that the colony decreases its investment into egg production when many eggs are present. Therefore, the larger egg population present in the colony and the larger investment in the brood care can have negative effects on the net egg production x; and $r = \hat{\gamma}p$, $\hat{c} = \hat{\gamma}(1-p)$ reflect the division of labor in workers of the colony.

(ii) *Outflow rate 1:* The egg cannibalism rate by worker population is modeled $\hat{\alpha}xy$ which follows the traditional Holling Type I functional response. In social insect colonies, such as ants, eggs are close to queen(s) and larvae, in general, there is no need for queens or larvae to search for eggs. In addition, workers also know the location of eggs.

(iii) *Outflow rate 2:* The maturation rate of egg population is βx. We assume that an egg leaves the egg stage at a per-capita rate β, and dies only by cannibalism, thus we do not incorporate an additional death rate of eggs in our current model. One explanation for no additional egg mortality is that even if egg dies naturally, it will be eaten and the nutrient will be recycled back to the colony.

2. **The worker population** $y(t)$**:** The population of workers that may have cannibalistic behavior $y(t)$ at time t is determined by two flow rates:

   (i) *Inflow rate* is modeled by $\beta x \cdot \frac{\hat{c}y}{1+ax+\hat{c}y}$ which is the product of the rate of egg leaving the egg stage, βx, and the probability of the survival rate $\frac{\hat{c}y}{1+ax+\hat{c}y}$ measured by the brood care effort of the worker population. After eggs leave the egg stage, they enter into larvae, pupae stage, respectively, before becoming adult workers where the survival ability of larvae depends on the investment of the brood care effort from workers. Our current model does not have the explicit stage structure of larvae, pupae stage, instead, we use $\frac{\hat{c}y}{1+ax+\hat{c}y}$ to model the survival rate during these stages which implies that the larger investment in brood care can have positive effects on the net population growth of adult worker population y.

   (ii) *Outflow rate:* The death rate of the older population in the absence of cannibalism (i.e. $\hat{\alpha} = 0$) can be determined by dy. However, in the presence of cannibalism (i.e. $\hat{\alpha} > 0$), dy can be decreased with the functional response $\frac{1}{1+c_a\hat{\alpha}x}$ which represents the benefit obtained from cannibalism. The parameter d is the death rate in the absence of cannibalism and c_a is a coefficient describing the functional response of survivability to an increasing presence of eggs (and therefore increasing the number of individuals cannibalized).

Given the above ecological assumptions, for further analysis, we rescale system (2.1) using the transformation $\tau = \beta t$, $E = ax$, and $A = \hat{c}y$, where $E' = \frac{dE}{d\tau}$, and

13

$A' = \frac{dA}{d\tau}$, then the above model (2.1) reduces to

$$E' = \frac{\gamma A}{1 + E + A} - \alpha AE - E,$$

$$A' = \frac{cEA}{1 + E + A} - \frac{\delta A}{1 + bE}, \tag{2.2}$$

whose biological meanings of the rescaled parameters have been listed in Table 2.1. We can see that the efficiency of energy investment c, the relative egg production rate γ, and the relative cannibalism rate α reflect the DOL in some degree as they all contain the p which is the ratio of workers engaging in foraging while $1 - p$ is the ratio of workers engaging in brood care.

Parameter	Definition
$c = \frac{\hat{c}}{a} = \frac{\hat{\gamma}(1-p)}{a}$	The efficiency of energy investment (reflecting the DOL)
$\gamma = \frac{ar}{\hat{c}\beta} = \frac{r}{\beta c} = \frac{ap}{\beta(1-p)}$	The relative egg production rate (reflecting the DOL)
$\alpha = \frac{\hat{\alpha}}{\beta\hat{c}} = \frac{\hat{\alpha}}{\beta\hat{\gamma}(1-p)}$	The relative cannibalism rate (reflecting the DOL)
$\delta = \frac{d}{\beta}$	Relative death rate.
$b = \frac{\hat{b}}{a} = \frac{c_a\hat{\alpha}}{a}$	Relative benefit rate from cannibalism.

Table 2.1: Description of Parameters in Model (2.2)

Mathematical Analysis

Dynamics of Ecological Model

The rescaled ecological Model (2.2) state space is $\mathbb{R}_+^2$ and we assume that all parameters α, b, c, δ, γ are strictly positive. We show that Model (2.2) is positive invariant and bounded in $\mathbb{R}_+^2$ in the following theorem:

Theorem 1 (Positive Invariance and Boundedness)**.** *System (2.2) is positive invariant in $\mathbb{R}_+^2$ and every trajectory is attracted to a compact set $D = \left[0, \frac{\gamma}{\alpha}\right] \times \left[0, \frac{\gamma\left(\frac{b\gamma}{\alpha}+1\right)}{\delta\alpha}\right]$.*

14

Moreover, Model (2.2) can have only equilibrium dynamics.

Notes: Theorem 1 suggests our model (2.2) is biologically well-defined and has no limit cycles according to Dulac-Bendixson Criterion.

Equilibria and Stability

Model (2.2) has always the extinction equilibrium: $\mathbf{E}_0 = (0,0)$, and can have two interior equilibria: $\mathbf{E}_i = (E_i^*, A_i^*)$, $i = 1, 2$. An interior equilibrium of the form (E^*, A^*) must satisfy the following equations:

$$\text{Let} \quad E' = 0, \quad \Rightarrow \quad 1 + E^* + A^* = \frac{\gamma A^*}{E^*(\alpha A^* + 1)}, \tag{2.3}$$

$$\text{and} \quad A' = 0, \quad \Rightarrow \quad 1 + E^* + A^* = \frac{cE^*(1 + bE^*)}{\delta} \tag{2.4}$$

Solving for A^* in equation (2.4) we obtain $A^* = f(E^*) = \frac{bcE^{*2} + (c - \delta)E^* - \delta}{\delta}$. Also, setting $(2.3) = (2.4)$ yields (more details on obtaining this equation can be found in A):

$$1 - \frac{1}{\alpha A + 1} = \frac{\alpha c E^2 (1 + bE)}{\delta \gamma} \tag{2.5}$$

From equation (2.5), we define $nf_1(E) = \frac{\alpha c E^2 (1 + bE)}{\delta \gamma}$ and $nf_2(E) = 1 - \frac{1}{\alpha A + 1} = 1 - \frac{1}{\alpha f(E) + 1} \leq 1$, such that $nf_1(E)$ and $nf_2(E)$ are subject to $E \geq E^c = \frac{\delta - c + \sqrt{(\delta - c)^2 + 4bc\delta}}{2bc}$. Depending on the values of $\gamma, \alpha, b, c, \delta$, the element E_i^* of an equilibrium of the form $(E_i^*, A_i^*) = (E_i^*, f(E_i^*))$, for $i = 1, 2$ is determined by the positive root(s) of the equation $nf_1(E) = nf_2(E)$ which can have none or at least two positive roots.

The stability of the equilibria is determined using the following Jacobian matrix evaluated at each of the equilibria $\mathbf{E}_i$, $i = 1, 2$.

$$J = \begin{pmatrix} -A\alpha - \frac{A\gamma}{(1+E+A)^2} - 1 & \frac{\gamma}{A+E+1} - \frac{A\gamma}{(1+E+A)^2} - \alpha E \\ \frac{cA}{1+E+A} - \frac{AEc}{(1+E+A)^2} + \frac{Ab\delta}{(1+bE)^2} & -\frac{\delta}{1+bE} + \frac{cE}{1+E+A} - \frac{cAE}{(1+E+A)^2} \end{pmatrix} \tag{2.6}$$

15

Proposition 1. *Model* (2.2) *can have the following dynamics depending on the values of its strictly positive parameters* $\alpha, d, c, \delta, \gamma$ *defined in Table 2.1.*

1. **Extinction:** *There is no interior equilibria if*

   $$\alpha(\delta - c + K)^2(c + \delta + K) > 8b^2c^2\gamma\delta \quad or \quad \alpha[\delta - c + K][c + 3(\delta + K)] > 4bc\gamma K,$$

   where $K = \sqrt{(\delta - c)^2 + 4bc\delta}$.

2. **Colony survival:** *Model* (2.2) *can have at least two interior equilibria* $\mathbf{E_i}$, $i = 1, 2$ *if for* $\ell = \frac{2\sqrt{bc\delta}}{bc}$, *we have* $nf_2(\ell) - nf_1(\ell) < 1$, *i.e.,*

   $$\frac{4\alpha}{c^2}(c + 2\sqrt{bc\delta})(2\alpha\sqrt{bc\delta}(\delta - c) - bc\delta(1 + 3\alpha)) > b^2\gamma\delta$$

3. **Stability:** *The extinction equilibrium is always locally asymptotically stable, while an interior equilibrium* $\mathbf{E_i} = (E_i^*, A_i^*)$ *for* $i = 1$ *or* 2 *is locally asymptotically stable whenever* $\alpha(bcE_i^{*2} + (c - \delta)E_i^* - \delta)^2 > \delta^2(1 + E_i^*)$ *for* $E_i^* > 0$.

(a) $c > \delta$; $b = 1, c = 1, \delta = 0.5$ (b) $c < \delta$; $b = 5, c = .7, \delta = 1.12$
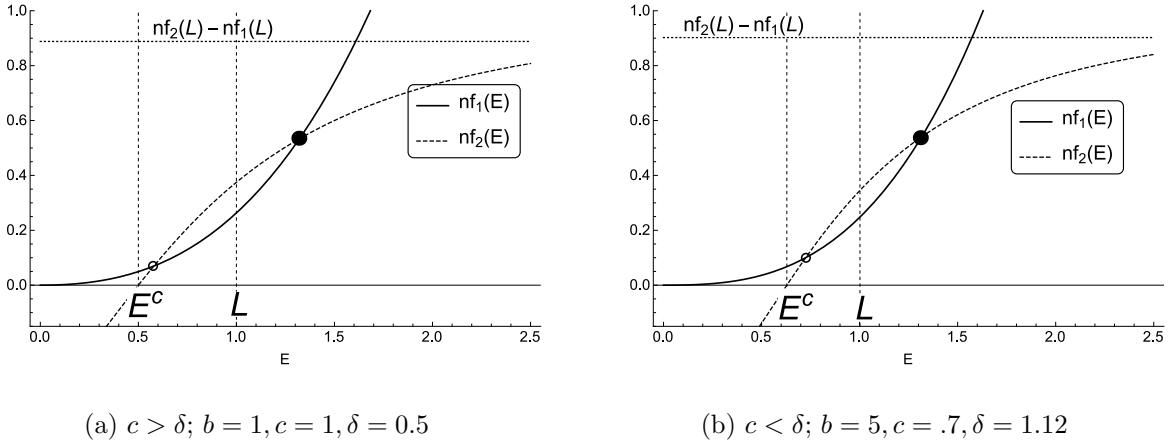
Figure 2.1: Nullclines $nf_1(E)$ and $nf_2(E)$ for Model (2.2) showing the existence of two interior equilibria when $\ell = L = \frac{2\sqrt{bc\delta}}{bc} > E^c$ and $nf_2(\ell) - nf_1(\ell) < 1$; ($\alpha = 0.3, \gamma = 4.56$); Stability is shown by ●: stable and ○:unstable.

Note: The detailed proof of Theorem 1 can be found in Appendix A. The number of interior equilibria of Model (2.2) is determined by the positive intercepts of

16

functions $nf_1(E) = \frac{\alpha c E^2 (1+bE)}{\delta \gamma}$ and $nf_2(E) = 1 - \frac{1}{\alpha f(E)+1}$. Figure 2.1 exemplify colony survival and stability conditions given in Proposition 1. If $E^c < 1$ and $nf_2(1) - nf_1(1) = 1 - \frac{\delta}{\delta + \alpha(c + bc - 2\delta)} - \frac{\alpha c (1+b)}{\delta \gamma} < 1$, we can have two interior equilibria. In Figure 2.1(a) with $c = 1 > \delta = 0.5$, we have two interior equilibria $\mathbf{E_1} = (0.58, 0.25)$ and $\mathbf{E_2} = (1.32, 3.82)$ with fixed parameters $b = 1, c = 1, \delta = 0.5, \alpha = 0.3, \gamma = 4.56$, where $E_2^* > E_1^*$. According to Proposition 1 part (3), $\mathbf{E_2}$ is locally asymptotically stable satisfying the condition $0.3(E_2^{*2} + 0.5E_2^* - 0.5)^2 > 0.25(E_2^* + 1)$ for $E_2^* = 1.32$, while $\mathbf{E_1}$ is saddle since $0.3(E_1^{*2} + 0.5E_1^* - 0.5)^2 < 0.25(E_1^* + 1)$ for $E_1^* = 0.58$. We can see similar behavior in Figure 2.1(b) with $c < \delta$. Figure 2.1 suggests that Model (2.2) has bistability of the extinction equilibrium $\mathbf{E_0}$ and one of the interior equilibria, in this case $\mathbf{E_2}$, which is generated by the choice of functional response in our model, a mechanism producing *Allee effects*. Depending on the initial conditions, Model (2.2) converges to $\mathbf{E_0}$ when these conditions are under some threshold, while it converges to $\mathbf{E_2}$ if the initial conditions are above that threshold. Moreover, Proposition 1 suggests that large α (i.e., the relative cannibalism rate), or too small c (i.e. efficiency of energy investment on DOL) is unsuitable for the colony since Model (2.2) goes to the extinction equilibrium $\mathbf{E_0}$, i.e. the colony dies out. If $\alpha = \frac{\hat{\alpha}}{\beta \hat{\gamma}(1-p)}$ is large or $c = \frac{\hat{\gamma}(1-p)}{a}$ is too small, this could imply that the brood care effort by workers is significantly smaller than the portion of workers foraging, and more individuals in the adult class may be engaging in cannibalism, which therefore this could suggest that the colony may die out due to low effort for brood care and excess of cannibalism.

For further insights of Model (2.2) on the synergistic effects of cannibalism, the benefit from cannibalizing, efficiency of energy invested in DOL, and relative death rate, we perform some numerical simulations by looking at one- and two-dimensional bifurcation diagrams.

In Figure 2.2, we study the **effects of b v.s. α, i.e., the relative benefit rate**

from cannibalism v.s. relative cannibalism rate. Figure 2.2a shows that large α can lead to colony extinction, while small α combined with small to large b leads to colony survival. Furthermore, looking at the effects of the population as α varies and fixing $b = 2$, Figure 2.2b shows that as the relative cannibalism rate α increases the total worker population size decreases. In Figure 2.2c, as b ranges from small to large, the total worker population size increases with $\alpha = 0.2$. Therefore, these results suggest that even though cannibalism may significantly reduce the colony's total population size, the colony can still survive due to the increase of adult's lifespan acquired through cannibalism. In general, an ideal scenario would consist of small $\alpha = \frac{\hat{\alpha}}{\beta\hat{\gamma}(1-p)}$ and large $b = \frac{c_a\hat{\alpha}}{a}$, i.e. if the brood care effort by workers is large enough with egg cannibalism rate being small or large, and a small enough such that b is large, then the colony can survive.

(a) $c = 2, \gamma = 2, \delta = 0.4$ (b) $\delta = 0.4, c = \gamma = b = 2$ (c) $\alpha = 0.2$
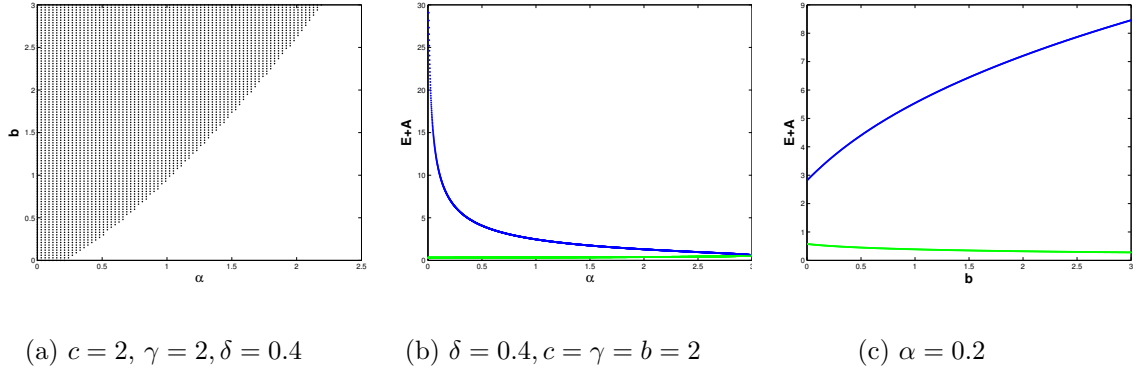
Figure 2.2: Two and one parameter bifurcation for Model (2.2). Figure (a) describes how the number of interior equilibria changes for different cannibalism rates and the benefit from cannibalism, α and b, respectively. White region has no interior equilibria while black region shows the existence of two interior equilibria. Figures (b) and (c) show the stability of the interior equilibria as we vary α or b, respectively. (stable; unstable)

In Figure 2.3a, we study the **effects c v.s. α, i.e., the effects of the efficiency of energy invested on DOL and the relative cannibalism rate.** In this case we see that for small c and any value of α the colony dies out and for larger values of c and any α, the colony can survive. We can conclude from Figure 2.3a that in order for the colony to survive in the presence of cannibalism, the brood care effort from workers should be large enough and a (i.e. quantity of the combination effects of crowding and resource allocation to egg production) is small.
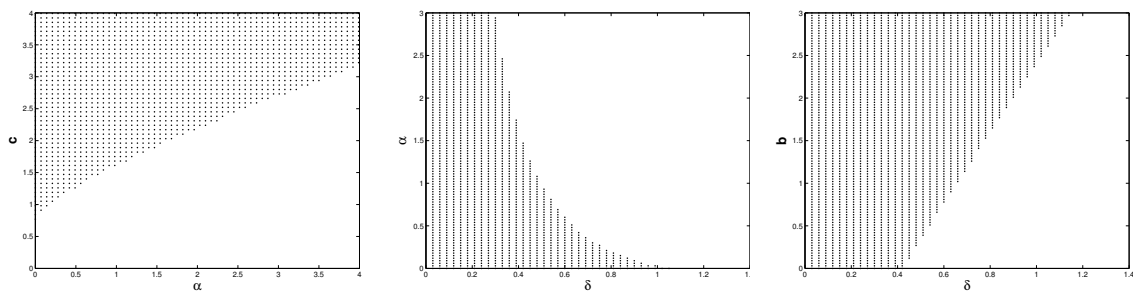
(a) $b = 2, \gamma = 1.5, \delta = 0.4$　　　(b) $\gamma = 1.5, c = 2, b = 2$　　　(c) $\gamma = 1.5, c = 2, \alpha = 0.1$

Figure 2.3: Two parameter bifurcation for Model (2.2) describing how the number of interior equilibria changes according to the variation of the respective parameters. Black region determines existence of two equilibria and white region determines extinction.

Figure 2.3b shows that for any α and small δ the population of young and adult workers survives, while for larger δ and any α the colony dies out. Figure 2.3c shows that for any b and small δ the worker population survives, while large δ leads to colony's death. In both of these cases, a decrease in maturation rate would induce an increase of $\delta = \frac{d}{\beta}$ leading to worker's population death. Biologically, both of these figures suggest that a colony can survive if there is high maturation rate from young to adult workers, the brood care effort by adults is large, and the adult workers within the colony engage in egg cannibalism as a strategy of survival which is reflected through the parameter b (i.e. relative benefit form cannibalism).

19

Colony dynamics outcomes of cannibalistic behavior.

Now, we consider the case when there is no egg and larval cannibalism (i.e. $\alpha = b = 0$). This case is represented in the following two-stage model:

$$E' = \frac{\gamma A}{1 + E + A} - E,$$

$$A' = \frac{cEA}{1 + E + A} - \delta A,$$

(2.7)

The dynamics of Model (2.7) can be summarized in the following theorem:

Theorem 2 (No cannibalism). *Model (2.7) is positive invariant in $\mathbb{R}^2_+$. It can have one or two interior equilibria depending on the values of its parameters c, δ, and γ. The necessary and sufficient conditions on their existence and stability are listed in Table 2.2. The global dynamics of Model (2.7) can be classified into the following scenarios:*

1. ***Extinction:*** *If $c < \delta$ or $\gamma < \frac{4c\delta}{(c-\delta)^2}$, then Model (2.7) has only the extinction equilibrium $\mathbf{E_0}$ which is globally stable. Under this conditions, the worker population is unable to survive and the colony dies out.*

2. ***Bistability of population:*** *If $c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$, then Model (2.7) has the extinction equilibrium $\mathbf{E_0}$ and two interior equilibria $\mathbf{E_i}$, $i = 1, 2$ where both $\mathbf{E_0}$ and $\mathbf{E_2}$ are locally asymptotically stable while $\mathbf{E_1}$ is saddle. Under this condition, colony exhibits strong Allee effects.*

Notes: The detailed proof of Theorem 2 can be found in Appendix A. The number of equilibria of Model (2.7) is determined by the positive intercepts of functions $g_1(E) = \frac{(c-\delta)E - \delta}{\delta}$ and $g_2(E) = \frac{cE^2}{\delta\gamma}$. Moreover, the local stability of the equilibria of (2.7) is determined by the eigenvalues $\lambda_i(E^*, A^*)$, $i = 1, 2$ (refer to (A.5)) of its

Equilibria	Existence Condition	Stability Condition
$\mathbf{E_0}$	Always exists for $\alpha \geq 0$	Locally asymptotically stable
$\mathbf{E_i}$, $i = 1, 2$	$c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$	$\mathbf{E_1}$ is saddle, while $\mathbf{E_2}$ is locally asymptotically stable.

Table 2.2: Equilibria And Stability Of Model (2.7) When $\alpha = 0$ and $b = 0$.

associated Jacobian matrix (A.29). Theorem 2 implies that: (i) Model (2.7) has only equilibrium dynamics, i.e., no limit cycles by Dulac-Bendixson criterion; (ii) The colony dies out if the relative death rate of the older population (e.g., workers) is greater than the efficiency of energy invested on division of labor ($\delta = \frac{d}{\beta} > c = \frac{\hat{\gamma}(1-p)}{a}$); (iii) Model (2.7) can have two interior equilibria whenever $\frac{ad}{\beta\hat{c}} + 2\sqrt{\frac{d}{r}} < 1$ ($\Leftrightarrow c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$ for $c = \frac{\hat{c}}{a}$ and $\delta = \frac{d}{\beta}$); (iv) Similarly as in Model (2.2), Model (2.7) can result in bistability when both the extinction equilibrium $\mathbf{E_0}$ and the interior equilibrium $\mathbf{E_2}$ are locally asymptotically stable (see Figure 2.5b); (v) Model (2.7) has one stable degenerate interior equilibrium which occurs when $c > \delta$ and $\gamma = \frac{4c\delta}{(c-\delta)^2}$ (see Figure 2.4).
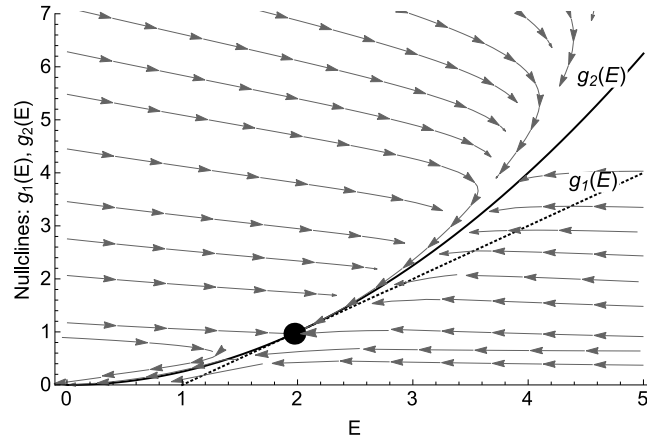
Figure 2.4: Phase Plane Showing the Stability of the Only Interior Equilibrium $\mathbf{E_1}$ when $c > \delta$ and $\gamma = \frac{4c\delta}{(c-\delta)^2}$. ($c = 1, \delta = 0.5, \gamma = 8$).
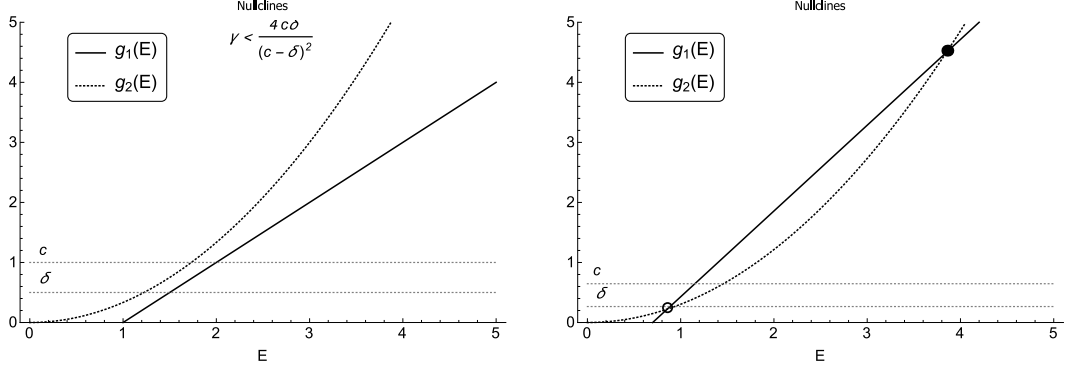
(a) No interior equilibria.($\delta = 0.5, \gamma = 6$) (b) Two interior equilibria.($\delta = 0.5, \gamma = 10$)

Figure 2.5: Nullclines for Model (2.2) without brood cannibalism such that when (a) $c > \delta$ and $\gamma < \frac{4c\delta}{(c-\delta)^2}$ there is no interior equilibria, and (b) if $c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$ there are two interior equilibria. ($c = 1$)

In the following simulations, we compare the dynamics of Model (2.2) and Model (2.7) by looking at the synergistic effects of the efficiency of energy investment in DOL, the relative egg production rate, and the relative death rate.

Figures 2.6(a-b) show the synergistic effects of c, δ, γ when egg and larval cannibalism is present, i.e., $\alpha, b > 0$, while Figures 2.6(d-f) show the effects of these parameters when $\alpha = b = 0$. In both cases, when $\alpha, b > 0$ and $\alpha = b = 0$, we have the following scenarios: (a) For small values of both $c = \frac{\hat{\gamma}(1-p)}{a}$ and $\gamma = \frac{ap}{\beta(1-p)}$ the colony dies out, while for large values of both c and γ the colony survives. Comparing Figure 2.6a and 2.6d, we can notice that the area where colony survives (both populations E and A are present) is larger when cannibalism is present (i.e. $\alpha, b > 0$). (b) For large values of c the colony can survive, while for large δ the colony goes extinct (see Figure 2.6b and 2.6e). Again, in this case, $\alpha, b > 0$ provide a larger area of colony survivability. (c) For large γ and small δ the worker populations can survive in both cases when $\alpha = b = 0$ and $\alpha, b > 0$, while for large δ the colony dies out (see Figure 2.6c and 2.6f). Once again, the presence of cannibalism provides a larger area where the colony is able to survive.

With egg and larval cannibalism, i.e., $\alpha = 0.2, b = 2$.

(a) $\delta = 0.4$ (b) $\gamma = 3$ (c) $c = 2$
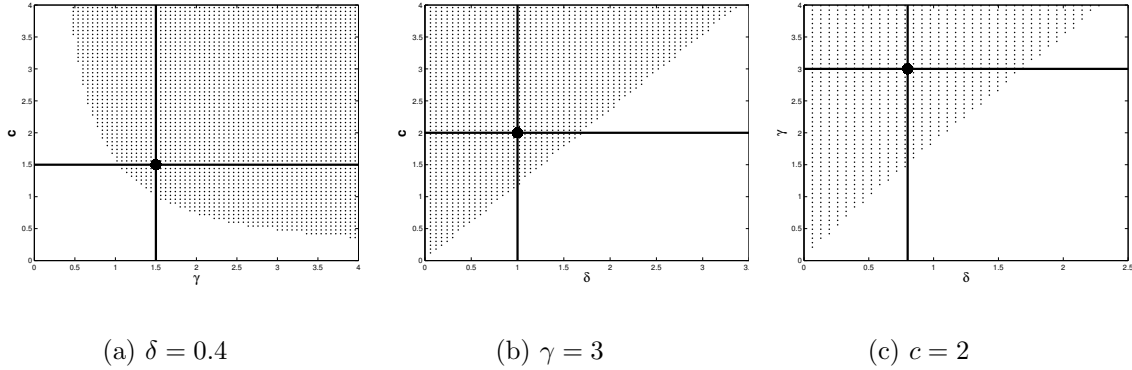
With no egg and larval cannibalism, i.e., $\alpha = b = 0$.

(d) $\delta = 0.4$ (e) $\gamma = 3$ (f) $c = 2$
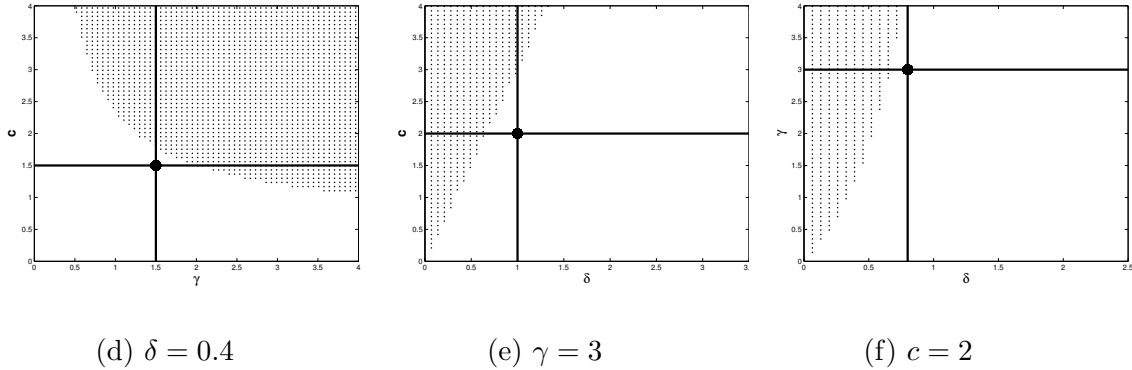
Figure 2.6: Two parameter bifurcation diagrams describing how the number of interior equilibria changes as c, δ, γ vary respectively. Figures (a-c) present cannibalistic behavior ($\alpha, b > 0$) and figures (d-f) $\alpha = b = 0$. Black region determines existence of two equilibria and white region determines extinction.

In general, these scenarios suggest that a higher brood care effort from workers and low maturation rate from egg stage to adult such that γ is large, are important for colony survival. However, we were also able to capture the importance of cannibalism in the worker population dynamics outcomes. Notice that for all the scenarios, cannibalism and the benefit from cannibalizing (i.e., when $\alpha, b > 0$) provide a larger area of colony survivability needing smaller values of c and γ than when the colony is non-cannibalistic, i.e., $\alpha = b = 0$. Also, a cannibalistic colony is able to survive with

smaller $\delta = \frac{d}{\beta}$, i.e., a low maturation rate and low death rate of adult workers is more beneficial for the colony.

In Figure 2.7 we can capture the individual effects of c, δ, γ in the total population size. Figures 2.7(a,b,d,e) show that c and γ have a positive effect on the the total worker population size as each of these parameters increase. We chose specific points to compare the effects of the relative cannibalism rate and its benefit (α and b). We can notice that when $\alpha, b > 0$ the worker population grows slower and reaches a smaller size at the end of the variation of c and γ than when $\alpha = b = 0$. Also a cannibalistic colony can survive and be stable with a smaller value of c and γ than a non-cannibalistic colony. Figures 2.7c and 2.7f show that δ has a negative effect in the total worker population with or without cannibalism. However, in a cannibalistic colony, the total worker population size decreases much slower as δ increases. This could mean that the colony is being benefited from cannibalizing on the young by slowing down the decrease of the population size and allowing a higher relative death rate before it dies out.

Biological Implications: Theorem 2 suggests that a non-cannibalistic colony can survive if the efficiency of energy invested in division of labor is greater than the relative death rate of the adult worker population (i.e. $c > \delta = \frac{ad}{\beta}$). Proposition 1 indicates that a cannibalistic colony, i.e., $\alpha, b > 0$, can survive if $c > \delta$ or $c < \delta$. However the colony can die out if α is too large, or if c is too small, i.e., if the brood care effort by workers is significantly smaller than the portion of workers foraging, and more individuals in the adult class engaging in cannibalism, then the colony may die out due to low effort for brood care and excess of cannibalism. In comparison, the dynamics of Model (2.2) and Model (2.7) suggest that higher brood care effort from workers and low maturation rate from the egg stage to adult class are important for the survival of a cannibalistic and non-cannibalistic colony. In general,

from our numerical simulations, cannibalism can increase or reduce the colony's total population size. This increase or decrease of colony size depends on the increase of adult's lifespan acquired through cannibalism. Furthermore both models (2.2) and (2.7) (with and without cannibalistic interactions) can experience *strong Allee effects* due to our choice of functional response describing division of labor.

With egg cannibalism, i.e., $\alpha = 0.2, b = 2$.

(a) $c = 2.5, \delta = 0.4$ (b) $\gamma = 3, \delta = 0.4$ (c) $\gamma = 3, c = 2.5$
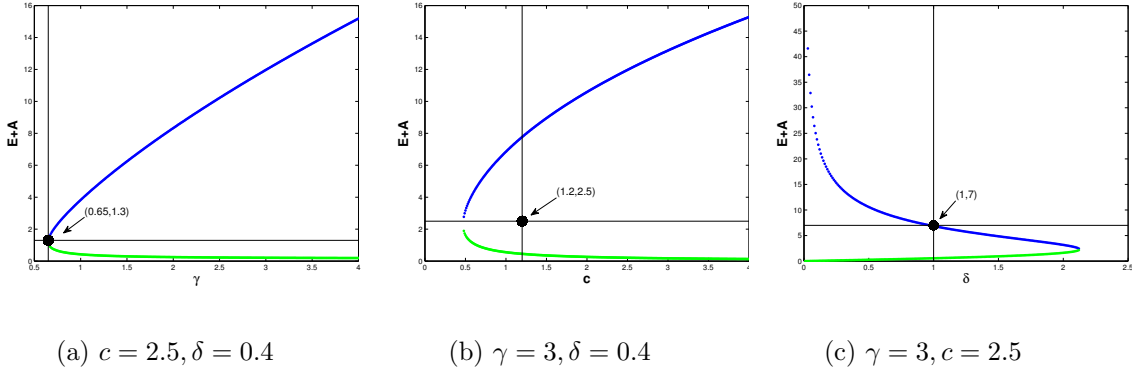
With no egg cannibalism, i.e., $\alpha = b = 0$.

(d) $c = 2.5, \delta = 0.4$.   (e) $\gamma = 3, \delta = 0.4$.   (f) $\gamma = 3, c = 2.5$.
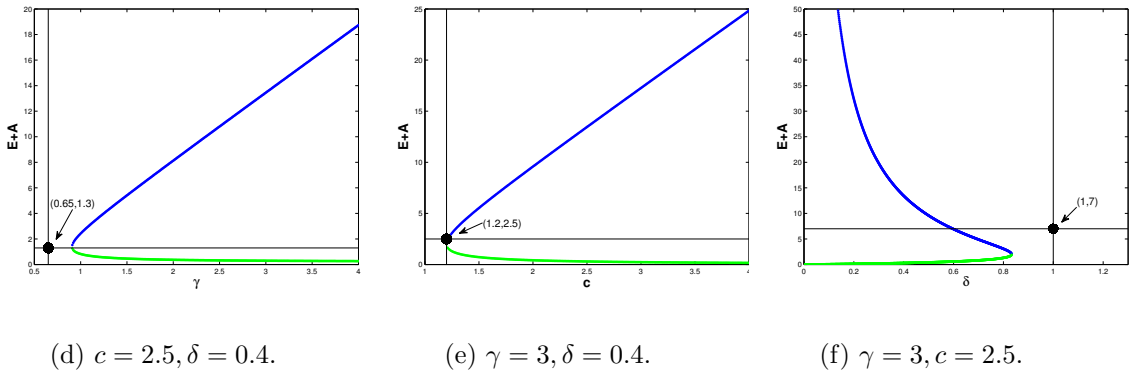
Figure 2.7: One parameter bifurcation showing the effects of the stability of the total population with respect to γ, c and δ in Model (2.2), (stable; unstable).

Evolutionary Model Derivation

In order to obtain further insights on how natural selection works on the life history parameter values and lead to different dynamic outcomes, we study an extended

evolutionary version of Model (2.2) by using the framework described by Vincent and Brown [2005]. We consider a colony of social insects, in a given environment, that have the same strategy set (i.e. a set of evolutionarily feasible phenotypes), and the same fitness consequences of possessing a particular strategy (pg. 75 on [Vincent and Brown, 2005]). Therefore, we apply a single fitness generating function to describe the fitness of all individuals within the colony [Vincent and Brown, 1984, 1988, 2005]. Let $u = u(t)$ denote the mean strategy (or trait) for the phenotypes of the population in a colony and v is the trait of a typical or focal individual which determines the fitness that would increase to a focal individual using any strategy of u. The related life history parameters considered, i.e $\gamma(u)$, $\alpha(u)$, $b(u)$, $\delta(u)$, and $c(u)$ are smooth and strictly positive functions of trait u. For a given trait value u, these parameters determine the ecological dynamics of Model (2.2). Let $N = E + A$ be the total population of the colony, then the fitness of a colony with the mean trait u is defined as follows:

$$\frac{N'}{N} = \frac{E' + A'}{N} = \frac{1}{N} \left(\frac{\gamma(u)A}{1 + E + A} - \alpha(u)AE - E + \frac{c(u)EA}{1 + E + A} - \frac{\delta(u)A}{1 + b(u)E} \right).$$

Let $G(v, u, E, A)$ be the fitness generating function of a focal individual that chooses a strategy v when the population in a colony has a mean trait u and population sizes E and A, which is defined as follows:

$$G(v, u, E, A) = \frac{1}{E + A} \left(\frac{\gamma(v)A}{1 + E + A} - \alpha(v)EA - E + \frac{c(v)EA}{1 + E + A} - \frac{\delta(v)A}{1 + b(v)E} \right)$$

Here we would like to point out that a general fitness generating function $G(v, u, E, A)$ should depend on the mean trait of a colony u, e.g., there is a intraspecific competition between population with trait u and trait v. However, for mathematical tractability, we assume that the fitness of a focal individual $G(v, u, E, A)$ that chooses strategy v is independent of the mean trait u. This simplified assumption is an initial point for

a general case when the formulation of $G(v, u, E, A)$ also depends on the mean trait u.

According to Vincent and Brown [2005], $G(v, u, x)$ is a fitness generating function; and the dynamics of trait u is determined by the fitness function H which is the partial derivative of the fitness generating function $G(v, u, x)$ with respect to v and the trait value v takes the mean trait value u, i.e., $H(u, E, A) = \frac{\partial G(v, u, E, A)}{\partial v}\big|_{v=u}$. Notice that either $A = 0$ or $E = 0$ leads to $A = E = 0$. Since $G(v, u, E, A) = \frac{1}{E+A}\left(\frac{\gamma(v)A}{1+E+A} - \alpha(v)EA - E + \frac{c(v)EA}{1+E+A} - \frac{\delta(v)A}{1+b(v)E}\right)$ will have singularity at $A = 0$ or $E = 0$ mathematically, thus we define the fitness function $H(u, E, A)$ in two parts: $AE = 0$ and $AE > 0$ as follows:

$$H(u, E, A)|_{AE>0} = \frac{\partial G(v, u, E, A)}{\partial v}\bigg|_{v=u}$$

$$= \frac{1}{E+A}\frac{\partial\left(\frac{\gamma(v)A}{1+E+A} - \alpha(v)EA - E + \frac{c(v)EA}{1+E+A} - \frac{\delta(v)A}{1+b(v)E}\right)}{\partial v}$$

$$= \frac{1}{E+A}\left(\frac{\gamma'(u)A + c'(u)EA}{1+E+A} - \alpha'(u)EA - \frac{\delta'(u)A}{1+b(u)E} + \frac{\delta(u)b'(u)EA}{(1+b(u)E)^2}\right),$$

$$H(u, E, A)|_{AE=0} = \frac{\partial\left(\frac{\gamma(v)A}{1+E+A} - \alpha(v)EA - E + \frac{c(v)EA}{1+E+A} - \frac{\delta(v)A}{1+b(v)E}\right)}{\partial v}$$

$$= \frac{\gamma'(u)A + c'(u)EA}{1+E+A} - \alpha'(u)EA - \frac{\delta'(u)A}{1+b(u)E} + \frac{\delta(u)b'(u)EA}{(1+b(u)E)^2}.$$

(2.8)

Hence, we derive an evolutionary model from the ecological model (2.2) as follows by using the modeling methodology for Evolutionary Game Theory presented in Vincent and Brown [2005] (also see Cushing and Hudson [2012], Kang and Udiani [2014], Rael *et al.* [2011]):

27

$$E' = \frac{\gamma(u)A}{1 + E + A} - \alpha(u)AE - E,$$

$$A' = \frac{c(u)AE}{1 + E + A} - \frac{\delta(u)A}{1 + b(u)E}$$

$$u'|_{AE>0} = \sigma^2 \frac{\partial G(v, u, E, A)}{\partial v}\bigg|_{v=u,AE>0} = \sigma^2 H(u, E, A)|_{AE>0} \tag{2.9}$$

$$= \frac{\sigma^2 A}{E + A}\left(\frac{\gamma'(u) + c'(u)E}{1 + E + A} - \alpha'(u)E - \frac{\delta'(u)}{1 + b(u)E} + \frac{\delta(u)b'(u)E}{(1 + b(u)E)^2}\right)$$

$$u'|_{AE=0} = \sigma^2\left(\frac{\gamma'(u) + c'(u)E}{1 + E + A} - \alpha'(u)E - \frac{\delta'(u)}{1 + b(u)E} + \frac{\delta(u)b'(u)E}{(1 + b(u)E)^2}\right).$$

The colony's mean strategy u changes in the direction of the upward slope of the adaptive landscape and the heritable variation within the colony [Vincent and Brown, 2005]. The adaptive landscape gives a visualization of the strategy dynamics, and its slope at any point represents the change in fitness for a given change in strategy [Vincent and Brown, 2005]. Therefore, the speed at which each population will evolve toward equilibrium depends on the increase of both the genetic variance and the change in fitness. Hence, σ^2 is the variance in traits present in the colony around the mean strategy u.

Mathematical Analysis

From the evolutionary model (2.9), if (E, A, u) is an equilibrium, then it satisfies the following equations:

$$0 = \frac{\gamma(u)A}{1 + E + A} - \alpha(u)AE - E,$$

$$0 = \frac{c(u)AE}{1 + E + A} - \frac{\delta(u)A}{1 + b(u)E}$$

$$0 = \frac{\gamma'(u) + c'(u)E}{1 + E + A} - \alpha'(u)E - \frac{\delta'(u)}{1 + b(u)E} + \frac{\delta(u)b'(u)E}{(1 + b(u)E)^2}$$

These equations imply that $(0, 0, u)$ is an equilibrium if $\gamma'(u) = \delta'(u)$. The existence and stability of this equilibrium is stated in the following theorem:

Theorem 3 (Extinction equilibrium). *Assume that $\gamma(u)$, $\alpha(u)$, $b(u)$, $\delta(u)$, and $c(u)$ are smooth and strictly positive functions of trait u. Then $(0, 0, u)$ is an extinction equilibrium of the evolutionary model (2.9) if there is a u such that $\gamma'(u) = \delta'(u)$. Also, $(0, 0, u)$ is locally asymptotically stable if $\gamma(u) < \delta(u)$, $\gamma'(u) = \delta'(u)$ and $\gamma''(u) < \delta''(u)$. However, if $\gamma''(u) > \delta''(u)$, then $(0, 0, u)$ is saddle.*

Notes: Theorem 3 suggests that the existence and stability condition of the extinction equilibrium is determined by the trait function of $\gamma(u)$ and $\delta(u)$ only and the relative egg cannibalism rate $\alpha(u)$ has no effect on its stability.

In nature, it is possible that $\gamma(u)$, $\alpha(u)$, $b(u)$, $\delta(u), c(u)$ may have different functional forms in u. However, mathematical analysis quickly loses its tractability. In order to continue studying the evolutionary model (9), we follow the approach of Cushing [2015] and Kang *et al.* [2015] and simplify the forms of these trait functions as a starting point. For further mathematical analysis, we assume that parameters $\gamma, \alpha, b, \delta, c$ have the same form of the trait function, i.e.

$$\gamma(u) = \gamma_0 \phi(u),\ \alpha(u) = \alpha_0 \phi(u),\ b(u) = b_0 \phi(u),\ , \delta(u) = \delta_0 \phi(u),\ c(u) = c_0 \phi(u)$$

where $\phi(u)$ be our trait function that is a strictly positive smooth function, i.e. $\phi : \mathbb{R} \to \mathbb{R}_+ \backslash \{0\}$, and the parameters $\gamma_0, \alpha_0, \delta_0, b_0, c_0$ are strictly positive. Moreover, $\phi(u)$ is bounded in its defined space. This assumption suggests that the life history parameters are proportional to each other and model the trade-off of growth, cannibalism and survivorship. For instance, increasing $\phi(u)$ with respect to u, increases the investment in reproduction, $\gamma(u)$, which is beneficial for the colony, while there will be an adverse effect as cannibalism rate will also increase but at the same

time the benefit from cannibalizing increases resulting another positive trade-off for the colony.

The evolutionary model (2.9) can be simplified as

$$
\begin{aligned}
E' &= \frac{\gamma(u)A}{1+E+A} - \alpha(u)AE - E = \phi(u)\left(\frac{\gamma_0 A}{1+E+A} - \alpha_0 EA - \frac{E}{\phi(u)}\right), \\
A' &= \frac{c(u)AE}{1+E+A} - \frac{\delta(u)A}{1+b(u)E} = \phi(u)A\left(\frac{c_0 E}{1+E+A} - \frac{\delta_0}{1+b\phi(u)E}\right) \\
u' &= \frac{\sigma^2 A}{E+A}\left(\frac{\gamma'(u)+c'(u)E}{1+E+A} - \alpha'(u)E - \frac{\delta'(u)}{1+b(u)E} + \frac{\delta(u)b'(u)E}{(1+b(u)E)^2}\right) \\
&= \frac{\sigma^2 A\phi'(u)}{E+A}\left(\left[\frac{c_0 E}{1+E+A} - \frac{\delta_0}{1+b_0\phi(u)E}\right]\right. \\
&\qquad\qquad \left. + \left[\frac{\gamma_0}{1+E+A} - \alpha_0 E + \frac{\delta_0\phi(u)b_0 E}{(1+b_0\phi(u)E)^2}\right]\right)
\end{aligned}
$$

$$(2.10)$$

which set space is $X = \{(E, A, u) : E \geq 0, A \geq 0, u \in \mathbb{R}\}$.

Let $\phi^* = \phi(u^*)$ and (E^*, A^*, u^*) be an interior equilibrium (i.e. $E^*, A^* > 0$), then the following equations satisfy Model (2.10):

$$
\frac{\gamma_0 A^*}{1+E^*+A^*} - \alpha_0 E^* A^* - \frac{E^*}{\phi^*} = 0
$$

$$
\frac{c_0 E^*}{1+E^*+A^*} - \frac{\delta_0}{1+b\phi^* E^*} = 0 \tag{2.11}
$$

$$
\frac{\gamma_0}{1+E^*+A^*} - \alpha_0 E^* + \frac{\delta_0\phi^* b_0^* E^*}{(1+b_0^*\phi^* E^*)^2} = 0 \quad \text{or} \quad \phi'(u^*) = 0
$$

From equations (2.11) we obtain $A^* = \frac{b_0 c_0 E^{*2}\phi(u^*) + E^*(c_0-\delta_0) - \delta_0}{\delta_0} \geq 0$.

Let $x = \phi(u)E$. We define the following equations as the nullclines of Model (2.11):

$$
ng_1(1, x) = \frac{\alpha_0 c_0 x^2(1+b_0 x)}{\gamma_0\delta_0}, \qquad ng_2(\phi(u), x) = \phi^2(u)\left(1 - \frac{1}{1+\alpha_0 F(\phi(u), x)}\right)
$$

and

$$
F(\phi(u), x) = \phi(u)A = \frac{b_0 c_0 x^2 + (c_0-\delta_0)x - \delta_0\phi(u)}{\delta_0}.
$$

30

Equations (2.11) indicate that if there exists a u^* such that $\phi'(u^*) = 0$, then according to Theorem 1, there exists at least two interior equilibria (E^*, A^*, u^*). Evaluating the eigenvalues of the Jacobian matrix of model (2.10) at the interior equilibria (E^*, A^*, u^*), we can determine the local stability of these by having $\alpha_0 \phi^* A^{*2} > E^* + 1$ and the sign of $\phi''(u)$.

Theorem 4. *The evolutionary model (2.10) always has the extinction equilibrium $(0, 0, u^*)$ if and only if there is some u^* such that $\phi'(u^*) = 0$. Stability conditions for this equilibrium are as follows: the boundary equilibrium is locally asymptotically stable if (i) $\gamma_0 < \delta_0$ and $\phi''(u^*) > 0$ or (ii) $\gamma_0 > \delta_0$ and $\phi''(u^*) < 0$, and saddle otherwise.*

Notes: Lemma 4.2 from Kang *et al.* [2015] can be similarly applied to show positive invariance and boundedness of model (2.10). Moreover, assume the trait function $\phi(u)$ is a strictly positive smooth function defined on a closed interval $[u^l, u^r]$ with the characteristic that $\phi'(u^l) = \phi'(u^m) = \phi'(u^r) = 0$, i.e., ϕ's only critical points are u^l, u^m, and u^r. The function $\phi(u)$ could be an increasing or decreasing function in $[u^l, u^r]$. Hence, without loss of generality, we assume that $\phi(u)$ is increasing in (u^l, u^m) and decreasing in (u^m, u^r), i.e., $\phi(u) > 0$, $\phi'(u) > 0$ in (u^l, u^m), $\phi'(u) < 0$ in (u^m, u^r), $\phi(u^l) = \phi(u^m) = \phi(u^r) = 0$ and $\phi''(u^l) > 0$, $\phi''(u^m) < 0$, $\phi''(u^r) > 0$. This condition is similar to recent work by Cushing [2015] and Kang *et al.* [2015]. Moreover, note that $\lim_{x \to \infty} ng_2(\phi(u), x) = \phi^2(u)$ and hence $ng_2(\phi(u), x)$ is an increasing function of $u \in (u^l, u^m)$ and decreasing for $u \in (u^m, u^r)$.

Theorem 5. *Assume that $\phi(u)$ is a function with characteristics: $\phi(u) > 0$, $\phi'(u) > 0$ in (u^l, u^m), $\phi'(u) < 0$ in (u^m, u^r), $\phi(u^l) = \phi(u^m) = \phi(u^r) = 0$ and $\phi''(u^l) > 0$, $\phi''(u^m) < 0$, $\phi''(u^r) > 0$. The evolutionary model (2.10) always has at most three boundary equilibria $(0, 0, u^j)$, $j = l, m, r$ with the following stability scenarios:*

31

1. If $\gamma_0 < \delta_0$, then $(0, 0, u^l)$ and $(0, 0, u^r)$ is locally asymptotically stable, while $(0, 0, u^m)$ is saddle.

2. If $\gamma_0 > \delta_0$, then $(0, 0, u^l)$ and $(0, 0, u^r)$ is saddle, while $(0, 0, u^m)$ is locally asymptotically stable.

Additionally, the following statements hold regarding the number of interior equilibria of the form (E_i^j, A_i^j, u_i^j), $i = 1, 2$, $j = l, m, r$ for the evolutionary model (2.10):

1. If $ng_1(1, x) > ng_2(\phi(u^i), x)$, $i = l, m, r$, there is no interior equilibrium.

2. If $ng_2(\phi(u^m), x) > ng_2(u^{l,r}) > ng_1(1, x) > ng_2(\phi(u^{r,l}), x)$, there are at most four interior equilibria.

3. If $ng_2(\phi(u^m), x) > ng_2(\phi(u^{l,r}), x) > ng_2(\phi(u^{r,l}), x) > ng_1(1, x)$, there are at most six interior equilibria.

The sufficient conditions on the existence and stability of these equilibria are listed in Table 2.3.

Notes: The precise mathematical definitions/criterions of evolutionary stability haven't been given in literature but see some recent work of [Cushing, 2015, Kang et al., 2015] where they define an equilibrium of the evolutionary model being evolutionary stability if it is locally asymptotically stable and satisfies *ESS maximum principle* [Vincent and Brown, 1988], i.e., $\max_{v \in \mathbb{R}}\{G(v, u^*, E^*, A^*)\} = G(u^*, u^*, E^*, A^*) = 0$. In this paper, we do not deal with evolutionary stability of an equilibrium, instead, we only focus on its locally stability.

For instance, define $\phi(u) = e^{-\frac{u^2}{2\sigma_\phi^2}}$, $u \in \mathbb{R}$. Notice that this is a decreasing function in (u^l, u^r). Then according to Theorem 4, $(0, 0, u^*)$ is an equilibrium of Model (2.10) if $u^* = 0$. Since $\phi_1''(u^*) = -\frac{1}{\sigma^2} < 0$, $(0, 0, 0)$ is locally asymptotically stable if $\gamma_0 > \delta_0$

and saddle if $\gamma_0 < \delta_0$. Figure 2.8 shows that using this trait function restricted in some interval $[u^l, u^r]$, Model (2.10) can have two extinction equilibria and up to four interior equilibria.

Another example is the trait function $\phi(u) = \sigma^2 u^2 (1-u)^2$ defined on $[0,1]$. The polynomial $\phi(u)$ is an increasing function in $(0, \frac{1}{2})$ and decreasing in $(\frac{1}{2}, 1)$. According to Theorem 4, Model (2.10) has the following three extinction equilibria $(0,0,0)$, $(0,0,\frac{1}{2})$, $(0,0,1)$ and up to six interior equilibria depending on the value of $u \in [0,1]$. The stability of the extinction equilibria is as follows: $(0,0,0)$ and $(0,0,1)$ are LAS whenever $\gamma_0 < \delta_0$ and $\phi''(0) = \phi''(1) = 2\sigma^2 > 0$, while $(0,0,\frac{1}{2})$ is saddle since $\phi''(\frac{1}{2}) = -\sigma^2 < 0$. If $\gamma_0 > \delta_0$, then $(0,0,\frac{1}{2})$ is LAS, while $(0,0,0$ and $(0,0,1)$ are saddle. Figure 2.9 shows that choosing this trait function, Model (2.10) can have a total of nine equilibria, in which three are extinction equilibria and can have up to six interior equilibria.
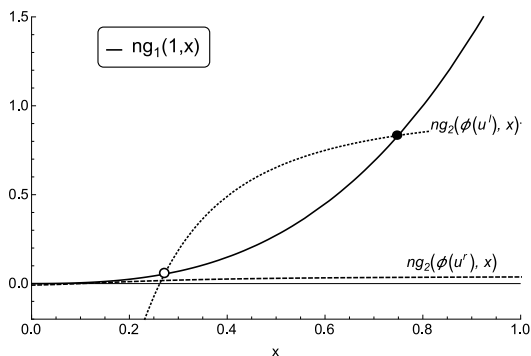
(a) Two attractors: $(0,0,u^l)$ and (E_2^l, A_2^l, u^l); two interior equilibria $(E_i^l, A_i^l, u^l); i = 1,2.$
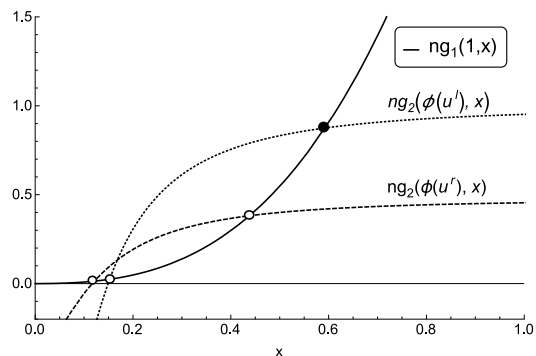
(b) One attractor: (E_2^l, A_2^l, u^l), with four interior equilibria (E_i^j, A_i^j, u^j), $i = 1,2; j = l, r.$

Figure 2.8: Let $x = \phi(u)E$ with $\phi(u) = e^{-\frac{u^2}{2\sigma_\phi^2}}$. The solid line is $ng_1(1,x) = \frac{\alpha_0 c_0 x^2 (1+b_0 x)}{\gamma_0 \delta_0}$ and the dotted lines are $ng_2(\phi(u), x) = \phi^2(u) \left(1 - \frac{1}{1+\alpha_0 F(\phi(u),x)}\right)$. On the left we have the case where $\gamma_0 > \delta_0$ and $ng_2(\phi(u^l), x) > ng_2(\phi(u^r), x) > ng_1(1,x)$ and on the right $\gamma_0 < \delta_0$ and $ng_2(\phi(u^l), x) > ng_1(1,x) > ng_2(\phi(u^r), x)$. The dark solid dot is $(u^l, x^l) = (u^l, \phi(u^l)E_2^l)$.

33
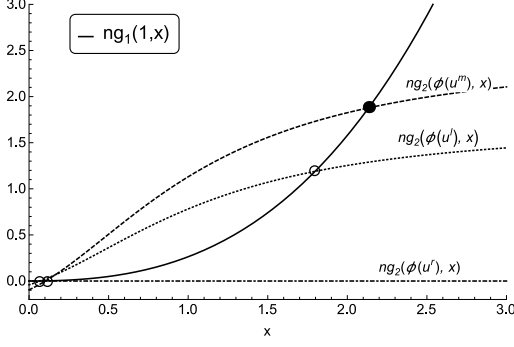
(a) $(\gamma_0 > \delta_0)$ Two attractors: $(0, 0, u^m)$ and (E_2^m, A_2^m, u^m), with four interior equilibria $(E_j^i, A_j^i, u^j), i = 1, 2, j = l, m.$
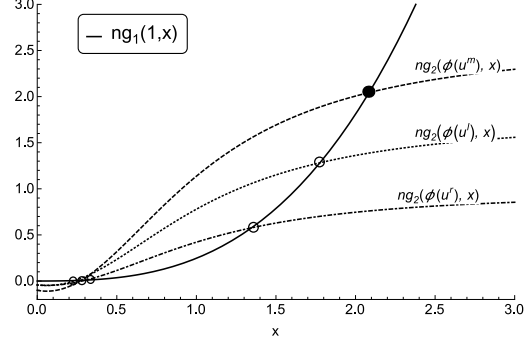
(b) $(\gamma_0 < \delta_0)$ One attractor: (E_2^m, A_2^m, u^m), with six int. equilibria $(E_i^j, A_i^j, u^j), i = 1, 2,$ $j = l, m, r.$

Figure 2.9: Let $x = \phi(u)E$ with $\phi_1(u) = \sigma^2 u^2(1-u)^2$. The solid line is $ng_1(1, x) = \frac{\alpha_0 c_0 x^2(1+b_0 x)}{\gamma_0 \delta_0}$ and the dotted lines are $ng_2\left(\phi(u), x\right) = \phi^2(u)\left(1 - \frac{1}{1+\alpha_0 F(\phi(u),x)}\right)$. The dark solid dot is $(u^m, x^m) = (u^m, \phi(u^m)E_2^m)$.

Evolutionary dynamics restricts the slope of the nullcline function

$$ng_2\left(\phi(u), x\right) = \phi^2(u)\left(1 - \frac{1}{1 + \alpha_0 F(\phi(u), x)}\right),$$

ranging from $\phi(u^r)$ to $\phi(u^l)$ with $x = \phi(u)E$ due to the assumption made about $\phi(u)$, where $\phi(u) > 0$, $\phi'(u) > 0$ in (u^l, u^m), $\phi'(u) < 0$ in (u^m, u^r), $\phi(u^l) = \phi(u^m) = \phi(u^r) = 0$ and $\phi''(u^l) > 0$, $\phi''(u^m) < 0$, $\phi''(u^r) > 0$ as we can see in Figures 2.8 and 2.9.

The potential impacts of the evolutionary settings for this model suggest that evolutionary dynamics may prevent colony's death when $ng_2(\phi(u^m), x) > ng_1(1, x) > ng_2(\phi(u^{r,l}), x)$. This occurs when the nullcline $ng_2\left(\phi(u^{r,l}), x\right)$ has no positive intercept with $ng_1(1, x)$ while $ng_2\left(\phi(u^m), x\right)$ intercepts twice with $ng_1(1, x)$. In the presence of evolution (i.e. with population and strategy dynamics), the population converges to the interior equilibrium (E_2^l, A_2^l, u^l) by choosing the trait u^l (see Figure). However, without evolution and with certain values of $\gamma, \alpha, b, c, \delta$, the ecological dynamics of model (2.2) may converge to the extinction equilibrium $(0, 0)$. Also, the inclusion

34

Equilibria	Existence Condition	Stability Condition
$(0,0,u^j)$, $j=l,m,r$	Always exists but has only* these three boundary equilibria if $ng_1(1,x) > ng_2(\phi(u^j),x)$, $j=l,m,r$	if $\gamma_0 > \delta_0$ and $\phi''(u^j) < 0$, or $\gamma_0 < \delta_0$ and $\phi''(u^j) > 0$, then $(0,0,u^j)$, $j=l,m$, or r is locally asymptotically stable while for $\phi''(u^j) > 0$ or $\phi''(u^j) < 0$, $(0,0,u^j)$ is saddle. *Moreover, $(0,0,u^j)$ is globally stable for each case.
(E_i^m, A_i^m, u_i^m), $i=1,2$	$ng_2(\phi(u^m),x) > ng_1(1,x) > ng_2(\phi(u^j),x)$, $j=l,r$	For $E_2^m > E_1^m$, (E_2^m, A_2^m, u^m) is locally asymptotically stable since $\alpha_0\phi(u^m)(A_2^m)^2 > E_2^m + 1$, while (E_1^m, A_1^m, u^m) is saddle since $\alpha_0\phi(u^m)(A_1^m)^2 < E_1^m + 1$
(E_i^j, A_i^j, u^j), $i=1,2$, $j=l,m,r$	$ng_2(\phi(u^m),x) > ng_2(\phi(u^{l,r}),x) > ng_2(\phi(u^{r,l}),x) > ng_1(1,x)$	For $E_2^j > E_1^j$, (E_i^j, A_i^j, u^j) can be locally asymptotically stable whenever $\alpha_0\phi(u^j)(A_i^j)^2 > E_i^j + 1$ and $\phi''(u^j) < 0$, while it can be saddle if $\phi''(u^j) > 0$.

Table 2.3: General Conditions for Existence of Equilibria and Respective Stability for $A^j = \frac{b_0 c_0 (E^j)^2 \phi(u^*) + E^j(c_0 - \delta_0) - \delta_0}{\delta_0} \geq 0$.

of evolutionary dynamics may produce an increase of colony's fitness. In this case, the nullcline function $ng_2(\phi(u),x)$ has up to six intercepts with $ng_1(1,x)$ for all $u \in [u^l, u^r]$ (see Figure 2.9). Five of these intercepts (i.e., (E_i^j, A_i^j, u^j), $i = 1,2$, $j = l, r$, and (E_1^m, A_1^m, u^m)) are less than the stable equilibrium (E_2^m, A_2^m, u^m). Since $\phi(u)$ is an increasing function in (u^l, u^m), then $x = \phi(u)E$ is also increasing, i.e. $\phi(u^m)E^m > \phi(u^l)E^l$, while of $\phi(u)$ is decreasing function in (u^m, u^r), then $x = \phi(u)E$

is also decreasing i.e., $\phi(u^m)E^m > \phi(u^r)E^r$. For a chosen $u \in (u^l, u^r)$, when there is evolution, the population converge to the interior equilibrium (E_2^m, A_2^m, u^m) by choosing the trait value u^m. However, in the situation in which no strategy changes are allowed, the ecological dynamics of model (2.2) may converge to the interior equilibrium (E^*, A^*) where $E_2^m > E^*$ and $A^* = \frac{bcE^{*2}+(c-\delta)E^*-\delta}{\delta}$. We say that (E^*, A^*) is ecologically stable.

Further, the choice of trait function for these settings is relevant. For example, choosing the trait function $\phi_1(u) = \sigma^2 u^2 (1-u)^2$ defined for all $u \in [0,1]$, can produce up to nine equilibria in which three can be extinction equilibria depending on the value of u and there can be up to six interior equilibria. On the other hand, the function $\phi_2(u) = e^{-\frac{u^2}{2\sigma_\phi^2}}$, $u \in \mathbb{R}$ can produce up to six equilibria in which two are extinction equilibria and four are interior equilibria. With respect to stability, using $\phi_1(u)$ as the trait function can produce up to two stable extinction equilibria and one stable interior equilibrium, while using $\phi_2(u)$ can produce only one stable extinction and one interior equilibrium. Also, both trait functions can make the system permanent when $\gamma_0 < \delta_0$ (see Figure 2.9).

Discussion

Here we proposed and studied a compartmental two-stage model for social insects in two different frameworks: ecological and evolutionary. Our model follows the assumptions: (1) Adult workers can cannibalize the brood (e.g., eggs or larvae or both); (2) Older population provide brood care to young ones and food resource to the colony through foraging which is in competition with brood care. We provide boundedness and positivity of the proposed model in Theorem 1. Analytical results are summarized in Proposition 1, Theorem 2, and Table 2.3 along with numerical simulations that give us insight and answer questions regarding the dynamics of these

models.

Our findings suggest that a non-cannibalistic colony can survive if the efficiency of energy invested in division of labor, c, is larger than the relative death rate, δ, of the older population. Otherwise, the colony dies out. In this case, a non-cannibalistic colony could experience an increase of mortality rate in adult workers in harsh environmental conditions when availability of food resources is poor or weather conditions are bad. In order to survive, the colony must invest more energy in brood care. Analytical results for a non-cannibalistic colony represented in Model 2.7, show bistability when the efficiency of energy invested in DOL is greater than the relative death rate $(c > \delta)$ and we have the quantity $\gamma > \frac{4c\delta}{(c-\delta)^2}$. For this case, the extinction equilibrium and the interior equilibrium $\mathbf{E_2} > \mathbf{E_1}$ are locally asymptotically stable meaning that for some initial conditions under some threshold, the colony can die out but if those initial conditions are above a certain threshold the colony survives (see Figure 2.6)e. Furthermore, in a colony presenting cannibalistic behavior, higher investment on brood care effort by workers and low maturation rate from egg stage to adult class, are factors that play an important role on the survivability and growth of the colony. Also, cannibalism and the benefit from it can increase the colony's population size (see Figure 2.7) allowing the colony to put less effort on brood care (compare Figure 2.7b with 2.7e) and providing a larger range for mortality rate in the adult class (compare Figure 2.7c with 2.7f).

In our evolutionary model, we assume there is a trait function $\phi(u)$ related to the life history parameters of social insects with a phenotypic trait u. This function determines the ecological dynamics for a given trait value. Our theoretical results for this model (see Theorem 5 and Table 2.3) indicate that evolutionary dynamics may prevent the colony from dying out by choosing the trait with large efficiency of energy invested in task allocation and with small cannibalism rate (see Figure 2.8a

and 2.9c). Our findings suggest that evolutionary dynamics may increase the colony's fitness as seen in Figure 2.8b and 2.9d where the total worker population within a colony converges to a higher equilibrium point, and the choice of the trait function is relevant as it produces different results in terms of number of equilibria and stability, but also can make the system permanent.

Studies on the evolution of cannibalism and how it affects population suggest that the most impactful factor of this behavior is the energetic benefit through the consumption of conspecific individuals representing a high-quality resource for the consumer [Nishimura and Isoda, 2004, Rudolf *et al.*, 2010]. However, if individuals fail to adopt cannibalism, they may be more likely to die due to crowding or low availability of alternate food resources, or both [Nishimura and Isoda, 2004]. On the other hand, ecological success of a colony has also been attributed to its social organization to perform particular tasks in response to varying conditions and colony needs [Bonabeau *et al.*, 1997, Gordon, 2015]. Some studies have shown that the colony regulates its activities depending on food availability, colony size and age etcetera [Gordon, 2015]. Our theoretical results suggest similar findings with respect to advantages of a cannibalistic colony and the feature that characterize social insects, division of labor. In addition, we would like to point out that social insects like honeybees have other methods of population control, such as swarming with a large fraction of the colony, that are more evolutionarily beneficial to the colony than cannibalizing the brood [Schmickl and Crailsheim, 2001].

Concluding Remarks

The use of dynamical systems to study complex biological systems has become a popular tool to describe the mechanistic and behavior of organisms, complex societies of social animals, and different phenomena affecting the population dynamics within

colonies. The consideration of many characteristics affecting the population dynamics of social insects has not been completely analyzed due to the complexity exhibited by such organisms in their natural habitat. The research presented in Chapter 2 analyzes from a general perspective two of the fundamental aspects in social insects that have an impact on species survival, i.e. brood cannibalism and division of labor. Given that the decision making of social insects in a colony is often shaped by the change in their natural surrounding, I investigate the population and evolutionary dynamic consequences of brood cannibalism and division of labor. In summary, the findings in this research suggest that both brood cannibalism and division of labor are adaptive strategies that increase the size of the worker population. However, one limitation of this work is that it does not include specific characteristics to a certain species. Therefore, in the next chapter, I propose a set models focusing on the population dynamics of multi-species interactions such as leafcutter ants, including *Atta* and *Acromyrmex*, to study the different ways brood cannibalism can benefit the colony for survival and the impacts of division of labor explicitly by including age-dependent task specialization.

Chapter 3

INTERACTIONS BETWEEN LEAFCUTTER ANTS AND FUNGUS GARDEN: EFFECTS OF DIVISION OF LABOR, AGE POLYETHISM, AND EGG CANNIBALISM

Abstract

Division of Labor (DOL), age polyethism, and egg cannibalism all play roles in shaping colony-level population dynamics in social insect colonies. However, the ways in which these factors interact with one another to shape population dynamics is not currently understood. In this study we examine how these factors influence population dynamics in colonies of fungus-gardening leafcutter ants by developing and studying two sets of models: (1) We study age polyethism contribution to the dynamics of a leafcutter ants and their fungus garden interaction model which incorporates other mechanisms of DOL; (2) We explore effects of egg cannibalism in colony dynamics and understand how to model such social conflict behavior realistically using different functional responses to incorporate benefits of egg cannibalism behavior. Our models and the related analytical and numerical analysis suggest that: (a) Age polyethism should be incorporated in the leafcutter ants and their fungus garden interaction model, otherwise, their population dynamics would be unstable. (b) If the maturation rate is too large, then the colony may die out. (c) If the mortality rate of the inside workers is greater than the outside's workers, then the colony is prone to extinction. (d) Small enough egg cannibalism rate benefits adult worker ant's growth and (or) development, large proportion of ants performing a given task can promote colony survival, and too large egg cannibalism rate can lead to colony's death. (f)

A non-linear functional response of egg cannibalism benefit can save the colony from extinction, while a linear fashion cannot provide survival. In addition, increasing energy invested on brood care and (or) the conversion rate between fungus and ants could induce oscillatory dynamics in models with cannibalism.

Introduction

Eusocial insects represent some of the most advanced social systems and are characterized by having cooperative brood care, an overlap of at least two generations in the same colony, and coexistence of reproductive and non-reproductive members [Hölldobler and Wilson, 2010]. Leafcutter ants are considered by many to represent one of the pinnacles of social evolution. They live in colonies that can reach population sizes in the millions, have a number of morphologically distinct subclasses, build nests over 30m wide, and are the greatest agricultural pest of the neotropics, with mature colonies devouring hundreds of pounds of leaves every year. The huge size of the colonies and success of the species is facilitated by their symbiosis with a fungus that they grow as their primary food source. The ants do not eat the pieces of fresh vegetation that they collect from the plants surrounding the colony, but instead provide them to their fungal symbiont which they consume in turn. They exhibit a complex system of division of labor by which task allocation depends on the age of the individual or on physical features, or on both [Hölldobler and Wilson, 2010]. Division of labor (DOL) in social insects, as defined by Gordon [2015], "describes a process in which one individual repeatedly performs a task while another individual repeatedly performs another".

Mechanisms of DOL include size polymorphism, age polyethism, variation in response thresholds, and learning [Beshers and Fewell, 2001]. Some of the tasks performed by non-reproductive individuals include caring for the queen and brood, nest

construction, foraging for resources, and cleaning and defending the nest, which have the overall purpose of increasing the colony's success [Hölldobler and Wilson, 2010, Yan *et al.*, 2014]. Age polyethism plays an important role in shaping division of labor in leafcutter ant colonies [Camargo *et al.*, 2007, Wilson, 1980]. This phenomenon is observed in many social insects in which individuals perform different tasks as they grow older [Oster and Wilson, 1978, Wilson *et al.*, 1971]. For example, workers in the smallest physical class take care of brood and the fungus inside the nest when they are young [Camargo *et al.*, 2007, Van Bael *et al.*, 2011], and can be seen riding on pieces of leaves being carried back to the nest by foragers when they are older, where they both protect the forager carrying the leaf from parasitic phorid flies and begin cleaning and processing the leaf fragment [Feener Jr and Moss, 1990, Vieira-Neto *et al.*, 2006, Camargo *et al.*, 2007, Hart *et al.*, 2002, Van Bael *et al.*, 2011, Linksvayer *et al.*, 2002]. Older workers from all size classes are also more likely to participate in the dangerous behavior of defending the nest [Hölldobler and Wilson, 2010]. Therefore, for social insect colonies with age polyethism, the tasks performed by individuals within a colony changes as they mature [Capinera, 2008]. One of the interesting questions is how age polyethism in a social insect colony contributes to population dynamic's including the distribution of workers performing different tasks.

Egg cannibalism behavior has been regularly observed in social insect colonies, including leafcutter ants and honeybees [Schmickl and Crailsheim, 2001, Monnin and Peeters, 1997, Woyke, 1977], and is suggested to be a selfish behavior influenced by environmental factors such as shortage of food resources [Matthews and Matthews, 2009, Richardson *et al.*, 2010, Schmickl and Crailsheim, 2001], and individual traits such as sex [Schultner, 2014]. Recent studies have shown that egg cannibalism is an adaptive life strategy that can increase growth and developmental rates [Kang *et al.*, 2015, Osawa, 1992, Roy *et al.*, 2007, Schultner *et al.*, 2013], adult body size [Osawa,

2002, Schultner *et al.*, 2013], improve colony survival [Kang *et al.*, 2015, Roy *et al.*, 2007, Schultner *et al.*, 2013], and reduce competition within the colony [Roy *et al.*, 2007, Schultner *et al.*, 2013, Wise, 2006]. There is a fair amount of literature devoted to the study of cannibalism behavior in both ecological and evolutionary settings (see [Cushing, 1991, 1992, Cushing and Li, 1995, Kang *et al.*, 2015]).

In leafcutter ants, egg cannibalism behavior plays an important role during the incipient stage of the leafcutter colony life cycle. When the first workers eclose in the new colony started by a recently-mated queen, the queen produces large malformed trophic eggs, formed by fusing multiple eggs in the ovariole, and the workers feed them to developing larvae to reduce consumption of the still-small fungus garden. The production of these trophic eggs is crucial to the survival of the colony until it reaches the size required for stable colony growth [Kang *et al.*, 2011]. One interesting question is whether the benefit of cannibalism behavior is reflected in a linear energy transfer from victim to consumer or in a nonlinear fashion.

A number of experimental studies have examined the respective roles of egg cannibalism [Kang *et al.*, 2015, Osawa, 1992, 2002, Roy *et al.*, 2007, Schultner *et al.*, 2013, Wise, 2006], division of labor [Beshers and Fewell, 2001], and age polyethism [Camargo *et al.*, 2007, Oster and Wilson, 1978, Wilson, 1980, Wilson *et al.*, 1971] in shaping population dynamics of social insects. However, it has been difficult to study how these factors interact with one another to shape overall colony-level population dynamics. Increasing our understanding of how these factors individually shape population dynamics, how the effects of the factors modulate the influence of one another, and their cumulative effects will be of great value to social insect scientists. In this paper we will use a mathematical modeling approach to facilitate study of the effects of these potentially interacting variables on colony-level population dynamics.

Mathematical models have been used to understand population dynamics observed

in natural environments. For instance, Karsai *et al.* [1996] developed a simple model to describe the colony dynamics from regulatory effects of feedback mechanisms such as brood production in eusocial paper wasps. Other models [Karsai and Schmickl, 2011, Schmickl and Karsai, 2014, 2016] have studied different mechanisms of division of labor. In Schmickl and Karsai [2014] and Karsai and Schmickl [2011], they focused on studying the regulation of task partitioning of hunting behavior in a Ponerine ant colony and in construction behavior in social wasps, respectively. Both Schmickl and Karsai [2014] and Karsai and Schmickl [2011] used a Stock and Flow modeling framework to develop a system of first-order ODEs explaining that task partitioning of hunting behavior and nest construction, can be done by regulation. In Schmickl and Karsai [2016], an ODE model approach was used to study the task regulation of collective behavior in honeybees predicting an adaptive strategy for both bees and plants. Also, Schmickl and Crailsheim [2007] proposed a model to study the population and resource dynamics of a honeybee colony emphasizing pollen supply and brood cannibalism. However, few models that could be applied to the interactions between leafcutter ants and their fungus garden have been produced (but see Kang *et al.* [2011]).

The model proposed in Kang *et al.* [2011] describes the mutualism interactions of leafcutter ants and their fungus with an implicit division of labor, which provides global dynamics suggesting that division of labor among worker ants is an important factor which determines survival and growth, or death of leafcutter ants colonies and their fungus garden. We adopt the modeling approach of Kang *et al.* [2011] to investigate the effects of age polyethism and egg cannibalism on colony population dynamics. More specifically, the main purpose of this paper is to learn the possible colony dynamic outcomes by studying the effects of the explicit division of labor through the subdivision of the worker ants into two task groups that perform tasks

44

according to their age such as tending the fungus garden and collecting leaves. We also explore how the colony may benefit from egg cannibalism behavior in linear or nonlinear fashions.

Model Derivation

Kang *et al.* [2011] proposed the following model (3.1) to study an incipient colony growth model for leafcutter ants and their fungus garden based on simple density-dependent growth and death rates coupled with a fungus growth model which can be described by a generalized Michaelis-Menten equation of enzyme kinetics [Kang *et al.*, 2011]:

$$F'(t) = \frac{r_f a A^2}{b + aA^2} F - d_f F^2 - r_c AF$$

$$A'(t) = r_a AF - d_a A^2$$

(3.1)

where r_f is the maximum growth rate of the fungus; $r_a = cr_f$ with c being the conversion rate between fungus and ants; b is the half-saturation constant; and d_a, d_f is the mortality rate of ants and the fungus, respectively. The parameter $a = p^2 q(1-q)$ measures implicit division of labor with p being the portion of the worker biomass of $A(t)$ performing an inside colony task such as brood care, and q being the portion of energy of each worker performing an outside colony task such as foraging. The ecological assumptions of (3.1) are listed as follows:

1. The numerical response function for ants is the Holling Type I function, i.e., fungus biomass F multiplied by a constant number r_a. In addition, we assume that ants suffer from density-dependent mortality due to energy consumed by foraging for leaves and taking care of the larvae and fungus garden, which will modify population growth through density-dependent self-limitation [Holland and DeAngelis, 2010].

2. The numerical response of fungus to ants is a Holling Type III function $\frac{aA^2}{b+aA^2}$ by applying the concept of the kinetics of functional response [Real, 1977]. Moreover, the fungus suffers from density-dependent mortality due to self-limiting [Holland and DeAngelis, 2010].

In the following subsections, we provide detailed model derivations and assumptions of the following two sets of models based on the modeling approach of (3.1) [Kang *et al.*, 2011]:

1. We derive two models with division of labor: leafcutter ants and their fungus garden interaction models with versus without age polyethism.

2. We derive two models with egg cannibalism behavior in the interactions of leafcutter ants and their fungus garden: (1) Consumption of eggs leads to the energy increasing linearly for consumer; and (2) Consumption of eggs decreases the mortality of the consumer in a nonlinear fashion.

Model with Division of Labor in leafcutter Ants with Fungus Garden

Let $F(t)$ represent the biomass of fungus, and $A(t) = A_i(t) + A_o(t)$ be the total biomass of workers in a colony where $A_i(t)$ is the biomass of ants working inside the colony, and $A_o(t)$ is the biomass of ants working outside the colony at any time t, respectively. We propose the following system of nonlinear differential equations describing the biomass rate of change of two task groups of leafcutter ants and their fungus with their related age polyethism effect as model (3.2). We assume that ants working inside the colony A_i will age into A_o to perform more risky tasks outside of the colony with maturation rate β.

46

$$F'(t) = \left[\frac{r_f A_i A_o}{b + A_i A_o} - d_f F - r_i A_i - r_o A_o \right] F$$

$$A_i'(t) = c_i r_i A_i F - \beta A_i - d_i A_i (A_i + A_o) \qquad (3.2)$$

$$A_o'(t) = c_o r_o A_o F + \beta A_i - d_o A_o (A_i + A_o)$$

The ecological assumptions of the leafcutter ants colony's dynamics of (3.2) are listed as follow:

1. **Biomass of fungus $F(t)$:**

   - $F(t)$ can only increase if there are ants tending the garden inside the colony and ants collecting leaves outside the colony, hence its growth will be a product thereof, taking into account the maximum growth rate of the fungus, r_f. By the kinetics of functional response, we can describe the response of the fungus as a Holling type III functional response, $\frac{r_f A_i A_o}{b + A_i A_o}$ where b is the half saturation constant.

   - $F(t)$ decreases due to natural mortality and consumption by ants, with d_f as the death rate of fungus, and r_i and r_o as the rate of consumption by ants working inside and outside, respectively.

   Thus, the dynamics of the fungus biomass $F(t)$ is described by the following equation:

   $$F'(t) = \left[\frac{r_f A_i A_o}{b + A_i A_o} - d_f F - r_i A_i - r_o A_o \right] F.$$

2. **Biomass of ants working inside and outside the colony, $A_i(t)$ and $A_o(t)$:**

   - $A_i(t)$ and $A_o(t)$ increase in proportion to the biomass of fungus and their own biomass according to the rate of consumption (r_i, r_o respectively) and the rate at which they can convert the biomass of consumed fungus to their own biomass (c_i, c_o respectively).

- $A_i(t)$ and $A_o(t)$ decreases due to density dependent mortality, i.e. the death rate of each of the task groups increases when the total population is too large and individuals are competing for space or resources.

- We consider a maturation rate of ants working inside the colony βA_i. We assume that ants working inside the colony leave this task group at a per-capita rate β.

In summary, model (3.2) has explicit division of labor that is measured by the population of inside colony workers A_i and outside colony workers A_o. In our model we assume that age polyethism is an additional DOL mechanism which includes the fact that younger workers A_i performing inside colony task will age into older workers A_o performing outside colony task at a rate of β. We aim to compare the dynamical outcomes of model (3.2) for $\beta = 0$ and $\beta > 0$ in order to explore the impacts of age polyethism described by the term βA_i. We also compare dynamics of the original model (3.1) to model (3.2) to study the effects of explicit DOL.

Model with Egg Cannibalism in leafcutter Ants with Fungus Garden

Let $F(t)$ be the total biomass of fungus as time t, and $E(t)+A(t)$ denote the total biomass of a focal colony of leafcutter ants at time t, where $E(t)$ represents the egg population biomass that can be cannibalized by $A(t)$ at time t, and $A(t)$ represents the population biomass of larvae and adult workers that may have cannibalistic behavior at time t. We propose the following sets of nonlinear equations describing a two-stage population model of leafcutter ants with egg cannibalism behavior and implicit DOL:

Model (3.3) describes the utilization of egg cannibalism leading to the growth benefit of A due to the linear energy transformation,

$$F'(t) = F\left[\frac{r_f a A^2}{b + a A^2} - d_f F - r_c A\right]$$

$$E'(t) = p_1 r_a A F - \alpha A E - \beta E \tag{3.3}$$

$$A'(t) = (1 - p_1) r_a A F + \beta E + c_1 \alpha A E - d_a A^2$$

Model (3.4) describes the utilization of egg cannibalism resulting in reduced mortality rate of A, and thus increase the lifespan of A. The benefits of egg cannibalism are modeled as nonlinear effects in the model (3.4). The detailed ecological assumptions for these models are described below.

$$F'(t) = F\left[\frac{r_f a A^2}{b + a A^2} - d_f F - r_c A\right]$$

$$E'(t) = p_1 r_a A F - \alpha A E - \beta E \tag{3.4}$$

$$A'(t) = (1 - p_1) r_a A F + \beta E - \frac{d_a A^2}{1 + c_2 \alpha E}$$

First, the derivations of the biomass fungus F in both model (3.3) and (3.4) follow the same assumptions in the original model (3.1) studied in Kang *et al.* [2011]. We also assume that the reproductive division of labor results in the ratio of energy gained through consuming fungus being $p_1 \in [0, 1]$ for the colony reproduction investment, i.e., the colony invests $p_1 r_a A F$ in reproduction and $(1 - p_1) r_a A F$ in the growth of A-class. We also assume that egg population $E(t)$ has no natural death but can only die through cannibalism by the A-class or mature into A-class. Egg cannibalism is modeled with the Holling Type I functional response $\alpha A E$, where α is the cannibalism rate; $E(t)$ matures into the A-class at the rate of βE. Thus, the population dynamics of E is described with the following equation:

$$E'(t) = p_1 r_a A F - \alpha A E - \beta E.$$

Regarding the population of A-class, this increases through the energy gained by consuming fungus $(1 - p_1) r_a A F$ and the maturation from E-class βE.

- In model (3.3), $A(t)$ can increase linearly its population/biomass by cannibalizing the egg population at a rate $c_1 \alpha A E$, where $c_1 \in (0,1)$ is the conversion efficiency between ants and eggs.

- In model (3.4), consuming eggs at a rate $\alpha A E$, $A(t)$ mortality rate $d_a A^2$ is decreased with the functional response $\frac{1}{1+c_2 \alpha E}$, which represents the benefit obtained from cannibalism. The parameter c_2 is a coefficient describing the functional response of survivability to an increasing presence of eggs which increases the number of individuals cannibalized.

The assumptions above imply that, if there is no egg cannibalism (i.e. $\alpha = 0$), model (3.3) and (3.4) are reduced to the following system:

$$
\begin{aligned}
F'(t) &= F\left[\frac{r_f a A^2}{b + a A^2} - d_f F - r_c A\right] \\
E'(t) &= p_1 r_a A F - \beta E \\
A'(t) &= (1 - p_1) r_a A F + \beta E - d_a A^2
\end{aligned}
\tag{3.5}
$$

A description to each of the parameters used in these models and intervals obtained from the approximations according to empirical work [Brown et $al.$, 2006, Clark and Fewell, 2014, Kang et $al.$, 2011], are shown below:

Parameter	Intervals	Reference
r_a: Maximum growth rate of ants	(0.05,0.3)	Kang *et al.* [2011]
r_f: Maximum growth rate of fungus	(0.01,1)	Kang *et al.* [2011]
r_c, c_i, c_o: Conversion rate between fungus and ants	(0.001,10)	Kang *et al.* [2011]
d_a, d_i, d_o: Death rate of adult workers	(0.001,1)	Kang *et al.* [2011]
d_f: Deterioration rate of fungus	(0.001,1)	Kang *et al.* [2011]
r_i, r_o: Consumption rate of fungus	variable	
b: Half-saturation constant	(0.001,10)	Kang *et al.* [2011]
a: Measurement of the division of labor	(0.0.25)	Kang *et al.* [2011]
p_1: Energy invested on brood care	(0,1)	variable
α: Cannibalism rate	variable	
β: Maturation rate	(0.015, 0.25)	Boulogne *et al.* [2014],Camargo *et al.* [2007]
c_1: Conversion efficiency between ants and eggs	(0,1)	variable
c_2: Regulation effect of an increase of cannibalism	arbitrary	variable

Table 3.1: Parameter Description and Interval Values Used in Models (3.2) and (3.3).

We aim to compare the dynamical outcomes of model (3.5) without egg cannibalism to model (3.3) with cannibalism to explore how may cannibalism behavior alter the colony dynamics; and compare equilibria dynamics of model (3.3) exploring both funtions $\Phi_{1,2}(E, A)$ to investigate how different modeling approaches of cannibalism's benefits could result in different outcomes.

Mathematical Analysis

First, we provide the following theorem regarding the basic dynamic properties of our proposed four models (3.2), (3.3) and (3.4) as follows:

Theorem 6 (Positive Invariance and Boundedness)**.** *The systems* (3.2)*,* (3.3) *and* (3.4) *are all positive invariant in* $\mathbb{R}^3_+$*. More specifically, every trajectory of model* (3.2)*is attracted to a compact set* $C = \left[0, \frac{r_f}{d_f}\right] \times \left[0, \frac{c\,r_f}{d\,d_f}\right]$*; and every trajectory of models* (3.3) *and* (3.4) *is attracted to a compact set* $D = \left[0, \frac{r_f}{d_f}\right] \times [0, M_3]$*.*

Models (2.2 - 2.4) are biologically well-defined, i.e. the populations' biomass is always positive and bounded. In addition, the extinction equilibrium $E_0 = (0, 0, 0)$ always exists for all models.

Effects of Age Polyethism

To determine the effects of age polyethism, we identify the conditions by which the colony of leaf-cutter ants can survive or perish. We do this by analyzing interior equilibria for the system (3.2) when $\beta = 0$ and $\beta > 0$. We define an interior equilibria in our model as a fix-point of the form (F^*, E^*, A^*) where $F^*, E^*, A^* > 0$. Let

$$\kappa = \frac{c_o r_o}{c_i r_i}$$

be the relative growth rate of workers performing inside colony tasks to workers performing inside colony tasks.

Let

$$A_i^* = A_o^* \left[\frac{(d_o - d_i \kappa) A_o^* - \beta \kappa}{\beta - (d_o - d_i \kappa) A_o^*} \right],$$

which depends on the positive solutions of the following nullcline equation:

$$g_2(A_o) = a_4 A_o^4 + a_3 A_o^3 + a_2 A_o^2 + a_1 A_o + a_0. \tag{3.6}$$

The complete expression for the constants a_i, for $i = 0, ..., 4$ are in the appendix.

The following theorem provides conditions for existence of interior equilibria for both considered cases of (3.2) (i.e., $\beta = 0$ and $\beta > 0$).

Theorem 7 (Existence of equilibria). *Model (3.2) always have the extinction equilibrium $\mathbf{E_0} = (0,0,0)$ which is always locally asymptotically stable. In addition, model (3.2) with $\beta = 0$ has interior equilibria if and only if $\kappa = \frac{d_o}{d_i}$. On the other hand, model (3.2) with $\beta > 0$ has an interior equilibrium if $\frac{d_o}{d_i} > \kappa$ and does not have an interior equilibria if $\frac{d_o}{d_i} < \kappa$.*

Numerical simulations

According to Theorem 7 and numerical simulations displayed in Figure 3.1, when $\kappa = \frac{d_o}{d_i}$, Model (2.2) without age polyethism (i.e. $\beta = 0$) has an attractor that consists of a line of equilibria where initial condition plays an important role in determining which equilibrium converges to. When the condition does not satisfy, Model (2.2) with $\beta = 0$ has only the extinction equilibrium.
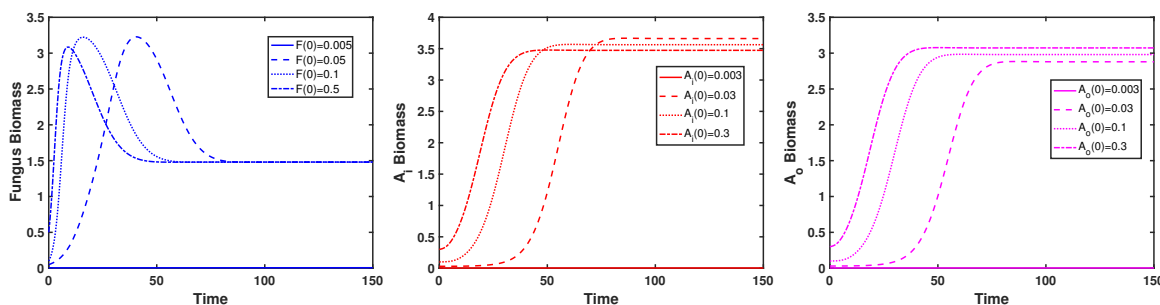
Figure 3.1: Time series solution for model (3.2) with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, d_i = 0.01, d_o = 0.0095, c_i = c_o = 0.7, r_o = 0.06$ with $\mathbf{r_i} = \frac{\mathbf{d_i c_o r_o}}{\mathbf{d_o c_i}}$, choosing different initial conditions.

The inclusion of age polyethism (i.e. $\beta > 0$) in model (3.2), gives us unique solutions as opposed to when $\beta = 0$ with either infinitely many solutions or non-existent positive solutions. Figure 3.2, shows the possible number of interior equilibria that model (3.2) with $\beta > 0$ can have and their stability. Fixing parameters $r_f = 0.7; b = 0.002; c_i = 0.5; c_o = 0.3; d_f = 0.2; d_i = 0.1; d_o = 0.2; r_i = 0.15; r_o = 0.2$ and varying β, which denotes the transition and maturation rate from inside worker

to outside worker, we can see the effect of this parameter in the biomass of fungus, inside the colony workers, and outside the colony workers. Figure 3.2a shows that as β increases, the total biomass of fungus is benefited by its increase. This could imply that as more inside worker ants transition into outside workers (i.e. workers which cut, collect, and bring back leaves to the colony), the biomass of fungus increases and benefits from A_o effort. Also, as β increases, the biomass of the population of ants working inside the colony decreases (see Figure 3.2b), while the biomass of the population of ants working outside increases (see Figure 3.2c). However, too high of a maturation rate could affect the whole colony and both species (fungus and ants) by inducing colony's death. *An explanation of this effect is that when inside the colony workers transition very quickly to outside workers, they are now exposed to greater risks outside the nest, resulting in increased mortality. At the same time, inside the nest, the production of new workers may not be fast enough to maintain a satisfactory number of inside workers need to contribute to the efforts to keep their fungus cultivar alive.*

| (a) | (b) | (c) |
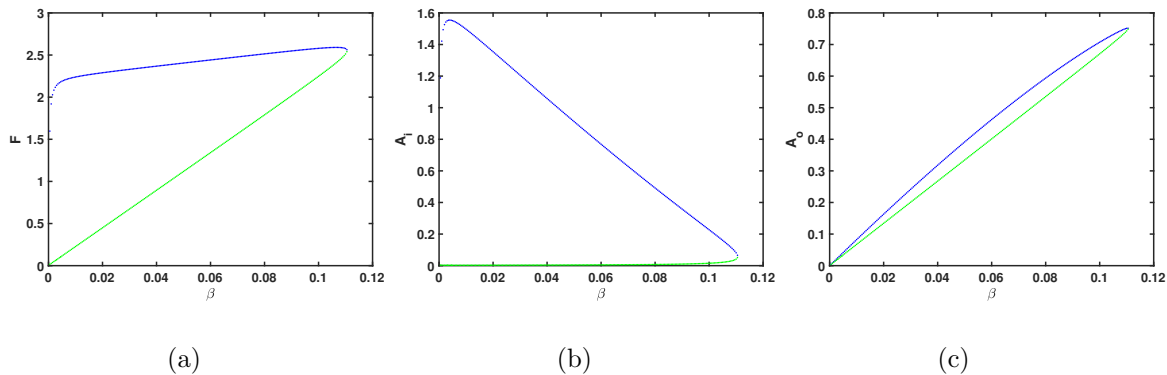
Figure 3.2: Bifurcation diagrams for model (3.2) studying the effect of β on biomass of fungus and worker ants where $r_f = 0.7; b = 0.002; c_i = 0.5; c_o = 0.3; d_f = 0.2; d_i = 0.1; d_o = 0.2; r_i = 0.15; r_o = 0.2$. (Blue: stable and green: unstable interior equilibria)

Figure 3.3 is a one-dimensional bifurcation of the death rate of outside workers to inside workers ratio showing coexistence and stability when $\frac{d_o}{d_i} > \kappa$. We also notice

that as $\frac{d_o}{d_i}$ increases, the biomass of fungus and the task group of ants working outside the colony decreases, while the biomass of the task group of ants working inside the colony increases.
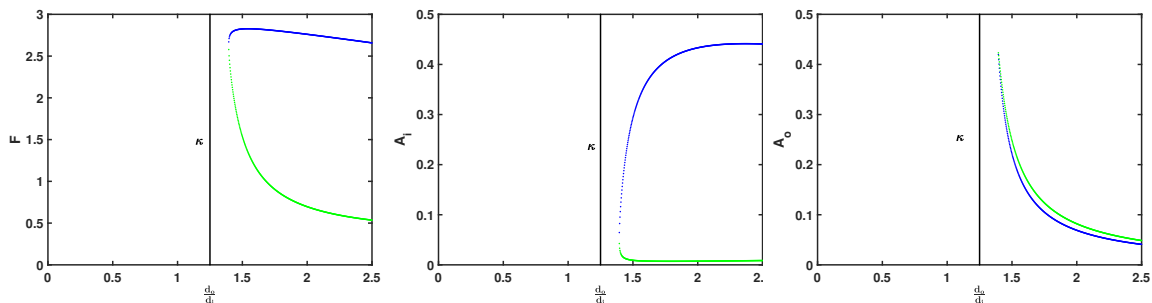
Figure 3.3: One-dimensional bifurcation of the ratio $\frac{d_o}{d_i}$ with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, c_i = c_o = 0.4, r_o = 0.25, r_i = 0.2$.

Figure 3.4 is a two-dimensional bifurcation diagram of $d_o \in (0, 1)$ and $d_i \in (0, 1)$ with different levels of maturation rate β by setting $c_i = c_o = 0.4; r_i = r_o = 0.2$, i.e. both task groups have the same consumption rate of fungus and conversion rate of fungus into their own biomass. *When the maturation rate is small, too large d_i can make the colony extinct. If the maturation rate is larger (e.g. $\beta = 0.1$), then the colony can go extinct if d_i is not large enough. In general if $d_i > d_o$ the colony of leafcutter ants can go extinct, otherwise it persists.*

Figure 3.5 shows the effects of the conversion rate of fungus into the biomass of worker ants. Here, we have $c_o \in (0, 1)$ versus $c_i \in (0, 1)$ by setting $\beta = 0.02, r_i = 0.2, r_o = 0.25$ and varying the death rate of each of the task groups of worker ants. Consider $d_i < d_o$, when d_i is really small (see Figure 3.5a), then when the conversion rate c_i of the worker ants belonging to the task group A_i is really small and for any value of c_o (white area in Fig. 3.5a), the colony cannot survive. *Now, if d_i increases but still less than d_o, the colony cannot survive for large c_o and small to medium c_i (see Figure 3.5b). However, small c_o and large c_i can promote coexistence of the two*
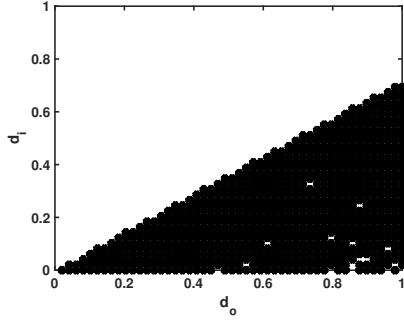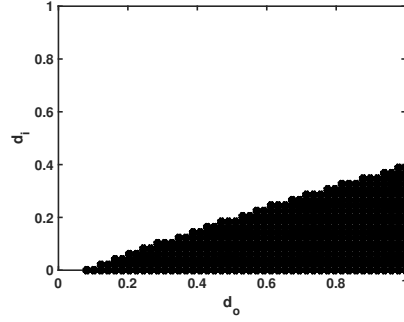
(a) $\beta = 0.02$ (b) $\beta = 0.1$

Figure 3.4: Two parameter bifurcation to study the effect of d_i and d_o on the existence of interior equilibria for model (3.2). $c_i = c_o = 0.4; r_i = 0.2; r_o = 0.2$. (Area in black denotes coexistence and white extinction)

task groups and fungus.
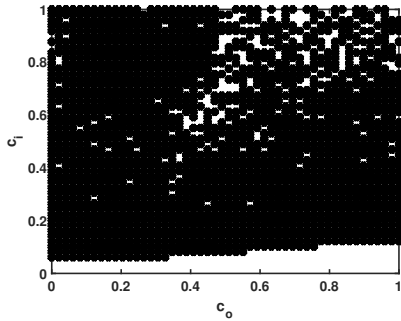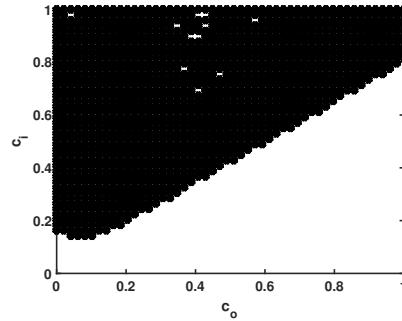
(a) $d_i = 0.03$ (b) $d_i = 0.3$

Figure 3.5: Two parameter bifurcation to study the effect of c_i and c_o on the existence of interior equilibria for model (3.2). $d_o = 0.5; \beta = 0.02; r_i = 0.2; r_o = 0.25$. (Area in black denotes coexistence and white extinction)

Effects of Egg Cannibalism

Next we investigate the effects of egg cannibalism α in both models (3.3) and (3.4).

If there is no egg cannibalism (i.e. $\alpha = 0$), system (3.3) and (3.4) reduces to system

(3.5).

Theorem 8 (No egg cannibalism)**.** *Let* $\gamma = \frac{4b(d_a d_f + r_a r_c)}{(r_a r_f)^2}$. *System* (3.5) *always have*

56

the extinction equilibrium and has the following equilibria scenarios:

1. *No interior equilibria: when $a < \gamma$.*

2. *One interior equilibria: when $a = \gamma$.*

3. *Two interior equilibria: when $a > \gamma$.*

The equilibrium dynamics of model (3.5) when the colony does not have egg cannibalism are similar to those in the model of Kang *et al.* [2011], i.e. $(0, 0, 0)$ is globally stable when it is the only equilibrium and (F_2^*, E_2^*, A_2^*) can be locally asymptotically stable when it exists.

Biological implications: Theorem 8 and equilibrium dynamics shown in Kang *et al.* [2011] for a similar case implies that division of labor plays an important role in determining whether a colony of leaf cutter ants can survive in the absence of egg cannibalism. When a is too small, the proportion of adult ants performing certain tasks is too small, therefore they are not investing enough energy to a given task. This leads to the extinction of the colony. However, if the proportion of adult ants performing given tasks is large enough, then the colony can survive.

Theorem 9. *If model (3.5) without cannibalism has no interior equilibria, then model (3.3) with cannibalism cannot have interior equilibria, i.e., the colony cannot survive. Moreover, model (3.4) with cannibalism can have the following dynamics:*

1. *Model (3.4) always have the extinction equilibrium and can have maximum two interior equilibria: $E_i = (F_i^*, E_i^*, A_i^*)$, $i = 1, 2$.*

2. *If $f_{\max} = \frac{r_f \sqrt{ab} - 2br_c}{2bd_f} < 0$, then model (3.4) has no interior equilibrium.*

3. *If $f_{\max} > \frac{\frac{d_a}{r_a}}{1 - p_1} > \frac{d_a}{r_a}$, then model (3.4) definitely has interior equilibria.*
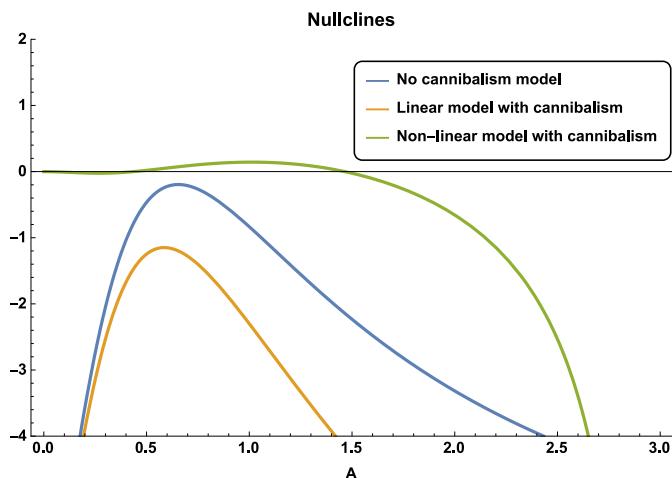
Figure 3.6: Nullclines of System (3.5) With No Egg Cannibalism and System (3.3) With Egg Cannibalism.

Biological implications: Theorem 9 supported by Figure 3.6 suggests that systems such as (3.5) and (3.3), i.e. without cannibalism and with cannibalism used for growth benefit of A biomass, respectively, cannot fully describe the positive mechanism that egg cannibalism represents in a colony of social insects. Under critical conditions when division of labor implicitly described by a is too small, both systems only have the extinction equilibrium. However, model (3.4) with cannibalism used to increase A lifespan improves the outcomes of model (3.3) and model (3.5) by providing two existent interior equilibrium where one of them can be stable (see Theorem 10). This suggests that the dynamics of model (3.4) provide survival of the colony when model (3.5) and (3.3) cannot.

Further analytical and graphical implications regarding the existence of interior equilibria of model (3.4) can be found in Appendix A.

The following theorem summarizes the conditions for existence of interior equilibria (F^*, E^*, A^*) for models (3.3) and (3.4), i.e. coexistence of fungus, eggs, and adult workers in a colony where egg cannibalism contributes to the growth of adult workers and increases adult worker lifespan, respectively.

58

Theorem 10 (Extinction and survival conditions). *Let $a, b, c_1, d_a, d_f, p_1, r_a, r_c$ be positive parameters. We define*

$$K_1 = \frac{a\beta r_a r_f}{b(d_a d_f + r_a r_c(1 - p_1(1 - c_1)))} \quad \text{and} \quad K_2 = \frac{\alpha b(d_a d_f + r_a r_c(1 - p_1(1 - c_1)))}{\beta r_a r_f}.$$

Model (3.3) and model (3.4) always have the extinction equilibrium which is always asymptotically stable. In addition, given the following conditions, both models can have maximum two interior equilibria: $\mathbf{E_i} = (F_i^*, E_i^*, A_i^*)$, $i = 1, 2$, such that all the components of $\mathbf{E_2}$ are larger than the components of $\mathbf{E_1}$ (i.e. $\mathbf{E_2} > \mathbf{E_1}$). For model (3.3):

1. *Colony dies out (zero and one interior equilibrium): If $\alpha > K_1$ or $a < K_2$, then the equilibrium $(0, 0, 0)$ is the only equilibrium of the system and it is global stable. On the other hand, when $\alpha = K_1$ or $a = K_2$, there is only one interior equilibrium which is saddle.*

2. *Colony survives (two interior equilibria): if $\alpha < K_1$ or $a > K_2$, $\mathbf{E_2}$ is locally asymptotically stable when*

$$r_a(1 - p_1)F_2^* + c_1\alpha E_2^* < 2d_a A_2^*.$$

Similarly, for model (3.4), when $(0, 0, 0)$ is the only equilibrium, it is globally stable, while if two interior equilibria exists under condition 3 in Theorem 9, then $\mathbf{E_2}$ is locally asymptotically stable when

$$r_a(1 - p_1)F_2^* < \frac{2d_a A_2^*}{1 + c_2\alpha E_2^*}.$$

Biological implication: Theorem 10 suggests that both egg cannibalism and division of labor are important factors for the survival of a colony of leaf cutter ants. For instance, if egg cannibalism rate is too large and the proportion of ants

performing a given task is too small, then the colony will die out. However, for a small egg cannibalism rate and large proportion of ants performing a given task, i.e., there are more ants investing energy on different tasks while using egg cannibalism as a way to regulate their growth, then the colony of leaf-cutter ants with fungus can survive. (See supplementary material in Appendix B).

The following numerical simulations will aid to understand the different dynamics of models (3.3) and (3.4). *We investigate the effects of egg cannibalism rate α, the parameter measuring the division of labor among the workers a, and the energy spent on brood care p_1 on the biomass of eggs E, adult workers A, and fungus F. We compare the dynamics of model (3.3) and model (3.4) with egg cannibalism used as energy for growth of the adult population described with the Holling Type I functional response $c_1 \alpha A E$ and for energy to decrease death rate (increase lifespan) of adult workers $\frac{d_a A^2}{1 + c_2 \alpha E}$.*

Numerical simulations

The time series solutions for model 3.3 and model 3.4 when testing the increase of p_1 and r_c, respectively, are shown in Figure 3.7 and Figure 3.8. Supplementary bifurcation diagrams in Appendix B show the destabilizing effects produced by the increase of parameters describing the energy gained through the consumption of fungus by the adult worker invested on brood care, p_1, and the conversion rate between fungus and ants, r_c.

For high energy invested on brood care p_1 by adult workers, and (or) high conversion rate between fungus and ants r_c, both model 3.3 and model 3.4 can have oscillatory solutions. Both of these systems models egg cannibalism and its benefits in two different fashions as previously described in our model derivation. Comparing the model 3.5 with no egg cannibalism, we observe that these fluctuation in popula-

tions dynamics emerge with the presence of egg cannibalism and other mechanisms related to brood care and nutrient consumption. Also, we want to point out that when r_c is too large, e.g. close to or greater than 2, the system goes through catastrophic event such that all solutions go to the extinction state.

Solution to model (3.3) with $c_1 = 0.85$ Solution to model (3.4) with $c_2 = 85$.
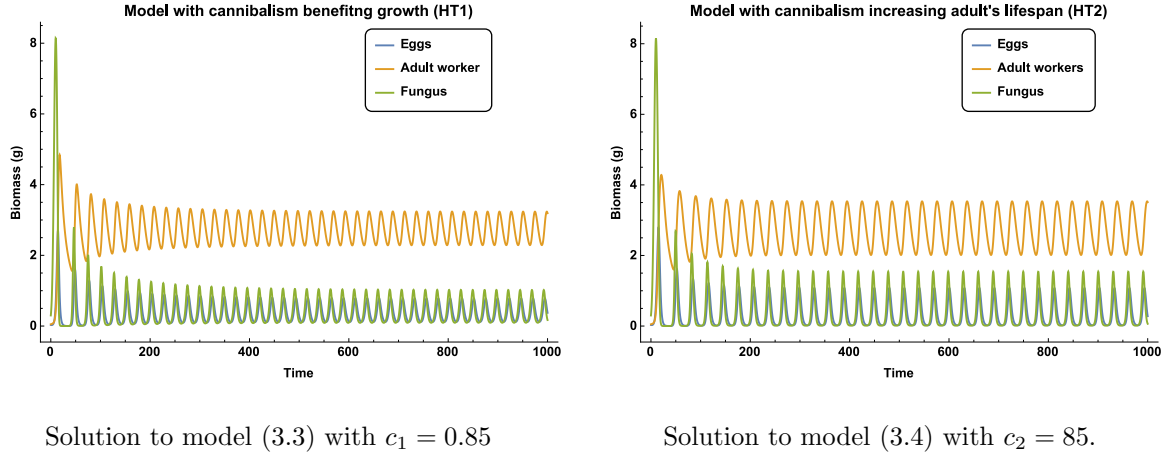
Figure 3.7: $p_1 = 0.85; \alpha = 0.08; r_c = 0.7; r_f = 2; b = 0.002; d_f = 0.2; a = 0.3; r_a = 0.15; d_a = 0.02; \beta = 0.15$

Solution to model (3.3) with $c_1 = 0.8$ Solution to model (3.4) with $c_2 = 10$.
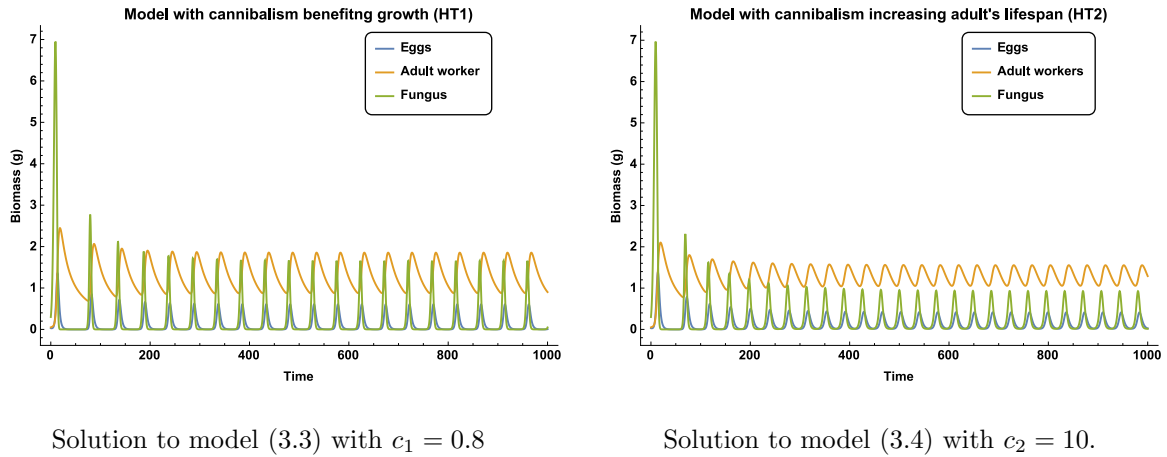
Figure 3.8: $r_c = 1.5; \alpha = 0.08; p_1 = 0.8; r_f = 2; b = 0.002; d_f = 0.2; a = 0.3; r_a = 0.15; d_a = 0.02; \beta = 0.15$

Next, we present 2-dimensional bifurcation diagrams in Figure 3.9, which shows the effects of egg cannibalism rate α with the parameter measuring the division of labor among the workers a in both models. In Figure 3.9a, we choose $c_1 = 0.1$ for

61

model (3.3) showing that with no egg cannibalism and with small or no division of labor, the colony can die out, while large egg cannibalism rate together with a higher response of division labor the colony can survive. Similarly, in Figure 3.9b, we choose $c_2 = 10$ for model (3.4) showing that for very small a the colony can die out, but larger a and any value of α the colony can survive. In this case, both of the models present similar results to those of model (3.1) and in Kang *et al.* [2011], in which division of labor plays a role on the survival of the colony.

(a) Linear model. $c_1 = 0.1$

(b) Non-linear model. $c_2 = 10$
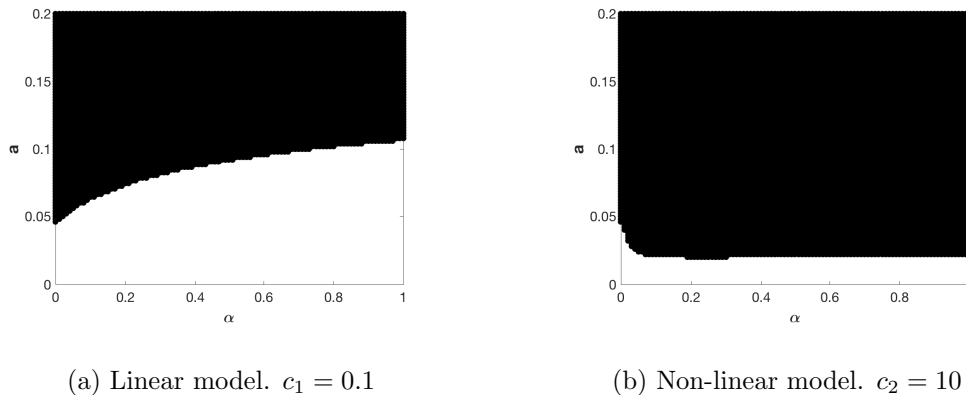
Figure 3.9: $r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$

In Figure 3.10 we can see the effects that energy spent on brood care p_1 and the egg cannibalism rate α have on the existence of interior equilibria for models (3.3) and (3.4). For model (3.3), we can see in Figure 3.10a that the colony can survive with low energy spent on brood care p_1 or low egg cannibalism rate α. For model (3.4), we can see in Figure 3.10b that the colony can survive almost under any value of p_1 and α. *However, with a high egg cannibalism rate and the majority of energy being spent on brood care and not on adult's growth, the colony will not survive.*
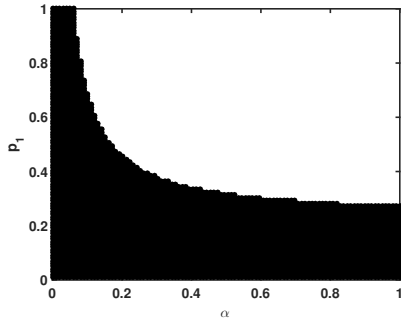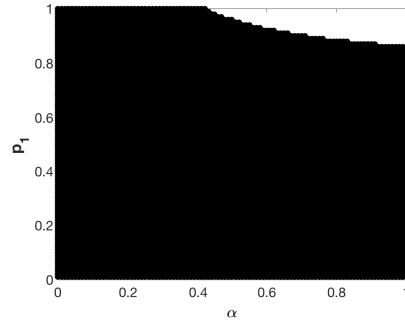
(a) Linear model. $c_1 = 0.1$ (b) Nonlinear model. $c_2 = 10$

Figure 3.10: $a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5$

Next, we provide 1-dimensional bifurcation diagrams in Figures 3.11-3.14, which show that both models can have two interior equilibria where one of them is stable and the other one is unstable. In Figures 3.11 and 3.12, we vary the parameter describing the egg cannibalism rate α with different c_1. In both figures, we notice that as α increases, the biomass of fungus, eggs, and adult workers decreases and eventually disappears. *However, increasing c_1 the conversion rate between ants and eggs, allows a higher cannibalism rate between adult workers and eggs. This suggests that if egg cannibalism is utilized to maximize adult growth, then the colony can survive under difficult conditions.*
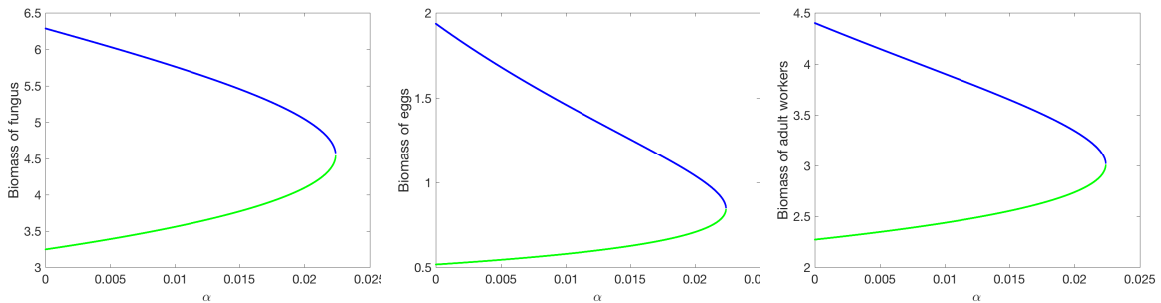
Figure 3.11: Linear model (3.3) $c_1 = 0.1; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (Blue: stable and green: unstable interior equilibria).
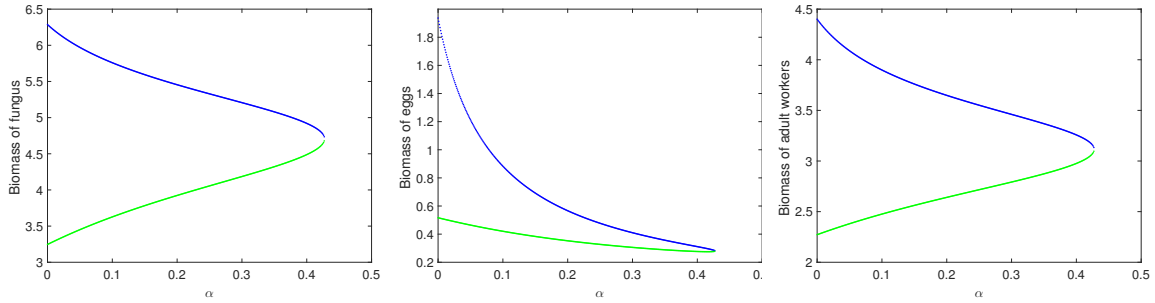
Figure 3.12: Linear model (3.3) $c_1 = 0.85; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (Blue: stable and green: unstable interior equilibria).

Figures 3.13 and 3.14 show the effects of egg cannibalism α and survival rate of adult workers due to cannibalism c_2 in model (3.4). The results in Figure 3.13 suggest that for small cannibalism rate the biomass in the colony can increase, but if the egg cannibalism is too large the colony dies out. However, for large c_2, the colony can survive even with very high egg cannibalism rate (see Figure 3.14). In this case, because the energy obtained from the eggs cannibalized is been used to decrease mortality rate of adult workers, these have the highest biomass in the colony.
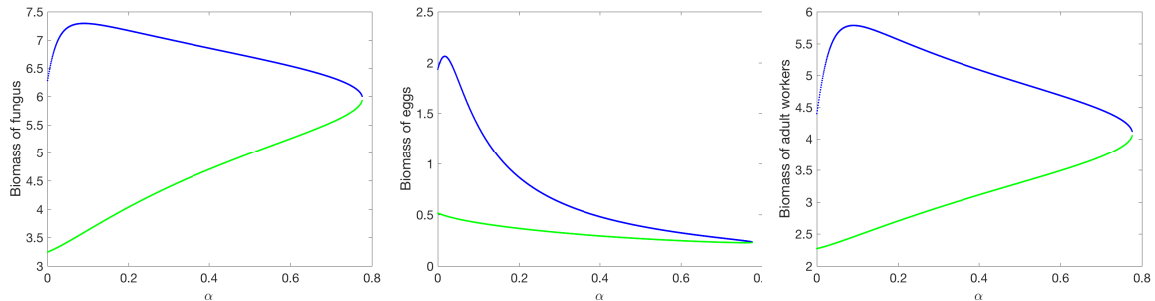
Figure 3.13: Nonlinear model (3.4) $c_2 = 4; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (Blue: stable and green: unstable interior equilibria).

64
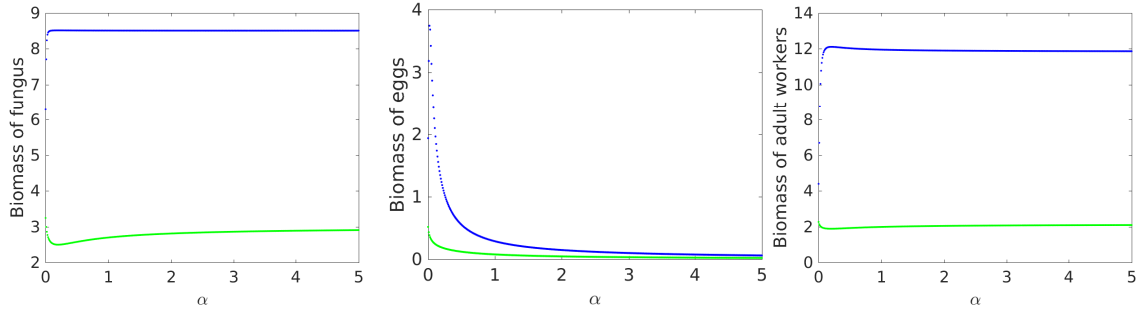
Figure 3.14: Nonlinear model (3.4) $c_2 = 10; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (Blue: stable and green: unstable interior equilibria).

Discussion

Modeling social insect biology has helped study the complex phenomena simple mechanisms can produce. Models proposed in Karsai *et al.* [1996], for instance, provide some advances on understanding the dynamics of brood production and colony development of paper wasps by considering oophagy in the models. In the work of Schmickl and Crailsheim [2001], through empirical study, they were able to determine that shortage of pollen can induce cannibalism of young honeybee larvae, and that cannibalism serves to recycle nutrients, mainly protein, to convert back into worker jelly. In Schmickl and Karsai [2014], showed that task partitioning can lead to self-regulation mechanisms.

In this work, we presented three different models to study the effects of age polyethism and egg cannibalism on the population dynamics of a leafcutter ant colony. System (3.2) models the explicit division of labor of (adult) worker ants in a leafcutter ant colony where we subdivided the total worker population $A(t)$ in two groups: worker ants in charge of processing and cultivating the fungus garden (inside workers) $A_i(t)$ and worker ants in charge of collecting leaves to grow the fungus garden (outside/forager workers) $A_o(t)$. This system models the work done by each of these

65

groups of ants, the consumption rate of fungus for growth/development of workers, and respective natural death rates. We considered the case when $\beta = 0$ in model (3.2) to study the effects of their age-based division of labor (i.e. age-polyethism) within the colony dynamics.

Our analytical and numerical results show that without age-polyethism (i.e. $\beta = 0$), the system (3.2) can have infinitely many solutions (i.e. infinitely many interior equilibria) under the condition $\frac{d_i}{c_i r_i} = \frac{d_o}{c_o r_o}$, which represents the ratio of mortality to growth in both task groups A_i and A_o. Including age-polyethism (i.e., $\beta > 0$), model (3.2) has a maximum of two interior equilibria. The effects of β (i.e. maturation rate) on the biomass of fungus, inside and outside workers are considered to be beneficial for certain ranges, i.e., a very high maturation rate could terminate the colony. An explanation of this situation could be that when inside workers begin to mature faster and switch to performing riskier tasks, this leads to an increase of mortality. Also, the production of new workers to perform inside tasks is not fast enough. Therefore, the colony experiences negative effects causing its collapse. Also, with the subdivision of workers into two task groups, we were able to capture in model (3.2) and Figure 3.2 that if one of the task groups decreases (in this case, A_i decreases as β increases) while the other task group A_o increases, then the fungus receives a greater contribution from the ants working outside the colony. Model (3.2) with $\beta > 0$ suggests that increasing the outside worker population has greater benefits for colony growth and development than increasing the inside worker population, as long as a certain necessary number of inside colony workers exist to care for the fungus and the brood. The evolutionary implications of this finding, and the role it plays in the life history of leafcutter ants, should be investigated in future studies.

Comparing the two different cases considered in model (3.2), i.e. $\beta = 0$ and $\beta > 0$, we conclude that age polyethism has clear benefits for the stability of a colony,

66

which is logically consistent with the important role it plays in the life of leafcutter ants [Hölldobler and Wilson, 2010]. However, it is interesting that the model also shows that the benefits of age polyethism are constrained by β, the maturation rate. Whether the maturation rate of leafcutter ants has been shaped by this restriction imposed by age polyethism should be investigated in future studies.

On the other hand, systems (3.3) and (3.4) model an implicit division of labor and egg cannibalism by including two developmental stages, i.e. eggs and adults, in which adults perform necessary tasks to maintain their fungus cultivar, and interact with eggs by providing brood care or cannibalizing them. Model (3.3) differs with model (3.4) by the choice of Holling Type functional response that models different ways egg cannibalism can contribute to the colony dynamics. In model (3.3), we use the Holling Type I functional response $c_1 \alpha A E$ to describe the positive input that egg cannibalism can provide to the adult class as a nutrient source for growth purposes, whereas model (3.4) has the Holling Type II functional response $\frac{d_a A}{1 + c_2 \alpha A E}$ that describes the contribution of egg cannibalism as nutrient source to decrease death rate of the adult class, thus providing an increase of worker lifespan (see Figures 3.11-3.14). This opens an opportunity to perform manipulative experimental work to determine whether egg cannibalism increase lifespan of adult workers, or if it has alternative benefits.

In the absence of egg cannibalism, i.e., when $\alpha = 0$, both model (3.3) and model (3.4) reduce to model (3.5) and have simple dynamics. The dynamics of model (3.5) with no egg cannibalism suggest that division of labor plays an important factor determining whether a colony of leaf cutter ants can survive or not in the absence of egg cannibalism. In such a case, if a is too small, i.e., the proportion of adult ants performing certain tasks is too small, then the energy invested to a given task is not enough to maintain a colony. This leads to colony collapse. However, if the proportion

of adult ants performing given tasks is large enough, then the colony can survive. This suggests that there may be an evolutionary relationship between division of labor and egg cannibalism, which it would be interesting to explore in future work. Moreover, the dynamics of model (3.3) suggest that in addition to division of labor, egg cannibalism could also play a role in the survival of the colony. This model can show the survival of a colony when egg cannibalism is not too large and the proportion of of adult ants performing necessary tasks is large enough. Even though model (3.3) has the addition of egg cannibalism as a mechanism of survival, it is not the best model to show the positive mechanisms that egg cannibalism represent in a colony. Therefore, the functional response introduced in model (3.4) improves this model by providing survival of the colony when model (3.5) with no egg cannibalism and model (3.3) with cannibalism described in the form of Holling Type I functional response cannot.

Another interesting result of model (3.3) is the possibility of destabilizing effects of population dynamics, i.e., fluctuations in populations size. Comparing the dynamics obtained in Kang *et al.* [2011] of a model with no egg cannibalism considered and our models with egg cannibalism, we conclude that this fluctuations arise due to the egg cannibalism behavior in the colony. These fluctuations, as seen in Figures 3.7-3.8, are also developed by the increase of energy invested in brood care and the conversion rate of between fungus and ants. Karsai *et al.* [1996] made similar findings with respect to the fluctuations in brood dynamics in paper wasps due to egg cannibalism. Their models assumed that adults prefer to feed the larvae with the younger eggs. This will produce a huge and fast decrease of eggs, but at the same time, there is a positive feedback mechanism due to an increase of egg-laying rate, which produce the fluctuations. From Karsai *et al.* [1996], we can consider the adults feeding the larvae with eggs as the brood care through egg cannibalism, and therefore, our model

produce similar results through this mechanisms.

Concluding Remarks

The findings of this chapter illustrate the role played by age polyethism in the population dynamics of leafcutter ants population. A colony undergoing certain environmental conditions may try to increase their likelihood of survival that could harm or benefit the colony in the long term. For instance, a fast transition to tasks outside the colony (e.g. foraging) may induce a higher mortality rate in a colony. In such scenario, it is possible that the colony collapses. However, an adequate maturation rate where the worker population performing task such as foraging can benefit the colony by increasing colony population size. While the proposed models neglects some of the environmental features that may produce different outcomes on the population dynamics of a colony (e.g. nutritional demands), I clearly illustrate the role played by egg cannibalism by implicitly incorporating the nutritional demands of the colony (including the fungus), which can regulate the foraging activity, into the life history parameters of leafcutter ants. My findings suggest that egg cannibalism benefiting the adult working class as a nutrient source for growth purposes, i.e. increasing the worker?s lifespan, provides colony survival. It will be interesting to investigate the population dynamics driven by the nutritional status of a colony influencing the age-based division of labor. I provide such study in the next chapter by investigating how nutritional status can promote division of labor of adult workers in honeybees (*Apis mellifera*).

Chapter 4

A MATHEMATICAL MODELING APPROACH ON THE IMPORTANCE OF NUTRITIONAL STATUS IN A HONEYBEE COLONY

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.

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

71

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 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, 2001, Fewell and Winston, 1992, Page Jr, 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 Jr 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, 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]. 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].

74

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. 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.

Model Derivation

The proposed model is nonlinear ordinary differential equations model with the following state variables: $B(t)$: represents the brood population size consisting of eggs and larvae, and $N(t) + F(t)$ represent the worker population size of the two main task groups in a colony, i.e. nurses and foragers, respectively, at time t. In addition, I 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 facts found in literature and assumptions from empirical findings:

1. The rate of change of brood population, $B'(t) = \frac{dB}{dt}$ 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.,

$$\underbrace{\frac{c_q \alpha_q V}{e_g}}_{\text{queen's egg-laying rate}},$$

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: $\beta_{bh} = \frac{1}{\tau_{bf}}$ where τ_{bf} is the developmental time from brood to nurse. Here, I assume that there is no additional brood death. Thus, the dynamics of the brood can be described by the following equation:

$$B' = \underbrace{\frac{c_q \alpha_q V}{e_g}}_{\text{queen's egg-laying rate}} - \underbrace{\beta_{bf}}_{\text{transition rate to nurse}} B. \tag{4.1}$$

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, $N'(t) = \frac{dN}{dt}$, is determined by:

Input: transition rate from brood $\beta_{bh}B$.

Outputs:

- Transition rate to forager, i.e., $\beta_{hf} = \frac{1}{\tau_{hf}}$ 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 $\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right)$ from nurse to forager is a decreasing function of the average of VG per nurse bee. An example of this transition rate can be $\beta_{hf} = \frac{\beta_{hf}^m N}{1+\alpha_v\left(\frac{V}{N}\right)^{-1}}$ 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 [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, i.e., $d_h\left(\frac{V}{N}, N\right)$. For simplification, we can just take d_h as a constant that is much smaller than the death rate of forager.

Thus, the dynamics of the hive can be described by the following equation:

$$N' = \underbrace{\beta_{bh}}_{\text{transition from brood}} B - \underbrace{\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right) N}_{\substack{\text{transition to forager} \\ \text{decreasing with V}}} - \underbrace{d_h\left(\frac{V}{N}, N\right)}_{\substack{\text{nurse mortality rate} \\ \text{depending on VG and N}}} N \qquad (4.2)$$

3. The rate of change of foraging worker population, $F'(t) = \frac{dF}{dt}$ is determined by:

Input: transition rate from nurse $\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right) N$.

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:

$$F' = \underbrace{\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right) N}_{\substack{\text{transition from nurse bee} \\ \text{to forager, decreasing with V}}} - \underbrace{d_f F}_{\text{forager mortality rate}} \qquad (4.3)$$

4. The rate of change of pollen storage $P'(t) = \frac{dP}{dt}$ 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 Jr, 1999, 2001], described by

$$\underbrace{\frac{rB}{1+aB+bP}}_{\text{Regulated pollen collecting rate}} F$$

   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 $\alpha P N$. 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 pollen stored less than 72 h [Anderson *et al.*, 2014].

   Thus, the dynamics of the pollen storage can be described by the following equation:

$$P' = \underbrace{\frac{rB}{1+aB+bP}}_{\text{regulated pollen collection rate}} F - \underbrace{\alpha N P}_{\substack{\text{removing rate of pollen} \\ \text{by nurse bee for VG production}}} - \underbrace{d_p P}_{\substack{\text{deterioration} \\ \text{rate of pollen}}} \quad (4.4)$$

5. The rate of change of VG in nurse bees, $V'(t) = \frac{dV}{dt}$, 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 αPH would be converted to VG with the amount of $c\alpha PH$.

- There are $\beta_{bh}B(t) = \frac{1}{\tau_{bf}}B(t)$ newly emerged adult bees whose content of VG could be estimated as follows:

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

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 $\alpha_q V$.

- The nurse bees use VG for their own metabolism, which is described by $\alpha_h NV$.

- The nurse bees dying during the nursing stage is described by $d_h V$.

- The nurse bees surviving and transitioning into foragers can be described by $\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right)V$.

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

$$V' = \underbrace{c\alpha NP}_{\substack{\text{VG production by nurse} \\ \text{bee with available pollen}}} - \underbrace{\alpha_b BV}_{\substack{\text{brood consumption} \\ \text{rate of VG}}} - \underbrace{\alpha_q V}_{\text{VG allocation to queen}}$$

$$- \underbrace{\alpha_h NV}_{\substack{\text{metabolic use of} \\ \text{VG by nurse bee}}} - \underbrace{\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right)V}_{\text{transition to forager}} - \underbrace{d_h\left(\frac{V}{N}, N\right)V}_{\substack{\text{removal rate due to} \\ \text{nurse bee death}}} \qquad (4.5)$$

$$+ \beta_{bh}\underbrace{\left[c_q\alpha_q V(t-\tau_{bf}) + \frac{c_q\alpha_q V(t-\tau_{bf})}{e_g}\int_{t-\tau_{bf}}^{t} V(\tau)d\tau\right]}_{\text{VG of newly emerged adult bees}}$$

A simplified version of (4.5) can be described as follows:

$$V' = \underbrace{c\alpha NP}_{\substack{\text{VG production by nurse} \\ \text{bee with available pollen}}} - \underbrace{\alpha_b BV}_{\substack{\text{brood consumption} \\ \text{rate of VG}}} - \underbrace{(1-c_q)\alpha_q V}_{\text{Metabolic costs of queen}}$$

$$\qquad (4.6)$$

$$- \underbrace{\alpha_h NV}_{\substack{\text{metabolic use of} \\ \text{VG by nurse bee}}} - \underbrace{\beta_{hf}\left(\left(\frac{V}{N}\right)^{-1}\right)V}_{\text{transition to forager}} - \underbrace{d_h\left(\frac{V}{N}, N\right)V}_{\substack{\text{removal rate due to} \\ \text{nurse bee death}}}$$
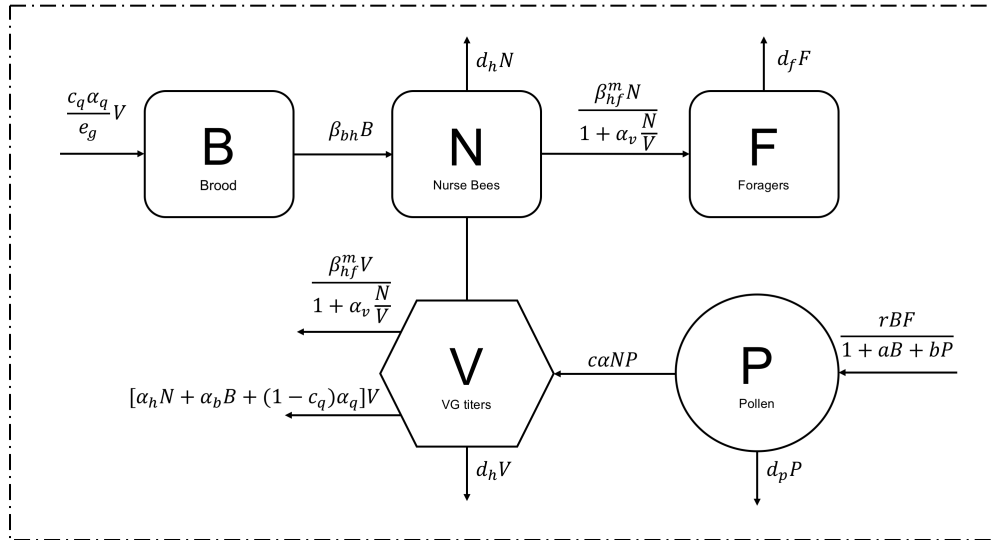
Figure 4.1: State Diagram of Model (4.7)

Parameter description	Value	Reference
r: Maximum collecting rate of pollen	avg. of [1,2] g/day/bee	Percival [1950]
a: regulation effect of brood for pollen coll.	(0,10)	estimated
b: reg. effect of stored pollen for pollen coll.	(0,10)	estimated
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 for egg production by queen	$(0,1)/g$	assumption
c: conversion rate of pollen per gram to VG	[0,0.003]/g of pollen (summer & autumn), [0,0.00012]/g in winter	[*]
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	[*]
α_h: metabolic use of VG by nurse	≤ 0.0001 g/day	[*]
α_q: feeding rate to queen	[0.00025,0.0007] g/day	estimated
α_v: reg. of VG/nurse in developmental time from nurse to forager	(0,1) g/unit	estimated
$\beta_{bh} = \frac{1}{\tau_{bh}}$: transition rate from brood to nurse	$\frac{1}{24}$/day	Winston [1992]
$\beta_{hf}^m = \frac{1}{\tau_{hf}}$: max. transition rate from nurse to forager	$(\frac{1}{3}, \frac{1}{21})$ per day	Winston [1992]
d_h : mortality rate of nurse bees	(0,0.17)/day	Rueppell *et al.* [2007][♣]
d_f: mortality rate of forager	(0,0.8)/day	♣
d_p: deterioration rate of pollen/day	(0.125,1)/day	Winston [1992]

Table 4.1: Parameters description and values for VG model

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

$$
\begin{aligned}
B' &= \frac{c_q \alpha_q}{e_g} V - \beta_{bh} B \\
N' &= \beta_{bh} B - \frac{\beta_{hf}^m N}{1 + \alpha_v \frac{N}{V}} - d_h N \\
F' &= \frac{\beta_{hf}^m N}{1 + \alpha_v \frac{N}{V}} - d_f F \\
P' &= \frac{rBF}{1 + aB + bP} - \alpha NP - d_p P \\
V' &= c\alpha NP - (1 - c_q)\alpha_q V - \alpha_h NV - \alpha_b BV - d_h V - \frac{\beta_{hf}^m V}{1 + \alpha_v \frac{N}{V}}
\end{aligned}
\tag{4.7}
$$

where we take $\beta_{hf}^m \left(\frac{N}{V} \right) = \frac{\beta_{hf}^m}{1 + \alpha_v \frac{N}{V}}$, $d_h \left(\frac{V}{N}, N \right) = d_h$, and the simplified version of V in equation (4.6). We define $\left. \frac{\beta_{hf}^m}{1 + \alpha_v \frac{N}{V}} \right|_{V=0} = 0$.

Variable	Description	
B	Population size of brood (eggs and larvae)	unit
N	Population size of nurse bees	unit
F	Population size of forager bees	unit
P	Stored pollen in the hive	grams
V	Total vitellogenin titers in nurse bees	grams

Table 4.2: Variables description and units

Mathematical Analysis and Numerical Simulations

In this section, I explore the dynamics of Model (4.7) analytically and provide biological implications. Note that an interior equilibria of Model (4.7) can be expressed in the following form:

$(P^*, V^*, B^*, N^*, F^*) =$

$$
\left(\Phi(\xi) + \frac{N^*}{c\alpha\xi} \left(\alpha_h + \frac{c_q \alpha_b \alpha_q}{e_g \beta_{bh} \xi} \right), \frac{N^*}{\xi}, \frac{c_q \alpha_q}{e_g \beta_{bh} \xi} N^*, N^*, \frac{\beta_{hf}^m N^*}{d_f (1 + \alpha_v \xi)} \right),
\tag{4.8}
$$

where

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

and N^* is a positive solution of the polynomial:

$$f(N) = c_3N^3 + c_2N^2 + c_1N + c_0, \tag{4.9}$$

where $c_i, i = 0, 1, 2, 3$ are polynomials of ξ (see details in A.33).

The parameter ξ measures nurse bees' nutritional status and can be expressed as follows:

$$\xi = \frac{c_q\alpha_q\alpha_v - d_he_g - \beta_{hf}^m e_g + \sqrt{(c_q\alpha_q\alpha_v - e_gd_h - e_g\beta_{hf}^m)^2 + 4c_q\alpha_q\alpha_vd_he_g}}{2\alpha_vd_he_g} \tag{4.10}$$

Note that $\xi^{-1} = \frac{V}{N}$ is the VG content per nurse bee. From simple analysis (see B), 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 $a, b, c, c_q, d_f, d_h, d_p, e_g, \alpha, \alpha_b, \alpha_q, \alpha_v, \beta_{hf}^m, \beta_{bh}$ be positive parameters. More details regarding the derivation of (4.8) can be found in B and the number of interior equilibria the model (4.7) have is determined with the following theorem.

Theorem 11 (Existence of interior equilibria). *System (4.7) is positive invariant in* $\mathbb{R}_+^5$. *Model (4.7) 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* $\alpha_b > cr\xi\frac{\beta_{hf}^m}{d_f(1+\alpha_v\xi)}$.

2. *Two interior equilibria if* $\alpha_b < cr\xi\frac{\beta_{hf}^m}{d_f(1+\alpha_v\xi)}$

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 (4.8) and stay stable at that point in the long term. Note that , $\alpha_b < cr\xi\frac{\beta_{hf}^m}{d_f(1+\alpha_v\xi)} = cr\frac{N}{V}\frac{\beta_{hf}^m}{d_f(1+\alpha_v\xi)} = \frac{cr}{V}F$, which can be simplified as $\frac{cr}{\alpha_b} > \frac{V}{F}$. 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 (4.8), 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, I 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 B). In Figure 4.2, 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 $\beta_{hf}^m \approx \frac{1}{7}$. 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 $\beta_{hf}^m = (\frac{1}{21}, \frac{1}{7})$. This range is consistent with empirical findings in [Tsuruda and Page, 2009] where the bees start foraging 2-3 weeks after emerging.
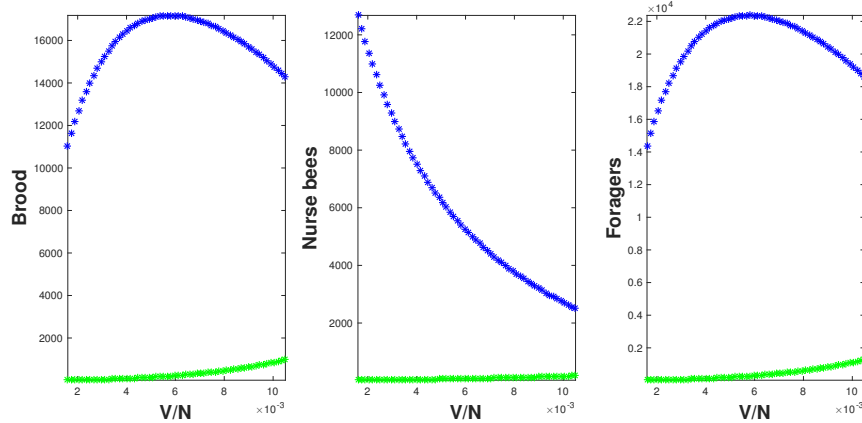
Figure 4.2: ($1/\xi$ varying with respect to β_{hf}^m) Effects of the levels of VG per nurse bee with respect to the maximum transition rate from nurse bee to forager β_{hf}^m across all populations. $r = 1; a = 0.3; b = 2; e_g = 3.82 * 10^{-6}; \alpha_q = 0.0007; \alpha_b = 5 * 10^{-5}; c_q = 0.124; d_h = .00001; d_f = 0.032; d_p = 1; c = 0.003; \alpha = 0.00688; \alpha_h = 0.0001; \alpha_v = .0005; \beta_{bh} = 1/24$. (Stability of equilibria: Stable and Unstable)

Figure 4.3 help us understand the impact of α_v 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 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 where α_v is too large and overemphasize the regulation effects of levels of VG. However, medium ranges for α_v could be most optimal. 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 realistic effects.
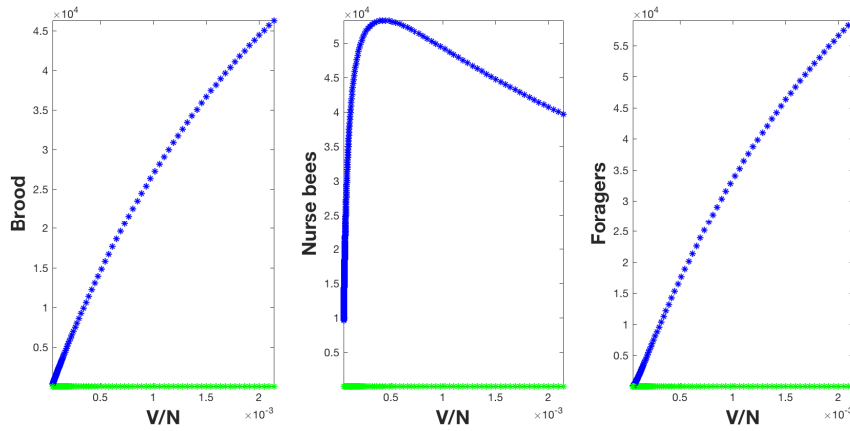
Figure 4.3: ($1/\xi$ varying with respect to α_v) Effects of the levels of VG per nurse bee with respect to the effect it has on the developmental rate of transitioning from nurse bee to forager over all populations. $.r = 1$; $a = 0.3$; $b = 2$; $e_g = 0.00000382$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_q = 0.0007$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable and Unstable)
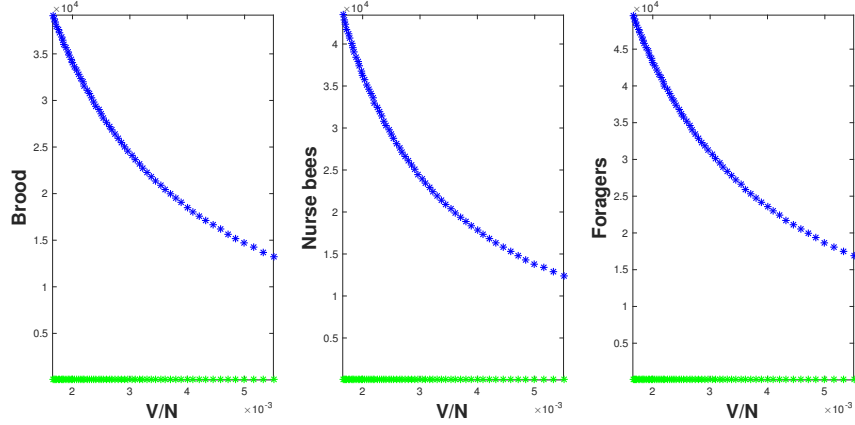
Figure 4.4: $(1/\xi$ varying with respect to α_q) Effects of the levels of VG per nurse bee over all populations with respect to the feeding rate to queen. $r = 1$; $a = 0.3$; $b = 2$; $e_g = 0.00000382$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable and Unstable)

In Figure 4.4 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 as 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 pollen, or synthesis of VG are in place.

In Figure 4.5 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.
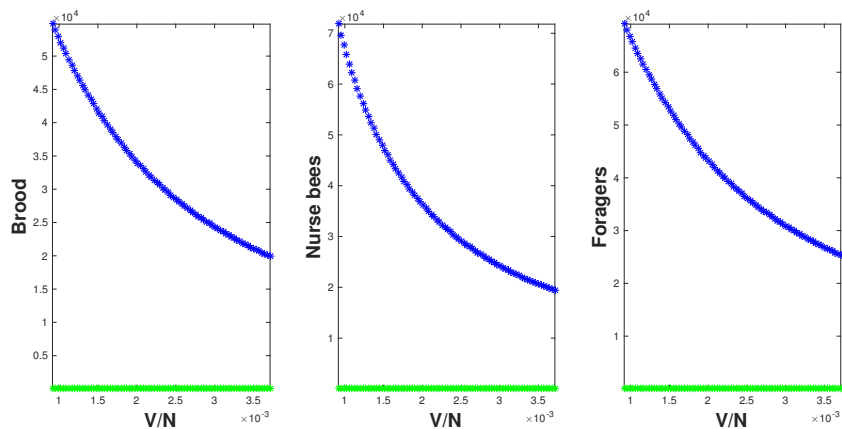
Figure 4.5: ($1/\xi$ varying with respect to e_g) Effects of the levels of VG per nurse bee over all populations with respect to the average levels of VG in one egg. $r = 1$; $a = 0.3$; $b = 2$; $a_b = 0.00005$; $c_q = 0.124$; $d_h = 0.001$; $d_f = 0.032$; $d_p = 0.008$; $c = 0.003$; $\alpha = 0.00688$; $a_h = 0.0001$; $\alpha_q = 0.0007$; $\alpha_v = 0.0005$; $\beta_{bh} = 1/24$; $\beta_{hf} = 1/21$; (Stability of equilibria: Stable and Unstable)

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 nutrient of VG for egg-laying by the queen, respectively. A low conversion rate of VG from pollen can cause colony collapse (see white region in Figure 4.6(a-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. However 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. 4.6b) and therefore the queen cannot use stored VG for egg-laying production (lower right-end white region in Fig. 4.6c). All these synergistic effects can cause colony's death.

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

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

Figure 4.6: Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;

Moreover, 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 Figures 4.6d and 4.6e). However, if the mortality rate of nurse bees increases or is too large, then our results show that the conversion rate of VG to pollen must be high in order to keep the colony alive (see Figure 4.6f).

From the simple analysis in B, we can tell 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 Figures 4.7a and 4.7b suggest that low collection rate of pollen r and low consumption rate of pollen by nurses α, together with low c_q can produce colony's death. 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. 4.7c). It is clear that the efficiency of converting VG for egg-laying production by the queen plays an important role in the colony survivability. In addition, a rapid depletion of food stores for brood feeding can cause the colony die of starvation [Le Conte and Navajas, 2008].

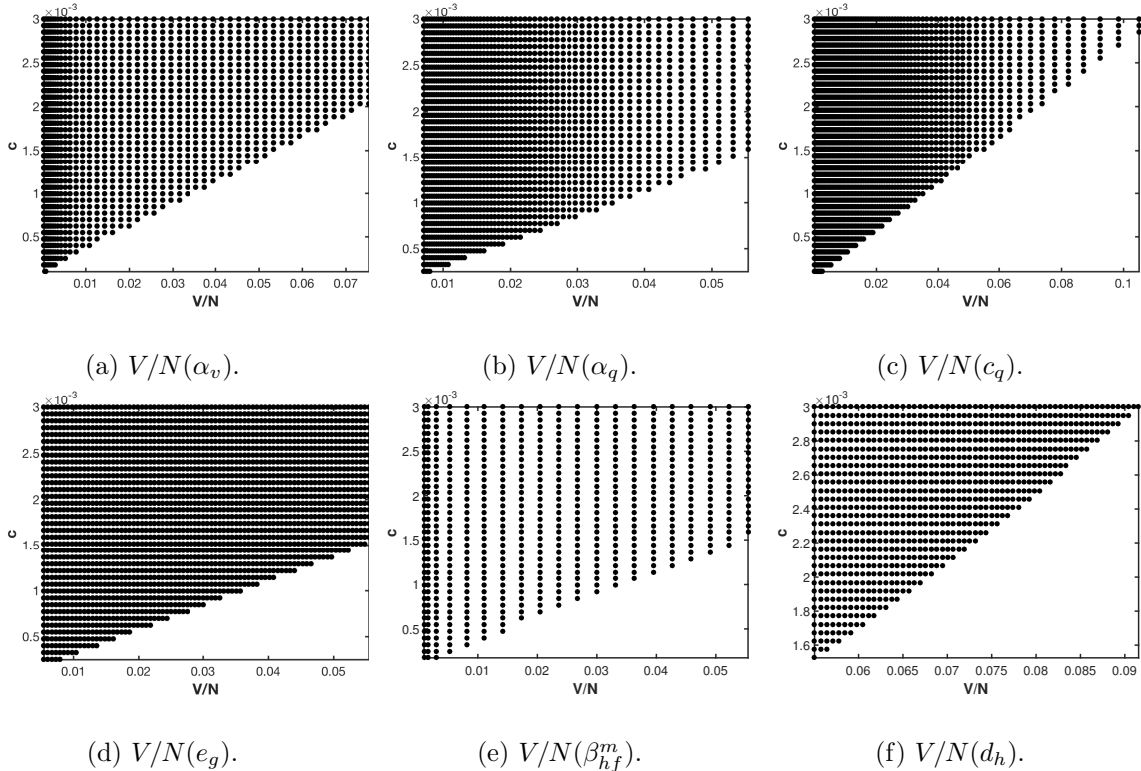(a) $V/N(c_q)$.　　　　　　(b) $V/N(c_q)$.　　　　　　(c) $V/N(c_q)$.

Figure 4.7: Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;

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 nurses won't have enough to feed brood and for their own metabolic use. Therefore, this extreme situation can cause colony's death (see Figure 4.8a). 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 Figures 4.8b,c) it will prompt a smaller overall pollen collection rate. A smaller overall pollen collection rate will cause a decrease and limited available pollen to be consumed by nurse bees and fed to brood and queen. This scenario will be critical on the survivability of the

colony and according to our numerical results in Figure 4.8b,c, respectively, shows that nurse bees will invest in the queen by feeding it at higher rates (reducing available VG per nurse bee) in order to produce 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.

(a) $V/N(\alpha_q)$.   (b) $V/N(\alpha_q)$.   (c) $V/N(\alpha_q)$.
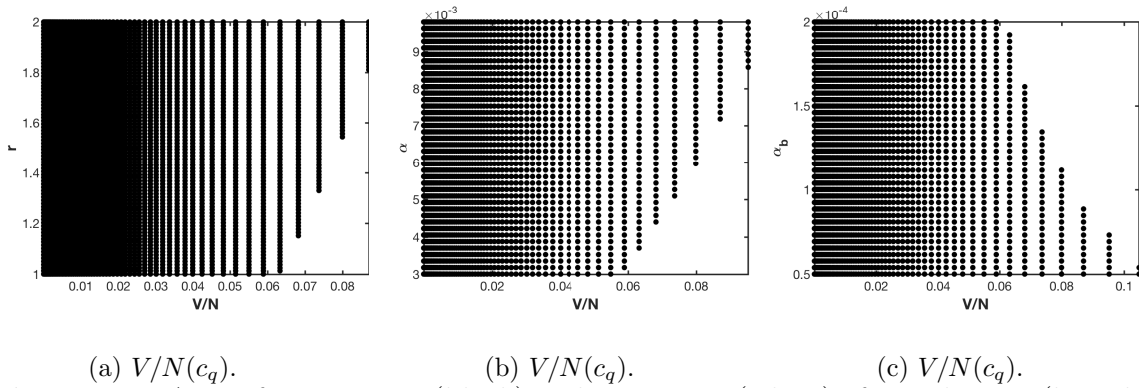
Figure 4.8: Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;

In Figures 4.9(a-c), I varied 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, I proceed to the explanations of each scenario. In Figure 4.9(a,b), we can see that low collection rate of pollen, r, and low consumption rate of pollen, α, can cause the colony to die when the levels of VG per nurse bee have no effect on task switching rates. Further implications can be made about these results. For instance, for our choice of $\beta_{hf}^m = 0.25$ (fast transition rate from nurse to forager) in these simulations given that r is relatively low (white region in Fig. 4.9a), 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. 4.9b). Moreover, if the brood's feeding rate of VG, α_b, is high (see white region in Fig. 4.9c), but there is no significant effect of the level of VG per nurse on task switching rates due to α_v been very small (as mentioned previously), 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.
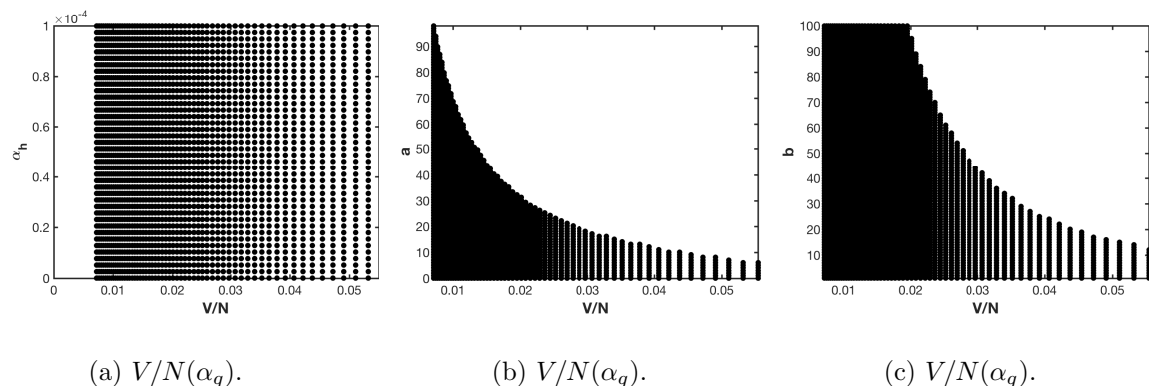

(a) $V/N(\alpha_v)$. (b) $V/N(\alpha_v)$. (c) $V/N(\alpha_v)$.

Figure 4.9: Area of coexistence and extinction of populations (brood, nurse bees and foragers) in a colony. $r = 2$; $a = 0.6$; $b = 4.5$; $e_g = 0.0000075$; $a_q = 0.00025$; $a_b = 0.00008$; $c_q = 0.1$; $d_h = 0.001$; $d_f = 0.006$; $d_p = 0.008$; $c = 0.0025$; $\alpha = 0.008$; $a_h = 0.00007$; $\alpha_v = 0.01$; $\beta_{bh} = 1/24$; $\beta_{hf}^m = .25$;

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 Figure 4.10a). 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 Figure 4.10b). Moreover, notice that

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 Figure 4.10c). 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.

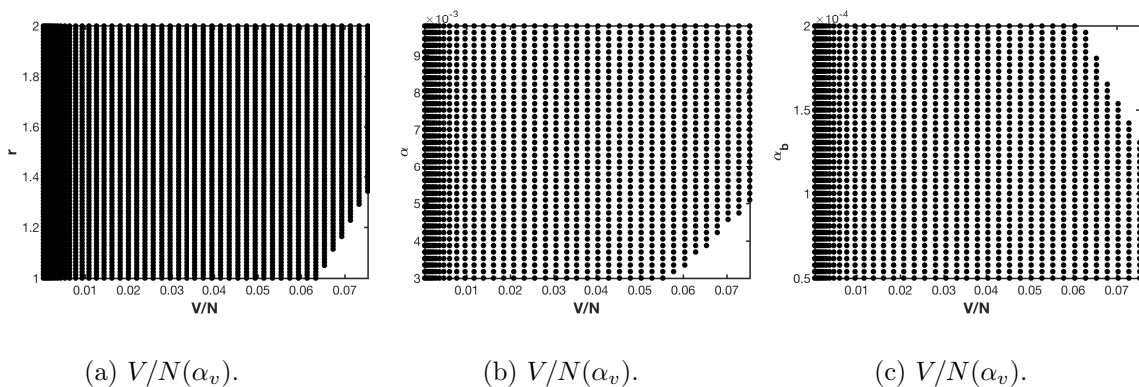(a)   (b)   (c)
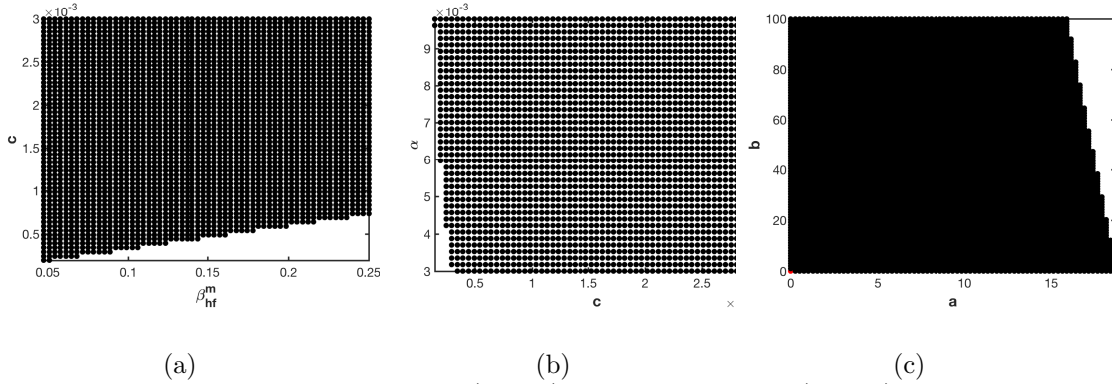
Figure 4.10: Area of coexistence (black) and extinction (white) of populations (brood, nurse bees and foragers) in a colony. $r = 1; a = 0.3; b = 2; e_g = 3.82 * 10^{-6}; \alpha_q = 0.0007; \alpha_b = 5 * 10^{-5}; c_q = 0.124; d_h = .00001; d_f = 0.032; d_p = 1; c = 0.003; \alpha = 0.00688; \alpha_h = 0.0001; \alpha_v = .0005; \beta_{bh} = 1/24; \beta_{hf}^m = 1/21.$

Lastly, I found that variation of V/N (or $\frac{1}{\xi}$) with respect to $\alpha_v, c_q, e_g, \beta_{hf}^m$ have no effect on the metabolic use of VG in nurse bees, α_h, 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 $\alpha_q, e_g, \beta_{hf}^m$ have no effect on the consumption rate of pollen to VG, α.

Seasonality Effects

First I 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. The numerical simulations compare results with empirical data from Harrís [1980]. In order to include seasonality in the model, I will 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.
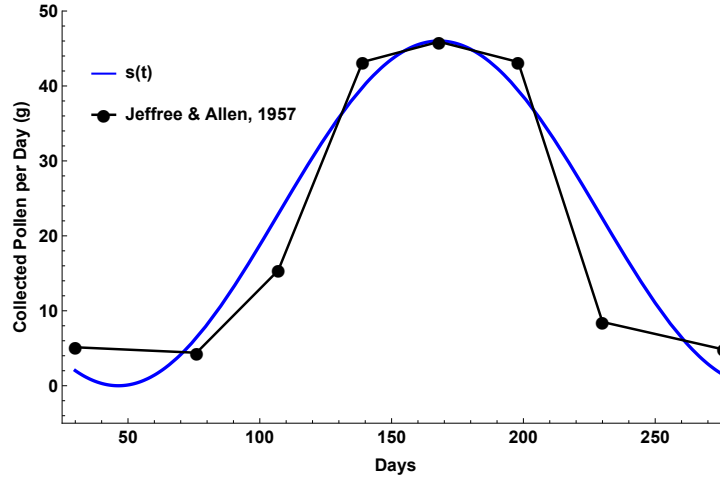
Figure 4.11: Data from Allen and Jeffree [1956] was normalized using the information provided in [Camazine *et al.*, 1990] where one full cell can contain 0.27 g of pollen (see also Schmickl and Crailsheim [2007]).

The regulated pollen collection rate in equation (4.4) is then modified as follows:

$$\frac{s(t)B}{1 + aB + bP}$$

The values of r and ϕ were chosen to fit best to our choice of empirical data. The rest of the parameters from model (4.7) were chosen by following the ranges in Table 4.1.

Figure 4.12 shows the population dynamics of brood and workers (nurses and foragers) for approximately one year. In order to perform this fitting and estimate parameters, I performed a numerical simulation using the command 'Manipulate' in Mathematica, Inc. [2018]. This commands allows to numerically evaluate the system of differential equations with an interactive object containing multiple controls to

vary the value of the parameters and initial conditions in model (4.7). This command allowed me to approximate the best fit for the given data.
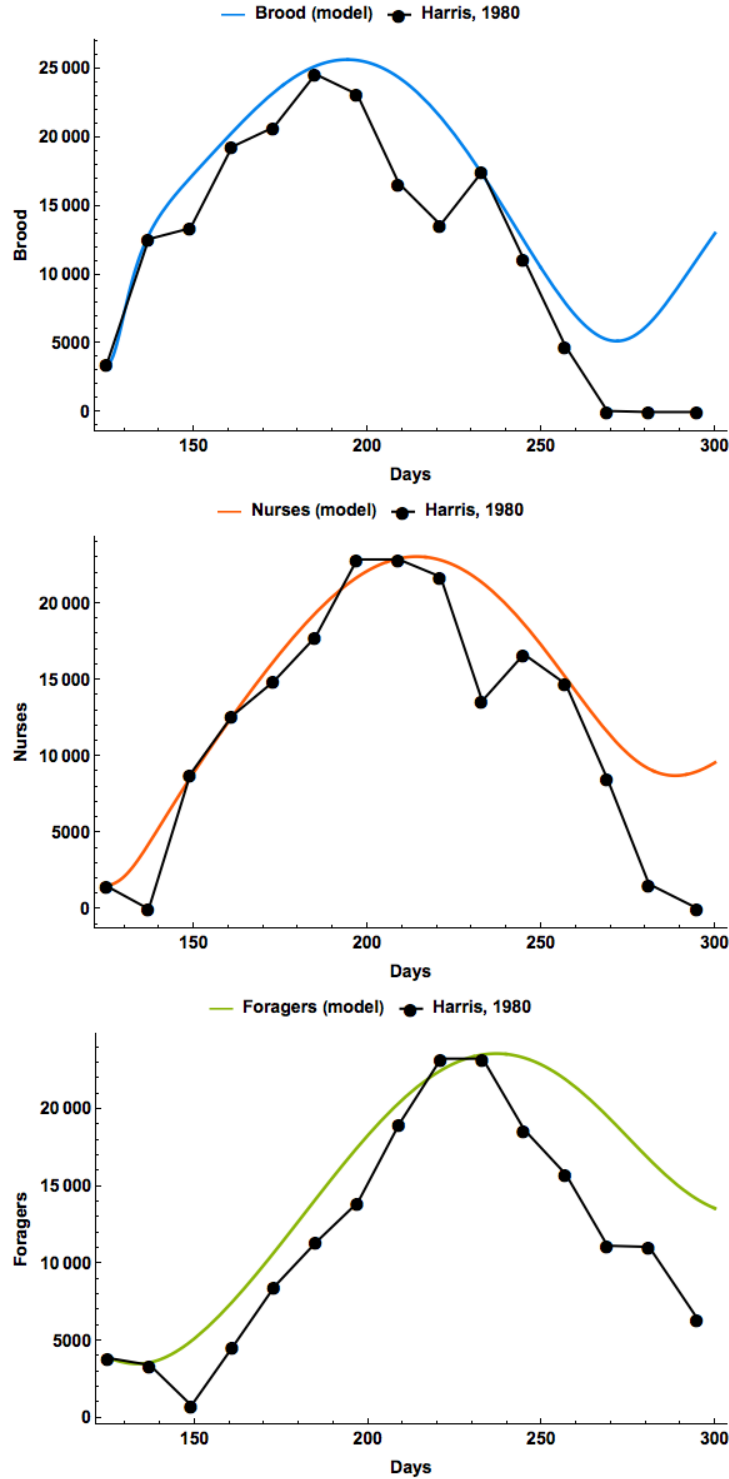
Figure 4.12: Empirical data from Harrís [1980]; $\phi = 135; r = 1.3; a = 0.3; b = 5; e_g = 7.32 * 10^{-6}; \alpha_q = 0.000688; \alpha_b = 5.48 * 10^{-5}; c_q = 0.125; d_h = .0008; d_f = 0.036; d_p = 1; \ c = 0.003; \alpha = 0.06; \alpha_h = 0.000046; \alpha_v = .00055; \beta_{bh} = 1/24; \beta_{hf}^m = 1/21;$ Initial conditions at $t = 125$ days: $P(t) = 17; V(t) = 2; B(t) = 3539; H(t) = 1487; F(t) = 3875.$

98

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 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 Figure 4.13).

(a) No seasonality showing colony survival. (b) Seasonality showing colony collapse.

Figure 4.13: 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: $P(t) = 20; V(t) = 2; B(t) = 100; H(t) = 5000; F(t) = 4000$.

Sensitivity Analysis

Up until this point, our model simulations, including bifurcations and time series, rely on parameter values (see Table 4.1) that have been collected from numerous em-

pirical 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 $NV^{-1} = \frac{1}{\xi}$.

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 $\pm 15\%$ 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 (4.7) 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 Figure 4.14b.

(a) Model with no seasonality
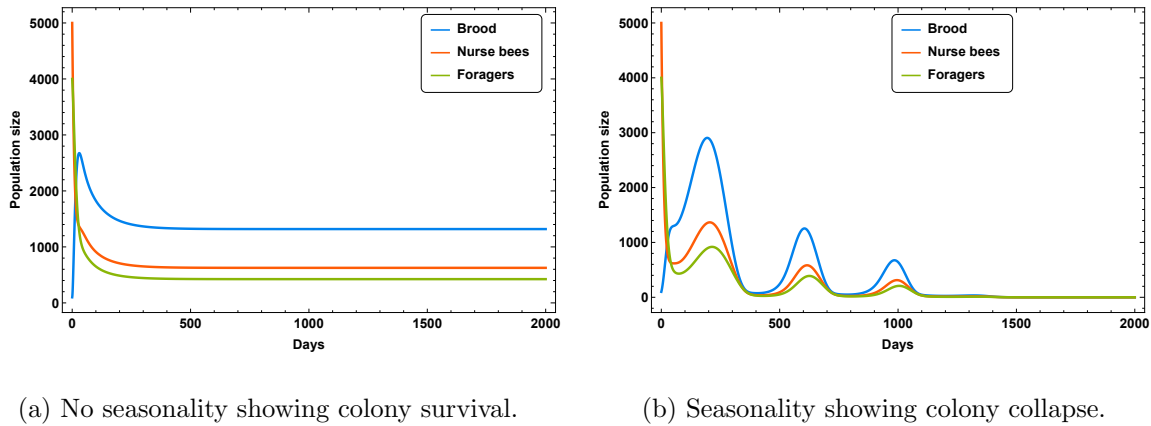

(b) Model with seasonality
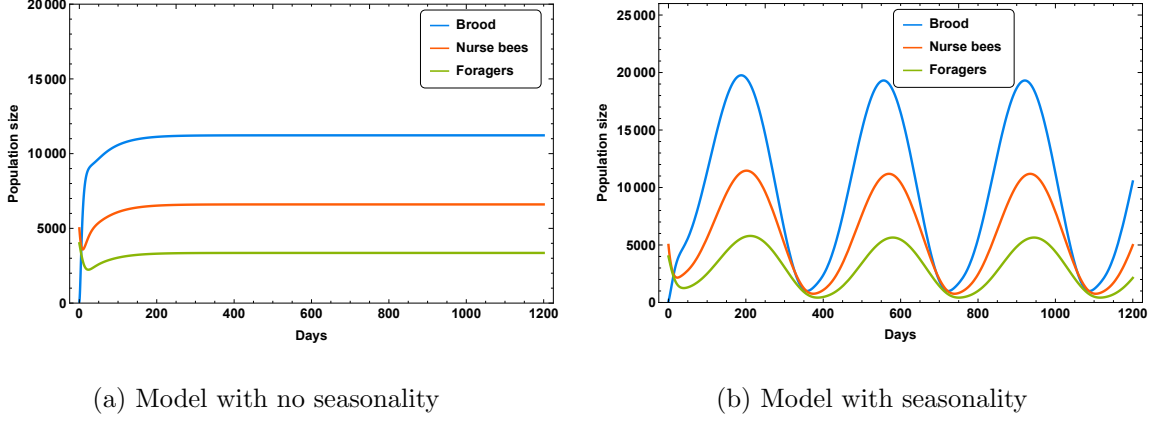
Figure 4.14: Time series of original model and model with seasonality showing different long term dynamics using parameter values: $r = 1; a = 0.95; b = 4; e_g = 4.88 * 10^{-6}; \alpha_q = 0.0007; \alpha_b = 5 * 10^{-5}; c_q = 0.4; d_h = .02; d_f = 0.1; d_p = 1; c = 0.003; \alpha = 0.006; \alpha_h = 0.0001; \alpha_v = 5 * 10^{-5}; \beta_{bh} = 1/24; \beta_{hf}^m = 1/21; \phi = 150;$ Initial conditions at $t = 0$ days: $P(t) = 20; V(t) = 2; B(t) = 100; H(t) = 5000; F(t) = 4000.$

In Figures 4.15-4.18, 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 Figure 4.15, sensitivity analysis of parameters at time $t = 360$, when population size is the lowest (Fig.) in the model with seasonality (in purple), shows a different outcome than at $t = 185$ (in purple). Here we observe that, when
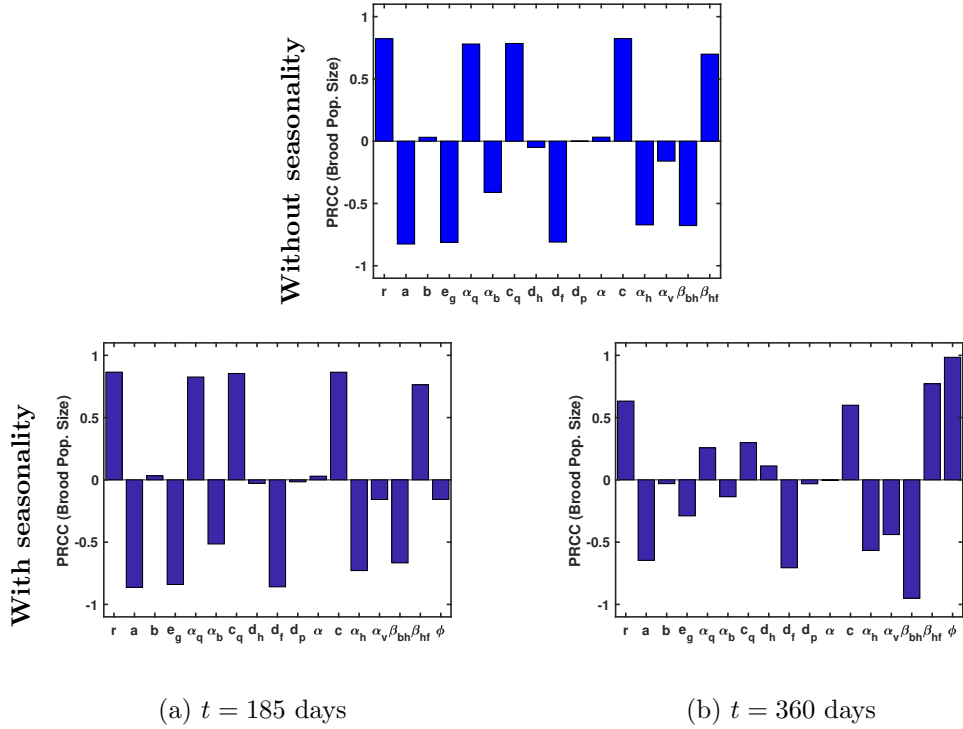
Figure 4.15: PRCC Values for the Parameters of Model (4.7) Using the Population Size of Brood as the Output of Interest.

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 Figure 4.16, 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.

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

Figure 4.16: PRCC Values for the Parameters of Model (4.7) Using the Population Size of Nurse Bees as the Output of Interest.

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

103

representing the availability of food source for the brood (available pollen foragers bringing back pollen to the hive for VG production).

In Figure 4.17, 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 Figure 4.18, 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

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

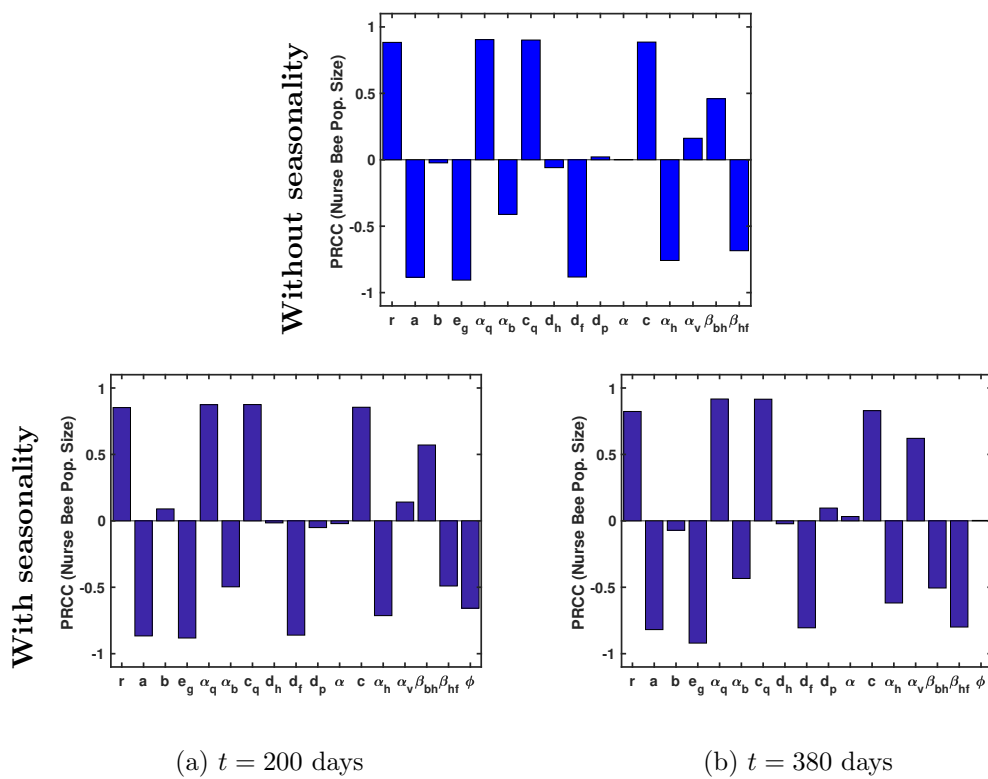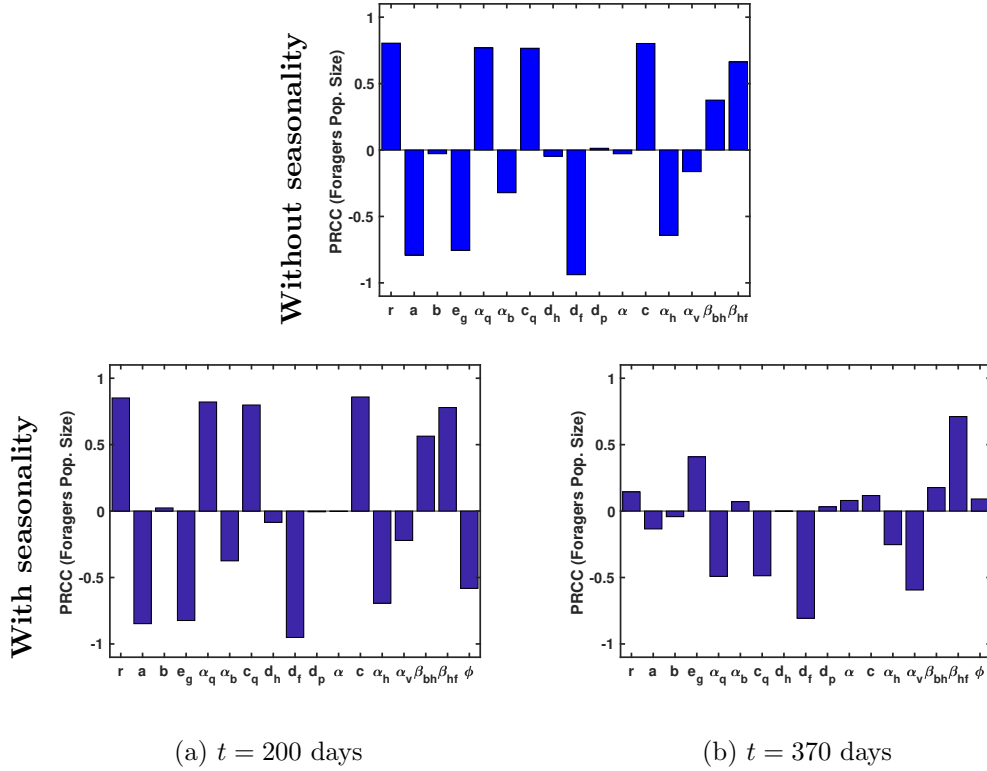**Figure 4.17:** PRCC Values for the Parameters of Model (4.7) Using the Population Size of Forager Bees as the Output of Interest.

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. 4.18(a) and 4.18(b) in purple).

(a) $t = 185$ days   (b) $t = 360$ days
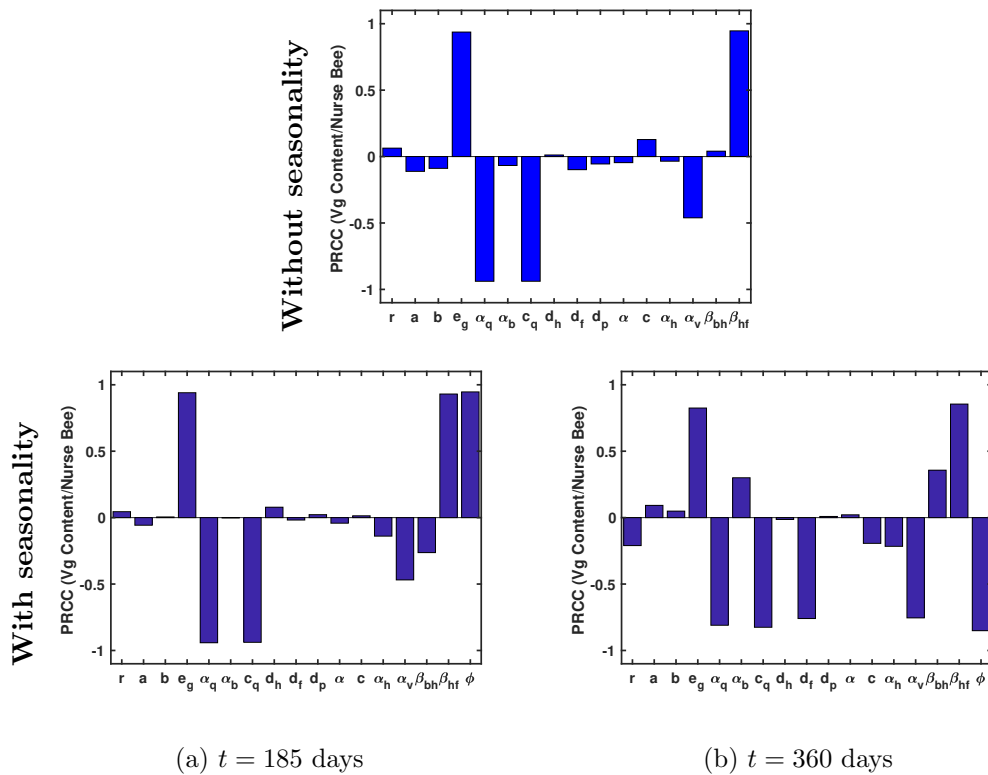
Figure 4.18: PRCC Values for the Parameters of Model (4.7) Using the level of Vitellogenin per Nurse Bee as the Output of Interest.

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 environmental variable influencing the age-based division of labor of worker honeybees is their nutritional status [Ament *et al.*, 2010, Avni *et al.*, 2014]. 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 (4.7) 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 Figure 4.4 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 Figure 4.7). 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 Figure 4.6f). 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 Figure 4.6a-4.6c). 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 Figures 4.6d and 4.6e). 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 corre-

sponding 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 (4.7), 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 Figure 4.13).

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 BEE-HAVE 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].

Chapter 5

FINAL REMARKS AND FUTURE WORK

Social insects have provided the best models for studying the evolution and main-
tenance of cooperative behavior. However, the study of mechanisms believed to have
shaped the observed division of labor structure in social insects such as nutrition and
age polyethism, and phenomena known to increase colony survival such as cannibal-
ism, has not yet been fully understood. In this dissertation, I illustrate the role played
by these mechanisms and phenomenon in the population dynamics of social insects
through a mathematical modeling approach.

Several models have addressed the dynamics of cannibalistic behavior in age-
structure models (see Kang *et al.* [2015], Cushing [1991]) and division of labor. How-
ever, the dynamics of both egg cannibalism and division of labor together have not
yet been studied. In this dissertation, I put together two of the most relevant mecha-
nisms in social insects that have an impact in colony survival, in both population and
evolutionary dynamics. Moreover, I illustrate the outcomes of explicit division of la-
bor through the inclusion of age-polyethism in a model describing the interactions of
leafcutter ants with their fungus garden, and the different ways the colony can benefit
from cannibalizing eggs. The results from this study open an opportunity to perform
manipulative experimental work to determine whether egg cannibalism increase lifes-
pan of adult workers, or if it has alternative benefits. Further results suggest that
division of labor plays an important factor determining whether a colony of leafcut-
ter ants can survive or not in the absence of egg cannibalism. For instance, if the
proportion of adult ants performing given tasks is large enough, then the colony can
survive. This suggests that there may be an evolutionary relationship between divi-

113

sion of labor and egg cannibalism, which it would be interesting to explore in future work.

Another interesting area to explore within leafcutter ants is the nutritional impact on colony growth to understand how different nutrients influence the physiology and behavior of ants. It is known that many herbivores such as leafcutter ants based their choices on leaf nutritional content [Clark, 2011]. Foragers collect macronutrients in a ratio to feed the fungus which the ants then eat. The switching of activities inside the nest depends on the colony feedback and individual decisions made by the foragers [Clark, 2011], who can switch between carbohydrate and protein foraging as the colony's necessities change and the level of starvation of the workers and larvae. The major drive for collected protein is growing larvae, whereas worker ants mainly require carbohydrate for energy [Cassill and Tschinkel, 1999, Dussutour and Simpson, 2012]. In this case, experimental work together with a mathematical model could bring important insights to answer questions such as: what is the optimal worker ratio collecting protein to carbohydrate material to increase or maintain colony survival?

There are genetic and physiological mechanism underlying the division of labor in social insects that are still poorly understood [Ikemoto *et al.*, 2009, Schmid-Hempel, 1992, Traniello and Rosengaus, 1997]. The role played by the nutritional status of a colony influencing the age-based division of labor in honeybees has been of great interest to biologist. Honeybees represent one of the most interesting social systems due to their complex division of labor structure and the organization within the colony. The model proposed in this dissertation captures the population dynamics over one season, i.e. spring and summer, where brood is available and foraging activity is necessary. This model helps us have a further understanding on 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. The

114

results obtained in this study opens the opportunity to further explore scenarios where nutrients are not available due to short summers in which bees opt to engage in brood cannibalism as a natural strategy to recycle protein. Other mechanism that can be included to the proposed model is the transition back from foraging to nursing under certain environmental conditions [Oettler *et al.*, 2015].

Currently, there are different known drivers of honeybee colony declines and losses which are causing serious environmental implications. Some of the most important indicators of colony losses are overall management issues, the role of pests such as *Varroa destructor*, and introduced pathogens such as deformed wing virus, acute bee paralysis virus, Kashmir bee virus, among others [Smith *et al.*, 2013]. An interesting extension to this model is the study of the population dynamics given 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]. Also, the use of pesticides has become part of colony losses [Smith *et al.*, 2013] and it is suspected, by some scientists and beekeepers, to be one of the main causes of colony-weakening processes [Henry *et al.*, 2012]. Some issues emerging from the use of pesticides according to some studies [Wu *et al.*, 2011] are delayed adult emergence leading to higher fecundity of *Varroa* mites, increased number of unhatched eggs leading to reduced egg-laying efficiency by the queen, and lower survivorship of worker bees leading to precocious foraging, which was shown in Chapter 4 and other studies (see Thompson *et al.* [2007]), to have an impact on colony size.

I am aware and acknowledge that the mathematical models presented in this dissertation have some limitations. However, I believe this work represents the first step to understand, mathematically, the underlying mechanisms of the emerging behaviors in social insects that ultimately influence the success of a colony.

REFERENCES

Abou-Shaara, H., "The foraging behaviour of honey bees, apis mellifera: a review.", Veterinarni Medicina **59**, 1 (2014).

Ahn, K., X. Xie, J. Riddle, J. Pettis and Z. Y. Huang, "Effects of long distance transportation on honey bee physiology", Psyche: A Journal of Entomology **2012** (2012).

Al-Tikrity, W., A. Benton, R. Hillman and W. Clarke Jr, "The relationship between the amount of unsealed brood in honeybee colonies and their pollen collection", Journal of Apicultural Research **11**, 1, 9–12 (1972).

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

Allen, M. D., "The honeybee queen and her attendants", Animal Behaviour **8**, 3, 201–208 (1960).

Allen, M. D. and E. P. Jeffree, "The influence of stored pollen and of colony size on brood rearing of honeybees", Annals of Applied Biology **44**, 4, 649–656, URL `http://dx.doi.org/10.1111/j.1744-7348.1956.tb02164.x` (1956).

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

Amdam, G. V., K. Norberg, A. Hagen and S. W. Omholt, "Social exploitation of vitellogenin", Proceedings of the national academy of sciences **100**, 4, 1799–1802 (2003).

Amdam, G. V. and S. W. Omholt, "The regulatory anatomy of honeybee lifespan", Journal of Theoretical Biology **216**, 2, 209–228 (2002).

Amdam, G. V. and S. W. Omholt, "The hive bee to forager transition in honeybee colonies: the double repressor hypothesis", Journal of theoretical biology **223**, 4, 451–464 (2003).

Amdam, G. V., O. Rueppell, M. K. Fondrk, R. E. Page and C. M. Nelson, "The nurseÕs load: early-life exposure to brood-rearing affects behavior and lifespan in honey bees (apis mellifera)", Experimental gerontology **44**, 6, 467–471 (2009).

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

Ament, S. A., Y. Wang and G. E. Robinson, "Nutritional regulation of division of labor in honey bees: toward a systems biology perspective", Wiley Interdisciplinary Reviews: Systems Biology and Medicine **2**, 5, 566–576 (2010).

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

Arathi, H. and R. Gadagkar, "Cooperative nest building and brood care by nest-mates and non nestmates in ropalidia marginata: implications for the evolution of eusociality", Oecologia **117**, 1-2, 295–299 (1998).

Avni, D., H. P. Hendriksma, A. Dag, Z. Uni and S. Shafir, "Nutritional aspects of honey bee-collected pollen and constraints on colony development in the eastern mediterranean", Journal of insect physiology **69**, 65–73 (2014).

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

BenVau, L. R. and J. C. Nieh, "Larval honey bees infected with nosema ceranae have increased vitellogenin titers as young adults", Scientific reports **7**, 1, 14144 (2017).

Beshers, S. N. and J. H. Fewell, "Models of division of labor in social insects", Annual review of entomology **46**, 1, 413–440 (2001).

Bitondi, M. and Z. P. Simoes, "The relationship between level of pollen in the diet, vitellogenin and juvenile hormone titres in africanized apis mellifera workers", Journal of Apicultural Research **35**, 1, 27–36 (1996).

Bonabeau, E., A. Sobkowski, G. Theraulaz, J.-L. Deneubourg *et al.*, "Adaptive task allocation inspired by a model of division of labor in social insects.", in "BCEC", pp. 36–45 (1997).

Bonabeau, E., G. Theraulaz and J.-L. Deneubourg, "Fixed response thresholds and the regulation of division of labor in insect societies", Bulletin of Mathematical Biology **60**, 4, 753–807 (1998).

Boulogne, I., H. Ozier-Lafontaine and G. Loranger-Merciris, "Leaf-cutting ants, biology and control", in "Sustainable Agriculture Reviews", pp. 1–17 (Springer, 2014).

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

Brown, M. J., A. Bot and A. G. Hart, "Mortality rates and division of labor in the leaf-cutting ant, atta colombica", Journal of insect science **6**, 1, 18 (2006).

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

Camargo, R., L. C. Forti, J. Lopes, A. Andrade and A. Ottati, "Age polyethism in the leaf-cutting ant acromyrmex subterraneus brunneus forel, 1911 (hym., formicidae)", Journal of Applied Entomology **131**, 2, 139–145 (2007).

Camazine, S., "The regulation of pollen foraging by honey bees: how foragers assess the colony's need for pollen", Behavioral Ecology and Sociobiology **32**, 4, 265–272 (1993).

Camazine, S., J. Sneyd, M. J. Jenkins and J. Murray, "A mathematical model of self-organized pattern formation on the combs of honeybee colonies", Journal of Theoretical Biology **147**, 4, 553–571 (1990).

Capinera, J. L., ed., *Encyclopedia of Entomology*, chap. Age Polythism, pp. 75–75 (Springer Netherlands, Dordrecht, 2008), URL `http://dx.doi.org/10.1007/978-1-4020-6359-6_107`.

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

Cassill, D. and W. Tschinkel, "Regulation of diet in the fire ant, Solenopsis invicta", Journal of Insect Behavior **12**, 3, 307–328 (1999).

Cicirello, V. A. and S. F. Smith, "Wasp-like agents for distributed factory coordination", Autonomous Agents and Multi-agent systems **8**, 3, 237–266 (2004).

Clark, R., *Behavioral and Nutritional Regulation of Colony Growth in the Desert Leafcutter Ant Acromyrmex versicolor*, Ph.D. thesis, Arizona State University (2011).

Clark, R. M. and J. H. Fewell, "Transitioning from unstable to stable colony growth in the desert leafcutter ant acromyrmex versicolor", Behavioral ecology and sociobiology **68**, 1, 163–171 (2014).

Courchamp, F., L. Berec and J. Gascoigne, "Allee effects in ecology and conservation", Environ. Conserv **36**, 80–85 (2008).

Crailsheim, K., "The flow of jelly within a honeybee colony", Journal of comparative physiology B **162**, 8, 681–689 (1992).

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

Cushing, J., "A simple model of cannibalism", Mathematical biosciences **107**, 1, 47–71 (1991).

Cushing, J. and J. T. Hudson, "Evolutionary dynamics and strong allee effects", Journal of biological dynamics **6**, 2, 941–958 (2012).

Cushing, J. and J. Li, "Oscillations caused by cannibalism in a size-structured population model", Can. Appl. Math. Quart **3**, 2, 155–172 (1995).

Cushing, J. M., "A size-structured model for cannibalism", Theoretical Population Biology **42**, 3, 347–361 (1992).

Cushing, J. M., "The evolutionary dynamics of a population model with a strong allee effect.", Mathematical biosciences and engineering: MBE **12**, 4, 643–660 (2015).

DeGrandi-Hoffman, G., Y. Chen, E. Huang and M. H. Huang, "The effect of diet on protein concentration, hypopharyngeal gland development and virus load in worker honey bees (apis mellifera l.)", Journal of insect physiology **56**, 9, 1184–1191 (2010).

Dercole, F. and S. Rinaldi, "Evolution of cannibalistic traits: scenarios derived from adaptive dynamics", Theoretical population biology **62**, 4, 365–374 (2002).

Dreller, C., R. E. Page Jr and M. K. Fondrk, "Regulation of pollen foraging in honeybee colonies: effects of young brood, stored pollen, and empty space", Behavioral Ecology and Sociobiology **45**, 3-4, 227–233 (1999).

Dussutour, A. and S. Simpson, "Ant worwork die young and colonies collapse when fed a high-protein diet", Proceedings of the Royal Society B **279**, 2402–2408 (2012).

Elgar, M. A. and B. J. Crespi, *Cannibalism: ecology and evolution among diverse taxa* (Oxford University Press, 1992).

Feener Jr, D. H. and K. A. Moss, "Defense against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment", Behavioral Ecology and Sociobiology **26**, 1, 17–29 (1990).

Fewell, J. and R. Page, "Genotypic variation in foraging responses to environmental stimuli by honey bees, apis mellifera", Cellular and Molecular Life Sciences **49**, 12, 1106–1112 (1993).

Fewell, J. H. and M. L. Winston, "Colony state and regulation of pollen foraging in the honey bee, apis mellifera l.", Behavioral Ecology and Sociobiology **30**, 6, 387–393 (1992).

Filmer, R. S., "Brood area and colony size as factors in activity of pollination units", Journal of Economic Entomology **25**, 2, 336–343 (1932).

Fox, L. R., "Cannibalism in natural populations", Annual review of ecology and systematics pp. 87–106 (1975).

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

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

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

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

Gordon, D. M., "From division of labor to the collective behavior of social insects", Behavioral Ecology and Sociobiology pp. 1–8 (2015).

Groot, A. P. d., *Protein and amino acid requirements of the honeybee (Apis mellifica L.)* (W. Junk, 1953).

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

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

Hart, A. G., C. Anderson and F. L. Ratnieks, "Task partitioning in leafcutting ants", Acta ethologica **5**, 1, 1–11 (2002).

Haydak, M. H., "Honey bee nutrition", Annual review of entomology **15**, 1, 143–156 (1970).

Henry, M., M. Beguin, F. Requier, O. Rollin, J.-F. Odoux, P. Aupinel, J. Aptel, S. Tchamitchian and A. Decourtye, "A common pesticide decreases foraging success and survival in honey bees", Science **336**, 6079, 348–350 (2012).

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

Holbrook, C. T., R. M. Clark, D. Moore, R. P. Overson, C. A. Penick and A. A. Smith, "Social insects inspire human design", Biology Letters **6**, 4, 431–433, URL `http://rsbl.royalsocietypublishing.org/content/6/4/431` (2010).

Holland, J. N. and D. L. DeAngelis, "A consumer-resource approach to the density-dependent population dynamics of mutualism", Ecology **91**, 5, 1286–1295 (2010).

Hölldobler, B. and E. O. Wilson, *The superorganism: the beauty, elegance, and strangeness of insect societies* (WW Norton & Company, 2009).

Hölldobler, B. and E. O. Wilson, *The leafcutter ants: civilization by instinct* (WW Norton & Company, 2010).

Hrassnigg, N. and K. Crailsheim, "Adaptation of hypopharyngeal gland development to the brood status of honeybee (apis mellifera l.) colonies", Journal of insect Physiology **44**, 10, 929–939 (1998).

Huang, Z., "Pollen nutrition affects honey bee stress resistance", Terrestrial Arthropod Reviews **5**, 2, 175–189 (2012).

Huang, Z. *et al.*, "Honey bee nutrition", American Bee Journal **150**, 8, 773–776 (2010).

Huang, Z.-Y. and G. Otis, "Factors determining hypopharyngeal gland activity of worker honey bees (apis mellifera l.)", Insectes Sociaux **36**, 4, 264–276 (1989).

Huang, Z.-Y., G. Robinson and D. Borst, "Physiological correlates of division of labor among similarly aged honey bees", Journal of Comparative Physiology A **174**, 6, 731–739 (1994).

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

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

Ikemoto, Y., Y. Ishikawa, T. Miura, H. Asama *et al.*, "A mathematical model for caste differentiation in termite colonies (isoptera) by hormonal and pheromonal regulations", Sociobiology **54**, 3, 841 (2009).

Inc., W. R., "Mathematica, Version 11.3", Champaign, IL, 2018 (2018).

Jeanne, R. L., "The organization of work in polybia occidentalis: costs and benefits of specialization in a social wasp", Behavioral Ecology and Sociobiology **19**, 5, 333–341 (1986).

Johnson, B. R., "Organization of work in the honeybee: a compromise between division of labour and behavioural flexibility", Proceedings of the Royal Society of London B: Biological Sciences **270**, 1511, 147–152 (2003).

Johnson, B. R., "Limited flexibility in the temporal caste system of the honey bee", Behavioral Ecology and Sociobiology **58**, 3, 219–226 (2005).

Johnson, B. R., "Division of labor in honeybees: form, function, and proximate mechanisms", Behavioral ecology and sociobiology **64**, 3, 305–316 (2010).

Kang, Y., K. Blanco, T. Davis, Y. Wang and G. DeGrandi-Hoffman, "Disease dynamics of honeybees with varroa destructor as parasite and virus vector", Mathematical biosciences **275**, 71–92 (2016).

Kang, Y., R. Clark, M. Makiyama and J. Fewell, "Mathematical modeling on obligate mutualism: Interactions between leaf-cutter ants and their fungus garden", Journal of theoretical biology **289**, 116–127 (2011).

Kang, Y., M. Rodriguez-Rodriguez and S. Evilsizor, "Ecological and evolutionary dynamics of two-stage models of social insects with egg cannibalism", Journal of Mathematical Analysis and Applications **430**, 1, 324–353 (2015).

Kang, Y. and O. Udiani, "Dynamics of a single species evolutionary model with allee effects", Journal of Mathematical Analysis and Applications **418**, 1, 492–515 (2014).

Karsai, I., Z. Pénzes and J. W. Wenzel, "Dynamics of colony development in polistes dominulus: a modeling approach", Behavioral ecology and sociobiology **39**, 2, 97–105 (1996).

Karsai, I. and T. Schmickl, "Regulation of task partitioning by a ?common stomach?: a model of nest construction in social wasps", Behavioral Ecology **22**, 4, 819–830 (2011).

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

Khoury, D. S., M. R. Myerscough and A. B. Barron, "A quantitative model of honey bee colony population dynamics", PloS one **6**, 4, e18491 (2011).

Klein, S., A. Cabirol, J.-M. Devaud, A. B. Barron and M. Lihoreau, "Why bees are so vulnerable to environmental stressors", Trends in ecology & evolution **32**, 4, 268–278 (2017).

Koenig, W. and J. Dickinson, *Animal social behaviour* (Encyclopædia Britannica, inc., 2017), URL https://www.britannica.com/topic/animal-social-behaviour.

Korb, J., M. Buschmann, S. Schafberg, J. Liebig and A.-G. Bagnères, "Brood care and social evolution in termites", Proceedings of the Royal Society of London B: Biological Sciences **279**, 1738, 2662–2671 (2012).

Krieger, M. J., J.-B. Billeter and L. Keller, "Ant-like task allocation and recruitment in cooperative robots", Nature **406**, 6799, 992 (2000).

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

Linksvayer, T. A., A. C. McCall, R. M. Jensen, C. M. Marshall, J. W. Miner and M. J. McKone, "The function of hitchhiking behavior in the leaf-cutting ant atta cephalotes1", Biotropica **34**, 1, 93–100 (2002).

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

Matthews, R. W. and J. R. Matthews, *Insect behavior* (Springer Science & Business Media, 2009).

Messan, K., G. DeGrandi-Hoffman, C. Castillo-Chavez and Y. Kang, "Migration effects on population dynamics of the honeybee-mite interactions", Mathematical Modelling of Natural Phenomena **12**, 2, 84–115 (2017).

Monnin, T. and C. Peeters, "Cannibalism of subordinatesÕ eggs in the monogynous queenless ant dinoponera quadriceps", Naturwissenschaften **84**, 11, 499–502 (1997).

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

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

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

Nicolson, S. W. and H. Human, "Bees get a head start on honey production", Biology letters **4**, 3, 299–301 (2008).

Nishimura, K. and N. Hoshino, "Evolution of cannibalism in the larval stage of pelagic fish", Evolutionary Ecology **13**, 2, 191–209 (1999).

Nishimura, K. and Y. Isoda, "Evolution of cannibalism: referring to costs of cannibalism", Journal of theoretical biology **226**, 3, 293–302 (2004).

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

Okasha, S., "Biological altruism", Stanford Encyclopedia of Philosophy (2008).

Oliver, R., "Fat bees. part 1", American bee journal (2007).

Osawa, N., "Sibling cannibalism in the ladybird beetleharmonia axyridis: Fitness consequences for mother and offspring", Researches on Population Ecology **34**, 1, 45–55 (1992).

Osawa, N., "Sex-dependent effects of sibling cannibalism on life history traits of the ladybird beetle harmonia axyridis (coleoptera: Coccinellidae)", Biological Journal of the Linnean Society **76**, 3, 349–360 (2002).

Oster, G. F. and E. O. Wilson, *Caste and ecology in the social insects* (Princeton University Press, 1978).

Page, R. E., Jr., O. Rueppell and G. V. Amdam, "Genetics of reproduction and regulation of honey bee (apis mellifera l.) social behavior", Annual review of genetics **46**, 97 (2012).

Page Jr, R. E., *The spirit of the hive* (Harvard University Press, 2013).

Pankiw, T. and R. E. Page, "Genotype and colony environment affect honeybee (apis mellifera l.) development and foraging behavior", Behavioral Ecology and Sociobiology **51**, 1, 87–94 (2001).

Pankiw, T. and R. Page Jr, "The effect of genotype, age, sex, and caste on response thresholds to sucrose and foraging behavior of honey bees (apis mellifera l.)", Journal of Comparative Physiology A **185**, 2, 207–213 (1999).

Pankiw, T. and R. E. Page Jr, "Brood pheromone modulates honeybee (apis mellifera l.) sucrose response thresholds", Behavioral Ecology and Sociobiology **49**, 2-3, 206–213 (2001).

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

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

Perry, C. J., E. Søvik, M. R. Myerscough and A. B. Barron, "Rapid behavioral maturation accelerates failure of stressed honey bee colonies", Proceedings of the National Academy of Sciences **112**, 11, 3427–3432 (2015).

Polis, G. A., "The evolution and dynamics of intraspecific predation", Annual Review of Ecology and Systematics **12**, 225–251 (1981).

Rael, R., T. Vincent and J. M. Cushing, "Competitive outcomes changed by evolution", Journal of Biological Dynamics **5**, 3, 227–252 (2011).

Real, L. A., "The kinetics of functional response", American Naturalist pp. 289–300 (1977).

Richardson, M. L., R. F. Mitchell, P. F. Reagel and L. M. Hanks, "Causes and consequences of cannibalism in noncarnivorous insects", Annual review of entomology **55**, 39–53 (2010).

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

Robinson, G. E., "Regulation of division of labor in insect societies", Annual review of entomology **37**, 1, 637–665 (1992).

Roy, H., H. Rudge, L. Goldrick and D. Hawkins, "Eat or be eaten: prevalence and impact of egg cannibalism on two-spot ladybirds, adalia bipunctata", Entomologia experimentalis et applicata **125**, 1, 33–38 (2007).

Rudolf, V. H., "Consequences of stage-structured predators: cannibalism, behavioral effects, and trophic cascades", Ecology **88**, 12, 2991–3003 (2007).

Rudolf, V. H., M. Kamo and M. Boots, "Cannibals in space: the coevolution of cannibalism and dispersal in spatially structured populations", The American Naturalist **175**, 5, 513–524 (2010).

Rueppell, O., C. Bachelier, M. K. Fondrk and R. E. Page, "Regulation of life history determines lifespan of worker honey bees (apis mellifera l.)", Experimental gerontology **42**, 10, 1020–1032 (2007).

Schmickl, T. and K. Crailsheim, "Cannibalism and early capping: strategy of honeybee colonies in times of experimental pollen shortages", Journal of Comparative Physiology A **187**, 7, 541–547 (2001).

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

Schmickl, T. and K. Crailsheim, "Hopomo: a model of honeybee intracolonial population dynamics and resource management", Ecological modelling **204**, 1, 219–245 (2007).

Schmickl, T. and I. Karsai, "Sting, carry and stock: How corpse availability can regulate de-centralized task allocation in a ponerine ant colony", PloS one **9**, 12, e114611 (2014).

Schmickl, T. and I. Karsai, "How regulation based on a common stomach leads to economic optimization of honeybee foraging", Journal of theoretical biology **389**, 274–286 (2016).

Schmickl, T. and I. Karsai, "Resilience of honeybee colonies via common stomach: A model of self-regulation of foraging", PloS one **12**, 11, e0188004 (2017).

Schmid-Hempel, P., "Worker castes and adaptive demography", Journal of Evolutionary Biology **5**, 1, 1–12 (1992).

Schultner, E., *Cannibalism and conflict in Formica ants*, Ph.D. thesis, University of Helsinki (2014).

Schultner, E., P. d'Ettorre and H. Helanterä, "Social conflict in ant larvae: egg cannibalism occurs mainly in males and larvae prefer alien eggs", Behavioral Ecology p. art067 (2013).

Schulz, D. J., Z.-Y. Huang and G. E. Robinson, "Effects of colony food shortage on behavioral development in honey bees", Behavioral Ecology and Sociobiology **42**, 5, 295–303 (1998).

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

Seehuus, S.-C., K. Norberg, U. Gimsa, T. Krekling and G. V. Amdam, "Reproductive protein protects functionally sterile honey bee workers from oxidative stress", Proceedings of the National Academy of Sciences of the United States of America **103**, 4, 962–967 (2006).

Seeley, T. D., *The wisdom of the hive: the social physiology of honey bee colonies* (Harvard University Press, 2009).

Smith, C. R., A. V. Suarez, N. D. Tsutsui, S. E. Wittman, B. Edmonds, A. Freauff and C. V. Tillberg, "Nutritional asymmetries are related to division of labor in a queenless ant", PloS one **6**, 8, e24011 (2011).

Smith, K. M., E. H. Loh, M. K. Rostal, C. M. Zambrana-Torrelio, L. Mendiola and P. Daszak, "Pathogens, pests, and economics: drivers of honey bee colony declines and losses", EcoHealth **10**, 4, 434–445 (2013).

Stenseth, N., "On the evolution of cannibalism", Journal of theoretical biology **115**, 2, 161–177, URL http://dx.doi.org/10.1016/S0022-5193(85)80093-Xhttp://www.sciencedirect.com/science/article/pii/S002251938580093X (1985).

Switanek, M., K. Crailsheim, H. Truhetz and R. Brodschneider, "Modelling seasonal effects of temperature and precipitation on honey bee winter mortality in a temperate climate", Science of The Total Environment **579**, 1581–1587 (2017).

Synge, A. D., "Pollen collection by honeybees (apis mellifera)", The Journal of Animal Ecology pp. 122–138 (1947).

Szabo, T. I., "Effect of weather factors on honeybee flight activity and colony weight gain", Journal of Apicultural Research **19**, 3, 164–171 (1980).

Thieme, H. R., *Mathematics in population biology* (Princeton University Press, 2003).

Thompson, H. M., S. Wilkins, A. H. Battersby, R. J. Waite and D. Wilkinson, "Modelling long-term effects of igrs on honey bee colonies", Pest management science **63**, 11, 1081–1084 (2007).

Thorp, R. W., "Structural, behavioral, and physiological adaptations of bees (apoidea) for collecting pollen", Annals of the Missouri Botanical Garden pp. 788–812 (1979).

Tofilski, A., "Influence of caste polyethism on longevity of workers in social insect colonies", Journal of theoretical biology **238**, 3, 527–531 (2006).

Torres, D. J., U. M. Ricoy and S. Roybal, "Modeling honey bee populations", PloS one **10**, 7, e0130966 (2015).

Toth, A. L., S. Kantarovich, A. F. Meisel and G. E. Robinson, "Nutritional status influences socially regulated foraging ontogeny in honey bees", Journal of Experimental Biology **208**, 24, 4641–4649 (2005).

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

Traniello, J. F. and R. B. Rosengaus, "Ecology, evolution and division of labour in social insects", Animal Behaviour **53**, 1, 209–213 (1997).

Traynor, K. S., Y. Le Conte and R. E. Page, "Queen and young larval pheromones impact nursing and reproductive physiology of honey bee (apis mellifera) workers", Behavioral ecology and sociobiology **68**, 12, 2059–2073 (2014).

Tsuruda, J. M. and R. E. Page, "The effects of young brood on the foraging behavior of two strains of honey bees (apis mellifera)", Behavioral ecology and sociobiology **64**, 2, 161–167 (2009).

Van Bael, S. A., C. Estrada and W. T. Wcislo, "Fungal-fungal interactions in leaf-cutting ant agriculture", Psyche: A Journal of Entomology **2011** (2011).

Vaudo, A. D., J. F. Tooker, C. M. Grozinger and H. M. Patch, "Bee nutrition and floral resource restoration", Current Opinion in Insect Science **10**, 133–141 (2015).

Vicens, N. and J. Bosch, "Weather-dependent pollinator activity in an apple orchard, with special reference to osmia cornuta and apis mellifera (hymenoptera: Megachilidae and apidae)", Environmental Entomology **29**, 3, 413–420 (2000).

Vieira-Neto, E., F. Mundim and H. Vasconcelos, "Hitchhiking behaviour in leaf-cutter ants: an experimental evaluation of three hypotheses", Insectes sociaux **53**, 3, 326–332 (2006).

Vincent, T. L. and J. S. Brown, "Stability in an evolutionary game", Theoretical Population Biology **26**, 3, 408–427 (1984).

Vincent, T. L. and J. S. Brown, "The evolution of ess theory", Annual Review of Ecology and Systematics pp. 423–443 (1988).

Vincent, T. L. and J. S. Brown, *Evolutionary game theory, natural selection, and Darwinian dynamics* (Cambridge University Press, 2005).

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

Wakano, J., Y. Kohmatsu and N. Yamamura, "Evolutionary dynamics of frequency-dependent growth strategy in cannibalistic amphibians", Evolutionary ecology research **4**, 5, 719–736 (2002).

Wakano, J., K. Nakata and N. Yamamura, "Dynamic model of optimal age polyethism in social insects under stable and fluctuating environments", Journal of theoretical biology **193**, 1, 153–165 (1998).

Wang, Y., O. Kaftanoglu, M. K. Fondrk and R. E. Page, "Nurse bee behaviour manipulates worker honeybee (apis mellifera l.) reproductive development", Animal behaviour **92**, 253–261 (2014).

Wheeler, D. E., "Developmental and physiological determinants of caste in social hymenoptera: evolutionary implications", The American Naturalist **128**, 1, 13–34 (1986).

Wheeler, M. M. and G. E. Robinson, "Diet-dependent gene expression in honey bees: honey vs. sucrose or high fructose corn syrup", Scientific reports **4** (2014).

Wilson, E. O., "Caste and division of labor in leaf-cutter ants (hymenoptera: Formicidae: Atta)", Behavioral Ecology and Sociobiology **7**, 2, 157–165 (1980).

Wilson, E. O. *et al.*, "The insect societies.", The insect societies. (1971).

Winston, M., "The honey bee colony: life history", The hive and the honey bee pp. 197–234 (1992).

Winston, M. L., *The biology of the honey bee* (Harvard University Press, 1991).

Winston, M. L. and L. A. Fergusson, "Influence of the amount of eggs and larvae in honeybee colonies on temporal division of labour", Journal of Apicultural Research **25**, 4, 238–241 (1986).

Wise, D. H., "Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations", Annu. Rev. Entomol. **51**, 441–465 (2006).

Woyke, J., "Cannibalism and brood-rearing efficiency in the honeybee", Journal of Apicultural Research **16**, 2, 84–94 (1977).

Wright, G. A., S. W. Nicolson and S. Shafir, "Nutritional physiology and ecology of honey bees", Annual review of entomology **63** (2018).

Wu, J. Y., C. M. Anelli and W. S. Sheppard, "Sub-lethal effects of pesticide residues in brood comb on worker honey bee (apis mellifera) development and longevity", PloS one **6**, 2, e14720 (2011).

Yan, H., D. F. Simola, R. Bonasio, J. Liebig, S. L. Berger and D. Reinberg, "Eusocial insects as emerging models for behavioural epigenetics", Nature Reviews Genetics **15**, 10, 677–688 (2014).

APPENDIX A

PROOFS

Proof of Theorem 1

Proof. Note that

$$x'|_{x=0} = \frac{ry}{1+cy} \geq 0$$

$$y'|_{y=0} = 0,$$

hence according to Theorem A.4 (p.423) in Thieme (2003) Thieme [2003], we can conclude that the system (2.1) is positively invariant in $\mathbb{R}_+^2$. Now, to show boundedness, by the property of positive invariance we have that

$$x' = \frac{ry}{1+ax+cy} - \hat{\alpha}xy - \beta x \leq ry - \hat{\alpha}xy = y(r - \hat{\alpha}x)$$

which implies that

$$\limsup_{t\to\infty} x(t) \leq \frac{r}{\hat{\alpha}}.$$

This indicates that for any $\epsilon > 0$, there exist T large enough such that

$$x(t) < \frac{r}{\hat{\alpha}} + \epsilon \quad \text{for all} \quad t > T.$$

Note that $\frac{\beta cxy}{1+ax+cy} \leq \frac{\beta cxy}{cy} = \beta x$. Therefore, we have

$$y' = \frac{\beta cxy}{1+ax+cy} - \frac{dy}{1+\hat{b}x} \leq \beta x - \frac{dy}{1+\hat{b}x} \leq \beta\left(\frac{r}{\hat{\alpha}} + \epsilon\right) - \frac{dy}{1+\hat{b}\left(\frac{r}{\hat{\alpha}} + \epsilon\right)}.$$

Since ϵ can be arbitrarily small, thus

$$\limsup_{t\to\infty} y(t) \leq \frac{\beta r\left(\frac{\hat{b}r}{\hat{\alpha}} + 1\right)}{d\hat{\alpha}}.$$

Therefore, the system is positively invariant and bounded in $\mathbb{R}_+^2$. More specifically, every trajectory starting from $\mathbb{R}_+^2$ converges to the compact set $C = \left[0, \frac{r}{\hat{\alpha}}\right] \times \left[0, \frac{\beta r\left(\frac{\hat{b}r}{\alpha} + 1\right)}{d\hat{\alpha}}\right]$.

Moreover, the rescaled model (2.2) is also positive invariant and bounded in $\mathbb{R}_+^2$. Thus we can restrict the dynamics of system (2.2) in the rescaled compact set $D = \left[0, \frac{\gamma}{\alpha}\right] \times \left[0, \frac{\gamma\left(\frac{b\gamma}{\alpha} + 1\right)}{\delta\alpha}\right]$.

Define $\phi(E, A) = \frac{1}{EA}$ which is positive in $\mathbb{R}_+^2$, then we have

$$\nabla \cdot (\phi(E', A')) = \frac{\partial}{\partial E}(\phi E') + \frac{\partial}{\partial A}(\phi A')$$

$$= \frac{\partial\left(\frac{\gamma}{E(1+E+A)} - \alpha - \frac{1}{A}\right)}{\partial E} + \frac{\partial\left(\frac{c}{1+E+A} - \frac{\delta}{E(1+bE)}\right)}{\partial A}$$

$$= \frac{\partial\left(\frac{\gamma}{E(1+E+A)}\right)}{\partial E} + \frac{\partial\left(\frac{c}{1+E+A}\right)}{\partial A} = -\frac{\gamma(1+2E+A)+c}{(1+E+A)^2} < 0.$$

This shows that system (2.2) has no limit cycle (i.e. only equilibrium dynamics) according to Dulac-Bendixson Criterion (Theorem A.12 on Thieme [2003]). $\qquad\square$

Details on derivation of equation (2.5)

$$\text{Set} \quad E' = 0, \quad \Rightarrow \quad 1 + E^* + A^* = \frac{\gamma A^*}{E^*(\alpha A^* + 1)}, \tag{A.1}$$

$$\text{and} \quad A' = 0, \quad \Rightarrow \quad 1 + E^* + A^* = \frac{cE^*(1+bE^*)}{\delta} \tag{A.2}$$

Setting (A.1) = (A.2) we obtain:

$$\frac{\gamma A^*}{E^*(\alpha A^* + 1)} = \frac{cE^*(1+bE^*)}{\delta}$$

$$\frac{A^*}{\alpha A^* + 1} = \frac{cE^{*2}(1+bE^*)}{\delta\gamma}$$

$$\frac{\alpha A^*}{\alpha A^* + 1} = \frac{\alpha cE^{*2}(1+bE^*)}{\delta\gamma}$$

$$\frac{\alpha A^* + 1 - 1}{\alpha A^* + 1} = \frac{\alpha cE^{*2}(1+bE^*)}{\delta\gamma}$$

$$\frac{\alpha A^* + 1}{\alpha A^* + 1} - \frac{1}{\alpha A^* + 1} = \frac{\alpha cE^{*2}(1+bE^*)}{\delta\gamma}$$

$$1 - \frac{1}{\alpha A + 1} = \frac{\alpha cE^2(1+bE)}{\delta\gamma}$$

Proof for Proposition 1

Proof. Let A^*, E^* be equilibrium of Model (2.2). Then it satisfies the following two equations:

$$A^* = f(E^*) = \frac{bcE^{*2} + (c - \delta)E^* - \delta}{\delta} > 0,$$

131

which is subject to

$$E^* \geq \frac{\delta - c + \sqrt{(\delta - c)^2 + 4bc\delta}}{2bc}.$$

$$\frac{\gamma A^*}{E^*(\alpha A^* + 1)} = \frac{cE^*(1 + bE^*)}{\delta} \quad \Rightarrow \quad \frac{\alpha A^*}{\alpha A^* + 1} = 1 - \frac{1}{\alpha A^* + 1} = \frac{\alpha c E^{*2}(1 + bE^*)}{\delta \gamma}$$

Hence, we can define the following two nullclines:

$$nf_1(E) = \frac{\alpha c E^2(1 + bE)}{\delta \gamma} \quad \text{and} \quad nf_2(E) = 1 - \frac{1}{\alpha A + 1} = 1 - \frac{1}{\alpha f(E) + 1} \leq 1,$$

which are subject to $E \geq \frac{\delta - c + \sqrt{(\delta - c)^2 + 4bc\delta}}{2bc}$.

Notice that $f(E)$ is increasing when $E \geq E^c = \frac{\delta - c + \sqrt{(\delta - c)^2 + 4bc\delta}}{2bc}$, thus both $nf_1(E)$ and $nf_2(E)$ are increasing functions of E. Therefore, we can conclude that $nf_1(E)$ and $nf_2(E)$ have no positive intercept if $nf_1(E^c) > 1$ holds or

$$nf_1(E)' = \frac{\alpha c E(2 + 3bE)}{\delta \gamma} \geq f'(E) > nf_2(E)' = \frac{\alpha f'(E)}{(\alpha f(E) + 1)^2}$$

where $f'(E) = \frac{2bcE + (c - \delta)}{\delta}$. Define $h(E) = \frac{\alpha c E(2 + 3bE)}{\delta \gamma} - \frac{2bcE + (c - \delta)}{\delta}$, then we can conclude that Model (2.2) has no interior equilibrium if $nf_1(E^c) > 1$ or $h(E^c) > 0$, i.e.

$$\alpha(\delta - c + K)^2(c + \delta + K) > 8b^2 c^2 \delta \gamma \quad \text{or} \quad \alpha[\delta - c + K][c + 3(\delta + K)] > 4bc\gamma K,$$

where $K = \sqrt{(\delta - c)^2 + 4bc\delta}$.

Note that as $c \to 0$, both conditions are satisfied.

Interior equilibria for Model (2.2) are determined by the positive roots of $nf_1(E) = nf_2(E)$. For $E^c > 0$, we claim that if $nf_1(E)$ is convex and $nf_2(E)$ is concave then $nf_1(\ell) < nf_2(\ell)$ for some $\ell > E^c$ and Model (2.2) can have at least two interior equilibria (see Fig 2.1).
Notice that $nf_1(E)$ is always convex since $nf_1''(E) = \frac{2\alpha c(3bE + 1)}{\delta \gamma} > 0$. Moreover, for $E > 0$, $nf_2(E)$ is an increasing function and $\lim_{E \to \infty} nf_2(E) = 1$. Therefore, this implies that $nf_1(E)$ and $nf_2(E)$ must intercept twice in $\mathbb{R}_+^2$.

Consider $\ell = \frac{2\sqrt{bc\delta}}{bc} \in \mathbb{R}_+$ such that $E^c < \ell$, then $nf_1(E_c) < nf_1(\ell)$ and $nf_2(E_c) < nf_2(\ell)$ since both $nf_1(E)$ and $nf_2(E)$ are increasing functions. First, notice that $nf_2(E^c) = 0$, then

$$nf_1(E^c) > 0$$
$$nf_1(E^c) > nf_2(E^c)$$
$$nf_1(E^c) - nf_2(E^c) > 0.$$

132

Now, suppose $nf_1(\ell) > nf_2(\ell)$, i.e.,

$$\frac{4\alpha(c + 2\sqrt{bc\delta})}{bc\gamma} + \frac{bc\delta}{(1 + 3\alpha)bc\delta + 2\alpha(c - \delta)\sqrt{bc\delta}} > 1.$$

However, since $nf_2(E) \to 1$ as $E \to \infty$, the interception of nf_1 and nf_2 must be less than 1. Therefore for $\ell > E^c$,

$$\frac{4\alpha(c + 2\sqrt{bc\delta})}{bc\gamma} + \frac{bc\delta}{(1 + 3\alpha)bc\delta + 2\alpha(c - \delta)\sqrt{bc\delta}} < 1$$

$$\frac{4\alpha(c + 2\sqrt{bc\delta})}{bc\gamma} < 1 - \frac{bc\delta}{(1 + 3\alpha)bc\delta + 2\alpha(c - \delta)\sqrt{bc\delta}}$$

$$nf_1(\ell) < nf_2(\ell).$$

The above shows that the function

$$\begin{aligned}
F(E) &= nf_2(E) - nf_1(E) \\
&= \alpha b^2 c^2 E^5 + \alpha bc(2c - \delta)E^4 + c(\alpha c - \alpha\delta + b\delta - \alpha b\delta)E^3 + c\delta(1 - \alpha - b\gamma)E^2 \\
&\quad + \gamma\delta(\delta - c)E + \gamma\delta^2,
\end{aligned}$$

can intercept at least twice in the positive quadrant and that $nf_2(E) - nf_1(E) \leq 1$. This implies that Model (2.2) can have at least two positive interior equilibria $\mathbf{E_i} = (E_i^*, A_i^*)$, $i = 1, 2$ if $nf_1(\ell) < nf_2(\ell)$ for $\ell > E^c$.

Now to study the stability of the existent equilibria when $\alpha, b > 0$ we consider the Jacobian matrix (A.30).

1. The stability of the extinction equilibrium $\mathbf{E_0} = (0, 0)$ is similarly determined by the eigenvalues $\lambda_i(0, 0)$, $i = 1, 2$ of the Jacobian matrix (A.30) evaluated at $\mathbf{E_0}$. Thus, we obtain the matrix (A.4) giving us the same result as before, i.e. the extinction equilibrium $\mathbf{E_0} = (0, 0)$ is always asymptotically stable for $\alpha \geq 0$.

Let (E^*, A^*) be an interior equilibrium of Model (2.2) with $\alpha > 0$. Then its stability can be determined by the eigenvalues $\lambda_i(E^*, A^*)$, $i = 1, 2$ of its associated Jacobian matrix (A.30).

Hence

$$J_{(E^*,A^*)} = \begin{pmatrix} -A^*\alpha - \frac{\gamma A^*}{(1+E^*+A^*)^2} - 1 & \frac{\gamma}{1+E^*+A^*} - \frac{\gamma A^*}{(1+E^*+A^*)^2} - \alpha E^* \\ \frac{A^*c}{1+E^*+A^*} - \frac{cA^*E^*}{(1+E^*+A^*)^2} + \frac{A^*b\delta}{(1+bE^*)^2} & -\frac{\delta}{1+bE^*} + \frac{cE^*}{1+E^*+A^*} - \frac{cA^*E^*}{(1+E^*+A^*)^2} \end{pmatrix}$$

$$= \begin{pmatrix} -\frac{(\alpha A^*+1)(A+2E^*+1)}{1+E^*+A^*} & \frac{E^*(1+E^*-\alpha A^{*2})}{A^*(1+E^*+A^*)} \\ \frac{cA^*(1+A^*)}{(1+E^*+A^*)^2} + \frac{\delta bA^*}{(1+bE^*)^2} & -\frac{cA^*E^*}{(1+E^*+A^*)^2} \end{pmatrix}$$

since

$$\frac{cE^*}{1 + E^* + A^*} = \frac{\delta}{1 + bE^*}, \quad \text{and} \quad \frac{\gamma A^*}{(1 + E^* + A^*)^2} = \frac{\alpha A^* E^* + E^*}{1 + E^* + A^*},$$

133

which gives

$$\lambda_1(E^*, A^*) + \lambda_2(E^*, A^*) = -\frac{(\alpha A^* + 1)(A + 2E^* + 1)}{1 + E^* + A^*} - \frac{cA^*E^*}{(1 + E^* + A^*)^2} < 0$$

and

$$\lambda_1(E^*, A^*)\lambda_2(E^*, A^*) = \left(\frac{(\alpha A^* + 1)(A + 2E^* + 1)}{1 + E^* + A^*}\right)\left(\frac{cA^*E^*}{(1 + E^* + A^*)^2}\right)$$

$$- \left(\frac{cA^*(1 + A^*)}{(1 + E^* + A^*)^2} + \frac{\delta b A^*}{(1 + bE^*)^2}\right)\left(\frac{E^*(1 + E^* - \alpha A^{*2})}{A^*(1 + E^* + A^*)}\right)$$

$$= \left(\frac{(\alpha A^* + 1)(A^* + 2E^* + 1)cA^*E^*}{(1 + E^* + A^*)^3}\right)$$

$$+ \frac{E^*(\alpha A^{*2} - E^* - 1)}{A^*(1 + E^* + A^*)}\left(\frac{cA^*(1 + A^*)}{(1 + E^* + A^*)^2} + \frac{\delta b A^*}{(1 + bE^*)^2}\right)$$

$$= \left(\frac{(\alpha A^* + 1)(A^* + 2E^* + 1)cA^*E^*}{(1 + E^* + A^*)^3}\right)$$

$$+ (\alpha A^{*2} - E^* - 1)\left(\frac{cE^*(1 + A^*)}{(1 + E^* + A^*)^3} + \frac{\delta b E^*}{(1 + bE^*)^2(1 + E^* + A^*)}\right)$$

with $A^* = f(E^*) = \frac{bcE^{*2} + (c - \delta)E^* - \delta}{\delta} > 0$.

Hence, one of the interior equilibrium $\mathbf{E_i} = (E_i^*, A_i^*)$ $i = 1$ or 2, is locally asymptotically stable if $0 < \frac{\alpha(bcE^{*2} + (c-\delta)E^* - \delta)^2}{\delta^2} - E^* > 1$, while the other one is saddle. $\qquad\square$

<div align="center">*Proof of Theorem 2*</div>

Proof. The positive invariance of Model (2.7) in its state space $\mathbb{R}_+^2$ can be easily established by applying Theorem A.4 in Thieme [2003]. Let $f(E, A) = \frac{\gamma A}{1 + E + A} - E$ and $g(E, A) = \frac{cAE}{1 + E + A} - \delta A$ and define $\phi(E, A) = \frac{1}{EA}$, then we have

$$\frac{\partial f(E, A)\phi(E, A)}{\partial E} = \frac{\partial\left[\frac{\gamma}{E(1 + E + A)} - \frac{1}{A}\right]}{\partial E} = \frac{\partial\left[\frac{\gamma}{E(1 + E + A)}\right]}{\partial E} < 0$$

$$\frac{\partial g(E, A)\phi(E, A)}{\partial A} = \frac{\partial\left[\frac{c}{1 + E + A} - \frac{\delta}{E}\right]}{\partial A} = \frac{\partial\left[\frac{c}{1 + E + A}\right]}{\partial A} < 0$$

Hence, this indicates that Model (2.7) has no limit cycle according to Dulac-Bendixson theorem Thieme [2003], which implies that this model has only equilibrium dynamics.

The equilibrium of Model (2.7) satisfies the following two equations:

$$\frac{\gamma A}{1 + E + A} - E = 0 \quad \Rightarrow \quad A = \frac{cE^2}{\delta\gamma}$$

$$\frac{cAE}{1 + E + A} - \delta A = 0 \quad \Rightarrow \quad A = \frac{(c - \delta)E - \delta}{\delta}$$

Define

$$g_1(E) = \frac{(c - \delta)E^* - \delta}{\delta} \quad \text{and} \quad g_2(E) = \frac{cE^{*2}}{\delta\gamma},$$

then E^* is determined by the positive root(s) of $g_1(E) = g_2(E)$. According to the values of c, δ, γ, the equation $g_1(E) = g_2(E)$ can have none, one, or two positive roots. Note that $g_1 - g_2$ gives

$$G(E) = -\frac{c}{\delta\gamma}E^2 + \frac{(c - \delta)}{\delta}E - 1,$$

which can have two roots, i.e.

$$E_1 = \frac{\gamma(c - \delta) - \sqrt{\gamma^2(c - \delta)^2 - 4c\delta\gamma}}{2c} \quad \text{and} \quad E_2 = \frac{\gamma(c - \delta) + \sqrt{\gamma^2(c - \delta)^2 - 4c\delta\gamma}}{2c}.$$

Hence $E_i > 0$, $i = 1, 2$ if and only if $c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$. Also, $G(E)$ can have a repeated root if $c > \delta$ and $\gamma = \frac{4c\delta}{(c-\delta)^2}$, i.e. $E_{1,2} = \frac{\gamma(c-\delta)}{2c} = \frac{2\delta}{c-\delta}$. Thus Model (2.2) can have, one or two interior equilibria.

Moreover, $G(E)$ has derivative

$$G'(E) = -\frac{2c}{\delta\gamma}E + \frac{c - \delta}{\delta}$$

Then $G(E)$ can have one positive critical point $E_c = \frac{\gamma(c-\delta)}{2c}$ if and only if $c > \delta$.

Note that $G(0) = -1 < 0$. Now, if $G(E_c) > 0$, then $G(E)$ can have a global maximum at E_c for $E > 0$ which is positive. Therefore, $G(0) < G(E_c)$ which implies that G is increasing on the interval $[0, E_c)$ and decreasing on (E_c, ∞). Hence, $G(E)$ has two positive roots if and only if $c > \delta$ and $\gamma > \frac{4c\delta}{(c-\delta)^2}$, and $G(E_c) > 0$ where

$$G(E_c) = \frac{\gamma(c - \delta)^2}{4c\delta} - 1.$$

1. The stability of the extinction equilibrium $\mathbf{E}_0 = (0, 0)$ is determined by the eigenvalues $\lambda_i(0, 0)$, $i = 1, 2$ of the following Jacobian matrix (A.29) evaluated at $\mathbf{E}_0$.

$$J = \begin{pmatrix} -\frac{A\gamma}{(1+E+A)^2} - 1 & \frac{\gamma}{1+E+A} - \frac{A\gamma}{(1+E+A)^2} \\ \frac{Ac}{1+E+A} - \frac{cEA}{(1+E+A)^2} & -\delta + \frac{cE}{1+E+A} - \frac{cEA}{(1+E+A)^2} \end{pmatrix} \qquad \text{(A.3)}$$

$$J_{(0,0)} = \begin{pmatrix} -1 & \gamma \\ 0 & -\delta \end{pmatrix}, \tag{A.4}$$

which gives

$$\lambda_1(0,0) + \lambda_2(0,0) = -1 - \delta < 0 \quad \text{and} \quad \lambda_1(0,0)\lambda_2(0,0) = \delta > 0$$

Hence, the extinction equilibrium $\mathbf{E}_0$ is asymptotically stable.

2. Let (E^*, A^*) be an interior equilibrium of Model (2.2) with $\alpha = 0$. Then its stability can be determined by the eigenvalues $\lambda_i(E^*, A^*)$, $i = 1, 2$ of its associated Jacobian matrix (A.29).

Hence

$$J_{(E^*,A^*)} = \begin{pmatrix} -\frac{A^*\gamma}{(1+E^*+A^*)^2} - 1 & \frac{\gamma}{1+E^*+A^*} - \frac{A^*\gamma}{(1+E^*+A^*)^2} \\ \frac{A^*c}{1+E^*+A^*} - \frac{cE^*A^*}{(1+E^*+A^*)^2} & -\delta + \frac{cE^*}{1+E^*+A^*} - \frac{cE^*A^*}{(1+E^*+A^*)^2} \end{pmatrix}$$

$$= \begin{pmatrix} -\frac{E^*}{1+E^*+A^*} - 1 & \frac{\gamma-E^*}{1+E^*+A^*} \\ \frac{cA^*-\delta A^*}{1+E^*+A^*} & -\frac{\delta A^*}{1+E^*+A^*} \end{pmatrix} \tag{A.5}$$

$$= \begin{pmatrix} -\left(1 + \frac{E^*}{1+E^*+A^*}\right) & \frac{\gamma-E^*}{1+E^*+A^*} \\ \frac{(c-\delta)A^*}{1+E^*+A^*} & -\frac{\delta A^*}{1+E^*+A^*} \end{pmatrix},$$

since

$$\frac{\gamma A^*}{1 + E^* + A^*} = E^* \quad \text{and} \quad \frac{cE^*A^*}{1 + E^* + A^*} = \delta A^*.$$

Therefore, $J_{(E^*,A^*)}$ give us

$$\lambda_1(E^*, A^*) + \lambda_2(E^*, A^*) = -\left(1 + \frac{E^*}{1+E^*+A^*}\right) - \frac{\delta A^*}{1+E^*+A^*} < 0$$

and

$$\lambda_1(E^*, A^*)\lambda_2(E^*, A^*)$$
$$= \frac{1}{(1+E^*+A^*)^2}\left[-(1+2E^*+A^*)(-\delta A^*) - (c-\delta)A^*(\gamma - A^*)\right]$$
$$= \frac{A^*}{(1+E^*+A^*)^2}\left[\delta(1+2E^*+A^*) - (c-\delta)(\gamma - E^*)\right]$$
$$= \frac{A^*}{1+E^*+A^*}\left[2cE^* - \gamma(c-\delta)\right], \quad \text{since } A^* = \frac{(c-\delta)E^*-\delta}{\delta}.$$

136

Now, we consider two cases:

<u>Case 1</u>: If $\gamma = \frac{4c\delta}{(c-\delta)^2}$, then we have one positive interior equilibria $\mathbf{E_1} = (E_1^*, A_1^*) = \left(\frac{\gamma(c-\delta)}{2c}, \frac{(c-\delta)E_1^*-\delta}{\delta}\right)$. Hence $\lambda_1(E_1^*, A_1^*)\lambda_2(E_1^*, A_1^*) = 0$.

This implies $\mathbf{E_1}$ is a stable degenerate equilibrium (see Figure 2.4).

<u>Case 2</u>: If $\gamma > \frac{4c\delta}{(c-\delta)^2}$ we have two interior equilibria $\mathbf{E_i}$, $i = 1, 2$ where

$$E_1^* = \frac{\gamma(c-\delta) - \sqrt{\gamma^2(\delta-c)^2 - 4c\delta\gamma}}{2c} \quad \text{and} \quad E_2^* = \frac{\gamma(c-\delta) + \sqrt{\gamma^2(\delta-c)^2 - 4c\delta\gamma}}{2c},$$

then

$$\lambda_1(E_1^*, A_1^*)\lambda_2(E_1^*, A_1^*) = -\frac{\delta\sqrt{\gamma(c-\delta)^2 - 4c\delta}}{c\gamma} < 0$$

and

$$\lambda_1(E_2^*, A_2^*)\lambda_2(E_2^*, A_2^*) = \frac{\delta\sqrt{\gamma(c-\delta)^2 - 4c\delta}}{c\gamma} > 0.$$

This implies $\mathbf{E_1} = (E_1^*, \frac{(c-\delta)E_1^*-\delta}{\delta})$ is saddle, while $\mathbf{E_2} = (E_2^*, \frac{(c-\delta)E_2^*-\delta}{\delta})$ is asymptotically stable.

□

Proof for Theorem 3

Proof. It is easy to check that $(0, 0, u^*)$ is an equilibrium of Model (2.9) if $\gamma'(u^*) = \delta'(u^*)$. The stability of $(0, 0, u^*)$ is determined by the eigenvalue of the following Jacobian matrix evaluated at $(0, 0, u^*)$

$$J_{(0,0,u^*)} = \begin{pmatrix} -1 & \gamma(u^*) & 0 \\ 0 & -\delta(u^*) & 0 \\ \sigma^2[c'(u^*) - \gamma'(u^*) - \alpha'(u^*) + \delta'(u^*)b(u^*) + \delta(u^*)b'(u^*)] & -\sigma^2\gamma'(u^*) & \sigma^2[\gamma''(u^*) - \delta''(u^*)] \end{pmatrix},$$

which eigenvalues are

$$\lambda_1(E^*, A^*, u^*) = -1, \qquad \lambda_2(E^*, A^*, u^*) = -\delta(u^*),$$

and

$$\lambda_3(E^*, A^*, u^*) = \sigma^2[\gamma''(u^*) - \delta''(u^*)].$$

Hence, the extinction equilibrium $(0, 0, u^*)$ exists if $\gamma'(u^*) = \delta'(u^*)$ and it is stable if $\lambda_3(E^*, A^*, u^*) < 0$, i.e., $\gamma''(u^*) < \delta''(u^*)$.

□

Proof for Theorem 4

Proof. Let (E^*, A^*, u^*) be an interior equilibrium (i.e. $E^*, A^* > 0$), then the following equations satisfy model (2.10)

$$\frac{\gamma_0 A^*}{1 + E^* + A^*} - \alpha_0 E^* A^* - \frac{E^*}{\phi^*} = 0 \tag{A.6}$$

$$\frac{c_0 E^*}{1 + E^* + A^*} - \frac{\delta_0}{1 + b\phi^* E^*} = 0 \tag{A.7}$$

$$\frac{\gamma_0}{1 + E^* + A^*} - \alpha_0 E^* + \frac{\delta_0 \phi^* b_0 E^*}{(1 + b_0 \phi^* E^*)^2} = 0 \quad \text{or} \quad \phi'(u^*) = 0 \tag{A.8}$$

From equation (A.7) we obtain $A^* = \frac{b_0 c_0 E^{*2} \phi^* + E^*(c_0 - \delta_0) - \delta_0}{\delta_0} > 0$. Now, using equation (A.6), we can equivalently express equation (A.8) as follows

$$\frac{\gamma_0}{1 + E^* + A^*} - \alpha_0 E^* + \frac{\delta_0 \phi^* b_0^* E^*}{(1 + b_0^* \phi^* E^*)^2} = \frac{E}{A^* \phi^*} + \frac{\delta_0 \phi^* b_0 E^*}{(1 + b_0 \phi^* E^*)^2} = 0,$$

then solving for A^*, we obtain $A^* = -\frac{(1 + b_0 \phi^* E^*)^2}{b_0 \delta_0 \phi^{*2}} < 0$. Hence we only consider $\phi'(u^*) = 0$ form equation (A.8). This implies that the equilibrium $(0, 0, u^*)$ exists if there is some u^* such $\phi'(u^*) = 0$.

Now, to study the stability of $(0, 0, u^*)$ we use the Jacobian matrix of the evolutionary model (2.10) evaluated at the boundary equilibrium can be represented as follows:

$$J_{(0,0,u^*)} = \begin{pmatrix} -1 & \gamma_0 \phi^* & 0 \\ 0 & -\delta_0 \phi^* & 0 \\ 0 & 0 & \sigma^2 \phi''(u^*)(\gamma_0 - \delta_0) \end{pmatrix}$$

The above Jacobian matrix gives three eigenvalues, which stability conditions must satisfy as follows:

$$\lambda_1(0, 0, u^*) + \lambda_2(0, 0, u^*) = -(1 + \delta_0 \phi^*) < 0, \qquad \lambda_1(0, 0, u^*)\lambda_2(0, 0, u^*) = \delta_0 \phi^* > 0$$

and

$$\lambda_3(0, 0, u^*) = \sigma^2 \phi''(u^*)(\gamma_0 - \delta_0).$$

By Theorem 3, we have that the equilibrium $(0, 0, u^*)$ is locally asymptotically stable if (i) $\frac{\gamma_0}{\delta_0} < 1$ and $\phi''(u^*) > 0$ or (ii) $\frac{\gamma_0}{\delta_0} > 1$ and $\phi''(u^*) < 0$, and saddle if any of these conditions fail and make $\lambda_3(0, 0, u^*) > 0$.

$\square$

Proof for Theorem 5

Proof. Since $\phi(u)$ is a function with the following characteristics: $\phi(u) > 0$, $\phi'(u) > 0$ in (u^l, u^m), $\phi'(u) < 0$ in (u^m, u^r), $\phi(u^l) = \phi(u^m) = \phi(u^r) = 0$ and $\phi''(u^l) > 0$, $\phi''(u^m) < 0$, $\phi''(u^r) > 0$, Proposition 1 suggests that the evolutionary model (2.10) can have the following interior equilibria:

1. If $ng_1(1, x) > ng_2(\phi(u^i), x)$, $i = l, m, r$, there is no positive solution in x.

2. If $ng_2(\phi(u^m), x) > ng_2(u^{l,r}) > ng_1(1, x) > ng_2(\phi(u^{r,l}), x)$, there are at most three positive solutions in x.

3. If $ng_2(\phi(u^m), x) > ng_2(\phi(u^{l,r}), x) > ng_2(\phi(u^{r,l}), x) > ng_1(1, x)$, there are at most six positive solutions in x.

Moreover, we study the stability of the interior equilibria by evaluating the respective Jacobian matrix of the evolutionary model (2.10) with (E^*, A^*, u^*):

$$J_{(E^*, A^*, u^*)} =$$

$$\begin{pmatrix} -\phi^* \left(\alpha_0 A^* + \frac{\gamma_0 A^*}{(1+E^*+A^*)^2} + \frac{A^*}{\phi^*} \right) & \phi^* A^* \left(\frac{E^*}{\phi^* A^{*2}} - \frac{\gamma_0}{(1+E^*+A^*)^2} \right) & 0 \\ \phi^* A^* \left(\frac{c_0}{1+E^*+A^*} + \frac{b_0 \delta_0 \phi^*}{(1+b_0\phi^* E)^{*2}} - \frac{c_0 E^*}{(1+E^*+A^*)^2} \right) & -\frac{c_0 \phi^* A^* E^*}{(1+E^*+A^*)^2} & 0 \\ 0 & 0 & \sigma^2 \phi''(u^*) K \end{pmatrix}$$

$$= \begin{pmatrix} -\frac{(1+\alpha_0\phi^* A^*)(1+2E^*+A^*)}{1+E^*+A^*} & \frac{E^*(1+E^*-\alpha_0\phi^* A^{*2})}{A^*(1+E^*+A^*)} & 0 \\ \phi^* A^* \left(\frac{c_0(1+A^*)}{(1+E^*+A^*)^2} + \frac{b_0 \delta_0 \phi^*}{(1+b_0\phi^* E)^{*2}} \right) & -\frac{c_0 \phi^* A^* E^*}{(1+E^*+A^*)^2} & 0 \\ 0 & 0 & \sigma^2 \phi''(u^*) K \end{pmatrix} \quad \text{(A.9)}$$

where $K = \left(\frac{E^*}{\phi^* A^*} + \frac{\delta_0 \phi^* b_0 E^*}{(1+b_0\phi^* E^*)^2} \right)$. According to Theorem 1, we can conclude that the three eigenvalues of (A.9) satisfy the following conditions:

$$\lambda_1(E^*, A^*, u^*) + \lambda_2(E^*, A^*, u^*) = -\frac{(1+\alpha_0\phi^* A^*)(1+2E^*+A^*)}{1+E^*+A^*} - \frac{c_0\phi^* A^* E^*}{(1+E^*+A^*)^2} < 0$$

$$\lambda_1(E^*, A^*, u^*)\lambda_2(E^*, A^*, u^*) = \left(\frac{(1+\alpha_0\phi^* A^*)(1+2E^*+A^*)(c_0\phi^* A^* E^*)}{(1+E^*+A^*)^3} \right)$$
$$+ \left(\frac{\phi^* E^*(\alpha_0\phi^* A^{*2} - E^* - 1)}{1+E^*+A^*} \right)$$
$$\left(\frac{c(1+A^*)}{(1+E^*+A^*)^2} + \frac{b_0\delta_0\phi^*}{(1+b_0\phi^* E^*)^2} \right)$$

$$\lambda_3(E^*, A^*, u^*) = \sigma^2 \phi''(u^*) \left(\frac{E^*}{\phi^* A^*} + \frac{\delta_0\phi^* b_0 E^*}{(1+b_0\phi^* E^*)^2} \right).$$

Since $\phi'(u^*) = 0$, then the interior equilibrium (E^*, A^*, u^*) is ecologically stable (i.e, given u^*, the interior equilibrium (E^*, A^*) is locally stable for the ecological model (2.2)), then (E^*, A^*, u^*) is locally stable if $\lambda_1(E^*, A^*, u^*)\lambda_2(E^*, A^*, u^*) > 0$ and $\phi''(u^*) \left(\frac{E^*}{\phi^* A^*} + \frac{\delta_0\phi^* b_0 E^*}{(1+b_0\phi^* E^*)^2} \right) < 0$ while it is saddle if $\lambda_1(E^*, A^*, u^*)\lambda_2(E^*, A^*, u^*) < 0$ or $\lambda_3(E^*, A^*, u^*) > 0$. More precisely, local stability is obtained if $\alpha_0\phi^* A^{*2} > E^* + 1$ and $\phi''(u^*) < 0$.

$\square$

Proof for Theorem 6

Proof. For any $F \geq 0, A_i \geq 0$, and $A_o \geq 0$ we have for system (3.2)

$$\frac{dF}{dt}|_{F=0} = 0, \quad \frac{dA_i}{dt}|_{A_i=0} = 0, \quad \frac{dA_o}{dt}|_{A_o=0} = 0$$

and for system (3.2)

$$\frac{dF}{dt}\bigg|_{F=0} = 0, \quad \frac{dA_i}{dt}\bigg|_{A_i=0} = 0, \quad \frac{dA_o}{dt}\bigg|_{A_o=0} = \beta A_i \geq 0$$

thus according to the Theorem A.24 in Thieme [2003], we can conclude that for model (3.2) are positive invariant in $\mathbb{R}^3_+$. Now we show boundedness of the system. First, we have the following inequalities due to the property of positive invariance:

$$\frac{dF}{dt} = \left[\frac{r_f A_i A_o}{b + A_i A_0} - d_f F - r_i A_i - r_o A_o\right] F \leq (r_f - d_f F) F$$

which implies that

$$\limsup_{t \to \infty} F(t) \leq \frac{r_f}{d_f} = M. \tag{A.10}$$

This indicates that for any $\epsilon_1 > 0$, there exists T_1 large enough, such that

$$F(t) \leq M + \epsilon_1 \quad \text{for all } t > T_1.$$

Now let $N = A_i + A_o$, then

$$N' = A'_i + A'_o = F(c_i r_i A_i + c_o r_o A_o) - N(d_i A_i + d_o A_o)$$
$$\leq cFN - dN^2)$$
$$\leq N(c(M + \epsilon_1) - dN) \quad \text{for all } t > T_1$$

which indicates

$$\limsup_{t \to \infty} N(t) \leq \frac{cr_f}{dd_f},$$

where $c = \max\{c_i r_i, c_o r_o\}$ and $d = \min\{d_i, d_o\}$. Then every trajectory starting from $\mathbb{R}^3_+$ converges to the compact set $C = \left[0, \frac{r_f}{d_f}\right] \times \left[0, \frac{cr_f}{dd_f}\right]$.

In system (3.3) and (3.4), for any $F \geq 0, E \geq 0$, and $A \geq 0$ we have that

$$\frac{dF}{dt}\bigg|_{F=0} = 0, \quad \frac{dE}{dt}\bigg|_{E=0} = p_1 r_a AF \geq 0, \quad \frac{dA}{dt}\bigg|_{A=0} = \beta E \geq 0.$$

Therefore, we conclude that model (3.3) is positive invariant in $\mathbb{R}^3_+$.

140

For the system (3.3)-Φ_2, let $A(t), E(t), F(t) > 0$ for $t \in \mathbb{R}_+$. From A.10 we have that

$$\limsup_{t \to \infty} F(t) \le \frac{r_f}{d_f}.$$

This indicates that for any $\epsilon > 0$, there exists T_1 large enough, such that

$$F(t) \le M_1 + \epsilon_1 \quad \text{for all} \quad t > T_1.$$

Similarly, from the second equation of (3.3)–Φ_2 we get

$$\frac{dE}{dt} = p_1 r_a AF - \alpha AE - \beta E \le A(p_1 r_a F - \alpha E) \le A\left(p_1 r_a \left(\frac{r_f}{d_f} + \epsilon_1\right) - \alpha E\right),$$

for all $t \ge T_1$, which indicates

$$\limsup_{t \to \infty} E(t) \le \frac{p_1 r_a r_f}{\alpha d_f}.$$

Therefore for any $\epsilon_2 > 0$, there exists T_2 large enough, such that

$$E(t) \le \frac{p_1 r_a r_f}{\alpha d_f} + \epsilon_2 \quad \text{for all} \quad t \ge T_1.$$

Let $N(t) = A(t) + E(t)$, then

$$N' = A\left(r_a F - \frac{d_a A}{1 + c_2 \alpha E} - \alpha E\right) \le A\left(r_a M_1 + \frac{d_a M_2}{1 + c_2 \alpha M_2} - \frac{d_a}{1 + c_2 \alpha M_2} N\right)$$

which implies

$$\limsup_{t \to \infty} N(t) \le \frac{d_a M_2 + (r_a M_1 - \alpha M_2)(1 + \alpha c_2 M_2)}{d_a} = M_3$$

Then every trajectory starting from $\mathbb{R}_+^3$ converges to the compact set $D = \left[0, \frac{r_f}{bd_f}\right] \times [0, M_3]$. This implies that all three populations are bounded and this also holds for the linear system (3.3).

$\square$

Proof of Theorem 7

Proof. The interior equilibria (F^*, A_i^*, A_o^*) of model (3.2) when $\beta = 0$ is determined with $\frac{dF}{dt} = \frac{dA_i}{dt} = \frac{dA_o}{dt} = 0$ as follows:

$$\frac{r_f A_i^* A_o^*}{b + A_i^* A_0^*} - d_f F^* - r_i A_i^* - r_o A_o^* = 0 \qquad \Rightarrow F^* = \frac{A_i^* A_o^* r_f - (A_i^* A_o^* + b)(r_i A_i^* + r_o A_o^*)}{(b + A_i^* A_o^*)d_f}$$

$$(A.11)$$

$$c_i r_i A_i^* F^* - d_i A_i^* (A_i^* + A_o^*) = 0 \qquad \Rightarrow \qquad F^* = \frac{(A_i^* + A_o^*)d_i}{c_i r_i} \tag{A.12}$$

$$c_o r_o A_o^* F^* - d_o A_o^* (A_i^* + A_o^*) = 0 \qquad \Rightarrow \qquad F^* = \frac{(A_i^* + A_o^*)d_o}{c_o r_o} \tag{A.13}$$

141

$$(A.12) = (A.13) \Rightarrow \quad (A_i^* + A_o^*)\left(\frac{d_i}{c_i r_i} - \frac{d_o}{c_o r_o}\right) = 0 \quad \Rightarrow \quad \frac{d_i}{c_i r_i} = \frac{d_o}{c_o r_o},$$

which implies $A_i^* + A_o^* > 0$.

From the equation above, we can conclude that the system has infinitely many positive solutions if and only if $\frac{d_o}{d_i} = \frac{c_o r_o}{c_i r_i}$.

We substitute (A.12) into (A.11) and we obtain

$$A_i = \frac{-c_i d_o(d_f d_o + c_o r_o^2)A_o^2 + c_i c_o d_o r_f r_o A_o - b(c_i d_f d_o^2 + c_o^2 d_i r_o^2)}{(c_i d_f d_o^2 + c_o^2 d_i r_o^2)A_o}$$

Figure A.1: Relation of A_i with A_o in model (3.2) when $\beta = 0$; $A_i = \frac{-c_i d_o(d_f d_o + c_o r_o^2)A_o^2 + c_i c_o d_o r_f r_o A_o - b(c_i d_f d_o^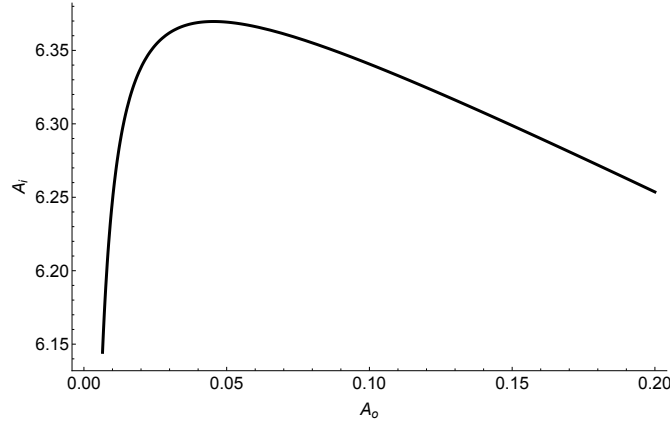2 + c_o^2 d_i r_o^2)}{(c_i d_f d_o^2 + c_o^2 d_i r_o^2)A_o}$ with parameters $r_f = 0.7, b = 0.002, d_f = 0.2, d_i = 0.01, d_o = 0.0095, c_i = c_o = 0.7, r_o = 0.06$ with $\mathbf{r_i} = \frac{\mathbf{d_i c_o r_o}}{\mathbf{d_o c_i}}$.

The interior equilibria (F^*, A_i^*, A_o^*) of model (3.2) is determined as follows:

From $A_i'(t) = 0$, yields

$$F^* = \frac{(A_i^* + A_o^*)d_i + \beta}{c_i r_i}, \tag{A.14}$$

and from $A_o'(t) = 0$, yields

$$A_i^* = \frac{A_o^*(d_o A_o^* - c_o r_o F^*)}{\beta - d_o A_o^*} \tag{A.15}$$

Substituting eq. (A.14) into (A.15) and solving for A_i, results in

$$A_i^* = A_o^*\left[\frac{(d_o - d_i\kappa)A_o^* - \beta\kappa}{\beta - (d_o - d_i\kappa)A_o^*}\right] \tag{A.16}$$

where $\kappa = \frac{c_o r_o}{c_i r_i}$.

Condition A1: Consider $c_i, c_o \in (0, 1)$, A_i^* is positive for $\kappa = \frac{c_o r_o}{c_i r_i} < 1$ whenever $\frac{\beta\kappa}{d_o - d_i\kappa} < A_o^* < \frac{\beta}{d_o - d_i\kappa}$, but also if $\kappa = \frac{c_o r_o}{c_i r_i} > 1$, then $\frac{\beta}{d_o - d_i\kappa} < A_o^* < \frac{\beta\kappa}{d_o - d_i\kappa}$, both cases satisfying $\frac{d_o}{d_i} > \kappa = \frac{c_o r_o}{c_i r_i}$.

Now substituting (A.16) into (A.11) we obtain the following nullcline:

$$g_2(A_o) = a_4 A_o^4 + a_3 A_o^3 + a_2 A_o^2 + a_1 A_o + a_0 = 0 \tag{A.17}$$

$a_4 = -c_i r_i (r_i - r_o)(d_o - d_i\kappa)^2$

$a_3 = -(d_o - d_i\kappa)(d_o r_f + r_o\beta) - \kappa(\beta(r_o - 2r_i) - d_i r_f)$

$a_2 = bc_i r_i (r_i - r_o)(d_o - d_i\kappa)^2 + \beta c_i r_i [d_o r_f - \kappa^2(d_i r_f + r_i\beta) + \kappa(d_o r_f + r_o\beta - d_i d_f)]$

$a_1 = -\beta r_i (b(c_i(r_i - 2r_o) + c_o r_o)(d_o - d_i\kappa) + c_i\beta\kappa)$

$a_0 = -b r_i r_o \beta^2 (c_i - c_o)$

The nullcline (A.17) always have at least two positive roots. However, if a root A_o from (A.17) does not satisfy Condition A1, then model (3.2) has no interior equilibria. Additional conditions for no interior equilibria are:

$$\frac{d_o}{d_i} < \kappa, \quad r_i < r_o \quad c_i < c_o, \quad \beta < \frac{d_i r_f}{r_o - 2r_i}, \quad d_o r_f(1+\kappa) + \kappa r_o\beta < \kappa^2 r_i(d_i + \beta) + \kappa d_i d_f$$

$\square$

Proof for Theorem 8

Proof. The interior equilibria (F^*, E^*, A^*) of model (3.5) are determined by setting $F' = E' = A' = 0$.

From the first equation of (3.5) we obtain

$$F^* = \frac{r_f a A^{*2}}{d_f(b + aA^{*2})} - \frac{r_c}{d_f} A^* = \frac{A^*}{d_f}\left[\frac{r_f a A^*}{b + aA^{*2}} - r_c\right] = A^* f(A^*) \tag{A.18}$$

By setting $E' + A' = 0$ yields

$$r_a F^* - d_a A^* = 0 \quad \Rightarrow \quad F^* = \frac{d_a}{r_a} A^* \quad \Rightarrow \quad f(A^*) = \frac{d_a}{r_a}$$

$$\Rightarrow \quad \frac{r_f a A^*}{d_f(b + aA^{*2})} - \frac{r_c}{d_f} - \frac{d_a}{r_a} = 0$$

Hence, by solving $f(A) = \frac{d_a}{r_a}$ for A, which is equivalent to $g(A) = -a(d_a d_f + r_a r_c)A^2 + ar_a r_f A - b(d_a d_f + r_a r_c)$, we obtain the following cases:

143

1. If $a > 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then by simple algebraic calculations, we can have the following two positive solutions of $g(A)$:

$$A_1^* = \frac{r_a r_f}{2(d_a d_f + r_a r_c)} - \sqrt{\left(\frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)^2 - \frac{b}{a(d_a d_f + r_a r_c)}}$$

$$A_2^* = \frac{r_a r_f}{2(d_a d_f + r_a r_c)} + \sqrt{\left(\frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)^2 - \frac{b}{a(d_a d_f + r_a r_c)}}.$$

Thus, when there is no egg cannibalism, the two interior equilibria of model (3.5) are:

$$(F_1^*, E_1^*, A_1^*) = \left(\frac{d_a}{r_a} A_1^*, \frac{d_a p_1 A_1^{*2}}{\beta}, A_1^*\right), \quad (F_2^*, E_2^*, A_2^*) = \left(\frac{d_a}{r_a} A_2^*, \frac{d_a p_1 A_2^{*2}}{\beta}, A_2^*\right).$$

2. If $a = 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then the system (3.5) has only one positive equilibria:

$$(F_1^*, E_1^*, A_1^*) = \left(\frac{d_a r_f}{2(d_a d_f + r_a r_c)}, \frac{d_a p_1 (r_a r_f)^2}{4\beta(d_a d_f + r_a r_c)^2}, \frac{r_a r_f}{2(d_a d_f + r_a r_c)}\right)$$

3. If $a < 4b(d_a d_f + r_a r_c)/(r_a r_f)^2$, then there is only one trivial equilibrium: $F = 0, E = 0$, and $A = 0$.

$\square$

Proof for Theorem 9

Proof. The interior equilibria (F^*, E^*, A^*) of model (3.3)-Φ_1 can be determined as follows:
From the first equation of (3.3)-Φ_1 we obtain

$$F^* = \frac{r_f a A^{*2}}{d_f(b + a A^{*2})} - \frac{r_c}{d_f} A^* = \frac{A^*}{d_f}\left[\frac{r_f a A^*}{b + a A^{*2}} - r_c\right] = A^* f(A^*) \qquad (A.19)$$

From the second equation of (3.3) we get

$$E^* = \frac{p_1 r_a A^* F^*}{\beta + \alpha A^*} = \frac{p_1 r_a A^{*2}}{d_f(\beta + \alpha A^*)}\left[\frac{r_f a A^*}{b + a A^{*2}} - r_c\right] = \frac{p_1 r_a A^{*2} f(A^*)}{\beta + \alpha A^*} \qquad (A.20)$$

Let $E' + A' = 0$, then we get

$$r_a F^* - d_a A^* - \alpha(1 - c_1) E^* = 0 \quad \Rightarrow \quad r_a A^* f(A^*) - d_a A^* - \alpha(1 - c_1)\frac{p_1 r_a A^{*2} f(A^*)}{\beta + \alpha A^*} = 0$$

144

$$\Rightarrow \qquad f(A^*) = \frac{d_a}{r_a}\left[\frac{\beta + \alpha A^*}{\beta + \alpha A^*[1 - p_1(1 - c_1)]}\right] \qquad\qquad \text{(A.21)}$$

$$\Rightarrow \qquad \frac{1}{d_f}\left[\frac{r_f a A^*}{b + a A^{*2}} - r_c\right] = \frac{d_a}{r_a}\left[\frac{\beta + \alpha A^*}{\beta + \alpha A^*[1 - p_1(1 - c_1)]}\right] \qquad \text{[from (A.19)]}$$

From the above, we obtain the nullcline

$$g(A) = A^3 + q_2 A^2 + q_1 A + q_0 \qquad\qquad \text{(A.22)}$$

where

$$q_2 = \frac{\beta(d_a d_f + r_a r_c) - r_a r_f \alpha[1 - p_1(1 - c_1)]}{\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])}$$

$$q_1 = \frac{\alpha b[d_a d_f + r_a r_c(1 - p_1(1 - c_1))] - a r_a r_f \beta}{a\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])}$$

$$q_0 = \frac{b\beta(d_a d_f + r_a r_c)}{a\alpha(d_a d_f + r_a r_c[1 - p_1(1 - c_1)])} > 0$$

Let $g(A) = A^3 + q_2 A^2 + q_1 A + q_0$ and $g'(A) = 3A^2 + 2q_2 A + q_1$.
Then $g(A)$ has the following critical points:

$$A_1^c = \frac{-q_2 - \sqrt{\Delta}}{3}, \qquad A_2^c = \frac{-q_2 + \sqrt{\Delta}}{3}$$

where $\Delta = q_2^2 - 3q_1$.
Since $q_0 > 0$, the sufficient condition for $g(A)$ to have positive real solutions is $q_2^2 - 3q_1 \geq 0$, i.e.,

$$\alpha \leq \frac{a\beta r_a r_f}{b(d_a d_f + r_a r_c(1 - p_1(1 - c_1)))},$$

otherwise, $g(A)$ has no positive real solutions.
When $q_2 < 0$, i.e. $\alpha > \frac{\beta(d_a d_f + r_a r_c)}{r_a r_f[1 - p_1(1 - c_1)]}$, and $\Delta > 0$ then $g(A)$ has two positive critical points $0 < A_1^c < A_2^c$.
Notice that $g''(A_1^c) = -2\sqrt{\Delta} < 0$ and $g''(A_2^c) = 2\sqrt{\Delta} > 0$, this implies that $g(A)$ has a local maximum at A_1^c and local minimum at A_2^c for $A > 0$, then $g(A)$ has two positive solutions if and only if $g(A_2^c) < 0$, otherwise it has no positive solutions, where

$$g(A_2^c) = \frac{27 q_0 + 6 q_1 \sqrt{\Delta} - q_2(9 q_1 + 2 q_2 \sqrt{\Delta} - 2 q_2^2)}{27}$$

Therefore, $g(A_2^c) < 0$, if $q_2(9 q_1 + 2 q_2 \sqrt{\Delta} - 2 q_2^2) > 27 q_0 + 6 q_1 \sqrt{\Delta}$.
Now, we will show that when model (3.5) has no interior equilibria, model (3.3)-Φ_1 cannot have interior equilibria. From Proposition 8 and (A), we have that $f(A) := \frac{1}{d_f}\left[\frac{r_f a A}{b + a A^2} - r_c\right]$ and has the following properties: $f(0) = -\frac{r_c}{d_f} < 0$, $f(A)$

145

is an increasing function on $(0, \sqrt{b/a})$ and decreasing on $(\sqrt{b/a}, \infty)$. Therefore, $f(A)$ has a maximum $f_{\max} = \max_{A>0}\{f(A)\} = f(A^c = \sqrt{b/a}) = \frac{r_f\sqrt{ab}-2br_c}{2bd_f}$. Hence, model (3.5) with $\alpha = 0$ can have interior equilibria if $f(A) = \frac{d_a}{r_a}$ and $f_{\max} \geq \frac{d_a}{r_a} > 0$. Therefore, if $f(A) < \frac{d_a}{r_a}$, then system (3.5) has no solutions in A, i.e., when $f_{\max} < \frac{d_a}{r_a}$, but also if $f_{\max} < 0 < \frac{d_a}{r_a}$, i.e., $\frac{r_f\sqrt{ab}}{2b} < r_c$, then model (3.5) can definitely not have interior equilibria, i.e., colony cannot survive. Similarly, from (A.21), model (3.3) can have interior equilibria if $f(A) = \frac{d_a}{r_a}\left[\frac{\beta+\alpha A}{\beta+\alpha A[1-p_1(1-c_1)]}\right]$. Hence, since

$$\frac{d_a}{r_a} < \frac{d_a}{r_a}\left[\frac{\beta+\alpha A}{\beta+\alpha A[1-p_1(1-c_1)]}\right] \quad \Rightarrow \quad f_{\max} < \frac{d_a}{r_a} < \frac{d_a}{r_a}\left[\frac{\beta+\alpha A}{\beta+\alpha A[1-p_1(1-c_1)]}\right],$$

this implies that when model (3.5) (model representing a colony with no cannibalism) does not have interior equilibria, then model (3.3)-Φ_1 can definitely have no interior interior equilibria.

Next, we show the dynamics of interior equilibria for model (3.3)-Φ_2.
An interior equilibrium (F^*, E^*, A^*) of model (3.3)-Φ_2 must satisfy the following three equations

$$0 = \frac{r_f a A^2}{b + a A^2} - d_f F - r_c A$$
$$0 = p_1 r_a A F - \alpha A E - \beta E \qquad\qquad (A.23)$$
$$0 = (1 - p_1) r_a A F - \frac{d_a A^2}{1 + c_2 \alpha E} + \beta E$$

From the first and second equation of (A.23) we get (A.19) and (A.20), respectively.

If there is no egg cannibalism, then the interior solutions satisfy the equation $f(A) = \frac{d_a}{r_a}$. Complete dynamics of this case has been provided in Proposition 8.

Now, if there is egg cannibalism, then the interior solutions satisfy the following equation:
From (A.23), let $E' + A' = 0$, then we get

$$r_a F - \alpha E - \frac{d_a A}{1 + c_2 \alpha E} = 0 \quad \Rightarrow \quad f(A) = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2 \alpha E}\right] + \frac{\alpha E}{r_a A}.$$

Therefore, using (A.20)

$$f(A) = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta+\alpha A}}\right] + \frac{\alpha p_1 A f(A)}{\beta + \alpha A}$$

$$\Rightarrow \quad f(A)\left[1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right] = \frac{d_a}{r_a}\left[\frac{1}{1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta+\alpha A}}\right]$$

$$\Rightarrow \quad f(A) = \frac{\frac{d_a}{r_a}}{\left[1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right]\left[1 + c_2 r_a A f(A)\frac{\alpha p_1 A}{\beta + \alpha A}\right]}$$

$$= \frac{\frac{d_a}{r_a}}{1 - \frac{\alpha p_1 A}{\beta + \alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right)\right]}.$$

Let $h(A) = \frac{\alpha p_1 A}{\beta + \alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right)\right]$. Thus

$$f(A) = \frac{\frac{d_a}{r_a}}{1 - h(A)} \tag{A.24}$$

From $h(A)$, we have

$$\frac{\alpha p_1 A}{\beta + \alpha A}(1 - c_2 r_a A f(A)) \le h(A) \le p_1.$$

Now, let A^* be the positive roots of the equation (A.24) subject to the condition $f(A^*) > 0$, so that the system (3.3)-Φ_2 have interior attractors.

Therefore, we can have the following conclusions about model (3.3)-Φ_2:

1. If $f_{\max} < 0$, i.e., $\frac{1}{d_f}\left(\frac{r_f \sqrt{ab}}{2b}\right) < r_c$, then our model has no interior equilibrium.

2. If $f_{\max} > \frac{\frac{d_a}{r_a}}{1 - p_1} > \frac{d_a}{r_a}$, then our model definitely has interior equilibria. This follows from the conclusion that model (3.5) can have interior equilibria when $f_{\max} > \frac{d_a}{r_a}$.

$\square$

Supplementary material for Theorem 9.
Note that an interior equilibrium (F^*, E^*, A^*) of model (3.3)-Φ_2 satisfies the equation

$$f(A) = \frac{d_a}{r_a[1 - h(A)]},$$

where

$$f(A) := \frac{1}{d_f}\left[\frac{r_f a A}{b + a A^2} - r_c\right] \quad \text{and} \quad h(A) := \frac{p_1 \alpha A}{\beta + \alpha A}\left[1 - c_2 r_a A f(A)\left(1 - \frac{\alpha p_1 A}{\beta + \alpha A}\right)\right].$$

Additionally to the proof and implications of Theorem 9, we have the following claims: If $f(A) = d_a/r_a$ has no positive solutions, then $f(A) = \frac{d_a}{r_a[1 - h(A)]}$ definitely has no solutions in A if $h(A) > 0$. In general, if $f_{\max} < \frac{\frac{d_a}{r_a}}{1 - h_{\min}}$ (see Figure A.2a), where $h_{\min}$ is the minimum of $h(A)$ over $[0, A^c]$, this implies that it is possible for $f(A) = \frac{d_a}{r_a}$ to have positive solutions but $f(A) = \frac{\frac{d_a}{r_a}}{1 - h(A)}$ does not have.
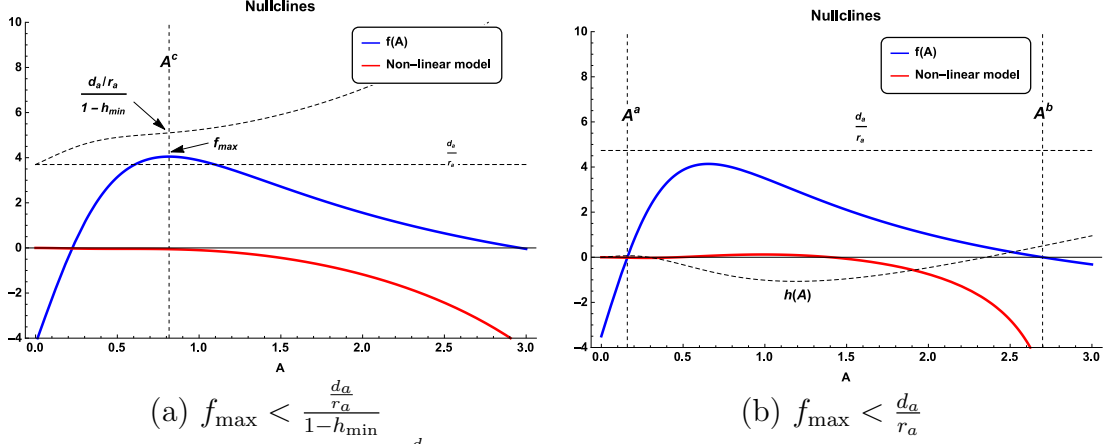
147

Figure A.2: Claims: $f_{\max} < \dfrac{\frac{d_a}{r_a}}{1 - h_{\min}}$ versus $f_{\max} < \dfrac{d_a}{r_a}$

If $f_{\max} < \frac{d_a}{r_a}$ (see Figure A.2b), then $f(A) = \dfrac{\frac{d_a}{r_a}}{1 - h(A)}$ can still have positive solutions in A if $h(A) < 0$ for a certain interval (A^a, A^b), where A^a and A^b are the smallest $A^a = \left((r_f/r_c) - \sqrt{(r_f/r_c)^2 - 4b/a} \right)/2$ and largest $A^b = \left((r_f/r_c) + \sqrt{(r_f/r_c)^2 - 4b/a} \right)/2$ roots of $f(A) = 0$.

<center>Proof for Theorem 7</center>

Proof. The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of model (3.2) is determined by the eigenvalues of the following Jacobian matrix J evaluated at the extinction equilibrium:

Jacobian Matrix for model (3.2):

$$J = \begin{pmatrix} -2d_f F + \frac{r_f A_i A_o}{b + A_i A_o} - r_i A_i - r_o A_o & \left(\frac{b r_f A_o}{(b + A_i A_o)^2} - r_i \right) F & \left(\frac{b r_f A_i}{(b + A_i A_o)^2} - r_o \right) F \\ c_i r_i A_i & c_i r_i F - (2A_i + A_o) d_i - \beta & -d_i A_i \\ c_o r_o A_o & \beta - d_o A_o & c_o r_o F - (A_i + 2A_o) d_o \end{pmatrix} \tag{A.25}$$

The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of model (3.2) when $\beta = 0$ is determined by the eigenvalues $\lambda_i(0, 0, 0)$, $i = 1, 2, 3$ of the Jacobian matrix (A.25), i.e., $J_{1(0,0,0)} = \mathbf{0}_{3 \times 3}$.

Hence, we will use Center Manifold Theory to determine the stability condition of system (3.2) when $\beta = 0$ at equilibrium $\mathbf{E_0}$. First, we simplify the system using Taylor series expansion (consider only up to the second order):

$$\begin{aligned} F'(t) &= -d_f F^2 - r_i A_i - r_o A_o F \\ A_i'(t) &= c_i r_i A_i F - d_i A_i (A_i + A_o) \\ A_o'(t) &= c_o r_o A_o F - d_o A_o (A_i + A_o) \end{aligned} \tag{A.26}$$

We replace A_0 in term of a function of F and A_o. For that, consider,

$$h(F, A_o) = a_1 F^2 + a_2 F A + a_3 A_o^2 + \mathcal{O}(F^3, A_o^3)$$

By some simple calculation, we get $h(F, A_o) \equiv 0$. Thus, the flow on the center manifold is given by

$$\begin{aligned} F'(t) &= -d_f F^2 - r_i A_i \\ A_i'(t) &= c_i r_i A_i F - d_i A_i^2 \end{aligned} \tag{A.27}$$

Again, both eigenvalues are zero for the system (A.27) at the trivial equilibrium $(0,0)$. Using center manifold theory for the stability at its extinction equilibrium. This system is already in the desired form to use center manifold theory. Replacing A_i in terms of a function of F, i.e., $g(F) = b_1 F^2 + b_2 F^3 + \mathcal{O}(F^4)$, and by simple calculation, it can be proved that $g(F) \equiv 0$. Therefore, the flow on the center manifold is given by

$$F' = -d_f F^2, \tag{A.28}$$

i.e., model (3.2) is always locally asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

Similarly, the stability of the extinction equilibrium for system (3.2) when $\beta > 0$ can be stablished by using Center Manifold Theory. It can be concluded that the flow on the center manifold for system (3.2) is given by (A.28), i.e., model (3.2) is always locally asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

$\square$

Proof for Theorem 10

Proof. The stability of the equilibrium $\mathbf{E_i}$, $i = 1, 2, 3$ of model (3.3) is determined by the eigenvalues of the following Jacobian matrix J associated to each model, respectively, evaluated at each equilibrium:

Jacobian for model (3.3)-Φ_1:

$$J = \begin{pmatrix} -2d_f F^* + A^* \left(\frac{a r_f A^*}{b + a A^{*2}} - r_c \right) & 0 & F^* \left(\frac{2abr_f A^*}{(b + aA^{*2})^2} - r_c \right) \\ p_1 r_a A^* & -(\beta + \alpha A^*) & p_1 r_a F^* - \alpha E^* \\ r_a(1 - p_1) A^* & \beta + \alpha c_1 A^* & r_a(1 - p_1) F^* - 2d_a A^* + \alpha c_1 E \end{pmatrix} \tag{A.29}$$

Jacobian for model (3.3)-Φ_2:

$$J = \begin{pmatrix} -2d_f F^* + A^* \left(\frac{a r_f A^*}{b + a A^{*2}} - r_c \right) & 0 & F^* \left(\frac{2abr_f A^*}{(b + aA^{*2})^2} - r_c \right) \\ p_1 r_a A^* & -(\beta + \alpha A^*) & p_1 r_a F^* - \alpha E^* \\ r_a(1 - p_1) A^* & \beta + \frac{\alpha c_2 d_a A^{*2}}{(1 + c_2 \alpha E^*)^2} & r_a(1 - p_1) F^* - \frac{2d_a A^*}{1 + c_2 \alpha E^*} \end{pmatrix} \tag{A.30}$$

149

1. Stability of extinction equilibrium for model (3.3)

The stability of the extinction equilibrium $\mathbf{E_0} = (0,0,0)$ for model (3.3) is determined by the eigenvalues $\lambda_i(0,0,0)$, $i = 1,2,3$ of the Jacobian matrix (A.29) and (A.30), respectively, evaluated at $\mathbf{E_0}$. i.e.

$$J_{(0,0,0)} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & -\beta & 0 \\ 0 & \beta & 0 \end{pmatrix}$$

which gives $\lambda_1 = \lambda_2 = 0$, $\lambda_3 = -\beta$.

Now we will use Center Manifold Theory to determine the stability condition of systems (3.3) at equilibrium $\mathbf{E_0} = (0,0,0)$. First, we simplify system (3.3) by using Taylor series expansion (consider only up to the second order). System (3.3) simplify as follows:

$$\begin{aligned} F'(t) &= -(d_f F^2 + r_c AF) \\ A'(t) &= (1 - p_1)r_a AF + \beta E - d_a A^2 \\ E'(t) &= -\beta E + (p_1 r_a F - \alpha E)A \end{aligned} \tag{A.31}$$

System (A.31) is already in the desired form with $C = \mathbf{0}_{2 \times 2}$, $P = -\beta$, $x = [F, A]$, $H(x, E) = p_1 r_a FA - \alpha EA$ and

$$G(x, E) = \begin{bmatrix} -d_f F^2 - r_c AF \\ (1 - p_1)r_a AF - d_a A^2 + \beta E \end{bmatrix}.$$

Let

$$\begin{aligned} h(x) &= a_1 F^2 + a_2 FA + a_3 A^2 + \mathcal{O}(F^3, A^3) \\ Dh(x) &= [2a_1 F + a_2 A + \cdots, \ a_2 F + 2a_3 A + \cdots] \\ Dh(x)[Cx + G(x, h(x))] &= [2a_1 F + a_2 A + \cdots, \ a_2 F + 2a_3 A + \cdots] \\ &\quad \begin{bmatrix} -d_f F^2 - r_c AF \\ (1 - p_1)r_a AF - d_a A^2 + \beta(a_1 F^2 + a_2 FA + a_3 A^2 + \cdots) \end{bmatrix} \\ Ph(x) + H(x, h(x)) &= -\beta(a_1 F^2 + a_2 FA + a_3 A^2 + \cdots) + p_1 r_a FA \\ &\quad - \alpha A(a_1 F^2 + a_2 FA + a_3 A^2 + \cdots) \end{aligned}$$

Setting $Dh(x)[Cx + G(x, h(x))] = Ph(x) + H(x, h(x))$ and collecting terms, we obtain

$$\begin{aligned} F^2 &: 0 = a_1 \beta &\Rightarrow \quad a_1 = 0 \\ FA &: 0 = a_2 \beta + p_1 r_a &\Rightarrow \quad a_2 = -\frac{p_1 r_a}{\beta} \\ A^2 &: 0 = 0 \end{aligned}$$

Hence, $h(F, A) = -\frac{p_1 r_a}{\beta} FA + \mathcal{O}(F^3, A^3)$. Thus, the flow of the center manifold is given by

$$F'(t) = -(d_f F + r_c A)F$$

$$A'(t) = (1 - p_1)r_a AF + \beta(-\frac{p_1 r_a}{\beta} FA + \mathcal{O}(F^3, A^3)) - d_a A^2 \qquad \text{(A.32)}$$

$$= (1 - 2p_1)r_a AF - d_a A^2 + \mathcal{O}(F^3, A^3)$$

Again, both eigenvalues are zero for system (A.32) at the trivial equilibrium $(0, 0)$. Therefore, we use center manifold theory for the stability at its extinction equilibrium. The system (A.32) is already in the desired form to use center manifold theory. Consider the function $g(F) = b_1 F^2 + b_2 F^3 + \mathcal{O}(F^4)$, then

$$Dg(F) = 2b_1 F + 3b_2 F^2 + \cdots$$
$$Dg(F)G(F, h(F))] = [2b_1 F + 3b_2 F^2 + \cdots][-d_f F^2 - r_c F(2b_1 F + 3b_2 F^2 + \cdots)]$$
$$H(x, h(x)) = 0$$

Similarly as before, by simple calculation and collecting terms we obtain $g(F) \equiv 0$. Therefore, the flow on the center manifold is given by the equation

$$F' = -d_f F^2,$$

this implies system (3.3) is always asymptotically stable at the extinction equilibrium $\mathbf{E_0}$.

2. *Stability of interior equilibria for model* (3.3)-Φ_1

Let (F^*, E^*, A^*) be an interior equilibrium of model (3.3)-Φ_1. Then its stability is determined by the eigenvalues $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ of its Jacobian matrix (A.29) at the interior equilibrium (F^*, E^*, A^*), where its characteristic equation is as follows:

$$\lambda^3 - \left[\sum_{i=1}^{3} \lambda_i\right] \lambda^2 + \left[\sum_{i,j=1, i\neq j}^{3} \lambda_i \lambda_j\right] \lambda - \prod_{i=1}^{3} \lambda_i$$

with $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ being the roots of the above characteristic equation:

$$\sum_{i=1}^{3} \lambda_i = -[d_f F + 2d_a A + \alpha A + \beta - (r_a(1 - p_1)F - c_1 \alpha E)] < 0$$

$$\sum_{i,j=1, i\neq j}^{3} \lambda_i \lambda_j = -\left[F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)(1 - p_1)r_a A + (p_1 r_a F - \alpha E)(\beta + \alpha c_1 A)\right.$$
$$\left. -(\beta + \alpha A)(d_f F)] - (r_a(1 - p_1)F + \alpha c_1 E - 2d_a A)(\beta + \alpha A + d_f F) > 0 \right.$$

$$\prod_{i=1}^{3} \lambda_i = F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)[p_1 r_a A(\beta + c_1 \alpha A) + (\beta + \alpha A)(1 - p_1)r_a A]$$
$$+ d_f F[(\beta + \alpha A)(r_a(1 - p_1)F + \alpha c_1 E - 2d_a A) - (p_1 r_a F - \alpha E)(\beta + \alpha + \alpha c_1 A)] < 0$$

According to the Routh-Hurwitz stability criterion for third-degree polynomial, the sufficient conditions for the above inequalities to be true, which provide the stability of interior equilibria are given by

$$r_a(1 - p_1)F + c_1\alpha E < 2d_a A, \qquad \frac{2abr_f A}{(b + aA^2)^2} < r_c, \qquad p_1 r_a F > \alpha E \quad (\Rightarrow \beta > 0).$$

3. Stability of interior equilibria for (3.3)-Φ_2

Let (F^*, E^*, A^*) be an interior equilibrium of model (3.3)-Φ_2. Then its stability is determined by the eigenvalues $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ of its Jacobian matrix (A.30) at the interior equilibrium (F^*, E^*, A^*), where its characteristic equation is as follows:

$$\lambda^3 - \left[\sum_{i=1}^{3} \lambda_i\right] \lambda^2 + \left[\sum_{i,j=1,i\neq j}^{3} \lambda_i\lambda_j\right] \lambda - \prod_{i=1}^{3} \lambda_i$$

with $\lambda_i(F^*, E^*, A^*)$, $i = 1, 2, 3$ being the roots of the above characteristic equation:

$$\sum_{i=1}^{3} \lambda_i = -\left[d_f F + \beta + \alpha A + \frac{2d_a A}{1 + c_2\alpha E} - r_a(1 - p_1)F\right] < 0$$

$$\sum_{i,j=1,i\neq j}^{3} \lambda_i\lambda_j = -\left[F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)r_a(1 - p_1)A + (p_1 r_a F - \alpha E)\left(\beta + \frac{\alpha c_2 d_a A^2}{(1 + c_2\alpha E)^2}\right)\right.$$
$$+ (\beta + \alpha A)\left(r_a(1 - p_1)F - \frac{2d_a A}{1 + c_2\alpha E}\right)$$
$$\left. + d_f F\left(r_a(1 - p_1)F - (\beta + \alpha A) - \frac{2d_a A}{1 + c_2\alpha E}\right)\right] > 0$$

$$\prod_{i=1}^{3} \lambda_i = F\left(\frac{2abr_f A}{(b + aA^2)^2} - r_c\right)\left[p_1 r_a A\left(\beta + \frac{\alpha c_2 d_a A^2}{(1 + c_2\alpha E)^2}\right) + (\beta + \alpha A)r_a(1 - p_1)A\right]$$
$$+ d_f F\left[\left(\frac{\beta^2 E}{A} + \frac{\alpha c_2 d_a \beta E A}{(1 + c_2\alpha E)^2}\right) + (\beta + \alpha A)\left(r_a(1 - p_1)F - \frac{2d_a A}{1 + c_2\alpha E}\right)\right] < 0$$

According to the Routh-Hurwitz stability criterion for third-degree polynomial, the sufficient conditions for the above inequalities to be true, which provide the stability of interior equilibria are given by

$$r_a(1 - p_1)F < \frac{2d_a A}{1 + c_2\alpha E}, \qquad \frac{2abr_f A}{(b + aA^2)^2} < r_c, \qquad p_1 r_a F > \alpha E \quad (\Rightarrow \beta > 0).$$

The sufficient condition of the interior equilibrium is given by $\frac{r_f a A}{b + aA^2} > r_c$ for model (3.3). Using this argument, it follows that the sufficient condition of the stability for interior equilibria is $A^2 > \frac{b}{a}$ or $A > \sqrt{\frac{b}{ab}}$. It can be easily verified that

$A_2^* > A^c > \sqrt{\frac{b}{a}}$, thus, it can be conclude that the interior equilibrium $\mathbf{E_2}$ is always locally asymptotically stable when it exists.

$\square$

Proof of Theorem 11

Proof. We start by showing positivity of Model 4.7 as follows:
Note that
$$P'|_{P=0} = \frac{rBF}{1+aB} \geq 0, \qquad V'|_{V=0} = c\alpha NP$$

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

hence according to Theorem A.4 (p.423) in Thieme [2003], we can conclude that the system (4.7) is positively invariant in $\mathbb{R}_+^5$.

To show existence of equilibria, notice that from equation (B.2), we can obtain the following polynomial, which is the nullcline of our model:

$$f(N) = c_3 N^3 + c_2 N^2 + c_1 N + c_0, \tag{A.33}$$

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

$$c_3 = d_f \alpha (1+\alpha_v \xi)(c_q \alpha_b \alpha_q + e_g \alpha_h \beta_{bh} \xi)(c_q \alpha_q (b\alpha_b + ac\alpha\xi) + be_g \alpha_h \beta_{bh} \xi) > 0$$

$$\begin{aligned}
c_2 = {}& bd_f(1+\alpha_v \xi)(c_q \alpha_b \alpha_q + e_g \alpha_h \beta_{bh} \xi)(c_q d_p \alpha_b \alpha_q + e_g \beta_{bh} \xi(d_p \alpha_h + 2c\alpha^2 \xi \Phi(\xi))) \\
& + c\alpha\xi(e_g \alpha \beta_{bh} \xi(d_f e_g \alpha_h \beta_{bh} \xi(1+\alpha_v \xi) + c_q \alpha_q(d_f \alpha_b(1+\alpha_v \xi) - cr\beta_{hf}^m \xi)) \\
& + ac_q d_f \alpha_q(1+\alpha_v \xi)(c_q d_p \alpha_b \alpha_q + e_g \beta_{bh} \xi(d_p \alpha_h + c\alpha^2 \xi \Phi(\xi))))
\end{aligned}$$

$$\begin{aligned}
c_1 = {}& cd_f e_g \alpha \beta_{bh} \xi^2 (1+\alpha_v \xi) \\
& (c_q d_p \alpha_q(\alpha_b + 2b\alpha_b \Phi(\xi) + ac\alpha\xi\Phi(\xi)) \\
& + e_g \beta_{bh} \xi(c\alpha^2 \xi \Phi(\xi)(1+b\Phi(\xi)) + d_p(\alpha_h(1+2b\Phi(\xi))))) > 0
\end{aligned}$$

$$c_0 = c^2 d_f d_p e_g^2 \alpha^2 \beta_{bh}^2 \xi^4 \Phi(\xi)(1+\alpha_v \xi)(1+b\Phi(\xi)) > 0$$

Let $f'(N) = 3N^2 + 3d_1 N + d_0$, where $d_1 = \frac{c_2}{c_3}$ and $d_0 = \frac{c_1}{c_3} > 0$. Note that $f(0) = c_0 > 0$, this implies that $f(N)$ has either no positive roots or it has two positive roots. If $\alpha_b > cr\xi \frac{\beta_{hf}}{d_f(1+\alpha_v \xi)}$, i.e. $d_1 > 0$, then $f(N) > 0$ and has two critical points $N_1^c < 0 < N_2^c$, where

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

153

This indicates $f(N)$ has no positive roots. If $\alpha_b < cr\xi\frac{\beta_{hf}}{d_f(1+\alpha_v\xi)}$, 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 $X_1 = \left(\frac{c_2}{c_3} + \sqrt{\left(\frac{c_2}{c_3}\right)^2 - 2\frac{c_0}{c_3}}\right) < 0$. 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 (4.7) has two interior equilibria.

Next, we show the stability conditions for the extinction equilibrium:
The Jacobian matrix (B.4) evaluated at the extinction equilibrium is as follows:

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

which eigenvalues are:

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

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

$\square$

APPENDIX B

SUPPLEMENTARY MATERIAL

The following bifurcation diagrams compares the dynamics of egg cannibalism in model 3.3 explained in Theorem 10. The figures display dashed blue and green lines representing the stable and unstable interior equilibria, respectively, for model 3.3-Φ_2. The solid blue and green lines represent the stable and unstable interior equilibria, respectively, for model 3.3-Φ_1. Figure B.1 helps us understand better that model 3.4 provides colony survival for a larger range of α (egg cannibalism rate).
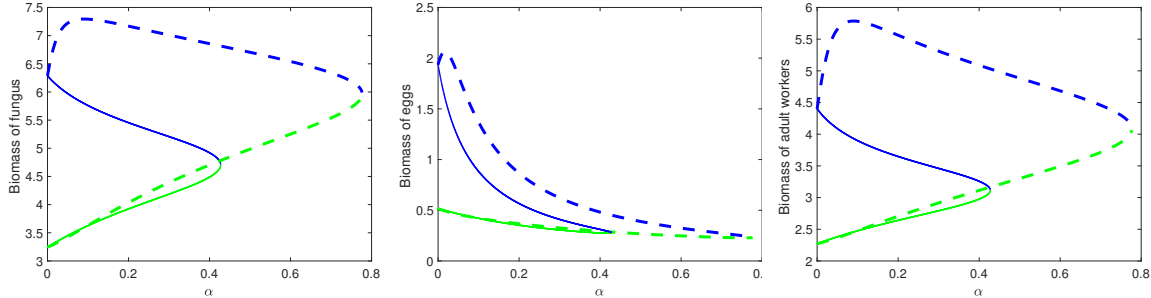
Figure B.1: Models comparison of egg cannibalism dynamics. $c_1 = 0.85; c_2 = 4; a = 0.05; r_f = 1; b = 0.5; r_a = 0.07; d_f = 0.1; r_c = .007; d_a = 0.1; \beta = 0.5; p_1 = 0.5$ (Blue: stable and green: unstable interior equilibria).

Supplementary bifurcation diagrams for time series Figure 3.7 and Figure 3.8

In Figures B.2-B.4 we compare the effects of p_1: the energy gained through the consumption of fungus by the adult workers which is then distributed (or invested) on brood care. In Figure B.2, which represents the case when there is no egg cannibalism, the biomass of fungus, eggs, and adult workers can have oscillatory solutions if the energy invested on brood care is medium to high. In Figures B.3, we introduce cannibalism ($\alpha > 0$) as represented in model (3.3)-Φ_1. In this case, the range in which oscillatory solutions can happen is decreased while the range of stable biomass is increased. This effect is produced by the way worker ants are using the converted energy from cannibalized eggs for their own growth. In Figure B.4, the energy from egg cannibalism is used to increase adult lifespan, therefore, higher levels of energy is available to invest on brood care keeping the biomasses stable. Moreover, model (3.3)-Φ_2 shows an increase of biomass of fungus, eggs, and adult workers as p_1 increases compared to that in model (3.3)-Φ_1, when there is no egg cannibalism. As a note, it seems that egg cannibalism can stabilize the dynamics with the nonlinear model (3.3)-Φ_2 having better stabilizing ability. In Figure B.5, we noticed that increasing r_c, i.e. the conversion rate between fungus and ants, can produce oscillatory solutions as p_1 increases. This suggests that r_c can potentially destablize the dynamics in the nonlinear model (3.3)-Φ_2.
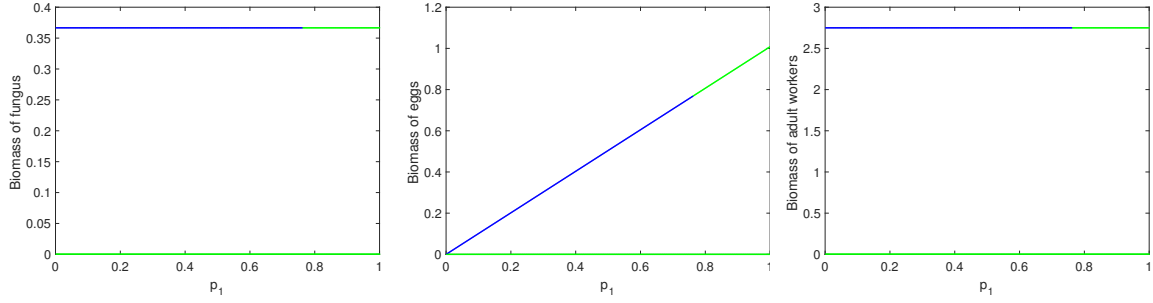
s

Figure B.2: Model (3.5) with no cannibalism. $\alpha = 0, r_c = 0.7, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15, c_1 = 0.8$ (Blue: stable and green: unstable interior equilibria).
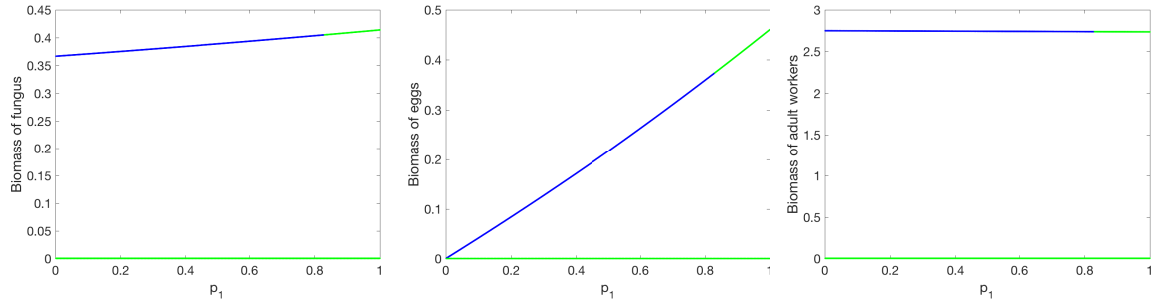

Figure B.3: Model (3.3)-Φ_1. $\alpha = 0.08, r_c = 0.7, c_1 = 0.8, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (Blue: stable and green: unstable interior equilibria).
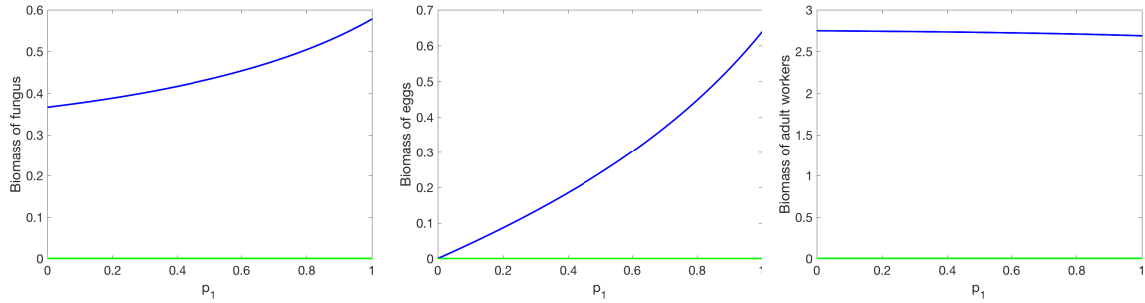

Figure B.4: Model (3.3)-Φ_2. $\alpha = 0.08, r_c = 0.7, c_2 = 10, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (Blue: stable and green: unstable interior equilibria).

Figure B.5: Model (3.3)-Φ_2. $\alpha = 0.08, r_c = 1.5, c_2 = 10, r_f = 2, b = 0.002, d_f = 0.2, a = 0.3, r_a = 0.15, d_a = 0.02, \beta = 0.15$ (Blue: stable and green: unstable interior equilibria).
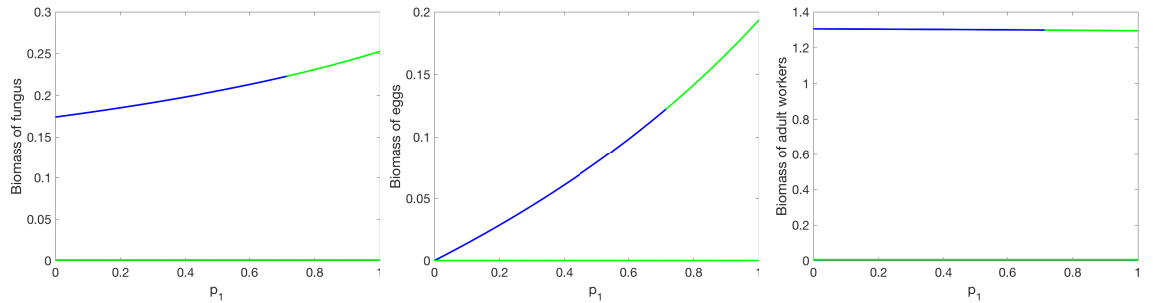
Assume that $(P^*, V^*, B^*, N^*, F^*)$ is an interior equilibrium of Model (4.7), then it satisfies the following five equations:

From $B' = 0$,

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

From $N' = 0$,

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

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

From $F' = 0$,

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

From $V' = 0$,

$$c\alpha NP - (1 - c_q)\alpha_q V - \alpha_h NV - \alpha_b BV = d_h V + \frac{\beta_{hf}^m V}{1 + \alpha_v \frac{N}{V}}$$

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

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

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

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

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

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

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

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

$$\tag{B.2}$$

where

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

$$= \frac{\frac{c_q\alpha_q\alpha_v - \beta_{hf}e_g}{d_h e_g} - 1 + \sqrt{(\frac{c_q\alpha_q\alpha_v - \beta_{hf}e_g}{d_h e_g} - 1)^2 + \frac{4c_q\alpha_q\alpha_v}{d_h e_g}}}{2\alpha_v} \quad \text{(B.3)}$$

$$\Phi(\xi) = \frac{[(1-c_q)\alpha_q + d_h]}{c\alpha\xi} + \frac{\beta_{hf}^m}{c\alpha\xi(1+\alpha_v\xi)} = \frac{(1-c_q)\alpha_q}{c\alpha\xi} + \frac{c_q\alpha_q}{c\alpha e_g\xi^2} = \frac{\alpha_q}{c\alpha\xi}\left[1 - c_q\left(1 - \frac{1}{e_g\xi}\right)\right].$$

Jacobian

The stability of the equilibria of Model (4.7) is determined using the following Jacobian matrix evaluated at each of the $\mathbf{E_i}$.

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

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

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

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

1. ξ is always increasing with α_q:

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

2. ξ is always increasing with c_q:

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

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

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

if $c_q\alpha_q\alpha_v(\beta_{hf}^m - d_h) > e_g(d_h + \beta_{hf}^m)^2$ when $\beta_{hf}^m > d_h$.

4. ξ always decreases with e_g:

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

because simplifying this inequality we obtain the following true inequality:

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

5. ξ always decreases with β_{hf}^m:

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

because simplifying this inequality we obtain the following true inequality:

$$4c_q d_h e_g \alpha_q \alpha_v > 0$$

6. ξ always decreases with d_h:

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

because simplifying this inequality we obtain the following inequality:

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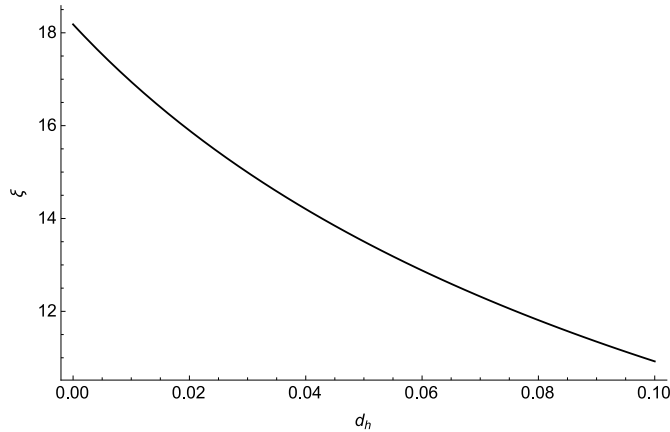

Figure B.6: Effects on ξ as d_h increases

APPENDIX C

STATEMENT OF AUTHORIZATION

The project "Colony And Evolutionary Dynamics Of A Two-Stage Model With Brood Cannibalism And Division Of Labor In Social Insects" (where I am the first author) published in the Journal of Natural Resource Modeling (Rodriguez-Rodriguez and Kang (2016)) is elaborated in Chapter 2 of the dissertation per request of the co-author Dr. Yun Kang.

The project "Interactions between leaf-cutter ants and fungus garden: Effects of division of labor, age polyethism, and egg cannibalism." (where I am the first author), which was recently accepted in the Journal of Mathematical Modeling of Natural Phenomena (Rodriguez-Rodriguez et al. (2018)) is elaborated in Chapter 3 of the dissertation per request of the co-authors Nathan Smith and Dr. Yun Kang.