

**Some models and their nonstandard  
discretizations for honey bee (*Apis mellifera L.*)  
colony population dynamics**

by

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# Declaration

I, the undersigned, hereby declare that the dissertation submitted herewith for the degree Master of Science to the University of Pretoria contains my own, independent work and has not been submitted for any degree at any other university.

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# Abstract

This dissertation focuses on two mathematical models to study biologically, theoretically and computationally the alarming declines of the colony population of honey bees, specifically the Colony Collapse Disorder (CCD) and *capensis calamity* (*cc*).

A comprehensive description of honey bees as model organisms is provided with the aim of understanding and elaborating the assumptions that are made in order to formulate the two models.

The first model is due to Khoury, Meyerscough and Barron [43]. Assuming that the rate at which the maximum eclosion is approached is sufficiently large, we have established the following result: There exists a critical value,  $m_c$ , of the foragers mortality rate,  $m$ , which is a transcritical bifurcation. More precisely, the CCD occurs for  $m > m_c$  in the sense that the trivial equilibrium point,  $(0,0)$ , is globally asymptotically stable (GAS) for such large values of the mortality rate. If  $m < m_c$ , the colony is healthy in the sense that a new interior equilibrium point which is GAS is born, while the trivial equilibrium point is unstable.

In the second step, we propose a social parasite (SP) model which is characterized by a low recruitment rate of the host population. We prove that the *cc* occurs in the sense that the total population of the host decays to zero.

We design nonstandard finite difference (NSFD) schemes that preserve the stability properties of the two continuous models including the CCD and *cc* phenomena. The faster decline in the SP setting is demonstrated theoretically for the NSFD scheme. Numerical simulations are provided to support the theory.

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# Chapter 1

## Introduction

In our daily lives, reference to the word honey is made to reflect a state of happiness, joy and comfort. Some of the most famous expressions include, “to go or be on honeymoon”, and “the promised land flowing with milk and honey”. Saint John Chrysostom goes deeper and hits the nail on the head when he says bees are more honored than other animals, not because they labor, but because they labor for others. This is because, among other pollinators, bees work to ensure food security and nutrition, maintain biodiversity as well as vibrant ecosystems for plants, humans, animals and bees themselves [31].

### Bees and the environment

Bees belong to the class Insecta (insects), phylum (Arthropod) in the kingdom of Animalia, group Aculeate and of order Hymenoptera. It is estimated that there are about 20 000 species of bees globally and 3000 of them are found in Africa [40]. Bees can be either solitary with one female in a nest, semi-social with more than one adult that take care of the nest or eusocial with distinct castes and a well organized division of labor like in stingless and honey bees [40]. Bees effectively pollinate plants as they visit flowers to collect pollen and nectar which they use as food for themselves [40, 101].

## Classification of bees

Bees are categorized into 7 families, namely; Colletidae, Stenotritidae, Andrenidae, Halictidae, Apidae, Megachillidae and Melittidae [28, 40, 81]. This classification is biologically based either on the type of nest they occupy, their colony organization or the way they collect pollen and nectar. Based on their nesting behavior, bees are further grouped into the following types [40]:

- **soil tunneling bees**- nests occur in distinct soil types, or termite mounds depending on the species.
- **plant tunnel nester**- they nest in dead plants (Fig 1.1(B)).
- **mud and resin daubers**- build nests of mud, sand or plants resin.
- **leafcutters bees**- they construct their nest in wood or ground tunnels (see Fig 1.1(D)).
- **carder bees**- they use grass seeds to construct their nests.
- **cavity nesters**- their nests are in cavities in the ground (see Fig 1.1(A)).
- **honey bees**- they either build their nests in ground cavities, or hollow trees, or in rocks crevices or under rocks.

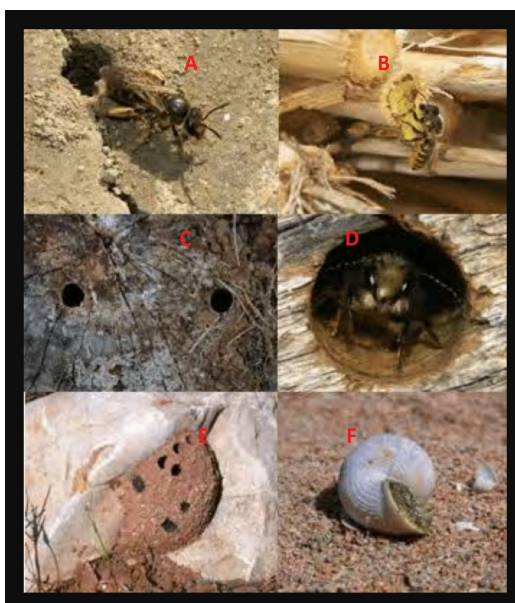


Figure 1.1: Different types of bee nests [100].

The features of the bee families mentioned above are described below. Our main references are [28, 40, 81].

#### **Family Colletidae**

Members in this family are short-tongued bees that secrete a plastic-like substance used to construct their nest. They nest under ground or in hollow twigs. Some subfamilies lack an external pollen carrying apparatus, as a result they carry pollen inside their crops.

#### **Family Andrenidae**

This is a family of mining bees that nest and burrow in the soil. Most species in this family do not sting, have short-tongues and are characterized by the presence of two subantennal suture. The females carry pollen on their hind legs.

#### **Family Halictidae**

They are called “sweat” bees. This family is the largest amongst the short-tongued bees. Possession of a single subantennal suture is their distinguishing feature. Depending on the species, members nest either in soil or wood. The family comprises of both social, solitary and cleptoparasitic bees (the ones that lay eggs in the nest of other species and steal the nest provisions of others because females do not carry pollen at all).

#### **Family Melittidae**

Members are short-tongued bees with one subantennal suture. They nest in dry regions. In addition to pollen harvesting, they also harvest oils from plants. They feed their larvae with the mixture of pollen and plant oils.

#### **Family Megachilidae**

These are the long-tongued bees. This family displays various types of nest constructing behavior. It comprises of carder bees, mason bees, leaf-cutters, and resin bees. Megachilid have no corbicula (pollen collecting structure), hence they collect pollen using the seta on their abdomen.

#### **Family Stenotritidae**

This family is only found in Australia and comprises of solitary bees that are large in size and fly very fast. They secrete plastic-like substance and build their nests in borrows. Their larvae are fed pollen and nectar.

## Family Apidae

This is the family of the long-tongued bees. Depending on species, they nest in wood, tunnels or use existing cavities. Although most members are solitary bees, there are also social and eusocial bees. Members includes, honey, bumble, digger, squash, and carpenter bees.

## Honey bees (*Apis mellifera* L.)

In this dissertation, the main interest is on *Apis mellifera* L. (honey-bearing) Western bees that belong to the family Apidae. There are about 24 races of *Apis mellifera* that are recognized by taxonomists of which about 10-12 of them occur in Africa and two are found in South Africa [40]. Figure 1.2 shows the distribution of *Apis mellifera* races in Africa and Europe. Races of *Apis mellifera* are categorized into four groups of genetic lineage, namely **A** (African), **O** (Eastern), **C** (European) and **M** (West European) groups [75]. *A.m. capensis* Escholtz (Cape honey bee) and *A.m. scutellata* Lepelerier (Savannah honey bee) races, which are the subject of this study, are found in South Africa and fall under the **A** lineage.



Figure 1.2: Distribution of *Apis mellifera* across Africa and Europe as modified from [37].

In addition to genetic variation among lineages, races of *Apis mellifera* are further classified according to their ability to adapt to climate. That is from temperate to tropical weather conditions and from high rainfall regions to semi-deserts [40]. The classification (taken from [37, 40]) is described as:

1. **Temperate races:** These races of *Apis mellifera* are able to survive winter temperature. They do not rear brood in winter and are large in size because they accumulate more proteins and fats which they use during the idle winter period.
2. **Tropical races:** These races comprise of the smaller populations that grow faster due to shorter developmental time. They either nest in cavities, bushes or underground. All races of *Apis mellifera* found in Africa (called African races) belong to this group. **African races:** The 10 *Apis mellifera* races found in Africa as shown in Fig 1.2 [40] occur in different vegetative zone on the continent [40, 75]. For instance: *A.m. capensis* is endemic to the cape floristic region of Southern Africa. *A.m. scutellata* has the widest distribution with ranges from the northern parts of South Africa up to the low lands of Eastern Africa (Fig 1.2). *A.m. adansonii* that is found in central and west Africa has the second widest distribution while *A.m. monticola* is found in the mountains of east Africa and *A.m. unicolor* on the islands of Madagascar. *A.m. litorea* in the east coast of the continent, *A.m. intemissa* occurs in the north, *A.m. sahariensis* is found in Atlas mountain ranges, *A.m. lamarckii* is distributed along the Nile river [75] (Fig 1.2).

In general, the classification of African races is based on natural zones of hybridization and introgression, the seasonal cycles of development, the swarming, migration and absconding, and the analysis of the bee flora of the continent [37].

## Honey bees and their importance

Honey bees are essential to man and his environment through services they provide directly or indirectly. The importance of honey bees can not be overemphasized for two main reasons described below.

- **Ecosystem services:** Honey bees play an important role in the ecosystem since they pollinate many plant species [91]. Because of the unique and crucial part they play in tropical ecosystems [91], bees from the Apidae family (honey, bumble, stingless bees, etc) are regarded as major pollinators in agricultural globally [1]. Thus, honey bees are viewed as keystone pollinators in ecosystem. Because for an ecosystem to function properly in terms of facilitating both plant and animal diversity, there is a critical need for pollination [91]. On one hand, flowering plant species need pollinators to transport pollen from anthers to their stigma or the stigma of other plants so that fertilization, that leads to development and maturity of fruits and seeds, can take place [91]. Pollination is very important in agriculture since it assists in the production of food and increasing crop yields. Although there are other insect and non-insect pollinators, honey bees are said to contribute approximately 9.5% to the global agriculture pollination [33]. The Western honey bees, *Apis mellifera*, contribute about USD 215 billion globally to ecosystem (specifically pollination) [86]. To carryout the ecosystem service of pollinating agricultural crops, managed honey bees are used as mobile pollinators in that they are moved from one place to another so they can pollinate crops where need arises [86]. Out of 300 crops grown globally, insects are said to pollinate about 80% [4]. This value, in agriculture is worth about USD 194 billion per year globally [6]. Both wild and managed honey bees are responsible for pollinating about 33% of crops [46]. This is why experts say “one of every three bites of our food depends on bees” [11].
- **Honey bee hive products:** Honey bee hive products are the basis for a multi-million dollar commercial industry globally [91], one of the reasons why humans have succeeded in partially domesticating them. These hive products includes honey, beeswax, propolis and royal jelly. In what follows, a brief description on how each of the hive-products is produced, used by both honey bees and humans is given. We start with honey, a sweet substance that honey bee workers produce. To produce honey, workers use their tube-shaped tongue to suck nectar (which is composed of water and sugars) from flowering plants as

they forage [101]. They store it (nectar) in their honey crop (honey stomach) and fly back to the hive. As they get to the hive, they regurgitate the nectar and pass it to other workers in the hive who mix it with enzymes so as to break the sugar contents and extracting water from the nectar, leaving a thick syrup (called honey) that they store in honeycomb cells [45,101]. Honey bees use honey as food for the hive during seasons when flowers have little or no nectar [101]. Humans use honey for medications such as cough drops and wound salves [48]. Honey is used as a food nutrient since it is a good source of energy [64] and as a replacement for sugar. It should be noted that one worker produces  $\frac{1}{12}$  of teaspoon for their lifetime which is achieved after  $800km$  of trip [11]. Thus, 12 workers are needed to produce one tablespoon full of honey. In European honey bees, a colony harvests approximately 240 kg of nectar and produces about 60 kg of honey per year [93] while African honey bees produce 15 kg of honey per season [87]. It should be noted that the amount of honey produced by the colony is influenced by factors such as the quantity and quality of nectar flow, laying rate of queen, pests and diseases in the hive and others [87]. Honey is often referred to as golden syrup because of health benefits associated with it to both honey bees and humans. The market value of honey is more expensive than oil and its demand is increasing globally [38]. In 2017, the total value of natural honey exported globally was USD 2.4 billion which is about 5% less compared to 2016 [103]. Table 1.1 below shows the top ten countries that imported natural honey in 2017, an estimated value of honey imported together with percentage [104]. Table 1.2 below shows the amount of natural honey produced in South Africa from the year 2013 to 2017 as recorded by Food and Agricultural Organization (FAO) [32].



Table 1.1: The top ten countries that imported natural honey in 2017, edited from [104].

<b>Country</b>	<b>Amount (in million USD)</b>	<b>ratio (in %)</b>
United States	568.8	24.4
Germany	281.9	12.1
Japan	143	6.1
United Kingdom	130.7	5.6
France	130.5	5.6
China	91.2	3.9
Italy	81.3	3.5
Belgium	79.7	3.4
Spain	76.8	3.3
Saudi Arabia	66.1	2.8

Table 1.2: The amount (in tonnes) of natural honey produced in South Africa from 2013 - 2017, edited from [32].

<b>Year</b>	<b>Amount (in tonnes)</b>
2017	1088
2016	1087
2015	1087
2014	1087
2013	1086

Honey bee wax or simply beeswax is a complex lipid that honey bee workers secrete from their wax-glands [101]. This wax consists mainly of hydrocarbons, monoesters, diesters, hydroxy polyesters and free acids [45, 93]. Workers use beeswax to construct their nests and comb cells (where they raise brood and store pollen and honey). Humans have originally used beeswax to make church candles [20]. Nowadays, beeswax is used in many products such as coating

pills in pharmaceutical industries, production of cosmetics like baby products and fragrances [64].

Royal jelly is a milky-substance which honey bee workers secrete from their hypopharangeal glands that are situated in the hypopharynx [45]. The workers use royal jelly to feed the brood at the larva stage. It is known that royal jelly is a designer-diet in the hive amongst the queen and the worker [93] because if workers in the hive want to raise a new queen due to various reasons such as, when the queen of the colony has left or the laying rate of the current queen has decreased. Then the workers feed the larva in the queen cell (honeycomb cell that look like a tea cup) more royal jelly than larvae in the other comb cells [45, 93]. Royal jelly provides bee larvae with an immunity against bacteria infection [93]. Humans mostly use royal jelly in anti-aging and wrinkle prevention creams [64]. It has been reported that long term consumption of royal jelly by humans does improve mental health and formation of red blood cells [60].

Propolis is made up of sticky resin collected by honey bee workers from trees and other botanical sources which is mixed with their saliva to produce propolis, known also as bee glue [45]. Workers use this glue as a sealant to close open spaces in the hive to protect the hive from rain, cold and diseases, to inhibit fungal, bacteria growth and parasites [101]. On the other hand, humans use propolis for the cure of dental cavities and in the production of cosmetics [64].

Therefore, beekeeping can be viewed as a conservation and poverty alleviation tool, which can be used to empower communities to boost economy.

## **Challenges facing beekeeping**

In the past decades, beekeepers have witnessed an increase in colony losses globally through phenomena known as Colony Collapse Disorder (CCD) which could not be associated with any pathogen or pests. But the result of interactions between pests, pathogens and pesticides [61]. Losses credited to CCD are in the range of 1.8% to

85% of total managed honey bee colonies [68]. In the case where the colony has fully collapsed, CCD is characterized by either the presence of food stores (pollen and honey), capped brood and no adult bees in the colony, with little or no build up of dead bees inside or in front of the colony. However, where the colony appears to be actively collapsing, there are few workers to maintain the present brood and the queen [43, 51]. Recent reports have revealed that pests, diseases, global honey trade and improper beekeeping management practices have contributed significantly towards colony losses [61, 68, 86].

In 2006, honey bee colony failures were reported globally [43], with South Africa reporting about 46.2% of colony losses in 2011 [74]. In this regard, we can mention the so-called *capensis calamity* (cc), which has, and is still causing great losses (up to 80%) of managed *A.m. scutellata* in the northern parts of South Africa [74]. In the process of writing this dissertation, it was reported that beekeepers were experiencing a massive loss of honey bees in the Cape region of South Africa. Thousands of bees along the Cape peninsula were reported dying where the cause of the death was assumed to be the poisonous insecticide from agricultural farming [71]. Without pollination in South Africa, it is estimated that about USD 700 billion per year of fruit export industry would be negatively affected while in seed production, between USD 5 and USD 6 million per year will decline [13]. It has been confirmed that there will be a miserable future without honey bees, and we were reminded of the price that we would pay due to the rapid loss of biodiversity and honey bees in particular which “could be the herald of a permanently diminishing planet” [98]. Thus, there has been significant concern over declines and losses of managed honey bee colonies due to their role as keystone pollinators of crops concurrent with existing concern regarding global pollinator declines [86]. Hence it is important to study honey bee population dynamics.

## **The purpose of the work**

The general purpose of this work is to study the dynamics of honey bee population within a colony from the modeling, theoretical and computational point of view,

specifically in the setting of the observed biological phenomenon of colony declines.

The interest and involvement in this fascinating topic of colony population dynamics of honey bees started in my honors project [50]. The purpose of the project was to understand as much as possible the fundamental paper [43] on this topic.

The specific purpose of this dissertation is four-fold.

1. Firstly, to provide a comprehensive description of honey bees as model organisms including their morphology, reproduction system, life cycle, division of labor and life span. We also focus on the biology behind honey bee races in South Africa, specifically the social parasite scenario as well as the cause(s) and symptoms of the *capensis calamity*.
2. Secondly, to build on the honors project [50] for a much better understanding of the paper [43]. More precisely:
  - (a) Thanks to the comprehensive biology of honey bees provided on the dissertation, we add, adjust, enhance and interpret the assumptions made in the formulation of the model (KMB) in [43].
  - (b) Provide details and proofs for the quantitative and qualitative results stated in [43] including global asymptotic stability results.
3. Thirdly, to improve the social parasite (SP) model that was proposed in [50] and do careful analysis that explains the *capensis calamity* in South Africa.
4. Lastly, to construct nonstandard finite difference (NSFD) schemes that are dynamically consistent with the KMB and SP models.

The tools used are fundamental results on continuous and discrete dynamical systems. These includes Gronwall inequality, Hartman-Grobman theorem, Lyapunov direct method and LaSalle invariance principle. Since our continuous models are two-dimensional dynamical systems, we also use the Poincaré-Bendixson theorem as well as the Dulac criterion. Note that these results (Poincaré-Bendixson theorem and Dulac criterion) apply neither to continuous dynamical system of dimension

greater than two nor to discrete dynamical systems. We use Wolfram Mathematica software for numerical simulations.

## Literature on honey bee modeling

The literature on the biology of honey bees is abundant. In particular, one can have an indication on the ever-growing publications in this field by looking at the “The South African Bee Journal” which is published quarterly by the South African Bee Industry Organization (SABIO). The biology of honey bees presented in this dissertation comes mostly from [93, 101].

As mentioned earlier, this dissertation originated from the mathematical model proposed in [43]. This specific choice is made for the following reasons:

1. To my best knowledge, this is the first mathematical model that predicts and explains colony collapse disorder (CCD) in terms of the foragers’ death rate without reference to any other factors.
2. The model is relatively simple, being restricted to only two compartments, namely the hives class and foragers class.
3. The restriction to only two compartments mentioned in (2) above has biological relevance. In particular:
  - The focus on workers only is justified by the fact that drones do not contribute to colony work [73, 80, 101]. Furthermore, there is a well recognized and documented division of labor among workers, which is age-based [83, 101], therefore it makes sense to classify them as hive bees and foragers.
  - Bearing in mind that in a healthy colony, the rate at which hive bees die is less significant to the overall population [80, 101], the death rate of hive bees is ignored while that of foragers can not.
  - Based on many reported cases on honey bee colony losses, it makes sense not to necessarily consider brood disease on colony failure and CCD [22,

69, 72]. Furthermore, given the complex relation that exists between the number of eggs reared in a colony and the number of bees in the hive, it makes sense to attempt to capture this relation by assuming that the eclosion rate is a saturated function that approaches the queen's laying rate as the total population of the hive bees increases.

- Whether the model is simple or not, death rate of the foragers is the underlying factor for the colony decline.

4. From the mathematical point of view, 2-dimensional dynamical systems allow the use of other results such as Poincaré-Bendixson Theorem, Dulac Criterion etc. system

This simplification permits therefore to easily gain some insight on the population dynamics and decline of honey bee colony.

We now want to comment on some of mathematical models that have additional compartments apart from the hive and foragers classes. While [16] improves the model in [43] by including the mortality rate of hive bees, it should be noted that the model in [43] was extended by the same authors in [44] where an additional compartment for brood is incorporated with an explicit dependence on food. These contributions, [44] and [16], fall under the category of works that explore the interactions of strategies (such as availability of food and climate change) and foragers death rate on colony fate [25, 27, 80].

The second category consists of works that model the colony failure as a contagion by a virus, which is transmitted by parasite varroa mites [25, 29, 47, 77]. In this category, models are enriched by additional compartments and factors such as infected bee class, mites class, demographics etc. In the two categories, the underlying factors for the decline is the foragers death rate.

To my best knowledge, our work [51] is the first publication on the NSFD method for differential equations model for honey bees. NSFD schemes are constructed using Mickens' rules [55], as formalized in [7], taking into account useful information such as the availability of exact schemes [79] and conservation laws [59].

## Outline of the dissertation

The rest of this dissertation is organized as outlined below. Chapter 2 deals with the review of some basic concepts on dynamical systems that are defined by ordinary differential equations and difference equations. These concepts are selected according to our needs for the quantitative and qualitative analysis of the mathematical models for honey bee population dynamics within the colony on which we focus in this work. The discrete dynamical systems on which we focus being nonstandard finite difference (NSFD) schemes, we present a directed overview of this approach.

In Chapter 3, we give an extensive description of the organizational structure of honey bee colonies. This includes their castes, morphology, reproduction system, division of labor, life cycle and lifespan. This knowledge of the biology of honey bees enables us to enhance the assumptions made in [43] so as to better understand how the model (KMB) proposed in [43] is derived. The main result on the existence and non existence of the CCD is proved in this chapter and reads as follows: The trivial equilibrium point  $(0,0)$  is globally asymptotically stable (GAS) whenever the death rate of foragers is above a critical value  $m_c$ ; the colony increases and stabilizes at a unique positive interior equilibrium point if the foragers' death rate is below  $m_c$ . This chapter is concluded by describing some mathematical models in the literature that explore other factors contributing to the declines of honey bee colonies.

Chapter 4 is devoted to the social parasite phenomenon in honey bees in South Africa. Our focal point is on how the host population of *A.m. scutellata* is affected by the presence of the parasites population of *A.m. capensis*. We discuss how the *capensis calamity*, which is still threatening South African beekeeping occurs and the symptoms associated with it. Assumptions are made, that enable us to formulate a mathematical (Social Parasite, SP) model. We show how colonies of *A.m. scutellata* are overtaken by parasitic clones of *A.m. capensis* in such a manner that colonies of *A.m. scutellata* decays exponentially to zero.

In Chapter 5, we design NSFD schemes for both the KMB and SP models. We theoretically prove that the constructed schemes are dynamically consistent with

their continuous models. This chapter is concluded by numerical simulations that support the theory and reliability of our schemes.

In the last chapter, we provide concluding remarks and show how our findings fit in literature. We also indicate how the work can be extended.



# Chapter 2

## Preliminaries on dynamical systems

The mathematical models investigated in this dissertation are in the framework of dynamical systems defined either by ordinary differential equations or difference equations. In this chapter, the main results and tools needed for the quantitative and qualitative analysis of continuous ordinary differential equations (from Section 2.1 to Section 2.5) and discrete dynamical systems (from Section 2.6 to Section 2.8) are collected. These results and tools are presented in the form that we will use them in this dissertation. Whenever it is necessary, we comment and provide suitable references on the general form of the results. Since the discrete dynamical systems that we have in mind are in the setting of the nonstandard finite difference (NSFD) method, we devote the last section of this chapter to it.

### 2.1 Generalities on continuous dynamical systems

We first consider dynamical systems defined by ordinary differential equations (ODEs). Our main reference on dynamical systems is [89]. We also mention the theses [42, 94] where most of the material that we need are presented in a way that we require.

The general setting of this dissertation is an autonomous first-order system of two-dimensional differential equations, in the dependent variable  $y \in \mathbb{R}^2$  and independent variable  $t \geq 0$  which has the form:

$$\dot{y} \equiv \frac{dy}{dt} = f(y), \quad y(0) = y_0, \quad (2.1.1)$$

where  $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  is a given vector-valued function and  $y_0 \in \mathbb{R}^2$  is the given initial data. We start by giving the definition of a dynamical system on a subset  $E \subseteq \mathbb{R}^2$ .

**Definition 2.1.1.** [42, 89, 94] *The initial value problem (2.1.1) is said to be a dynamical system on a set  $E \subseteq \mathbb{R}^2$  if for every  $y_0 \in E$ , there exists a unique continuously differential function  $y : [0, \infty) \rightarrow E$  which solves the Equation (2.1.1).*

**Remark 2.1.2.** *The system (2.1.1) and Definition 2.1.1 of a dynamical system can be considered for any vector-valued function  $f : \mathbb{R}^m \rightarrow \mathbb{R}^m$ , and any given initial data  $y_0 \in \mathbb{R}^m$ , such that  $y(t) \in \mathbb{R}^m$  is a solution defined for all  $t \geq 0$ , where  $m \in \mathbb{N}$ . Throughout this dissertation, we will be focusing on dynamical systems in  $\mathbb{R}^2$  which is the setting of population dynamics of hives and foragers in the honey bee colonies. It should also be noted that two-dimensional dynamical systems have specific features (e.g. Poincaré-Bendixson Theorem) that do not apply to higher order dimensional systems.*

At this stage, we introduce the concept of evolution semigroup operator for a dynamical system that helps to describe the evolution of the solution as time increases.

**Definition 2.1.3.** *For a dynamical system on  $E \subseteq \mathbb{R}^2$ , its evolution semigroup operator or solution operator is defined to be the map;*

$$\phi(t) : E \rightarrow E \quad \text{such that} \quad y(t) = \phi(t)y_0,$$

where  $y(t)$  is the unique solution of the system (2.1.1).

The terminology in Definition 2.1.3 is inspired by the following properties:

1. For all  $t > 0$ ,  $s > 0$ , we have  $\phi(t + s) = \phi(s)\phi(t) = \phi(t)\phi(s)$ ,
2. If  $t = 0$  then  $\phi(0) = I$ , the identity operator.

Definition 2.1.3 is a convenient notation for the advancement of the solution through time  $t$ . Taking this definition into account, we introduce the set

$$\Gamma^+(y_0) = \left\{ \phi(t)y_0 : t \in [0, \infty) \right\} \subset E$$

which is called the positive or forward orbit/trajectory of the initial data  $y_0$ .

**Remark 2.1.4.** *Stating that the initial value problem (2.1.1) is a dynamical system is linked to saying that the problem (2.1.1) is well-posed in the sense of Hadamand. That is:*

1. *A solution,  $y(t)$ , to the problem (2.1.1) exists.*
2. *The solution is unique.*
3. *The solution depends continuously on the given initial data.*

The minimal condition to be imposed on the function  $f$  in Equation (2.1.1) is contained in the next definition:

**Definition 2.1.5.** *The function  $f(y)$  is said to be locally Lipschitz if for every compact set  $B \subset E \subseteq \mathbb{R}^2$ , there exists a real number  $K \geq 0$  (called the Lipschitz constant) depending on  $B$  such that*

$$\|f(y_1) - f(y_2)\| \leq K \|y_1 - y_2\| \quad \text{for all } y_1, y_2 \in B. \quad (2.1.2)$$

Here  $\|\cdot\|$  denotes the Euclidean norm. If Condition (2.1.2) is satisfied for  $B = E$  then the function  $f$  is said to be globally Lipschitz. The Lipschitzian nature of functions plays a major role in proving the existence and uniqueness results for many mathematical problems [105]. To be more specific, we have the following theorem which guarantees the existence and uniqueness of the local solution.

**Theorem 2.1.6.** [42] *Assume that the function  $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  satisfies the Lipschitz condition on the ball  $\bar{B} = \bar{B}(y_0, r)$  with Lipschitz constant  $L_B$ . Consider the finite time*

$$T_B = \frac{r}{\sup_{y \in \bar{B}} \|f(y)\|}.$$

*Then the initial value problem (2.1.1) has a unique solution  $y(t)$  in the interval  $[0, T_B]$ .*

The global solution is obtained by proving some a priori estimates as stated in the following result.

**Theorem 2.1.7.** [42, 89] *Let  $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  be locally Lipschitz on an  $\epsilon$ -neighborhood  $E_\epsilon$  of a bounded set  $E \subseteq \mathbb{R}^2$ . If for any  $y_0 \in E$ , the solution  $y(t)$  of (2.1.1) satisfies*

$y(t) \in E$  for each time  $t \geq 0$  where the solution exists, then (2.1.1) defines a dynamical system on  $E$ .

The next result is the so-called Gronwall's Inequality. The general forms of which can be found in the literature [99]. Gronwall's Inequality helps in obtaining a priori bounds for solutions of differential equations. We provide below a simple version of the Gronwall's Inequality which is relevant to our needs in this dissertation.

**Lemma 2.1.8.** [89][Gronwall's Inequality] *For a real-valued function*

$$z : [0, +\infty) \rightarrow \mathbb{R}$$

*that satisfies the inequality*

$$\dot{z} := \frac{dz}{dt} \leq az + b \quad ; \quad z(0) = z_0$$

*where  $a$  and  $b$  are constants, there holds the following inequalities:*

$$z(t) \leq \begin{cases} z_0 e^{at} + \frac{b}{a} (e^{at} - 1) & \text{if } a \neq 0 \\ z_0 + bt & \text{if } a = 0 \end{cases}$$

In many cases, it is not possible to explicitly solve dynamical systems even though it is known that the solution exists and is unique. Thus the importance of studying the behavior of the solutions. In order to do the qualitative analysis, the concepts in the next definition are essential regarding the action of the evolution semigroup operator  $\phi(t)$  on  $E \subseteq \mathbb{R}^2$ .

**Definition 2.1.9.** [42, 89, 94] *For a dynamical system defined by (2.1.1), a set  $E$  is said to be*

1. *positively invariant under the map  $\phi$  if  $\phi(t)E \subseteq E$  for all  $t \geq 0$ ,*
2. *negatively invariant under  $\phi$  if  $\phi(t)E \supseteq E$  for all  $t \geq 0$ ,*
3. *invariant under  $\phi$  if it is both positively and negatively invariant so that  $\phi(t)E = E$  for all  $t \geq 0$ .*

Special trajectories play a crucial role in the qualitative analysis of dynamical systems. The simplest of such trajectories are equilibrium points which turn out to be the simplest invariant sets. In what follows, we define an equilibrium point of the dynamical system and explain its properties.

**Definition 2.1.10.** A point  $y^* \in \mathbb{R}^2$  is said to be an equilibrium point of the autonomous system (2.1.1) if

$$f(y^*) = 0.$$

**Remark 2.1.11.** It is with no doubt from Definition 2.1.10 that the point  $y^*$  is an equilibrium point of the system (2.1.1) if and only if it is a fixed point of the semigroup operator, that is  $\phi(t)y^* = y^*$ .

In order to compare the other trajectories to the simplest invariant sets, equilibrium points, we use the following definition

**Definition 2.1.12.** [89] An equilibrium point,  $y^*$ , for a dynamical system on  $E \subset \mathbb{R}^2$  is said to be:

- (a) stable if for every  $\epsilon > 0$ , there exists  $\delta > 0$  such that  $\|y_0 - y^*\| < \delta$  implies  $\|y(t) - y^*\| < \epsilon$  for all  $t > 0$ ,
- (b) locally attractive, if there exists  $\eta > 0$  such that  $\|y_0 - y^*\| < \eta$  implies that  $\lim_{t \rightarrow \infty} y(t) = y^*$ ,
- (c) locally asymptotically stable if  $y^*$  is stable and locally attractive
- (d) globally attractive if (b) holds for any  $y_0 \in E$ ,
- (e) globally asymptotically stable if (a) and (d) hold.
- (f) unstable whenever (a) fails to hold.

## 2.2 Linearization for continuous dynamical systems

In practice, it is not easy to determine the stability/instability of equilibrium point of a dynamical system through Definition 2.1.12. The simplest way to investigate the stability property of the equilibrium point is through linearization process, which we explain below. The type of the equilibrium point for which the linearization process works is described in the following definition.

**Definition 2.2.1.** [15, 89] *An equilibrium point  $y^*$  is said to be hyperbolic if the eigenvalues,  $\lambda$ , of the Jacobian matrix,  $J \equiv J(y^*)$  of the function  $f$  at the equilibrium point  $y^*$ , have non-zero real parts, that is,  $\text{Re}(\lambda) \neq 0$ . Otherwise, the equilibrium point is called non hyperbolic.*

In what follows, we explain the linearization process of the dynamical system (2.1.1) about the equilibrium point  $y^*$ .

Suppose that  $y^*$  is a hyperbolic equilibrium point of the dynamical system (2.1.1) and that the function  $f$  is sufficiently smooth. Then, the Taylor expansion of the function  $f$  about the equilibrium point  $y^*$  yields:

$$f(y) = f(y^*) + J(y^*)(y - y^*) + \mathcal{O}((y - y^*)^2) \quad (2.2.1)$$

or, where  $u = y - y^*$ ,

$$\dot{u} = Ju + \mathcal{O}(u^2). \quad (2.2.2)$$

Since  $\mathcal{O}(u^2)$  is small whenever  $u$  is, it makes sense to assume that  $u_0$  near the origin the solutions of (2.2.2) behaves in a similar manner as solutions of

$$\dot{u} := \frac{du}{dt} = Ju, \quad (2.2.3)$$

which are given by

$$u(t) = u_0 e^{tJ}. \quad (2.2.4)$$

Equation (2.2.3) is called the linearization of the system (2.1.1) at  $y^*$ .

The stability of the non-linear dynamical system (2.1.1) via the linear dynamical system (2.2.3) is guaranteed by the following theorem, which is an important result about the local behavior of dynamical systems in the neighborhood of a hyperbolic equilibrium point.

**Theorem 2.2.2.** [89] [Hartman-Grobman Theorem] *Assume that the function  $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  is of class  $C^1$  and consider a hyperbolic equilibrium point  $y^*$  of a dynamical system (2.1.1). Then there exists  $\delta > 0$ , a neighborhood  $\mathcal{N} \subset \mathbb{R}^2$  of the origin, and a homeomorphism  $h : B(y^*, \delta) \rightarrow \mathcal{N}$  such that  $u(t) := h(y(t))$  solves (2.2.3) if and only if  $y(t)$  solves (2.1.1).*

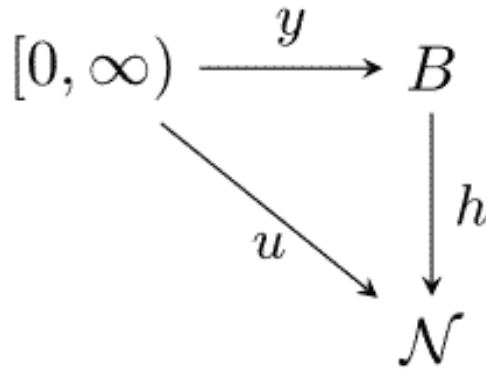


Figure 2.1: Hartman-Grobman Theorem for the continuous system

Theorem 2.2.2 implies that, for a hyperbolic equilibrium point  $y^*$  of a dynamical system, the behavior of the solution,  $y(t)$  of the non-linear system (2.1.1) near  $y^*$ , as  $t \rightarrow +\infty$  is the same as the behavior of the solution,  $u(t)$ , of the linear System (2.2.3) near the origin.

**Remark 2.2.3.** *With the matrix  $J$  of order two having entries  $J_{ij}$ , we have*

$$\text{tr}J = \lambda_1 + \lambda_2 = J_{11} + J_{22} \quad \text{and} \quad \det J = \lambda_1 \lambda_2 = J_{11}J_{22} - J_{12}J_{21},$$

where the eigenvalues  $\lambda_1$  and  $\lambda_2$  of  $J$  are the roots of the characteristic equation

$$\det(J - \lambda I) = 0 \quad \text{which is equivalent to} \quad \lambda^2 - \lambda \text{tr}J + \det J = 0.$$

Taking into consideration the equation (2.2.4), we have the following precise result:

**Corollary 2.2.4.** *For  $y_0$  close to  $y^*$ , the equilibrium point  $y^*$  is asymptotically stable if and only if  $\text{Re}(\lambda) < 0$  for all  $\lambda \in \sigma(J)$  or equivalently, the trace,  $\text{tr}J$ , of  $J$  is negative and the determinant,  $\det J$ , is positive.*

## 2.3 Poincaré-Bendixson Theorem

We address, in this section, the situation when the Linearization process does not hold, resulting in a more complex structure of the final state of the trajectories. It should be noted that the results in this section do not hold true for dynamical systems of dimension higher than two. The complex structure of the trajectories can be either one of the following [15]:

1. the system does not have asymptotically stable equilibrium points,
2. the solution does not start near an equilibrium point,
3. the equilibrium point of the system is non hyperbolic.

To carryout the qualitative analysis of a dynamical system that has one of the above feature, we study the structure of the  $\omega$ -limit set that we define below.

**Definition 2.3.1.** [15] *Let  $y_0 \in \mathbb{R}^2$  be the initial data of the system (2.1.1) with its forward orbit  $\Gamma^+ \equiv \Gamma^+(y_0)$ . The limit set of  $\Gamma^+$ , known also as the  $\omega$ -limit set of the point  $y_0$ , is denoted by  $L(\Gamma^+) = \omega(y_0)$ , and defined by*

$$L(\Gamma^+) \equiv \omega(y_0) := \left\{ \bar{y} \in \mathbb{R}^2 : \exists \{t_n > 0\} \rightarrow \infty : \lim_{n \rightarrow \infty} \phi(t_n)(y_0) = \bar{y} \right\}.$$

The Poincaré-Bendixson Theorem in its general form can be found in [36, 88]. Here we state the theorem in the setting of a dynamical system on  $E$  in the sense of Definition 2.1.1 whereby the existence and uniqueness of a global solution that remains in  $E$  is guaranteed.

**Theorem 2.3.2.** [36][Poincaré-Bendixson Theorem] *Suppose that a subset  $E$  of  $\mathbb{R}^2$  is compact, positively invariant and has a finite number of equilibrium points (possibly zero) of the two-dimensional dynamical system (2.1.1). Let  $y_0 \in E$ . Then one of the following possibilities holds for the bounded forward orbit  $\Gamma^+$  and for the structure of the  $\omega$ -limit set of  $y_0$ :*

1. *The  $\omega$ -limit set,  $\omega(y_0)$ , is a single point  $\bar{y}$  which is an equilibrium point and the solution is such that  $\lim_{t \rightarrow \infty} \phi(t)(y_0) = \bar{y}$ .*
2. *The  $\omega$ -limit set,  $\omega(y_0)$ , is a periodic orbit  $\Gamma$ . In this case either  $\Gamma^+(y_0) = \omega(y_0) = \Gamma$  or else  $\Gamma^+(y_0)$  spirals with increasing time towards  $\Gamma$  on one side of  $\Gamma$ .*
3. *The  $\omega$ -limit set,  $\omega(y_0)$ , consists of equilibrium points and an orbit joining them.*

**Remark 2.3.3.** *In the case when the positively invariant and compact set  $E$  does not contain equilibrium points of the dynamical system, only the scenario 2 in Theorem*



2.3.2 will apply. One interesting situation in this scenario is when  $\Gamma^+(y_0) \neq \Gamma$ . In this case  $\Gamma$  is called the limit cycle [36].

From Remark 2.3.3, Poincaré-Bendixson Theorem is very useful in identifying the existence of the periodic solutions and to find out whether the system under consideration has a confined set. At the same time it is important to determine whether a 2-dimensional system has periodic orbits or not. The next theorem addresses this situation in a manner that is sufficient to this dissertation.

**Theorem 2.3.4.** [15][Dulac Criterion] *Let  $\beta$  be a function of class  $C^1$  on a simply connected domain  $E$  on which the system (2.1.1) is considered. If the divergence of the vector-valued function,  $\beta f$ ,*

$$\operatorname{div}(\beta f) = \frac{\partial(\beta f_1)}{\partial y_1} + \frac{\partial(\beta f_2)}{\partial y_2},$$

*has a constant sign then there are no periodic orbits of the system (2.1.1) in  $E$ .*

**Remark 2.3.5.** 1. *If  $\beta = 1$  in Theorem 2.3.4 above then Theorem 2.3.4 is known as Bendixson Theorem.*

2. *Other sufficient conditions for the system (2.1.1) not to have periodic solutions include:*

(i) *the vector function  $f$  is a gradient system as defined below  $f = -\nabla\gamma$ .*

(ii) *the system admits a strict Lyapunov function as defined below (conclusion 1 in Theorem 2.3.2 will apply).*

## 2.4 Lyapunov direct method for continuous dynamical systems

In this section, we consider the Lyapunov direct method (also called the second method of Lyapunov) to determine the stability or instability of the equilibrium point of dynamical systems. Apart from being also suitable for situations where the Poincaré-Bendixson theorem and linearization process do not apply, this approach permits one to establish global stability results. First, we define a Lyapunov function.

**Definition 2.4.1.** [36, 53, 88, 89, 99] Assume that the system (2.1.1) defines a dynamical systems on an open  $E \subset \mathbb{R}^2$  and  $y^* \in E$  is an equilibrium point.

1. A function  $V \in C^1(E, \mathbb{R})$  is called a Lyapunov function of System (2.1.1) for  $y^*$  on a neighborhood  $B \subset E$  of  $y^*$  if it satisfies the following two properties:

(i)  $V$  is positive definite in the sense that

$$V(y^*) = 0 \quad \text{and} \quad V(y) > 0 \quad \text{for all} \quad y \in B \setminus \{y^*\},$$

(ii)

$$\dot{V}(y) \leq 0 \quad \text{for all} \quad y \in B \tag{2.4.1}$$

where  $\dot{V}(y)$  is the directional derivative of  $V$  in the direction of the vector-function  $f$  and is given by

$$\dot{V}(y) := \lim_{h \rightarrow 0} \frac{V(y + hf(y)) - V(y)}{h}.$$

2. A Lyapunov function  $V$  is called a strict Lyapunov function whenever

$$\dot{V}(y) < 0 \quad \text{for all} \quad y \in B.$$

Note that by Taylor expansion

$$\dot{V}(y) = \nabla V(y)f(y). \tag{2.4.2}$$

Moreover, if  $y(t)$  is the solution of the differential equation (2.1.1), then by the chain rule from Equations (2.4.2) and (2.1.1), we obtain

$$\dot{V}(y(t)) = \frac{d}{dt}V(y(t)). \tag{2.4.3}$$

The relation (2.4.3) motivates the fact that  $\dot{V}$  is often called the derivative of  $V$  along trajectories. The Lyapunov function and the relation (2.4.3) give information on the solution  $y(t)$  of the dynamical system (2.1.1) without its prior knowledge. As a matter of fact, we have the following result:

**Theorem 2.4.2.** [53, 89, 94] Let  $V$  be a positive definite Lyapunov function of the dynamical system (2.1.1) on a neighborhood set  $B \subset E$  of an equilibrium point  $y^*$ . Then the following holds true:

1. The equilibrium point  $y^*$  is stable,
2. The equilibrium point  $y^*$  is locally asymptotically stable if  $\dot{V}(y) < 0$  for all  $y \in B \setminus \{y^*\}$  (i.e  $V$  is strictly a Lyapunov function).
3. The equilibrium point  $y^*$  is unstable if  $\dot{V} > 0$  for all  $y \in B \setminus \{y^*\}$ .

The main challenge associated with the use of a Lyapunov function is that it is not easily constructed. But once it is available, it has the advantage of leading to some global stability properties of an equilibrium point especially if the system under consideration is dissipative.

**Definition 2.4.3.** [89, 94] A dynamical system defined on a set  $E \subseteq \mathbb{R}^2$  is said to be dissipative if there exists a bounded, positively invariant set  $U$  with the property that for any bounded set  $B \subseteq \mathbb{R}^2$ , there exists a time  $t^* = t^*(U, B) \geq 0$  such that  $\phi(t)B \subseteq U$  for all  $t > t^*$ . The set  $U$  is called an absorbing set.

With Definition 2.4.3 in mind, the global stability result is the LaSalle Invariance Principle that reads as follows:

**Theorem 2.4.4.** [94][LaSalle Theorem] Let  $y^*$  be an equilibrium point of a dissipative dynamical system on a set  $E$ , defined by (2.1.1). Let  $V$  be a positive definite Lyapunov function for  $y^*$  on the set  $E$ . Furthermore, let  $\mathcal{E} = \{y \in E : \dot{V}(y) = 0\}$ . If  $\mathcal{M}$  is the largest invariant subset of  $\mathcal{E}$ , then  $y^*$  is globally asymptotically stable on  $E$  if and only if it is globally asymptotically stable for the system restricted to  $\mathcal{M}$ . In particular,  $y^*$  is globally asymptotically stable on  $E$  if  $\mathcal{E} = \{y^*\}$ .

## 2.5 Bifurcation of equilibrium points

To conclude the preliminaries on continuous dynamical system, we consider the concept of bifurcation of equilibrium points. Bifurcation theory is well documented. However, to make this part of the dissertation self-contained, we follow the presentation given in [94].

Let us assume that the right-hand side of the dynamical system (2.1.1) depends on

a real parameter, say  $\mu$ . That is, the system

$$\dot{y} = f(y)$$

is replaced by

$$\dot{y} = f(y, \mu). \tag{2.5.1}$$

The equilibrium points of the system (2.5.1) are the roots  $(y, \mu)$  of the equation

$$f(y, \mu) = 0. \tag{2.5.2}$$

In a nutshell, we say that a bifurcation occurs at a critical point  $\mu = \mu_0$  of the parameter  $\mu$  whenever the behavior of the system changes as the parameter passes through  $\mu_0$ , namely for  $\mu < \mu_0$  and for  $\mu > \mu_0$ . In fact, according to Fred-Brauer and Castillo-Chavez [15], a bifurcation is defined by a point in the parameter space, say  $\mu - y$ , where equilibrium points appear, disappear or change stability. More specifically, we have the following definition:

**Definition 2.5.1.** [94, 102] *An equilibrium point  $(y^*, \mu_0)$  of System (2.5.1) is said to undergo a bifurcation at the point  $\mu = \mu_0$  or alternatively the parameter  $\mu = \mu_0$  is said to be a bifurcation value for the system (2.5.1) if the dynamics of (2.5.1) near both  $y = y^*$  and  $\mu = \mu_0$  is not the same as the dynamics near  $y = y^*$  at  $\mu = \mu_0$ .*

Though there are several types of bifurcation (e.g pitchfork bifurcation, saddle node bifurcation, hopf bifurcation) we will, in this work, mostly be interested in the following type of bifurcation:

**Definition 2.5.2.** [94, 102] *The dynamical system (2.5.1) is said to undergo a transcritical bifurcation at  $\mu = \mu_0$  if there holds the following conditions:*

1. *At least two curves  $y = y(\mu)$  of equilibrium points exist in the  $\mu - y$  space for  $\mu < \mu_0$  and  $\mu > \mu_0$ ;*
2. *The curves of the equilibrium point branch at  $\mu = \mu_0$  or intersect at the point  $(y^*, \mu_0)$ ;*
3. *The stability of the equilibrium point along a given curve changes as it passes the point  $\mu = \mu_0$ .*

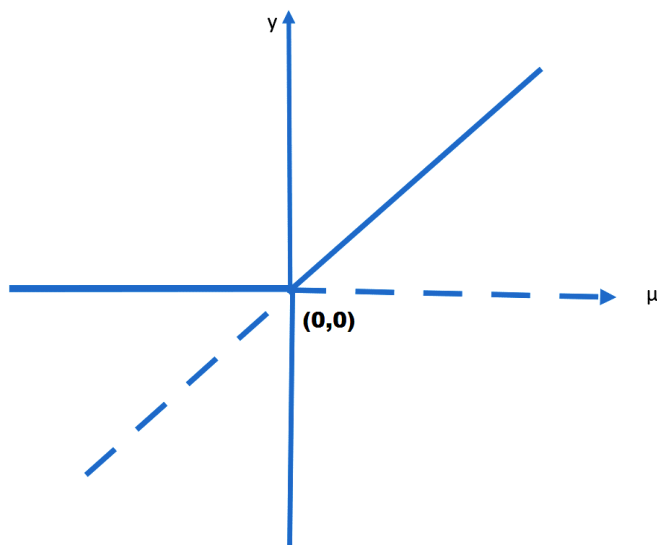


Figure 2.2: Bifurcation diagram of  $\dot{y} = y(\mu - y)$  [102]; solid lines represent stable equilibrium points and dashed lines represent unstable equilibrium points.

**Remark 2.5.3.** Typically, the bifurcation points of the system (2.5.1) are represented on a bifurcation diagram, which is the parameter space  $\mu - y$  where curves  $y = y(\mu)$  of equilibrium points and their stability properties are displayed. Fig 2.2 illustrates Definition 2.5.2, with  $\mu = 0$  being a transcritical bifurcation for the involved scalar equation: for  $\mu < 0$ ,  $y = 0$  is asymptotically stable while  $y = \mu$  is unstable; for  $\mu > 0$ ,  $y = 0$  becomes unstable while  $y = \mu$  is asymptotically stable.

## 2.6 Generalities on discrete dynamical systems

Dynamical systems generated by the mappings from  $\mathbb{R}^2$  to  $\mathbb{R}^2$  are presented in this section. Discrete dynamical system concepts are in some sense the same as those of continuous dynamical systems on the understanding that the time variable  $t \geq 0$  is now replaced by the discrete variable  $n \in \mathbb{N}$ . Our main references are [42, 94] in the specific form adapted in [89].

Here and after, we consider a sequence  $\{y_n\}_{n=0}^{\infty}$  in  $\mathbb{R}^2$  defined recursively from  $y_0$  by

$$y_{n+1} = G(y_n), \quad (2.6.1)$$

where  $G : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  is a map.

**Definition 2.6.1.** Equation (2.6.1) defines a discrete dynamical system on a set  $E \subseteq \mathbb{R}^2$  if, for every  $y_0 \in E$ , the sequence  $\{y_n\}_{n=0}^{\infty}$  is such that  $y_n$  remains in  $E$  for all  $n \geq 0$ .

**Definition 2.6.2.** The evolution semigroup operator for a discrete dynamical system of  $E$  is defined to be the map  $S^n : E \rightarrow E$  such that  $y_n = S^n y_0 = G \circ G \dots \circ G y_0$ .

The following are the properties of the evolution semigroup operator:

1.  $y_{m+n} = S^m y_n = S^n y_m = S^{m+n} y_0$  for all  $m, n \geq 0$ ,
2.  $S^0 = I$ , the identity operator.

The discrete analogue of Gronwall's Inequality, as stated in Lemma 2.1.8, reads as follows:

**Lemma 2.6.3.** [Gronwall's Inequality] Let a positive sequence  $\{y_n\}_{n=0}^N$  satisfy

$$y_{n+1} \leq C y_n + D \quad \text{for all } n = 0, 1, \dots, N-1,$$

where  $C$  and  $D$  are constants and  $C > 0$ . Then, there holds the following:

$$y_n \leq \frac{D}{1-C}(1-C^n) + y_0 C^n \quad \text{for all } n = 0, 1, \dots, N \quad \text{if } C \neq 1$$

and

$$y_n \leq nD + y_0 \quad \text{for all } n = 0, 1, \dots, N \quad \text{if } C = 1.$$

We deal with the behavior of the discrete dynamical system on  $E \subseteq \mathbb{R}^2$  defined by the system (2.6.1).

**Definition 2.6.4.** [42, 89, 94] A subset  $B \subset E \subseteq \mathbb{R}^2$  is said to be

1. positively invariant under the map  $S^n$  if  $S^n B \subseteq B$  for all  $n \geq 0$ ,
2. negatively invariant under the map  $S^n$  if  $S^n B \supseteq B$  for all  $n \geq 0$ ,
3. invariant if it is both positively and negatively invariant; That is,  $S^n B = B$  for all  $n \geq 0$ .

**Definition 2.6.5.** A point  $y^* \in \mathbb{R}^2$  is called a fixed-point of the discrete dynamical system (2.6.1) if  $y^* = G(y^*)$  or  $y^* = S^n y^*$  for all  $n \geq 0$ .

**Definition 2.6.6.** [42, 89, 94] Let  $y^* \in \mathbb{R}^2$  be a fixed point of the discrete dynamical system. Then,  $y^*$  is:

1. stable if, for any  $\epsilon > 0$ , there exists  $\delta(\epsilon) > 0$  such that if  $\|y_0 - y^*\| < \delta$ , then  $\|y_n - y^*\| < \epsilon$  for all  $n \geq 0$ ;
2. locally attractive if there exists  $\eta > 0$  such that  $\|y_0 - y^*\| < \eta$  implies that  $\lim_{t \rightarrow \infty} y(t) = y^*$
3. locally asymptotically stable if (1) and (2) hold
4. globally attractive if (2) holds for all  $y_0 \in E$
5. globally asymptotically stable if (1) and (4) holds
6. unstable if (1) does not hold.

In practice, it is difficult to investigate the stability of fixed points of the discrete dynamical system using Definition 2.6.6. In the next section, we explain the practical way of determining the stability or instability of the fixed points.

## 2.7 Linearization for discrete dynamical systems

To investigate the stability or instability of the fixed-point  $y^*$  of the discrete dynamical system, we assume that the map  $G$  in Equation (2.6.1) is of class  $C^1$  and we denote the Jacobian matrix of  $G$  at  $y^*$  by  $J = JG(y^*)$ . Then,

$$u_{n+1} = Ju_n \quad \text{for } n = 0, 1, 2, \dots \quad (2.7.1)$$

is the linearization of (2.6.1) around the fixed point  $y^*$  where  $u_n = y_n - y^*$ . The stability properties of the discrete linear system (2.7.1) is determined by the eigenvalues of the Jacobian matrix  $J$ . Thus, the stability property of the fixed point  $y^*$  of (2.6.1) would be easily related to the stability property of the fixed point  $u^* = 0$  of the linear system (2.7.1). Below, we define the type of the fixed point for which the linearization process works.

**Definition 2.7.1.** [89] A fixed point  $y^*$  of the discrete dynamical system is said to be hyperbolic if no eigenvalues of the Jacobian matrix  $J$  lie on the unit circle. That is,  $|\lambda| \neq 1$  for all  $\lambda \in \sigma(J)$ . Otherwise, the fixed point is called non-hyperbolic.

**Theorem 2.7.2.** [89][Hartman-Grobman Theorem] Let the discrete dynamical system (2.6.1), with map  $G : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  of class  $C^1$ , have hyperbolic fixed point  $y^*$ . Then, there exist  $\delta > 0$ , a neighborhood  $\mathcal{N} \subset \mathbb{R}^2$  of the origin and a homeomorphism  $h : B(y^*, \delta) \rightarrow \mathcal{N}$  such that

$$h(G(y_0)) = Jh(y_0) \quad \text{for all } y_0 \in B(y^*, \delta).$$

Consequently, by setting  $u_n = h(y_n)$  for all  $n \geq 0$ , the mapping (2.6.1) in the neighborhood  $B(y^*, \delta)$  of  $y^*$  is equivalent to the mapping (2.7.1) in the neighborhood  $\mathcal{N}$  of the origin.

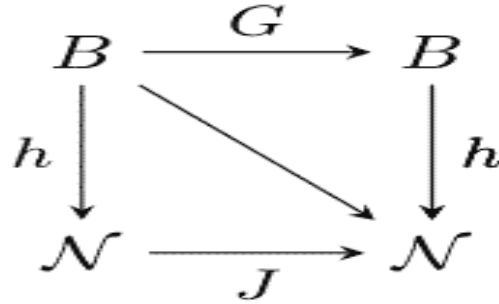


Figure 2.3: Hartman-Grobman Theorem for the discrete system

The practical use of Theorem 2.7.2 is stated in the next result.

**Theorem 2.7.3.** [89, 94, 99] Let a dynamical System (2.6.1), with  $G : \mathbb{R}^2 \rightarrow \mathbb{R}^2$  of class  $C^1$ , have hyperbolic fixed-point  $y^*$ . Then,

1. The fixed-point  $y^*$  is asymptotically stable if and only if for

$$u_n = J^n u_0,$$

solution of (2.7.1), with  $\|u_0\| := \|y_0 - y^*\|$  small enough, we have

$$\lim_{n \rightarrow \infty} u_n = 0 \quad \text{or equivalently} \quad |\lambda| < 1 \quad \text{for all } \lambda \in \sigma(J).$$



2. The fixed-point is unstable if there exists at least one eigenvalue,  $\lambda \in \sigma(J)$ , of the Jacobian matrix such that

$$\lim_{n \rightarrow \infty} \|u_n\| = \infty \quad \text{or equivalently} \quad |\lambda| > 1.$$

## 2.8 Lyapunov direct method for discrete dynamical systems

In this section, we assume that a fixed-point  $y^*$  of the discrete dynamical system (2.6.1) can be non-hyperbolic, in which case Theorem 2.7.2 and Theorem 2.7.3 do not apply. In order to address the stability or instability property of the fixed point, we use a Lyapunov function in conjunction with LaSalle Invariance Principle just as explained in the continuous dynamical system case (section 2.4).

**Definition 2.8.1.** [53, 89, 94] Let  $y^*$  be a fixed point of the discrete dynamical system (2.6.1) defined on  $E \subseteq \mathbb{R}^2$ . A function  $V \in C^1(E, \mathbb{R}^2)$  is said to be a Lyapunov function for  $y^*$  on some neighborhood  $B \subset E$  if

1. the function  $V$  satisfies  $V(y^*) \leq V(y)$  for all  $y \in B$ ,
2. the inequality  $V(G(y)) \leq V(y)$  holds for all  $y \in B$ .

If, in addition,  $V(y^*) = 0$  and  $V(y) > 0$  for all  $y \in B \setminus \{y^*\}$ , then  $V$  is said to be positive definite function at  $y^*$ .

Like in the case of continuous dynamical systems, construction of Lyapunov function is not easy. But once determined, it becomes possible to check the stability properties of a fixed-point as specified in the next result.

**Theorem 2.8.2.** [53, 89, 94] If there exists a Lyapunov function  $V(y)$  for the fixed-point  $y^*$  on the ball  $B(y^*, \delta)$ , then the fixed point  $y^*$  is stable. If  $V(G(y)) < V(y)$  for all  $y \in B(y^*, \delta) \setminus \{y^*\}$  then  $y^*$  is locally asymptotically stable, whereas  $y^*$  is unstable if  $V(G(y)) > V(y)$  for all  $y \in B(y^*, \delta) \setminus \{y^*\}$

The following concept plays a major role for the global asymptotic stability of the fixed-point.

**Definition 2.8.3.** [53, 89, 94] A discrete dynamical system on  $E$  is said to be dissipative if there exists a compact, positively invariant set  $B \subset \mathbb{R}^2$  with the property that for any bounded set  $D \subseteq E$ , there exists  $n^* = n^*(B, D) \geq 0$  such that  $S^n D \subseteq B$  for all  $n > n^*$ . The set  $B$  is called an absorbing set. In the case when set  $D$  is replaced by each point  $y_0 \in E$ , the dynamical system is said to be point dissipative.

The following result describes how the global asymptotic stability can be achieved.

**Theorem 2.8.4.** [53, 89, 94] Suppose that  $y^*$  is a fixed-point of the discrete dynamical system (2.6.1) defined on  $E$ . Assume further that the system (2.6.1) is dissipative. Assume also that there exists a continuous function  $V : \bar{E} \rightarrow \mathbb{R}$  such that

1. the function  $V$  is bounded from below on  $E$ ,
2. the inequality  $V(G(y)) \leq V(y)$  holds true for all  $y \in E$ ,
3. the fixed-point is globally asymptotically stable when the system (2.6.1) is restricted to the set  $\mathcal{M}$ , which is the largest invariant set contained in

$$\mathcal{E} = \{y \in E : V(G(y)) = V(y)\}.$$

Then, the fixed-point  $y^*$  is globally asymptotically stable on the whole set  $E$ , which is in particular the case when  $\mathcal{M} = \{y^*\}$ .

**Remark 2.8.5.** Theorem 2.8.4 is a version of the LaSalle Invariance Principle. The function  $V$  is some kind of Lyapunov function even though the lower bound required for  $V(y)$  is not specifically for  $V(y^*)$  as stated in the first part of Definition 2.8.1. The invariance principle nature is contained in part (3) of Theorem 2.8.4.

## 2.9 Nonstandard finite difference schemes

In general, the continuous system (2.1.1) cannot be completely solved by analytic techniques. Consequently, numerical methods are of fundamental importance in gaining more useful insights on the solution of the differential equation.

We consider a difference equation

$$D_{\Delta t} y_n = G_{\Delta t}(f, y_n), \tag{2.9.1}$$

which gives rise to a sequence  $\{y_n\}_{n=0}^{\infty}$  of approximations to the solution  $y(t)$  of the system (2.1.1) at the discrete time  $\{t_n = n\Delta t\}_{n=0}^{\infty}$ , where  $\Delta t \equiv h$  is the step size and

$$y(t_n) \approx y_n. \quad (2.9.2)$$

It is implicitly understood that  $D_{\Delta t}y_n$  is an approximation of the derivatives  $\frac{dy}{dt}$ , while  $G_{\Delta t}(f, y_n)$  approximates the function  $f(y)$ . It is also important to note that the algorithm (2.9.1) permits to find the discrete solution  $y_{n+1}$  at the time  $t_{n+1}$  assuming that the discrete solution  $y_n$  is known at the time  $t_n$ .

We start with some general concepts about the numerical method (2.9.1). We fix a time  $t^*$  which can be represented in the form

$$t^* = n\Delta t = t_n \quad (2.9.3)$$

for different values of  $n$  and  $\Delta t$ .

**Definition 2.9.1.** [49] *The difference scheme (2.9.1) of a well-posed initial value problem (2.1.1) is said to be convergent if, we have that*

$$\lim_{\substack{\Delta t \rightarrow 0 \\ t^* = n\Delta t}} y_n = y(t^*) \quad (2.9.4)$$

*holds for all  $t^* \geq 0$  and for all solutions  $\{y_n\}$  of the difference Equation (2.9.1).*

As mentioned earlier, the exact solution  $y(t^*)$  is not known. It is therefore difficult to check the convergence based on Definition 2.9.1. To overcome this difficulty, we consider three additional concepts.

**Definition 2.9.2.** [49] *The local truncation error,  $R_{n+1}$ , of the numerical method (2.9.1) is the amount by which the exact solution  $y(t)$  fails to satisfy the relation (2.9.1). That is*

$$R_{n+1} := D_{\Delta t}y(t_n) - G_{\Delta t}(f, y(t_n)).$$

**Definition 2.9.3.** [49] *The method (2.9.1) is said to be consistent with the differential equation if, for all initial value problems, the local truncation error  $R_{n+1}$  satisfies*

$$\lim_{\substack{\Delta t \rightarrow 0 \\ t^* = n\Delta t}} R_{n+1} = 0. \quad (2.9.5)$$

**Definition 2.9.4.** [49] *Let  $\{\delta_n\}_{n=0}^\infty$  and  $\{\delta_n^*\}_{n=0}^\infty$  be any two perturbation of the scheme (2.9.1), and let  $\{Z_n\}_{n=0}^\infty$  and  $\{Z_n^*\}_{n=0}^\infty$  be the resulting pertubated solutions. If there exist constants  $S$  and  $\Delta t_0$  such that for all  $\Delta t \in (0, \Delta t_0]$ , we have*

$$\|Z_n - Z_n^*\| \leq S\epsilon \quad \text{whenever} \quad \|\delta_n - \delta_n^*\| \leq \epsilon \quad \text{for} \quad n \geq 0,$$

*then the scheme (2.9.1) is said to be zero-stable.*

The challenge mentioned earlier about checking the convergence of the scheme is addressed by the following fundamental result:

**Theorem 2.9.5.** [49] *Assume that the problem (2.1.1) is well-posed. Then the difference scheme (2.9.1) is convergent if and only if it is both consistent with differential equation and zero-stable.*

Convergence of the scheme is important. A numerical method that is not convergent is not useful. In addition to convergence, we want schemes which replicate dynamics of the continuous systems. A typical example is the so called exact scheme. For the exact scheme, the local truncation error is zero.

**Definition 2.9.6.** *The numerical method (2.9.1) that approximates (2.1.1) is called an exact scheme whenever the difference equation (2.9.1) and the differential equation (2.1.1) have the same general solutions at the discrete time  $t = t_n$ . In particular, with  $y(t)$  being the solution of the initial value problem (2.1.1,) we have  $y_n = y(t_n)$*

A lot of work has been done in providing exact schemes of a wide range of models that arise in applications. Typical references for this include [55–57, 79]. We restrict ourselves to give the exact schemes of two equations that we will deal with in this dissertation. The first model is the decay equation which will arise, in the KMB model for the honey bee colony population, when the hive bees are ignored (see Section 5.1).

**Proposition 2.9.7.** *The exact scheme of the decay equation*

$$\frac{dy}{dt} = -my, \quad y(0) = y_0, \tag{2.9.6}$$

*is*

$$\frac{y_{n+1} - y_n}{(1 - e^{-m\Delta t})/m} = -my_n \tag{2.9.7}$$

or equivalently

$$\frac{y_{n+1} - y_n}{(e^{m\Delta t} - 1)/m} = -my_{n+1}. \quad (2.9.8)$$

*Proof.* By separation of variables, the solution of (2.9.6) is  $y(t) = y_0 e^{-mt}$ . Thus, the solution of (2.9.6) at time  $t = t_{n+1}$ , is

$$y(t_{n+1}) = y_0 e^{-mt_{n+1}}. \quad (2.9.9)$$

By subtracting  $y(t_n)$  and doing some manipulations, (2.9.9) leads successively to

$$\begin{aligned} y(t_{n+1}) - y(t_n) &= y_0 e^{-mt_{n+1}} - y(t_n) \\ &= y_0 e^{-m(t_n + \Delta t)} - y(t_n) \\ &= y(t_n) e^{-m\Delta t} - y(t_n) \\ &= -my(t_n) (e^{-m\Delta t} - 1) / (-m). \end{aligned}$$

Therefore, setting  $y_n := y(t_n)$  allows us to re-write (2.9.9) in the equivalent form (2.9.7). To obtain relation (2.9.8), we divide both sides of (2.9.7) by  $e^{m\Delta t}$ . That is

$$\frac{y_{n+1} - y_n}{e^{m\Delta t} \left( \frac{1 - e^{-m\Delta t}}{m} \right)} = -my_n e^{-m\Delta t},$$

which implies that

$$\frac{y_{n+1} - y_n}{\frac{e^{m\Delta t} - 1}{m}} = -my_{n+1} \quad \text{since} \quad y_{n+1} = y_n e^{-m\Delta t}.$$

□

The second model of interest in this dissertation is the Michaeli-Menten (M-M) equation

$$\frac{dH}{dt} = \frac{LH}{\omega + H}. \quad (2.9.10)$$

While the M-M model arises directly from the KMB model in the absence of foragers (Section 5.1), we motivate below how the M-M equation is of great use in applications. As reported in [18] and [19], the M-M equation represents one of the most basic enzymatic reactions that was proposed more than a century ago by Michaelis-Menten. This equation models the enzyme kinetics in pharmacology and was solved in [70, 84] with a singular perturbation where for our case for instance,  $H$  is one of the leading order terms of the expansion of the outer solution. The right-hand side

of the M-M equation also arises as a functional response in the predator-prey and infectious disease models in specific extended forms ranging from the M-M type, the ratio-dependent type, the Beddington-De Angelis type, to the general Holling type II considered in the Rosenzweig-Mac Arthur model [18]. To derive its exact scheme, we need to use the Lambert  $W$  function, known also as the Omega function, which is given by the relation [21]

$$z = W(z) \exp(W(z))$$

as the multivalued inverse of the non-injective complex-valued function

$$v \mapsto v \exp(v).$$

Note that the Lambert  $W$  function satisfies the differential equation

$$\frac{dW}{dz} = \frac{W(z)}{z(1+W(z))}. \quad (2.9.11)$$

The next result is due to Mickens [58].

**Proposition 2.9.8.** *The exact scheme of the M-M equation (2.9.10) is*

$$H_{n+1} = \omega W \left[ \frac{H_n}{\omega} \exp \left( \frac{H_n}{\omega} \right) \exp \left( \frac{L}{\omega} \Delta t \right) \right]. \quad (2.9.12)$$

*Proof.* By separation of variables and integration in Eq.(2.9.10) we have

$$\left( \frac{H + \omega}{H} \right) dH = L dt$$

and

$$\omega \ln H(t) + H(t) = Lt + C. \quad (2.9.13)$$

Setting  $t = t_0$ , we obtain the constant  $C$  as follows:

$$C = \omega \ln H_0 + H_0 - Lt_0.$$

Thus, the solution of Equation (2.9.10) is given implicitly by the relation,

$$\omega \ln H(t) + H(t) = L(t - t_0) + \omega \ln H_0 + H_0$$

or

$$\ln H(t) + \frac{H(t)}{\omega} = \frac{L}{\omega}(t - t_0) + \ln H_0 + \frac{H_0}{\omega}$$

or

$$H \exp\left(\frac{H}{\omega}\right) = H_0 \exp\left(\frac{H_0}{\omega}\right) \exp\left(\frac{L}{\omega}(t - t_0)\right)$$

or

$$\frac{H}{\omega} \exp\left(\frac{H}{\omega}\right) = \frac{H_0}{\omega} \exp\left(\frac{H_0}{\omega}\right) \exp\left(\frac{L}{\omega}(t - t_0)\right).$$

By definition of the Lambert  $W$  function, we have

$$\frac{H}{\omega} = W\left[\frac{H_0}{\omega} \exp\left(\frac{H_0}{\omega}\right) \exp\left(\frac{L}{\omega}(t - t_0)\right)\right].$$

Thus

$$H(t) = \omega W\left[\frac{H_0}{\omega} \exp\left(\frac{H_0}{\omega}\right) \exp\left(\frac{L}{\omega}(t - t_0)\right)\right]. \quad (2.9.14)$$

For  $t = t_{n+1}$ , using the semi-group property of the evolution operator in Definition 2.6.2, we have

$$H(t_{n+1}) = \omega W\left[\frac{H(t_n)}{\omega} \exp\left(\frac{H(t_n)}{\omega}\right) \exp\left(\frac{L}{\omega}\Delta t\right)\right]. \quad (2.9.15)$$

Thus, setting  $H_n := H(t_n)$  allows us to re-write the relation (2.9.15) in the equivalent form (2.9.12) which by a theorem on page 71 in Mickens [55] is the exact scheme of M-M Equation. (2.9.10).  $\square$

**Definition 2.9.9.** [7] *The difference equation (2.9.1) is called a nonstandard finite difference (NSFD) scheme if at least one of the following conditions is satisfied:*

1. *In the first order discrete derivative  $D_{\Delta t}y_n \approx \dot{y}(t_n)$ , the classical denominator  $h = \Delta t$  is replaced by a nonnegative function  $\phi : (0, \infty) \rightarrow (0, \infty)$  satisfying the asymptotic relation (**Rule 2**)*

$$\phi(\Delta t) = \Delta t + \mathcal{O}([\Delta t]^2). \quad (2.9.16)$$

*For example in Proposition 2.9.7, we have*

$$\phi(\Delta t) = \frac{1 - e^{-m\Delta t}}{m} \quad \text{or} \quad \phi(\Delta t) = \frac{e^{m\Delta t} - 1}{m}.$$

2. *In the expression  $G_{\Delta t}(f, y_n)$ , non-linear terms are approximated in a non-local manner. For example, a term like  $y^2(t_n)$  is approximated by  $y_{n+1}y_n$  instead of  $y_n^2$ . (**Rule 3**)*

**Remark 2.9.10.** Note that Definition 2.9.9 retains only two rules out of the five rules proposed by Mickens [55] to construct NSFD schemes. For convenience, the other three rules are stated below.

1. The order of the discrete derivative should be equal to the order of the corresponding derivative of the differential equation. (**Rule 1**)
2. The special condition that holds for the solution of differential equations should also hold for the solutions of the finite difference scheme. (**Rule 4**)
3. The scheme should not introduce extraneous or spurious solutions. (**Rule 5**)

In order to illustrate Definition 2.9.9, we construct below a NSFD scheme for the M-M equation (2.9.10) that we will be using throughout this dissertation. This is particularly important because the exact scheme (2.9.12) involves the Lambert  $W$  function, which is not explicitly known and is therefore of limited use in practice. To proceed with the said construction, we first note that the linearized equation of the M-M equation (2.9.10) around the unique fixed point  $\bar{H} = 0$ , is the exponential equation

$$\frac{dH}{dt} = \frac{L}{\omega}H, \quad (2.9.17)$$

which has exact scheme

$$\frac{H_{n+1} - H_n}{\phi_1} = \frac{L}{\omega}H_n \quad (2.9.18)$$

or equivalently

$$\frac{H_{n+1} - H_n}{\phi_2} = \frac{L}{\omega}H_{n+1} \quad (2.9.19)$$

where

$$\phi_1 \equiv \phi_1(\Delta t) = \frac{\exp(\frac{L}{\omega}\Delta t) - 1}{\frac{L}{\omega}} \quad \text{and} \quad \phi_2 \equiv \phi_2(\Delta t) = \frac{1 - \exp(-\frac{L}{\omega}\Delta t)}{\frac{L}{\omega}}.$$

Therefore the exact scheme of the M-M equation in Equation (2.9.12) can be written as

$$\frac{H_{n+1} - H_n}{\phi_1} = \frac{\omega W\left(\frac{H_n}{\omega} \exp\left(\frac{H_n}{\omega}\right) \exp\left(\frac{L}{\omega}\Delta t\right)\right) - H_n}{\phi_1(\Delta t)} \quad (2.9.20)$$

In the formulation (2.9.20), it is clear that the right hand side is an approximation of  $\frac{LH}{H + \omega}$ . Indeed, since

$$W\left(\frac{H_n}{\omega} \exp\left(\frac{H_n}{\omega}\right)\right) = \frac{H_n}{\omega},$$



we have

$$\begin{aligned} \frac{\omega W\left(\frac{H_n}{\omega} \exp\left(\frac{H_n}{\omega}\right) \exp\left(\frac{L}{\omega} \Delta t\right)\right) - H_n}{\phi_1(\Delta t)} &= \frac{\omega W\left(\frac{H_n}{\omega} e^{\frac{H_n}{\omega}} e^{\frac{L}{\omega} \Delta t}\right) - \omega W\left(\frac{H_n}{\omega} e^{\frac{H_n}{\omega}}\right)}{\phi_1(\Delta t)} \\ &= \frac{\omega \frac{dW}{dz}(z_n) \frac{H_n}{\omega} e^{\frac{H_n}{\omega}} \left(e^{\frac{L}{\omega} \Delta t} - 1\right)}{\phi_1(\Delta t)}; \end{aligned}$$

by the mean value theorem, for some  $z_n \in \left(\frac{H_n}{\omega} e^{\left(\frac{H_n}{\omega}\right)} \quad ; \quad \frac{H_n}{\omega} e^{\left(\frac{H_n}{\omega}\right)} e^{\left(\frac{L}{\omega} \Delta t\right)}\right)$

$$\begin{aligned}
&= L \frac{\frac{dW}{dz}(z_n) \frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \left( \exp(\frac{L}{\omega} \Delta t) - 1 \right)}{\exp(\frac{L}{\omega} \Delta t) - 1} \quad \text{by definition of } \phi_1 \\
&= L \frac{dW}{dz}(z_n) \frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \\
&= L \frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \frac{W(z_n)}{z_n(1+W(z_n))} \quad \text{by Equation (2.9.11)} \\
&= \frac{L \frac{H_n}{\omega} \exp(\frac{H_n}{\omega})}{z_n} \frac{\omega W(z_n)}{\omega(1+W(z_n))} \\
&\approx L \begin{cases} \frac{\omega W\left(\frac{H_n}{\omega} \exp(\frac{H_n}{\omega})\right)}{\omega + \omega W\left(\frac{H_n}{\omega} \exp(\frac{H_n}{\omega})\right)} & \text{if } z_n = \frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \\ \frac{\omega W\left(\frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \exp(\frac{L}{\omega} \Delta t)\right)}{\omega + \omega W\left(\frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \exp(\frac{L}{\omega} \Delta t)\right)} & \text{if } z_n = \frac{H_n}{\omega} \exp(\frac{H_n}{\omega}) \exp(\frac{L}{\omega} \Delta t) \end{cases} \\
&\approx L \begin{cases} \frac{H(t_n)}{\omega + H(t_n)} \\ \frac{H(t_{n+1})}{\omega + H(t_{n+1})} \end{cases} \\
&\approx L \begin{cases} \frac{H_n}{\omega + H_n} \\ \frac{H_{n+1}}{\omega + H_{n+1}}. \end{cases}
\end{aligned}$$

Thus, we retrieve the following NSFD schemes that were proposed by Chapwanya et al. in [18].

$$\frac{H_{n+1} - H_n}{\phi_1} = \frac{LH_n}{\omega + H_n} \quad (2.9.21)$$

$$\frac{H_{n+1} - H_n}{\phi_1} = \frac{LH_{n+1}}{\omega + H_{n+1}} \quad (2.9.22)$$

In addition to these, and whenever  $L < 0$ , Chapwanya et al. [19] considered the NSFD scheme

$$\frac{H_{n+1} - H_n}{\phi_2} = \frac{LH_{n+1}}{\omega + H_n}, \quad L < 0, \quad (2.9.23)$$

in which Rule 3 on the non-local approximation of the non linear term  $\frac{LH}{\omega + H}$  is reinforced. The NSFD scheme of interest in this dissertation is the one given in (2.9.21).

The power of NSFD schemes over usual numerical schemes is their potential to be dynamically consistent with respect to the continuous model as clarified in the next definition.

**Definition 2.9.11.** [7, 8] *Assume that the solution of (2.1.1) satisfies a property  $P$ . The difference equation (2.9.1) is said to be qualitatively stable or dynamically consistent with respect to property  $P$  if for all step sizes  $\Delta t > 0$ , the discrete solution for (2.9.1) satisfies  $P$ .*

Below, we describe the minimal desirable property  $P$  for any scheme.

**Definition 2.9.12.** [89, 94] *The difference scheme (2.9.1) that approximates differential Equation (2.1.1) is said to be elementary stable if, for any value of the step size  $\Delta t$ , its fixed points are exactly the equilibrium points of the differential system (2.1.1) and these fixed points for the difference scheme have the same linear stability or instability properties as the differential system.*

To illustrate Definition 2.9.12, we have the following result:

**Theorem 2.9.13.** *The NSFD schemes (2.9.21), (2.9.22) and (2.9.23) are elementary stable.*

*Proof.* For all these NSFD schemes, it is obvious that the equilibrium point  $\bar{H} = 0$  of the continuous system (2.9.10) is their unique fixed point. Regarding the stability, we start with the scheme (2.9.23). Solving for  $H_{n+1}$  we have

$$H_{n+1} = \frac{\omega H_n + H_n^2}{\omega + H_n - \phi_2 L}. \quad (2.9.24)$$

Differentiating with respect to  $H_n$  and evaluating the derivative at  $H_n = 0$ , we get

$$\left. \frac{dH_{n+1}}{dH_n} \right|_{H_n=0} = \frac{\omega}{\omega - \phi_2 L}.$$

It follows that the linearized equation of (2.9.24) about  $H_n = 0$  is

$$H_{n+1} = \left( \frac{\omega}{\omega - \phi_2 L} \right) H_n, \quad \text{or equivalently} \quad H_{n+1} = \left( \frac{\omega}{\omega - \phi_2 L} \right)^n H_0.$$

Therefore

$$H_n \rightarrow 0 \quad \text{as} \quad n \rightarrow \infty \quad \text{because, with} \quad L < 0, \quad \frac{\omega}{\omega - \phi_2 L} < 1.$$

This shows that the fixed point  $\bar{H} = 0$  is asymptotically stable as is the equilibrium point  $\bar{H} = 0$  for (2.9.10).

We next check the stability of the scheme in Equation (2.9.21). Making  $H_{n+1}$  the unknown of the formula in (2.9.21), we obtain

$$H_{n+1} = \frac{\phi_1 L H_n + H_n^2 + \omega H_n}{\omega + H_n}. \quad (2.9.25)$$

Thus

$$\left. \frac{dH_{n+1}}{dH_n} \right|_{H_n=0} = \frac{\phi_1 L + \omega}{\omega}.$$

This leads to the linearized equation

$$H_{n+1} = \left( \frac{\phi_1 L + \omega}{\omega} \right) H_n, \quad \text{or equivalently} \quad H_{n+1} = \left( \frac{\phi_1 L + \omega}{\omega} \right)^n H_0.$$

Therefore  $H_n \rightarrow \infty$  as  $n \rightarrow \infty$  since  $\frac{\phi_1 L + \omega}{\omega} > 1$  for  $L > 0$ . Hence  $\bar{H} = 0$  is unstable for both NSFD scheme (2.9.21) and the continuous model (2.9.10).

Lastly, we examine the stability of the scheme in Equation (2.9.22). We observe that Equation (2.9.22) is equivalent to a quadratic in  $H_{n+1}$ . That is:

$$H_{n+1}^2 - (\phi_1 L + H_n - \omega) H_{n+1} - \omega H_n = 0. \quad (2.9.26)$$

The unique positive root of (2.9.26) is

$$H_{n+1} = \frac{(\phi_1 L + H_n - \omega) + \sqrt{(\phi_1 L + H_n - \omega)^2 + 4\omega H_n}}{2}. \quad (2.9.27)$$

Evaluating the derivative of (2.9.27) at  $H_n = 0$ , we get

$$\left. \frac{dH_{n+1}}{dH_n} \right|_{H_n=0} = \frac{\phi_1 L}{\phi_1 L - \omega}.$$

From the linearized equation

$$H_{n+1} = \left( \frac{\phi_1 L}{\phi_1 L - \omega} \right) H_n \quad \text{or equivalently} \quad H_{n+1} = \left( \frac{\phi_1 L}{\phi_1 L - \omega} \right)^n H_0,$$

of (2.9.22), it follows that  $H_n \rightarrow \infty$  as  $n \rightarrow \infty$ , which shows the instability of  $\bar{H} = 0$  for the continuous and discrete equation.  $\square$

# Chapter 3

## The KMB model

### 3.1 The western honey bee as a model organism

In this section, we provide some biology of the western honey bees. Most of the material appears in [50] and is taken from [46, 93, 101]. The western honey bee known also as *Apis mellifera L.* (honey-carrying bees [93]) is a eusocial insect, that has well organized division of labor among themselves [101]. A colony of honey bees consist of one queen, which is responsible for laying brood reared in the hive, thousands workers and some drones (during reproduction season) [77, 101].

The population within the honey bee colony is made up of related and closely interacting individuals that form a highly complex society [43]. Their dynamics is complicated [43, 80], because the organizational level is influenced by the number of bees within the colony [80]. As a result of this, the fate of bees within the colony is not independent on their macro and micro habitat [43, 80], and the survival of the colony is mostly determined by dynamic interactions of individuals [80]. Therefore, the lifespan of an individual is influenced by the role they play in and outside the colony [43].

Depending on the season and time, honey bee colonies have three types of individuals, namely; the fertile female (queen), the sterile females (workers) and the males (drones). The main differences between these individuals are that: the queen hatches from a diploid egg and has fully functional reproductive system. She is character-

ized by an elongated body, large abdomen, shorter wings, small head, moderately developed eyes and her three pairs of legs are the same with a total body length of approximately 20mm (see Fig 3.1) [45, 101]. The workers, that have body length of about 15mm, Fig 3.1, [45], hatch from diploid eggs and are regarded as the main essential elements of the colony due to the roles they play [101]. Though the queen and worker hatch from diploid eggs, the difference between them is that workers' reproductive system is suppressed in the presence of the queen. Workers are characterized by the well developed wings, stingers, corbicula-hind legs designed to carry pollen and they have completely developed and long proboscis for collecting nectar. Workers have glands that produce wax and royal jelly [45, 101]. Drones are haploid males produced from unfertilized eggs of the workers or the queen and have heavily built body with an average length of 19mm, Fig 3.1, [45]. They are characterized by long wings that cover their bodies, developed eyes that are large and joined behind the occiput.

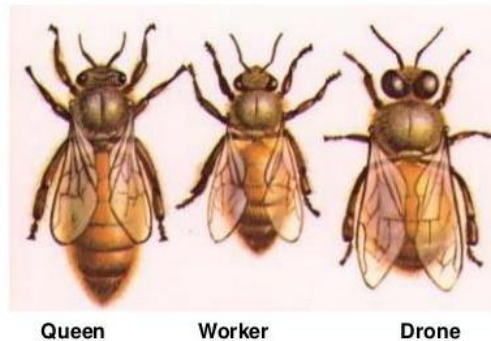


Figure 3.1: The morphology of queen, worker and drone honey bees [76].

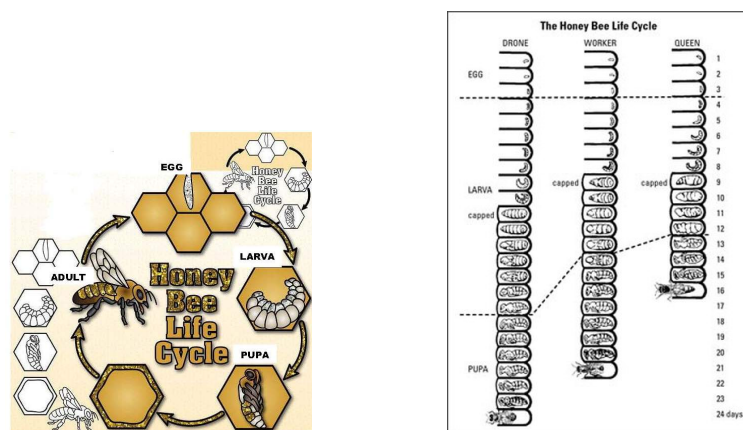
### **Reproduction of honey bees**

In this paragraph, we explain briefly what is meant by “functional and non functional reproductive system” in honey bees. Starting with the queen: as mentioned previously, her reproductive system is fully functional because her genital apparatus is well developed and comprises of two piriform ovaries [45]. She (queen) has a spermatheca (that stores sperm cells collected during mating flights with the drones). Drones, as well, have functional reproductive tracts and an evagiable endophallus which they use to ejaculate sperms into the queen during mating [101]. It should

be noted that drone dies soon after mating as his abdomen rips open when his endophallus is removed [101]. In the presence of the queen, the reproductive system of workers is suppressed by pheromones secreted by the queen. These pheromones restrict workers to produce but to focus on other hive activities [41, 45, 101]. Thus, workers are considered to have non functional reproductive system in the presence of the queen (under normal circumstances). We will elaborate later the unusual scenario where workers become reproductive in the presence of the queen.

### Life cycle

Honey bees undergo a complete metamorphosis, that is; egg, larva, pupa and adult, but the eclosion period differs by caste and sex [16]. The egg, hatched from either queen or worker, develops into a larva after 3 days. If it is an unfertilized (resulting to the birth of drone), it develops into pupa in 18 days while the fertilized (worker) egg becomes a pupa at day 14 and that give rise to queen by day 12. From the pupa stage, drones develop into an adult bee in 6 days while workers reach adulthood in 7 days and queens have a shorter development time which only takes 4 days from pupa to adult [101]. This shows that queen, worker and drone complete their metamorphosis in 16, 21 and 24 days respectively. Figure 3.2 shows the life cycle (Fig 3.2(a)) and the developmental stages of honey bees with time taken from one stage to the next, depending on the caste (Fig 3.2(b)).



(a) Honey bee life cycle [9]. (b) Honey bee eclosion period [12].

Figure 3.2: Honey bee life cycle with eclosion period adapted from [9] and [12].

## **Division of labor amongst honey bees**

Division of labor among honey bees is the most researched topic in the study of animal behavior [41]. There are two basic classes of division of labor across honey bees. The first one is between the queen and workers in relation to reproduction of the brood reared in the hive and the second one is between the workers themselves regarding the duties (that are not related to reproduction) in the hive [41]. In what follows, we describe duties each set of individuals perform within the colony.

### **Queen**

Before laying eggs, the queen takes mating flights where she mates with many drones [78]. Upon the completion of the mating period, she stays in the hive for the rest of her life and lays both fertilized and unfertilized eggs that develop into workers/queen and drones respectively, depending on the demands of the colony [101]. She also secretes pheromones that are used to control the hive [45,78,101].

### **Drones**

Haploid individuals that are ideal models for population studies as well as studies aimed at understanding the dynamics of honey bee pests such as *Varroa* mites has shown, recently, that drones do communicate with each other in the colony using drone pheromones [97], to give signal of where other drones are. They also mate with the queens at a specific area called drone congregation areas (DCA) [101], which is about 10 – 40 meters above the ground [14]. This is where the queen goes and secrete pheromones so that drones get attracted to her [14].

### **Workers**

The division of labor amongst honey bee workers is highly complex and flexible in that workers quickly adapt to changing colony needs and accelerate or reverse their behavioral development [78]. For instance; if there are few foragers to sustain the colony, young workers start foraging precociously [43,78]. Or young foragers can revert back to nursing behavior and develop fully functional brood food glands when there are few nurse bees [78].

We describe the division of labor amongst honey bees under normal circumstances



(when there is no precocious foraging or the reversion from forager class to hive class). This division of labor is age-dependent [41, 43, 45, 78, 101]. Since the newly hatched honey bees are developmentally immature [41, 101], their duties consist of cleaning cells by removing the remains of larvae and pupae from the cells [41], eliminate excess water vapor and regulate temperature in the hive by rapidly beating their wings [45]. As they mature, they become nurse bees. During the nursing period, they feed the brood with honey, pollen and glandular secretions [41, 45]. Later on, they secrete royal jelly that is fed to the brood during larval stage [101]. They also care for the queen by surrounding her as attendants, monitoring how she eats as well as sending pheromones secreted by the queen within the colony [41]. It is during the nursing period when they (workers) become stokers. That is; they receive nectar and pollen from foragers and process nectar into honey then store them (pollen and honey) in the combs [41, 45]. From being stokers, they grow to become comb-makers. At this stage, they secrete beeswax and use it to build and repair comb cells [41]. Graduating from the comb-making stage, they become guards and prevent intruders like insects or workers from foreign hives from entering their hive [41, 45]. They later become foragers [83, 101] where, they leave the hive to collect resources (water, pollen, nectar, propolis) needed in the colony [41, 45, 83, 101]. In general, the division of labor among honey bee workers as thoroughly observed was recorded by Seeley [83] and is listed in Table 3.1.

Table 3.1: Summary of age-dependent division of labor amongst honey bee workers [83].

<b>Age</b>	<b>Main activity</b>
From birth till day 2	Cleaners
From day 3 to day 11	Brood care
From day 12 to day 20	Store provisions guarding
From day 21 till death	Foragers

### **Life span**

The lifespan of honey bees varies by caste, sex and season and is strongly influenced by the role they play in the colony [43]. The queen lives between 3 and 5 years [45]. The drones live longer in mid-summer at an average of 90 days while in spring their lifespan is between 21 and 32 days [16], and in winter they are expelled from the hive [43]. The workers live longer in winter, since they are inactive, as compared to summer, when foraging (that exposes them to a lot of stress and adverse weather conditions [80]) is at its most, with an average of 140 days in winter and between 15 to 38 days in summer [101].

## **3.2 Formulation of the Mathematical model**

Khoury, Meyerscough and Barron considered several models for the dynamics of honey bee population [43, 44]. In this work, we focus on the basic mathematical model proposed in [43]. The assumptions they used are stated below with more motivation from the biology of honey bees.

### **Assumptions**

1. We neglect factors that compromise the health of the queen. Thus, we assume that the queen does not die, or if there arise a need for her to be replaced, this is done without affecting the overall performance of the colony [73].
2. The model focuses on workers only since drones do not contribute to colony work [43, 73, 80] and because they are not present in the colony during winter [101].
3. Workers are classified either as hive bees,  $H$ , or foragers,  $F$ , and there is no overlap between these two behavioral classes. This assumption is motivated by the fact that there is a well recognized division of labor among workers which is age-based (as discussed in Section 3.1)
4. Because many reported cases of honey bee colony declines are not associated with brood disease [22, 43, 69, 72], and since brood is maintained at the humidity levels within narrow limits inside the hive and constant temperature that is

crucial for normal development and growth [90]. It makes sense not to consider brood disease on colony failure.

5. Death rate of hive bees is ignored. This is because in a healthy colony, the rate at which hive bees die is extremely low [43] and is less significant to the overall population [80].
6. Workers are recruited from the hive class to the forager class at the maximum rate  $\alpha$ .
7. Foragers die at the rate  $m$ .
8. The maximum rate of eclosion is equivalent to the queen's laying rate,  $L$ , and eclosion rate approaches this maximum as the total number of workers,  $N := H + F$ , in the hive increases. This assumption is an attempt to capture the complex relation that exists between the number of eggs reared in a colony (eclosion rate) and the number of bees in the hive [43].
9. In the absence of foragers, new workers become foragers in  $\frac{1}{\alpha} \geq 4$  days after eclosion.
10. There is a reversion from the foragers class to hive bee class at the rate  $\sigma > \alpha$  if more than  $\frac{\alpha}{\sigma}N$  are foragers.
11. The eclosion approaches  $L$  at the rate  $\omega$ .

**Remark 3.2.1.** *Regarding Assumption 8, the relationship between the number of eggs reared in the colony and the number of bees in the hive is expressed by using, as eclosion function, the Michaelis-Menten or Holling function of type II, as follows:*

$$E(H, F) = \frac{L(H + F)}{H + F + \omega} = \frac{LN}{N + \omega} := f(N). \quad (3.2.1)$$

*Other possible functions include ,*

$$g(N) = L \tanh(N), \quad N \geq 0. \quad (3.2.2)$$

*More generally, we can use a saturated function  $f(N)$  which is bounded and increasing such that  $f(N) \rightarrow L$  as  $N \rightarrow \infty$ . However, we will use the function (3.2.1)*

because it is extensively applied in several population dynamics frameworks such as predator-prey models [15], epidemiological models [15] and reaction kinetics [63]. Figure 3.3 illustrates Assumption 11.

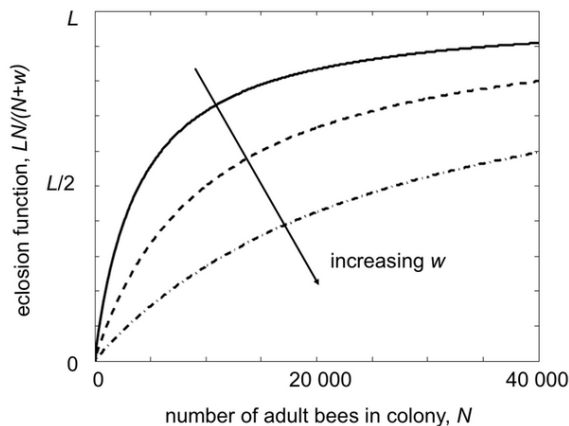


Figure 3.3: Eclosion function,  $E(H, F) = \frac{L(H + F)}{\omega + H + F}$  [43].

To describe the recruitment function, we follow an approach which is similar to the standard incidence formulation in epidemiology of infectious diseases [15]. The presentation outlined in [50] is detailed below. In view of Assumption 10, we note that social inhibition will take place whenever the hive bees are in contact with the foragers. The probability for the hive bees to be in contact with one forager is

$$\frac{H}{N}.$$

Thus the total number of contacts between hive bees and foragers is

$$\frac{H}{N}F.$$

However, not all the bees

$$\frac{H}{N}F$$

become foragers. Instead, the social inhibition process is such that

$$\sigma \frac{H}{N}F$$

are returned to the hive compartment on the grounds of being immature. Consequently, with Assumption 6 in mind, the recruitment rate function is, for  $H > 0$  and  $F > 0$  given by

$$R(H, F) = \left( \alpha - \sigma \frac{F}{H + F} \right) H.$$

With the above assumptions and the comments as well as the flow diagram in Figure 3.4, we are led to the following model (as proposed in [43]):

$$\begin{cases} \frac{dH}{dt} = \frac{L(H+F)}{H+F+\omega} - \left(\alpha - \sigma \frac{F}{H+F}\right)H =: f_1(H, F) \\ \frac{dF}{dt} = \left(\alpha - \sigma \frac{F}{H+F}\right)H - mF =: f_2(H, F) \end{cases} \quad (3.2.3)$$

$$H(0) = H_0 \quad \text{and} \quad F(0) = F_0 \quad (3.2.4)$$

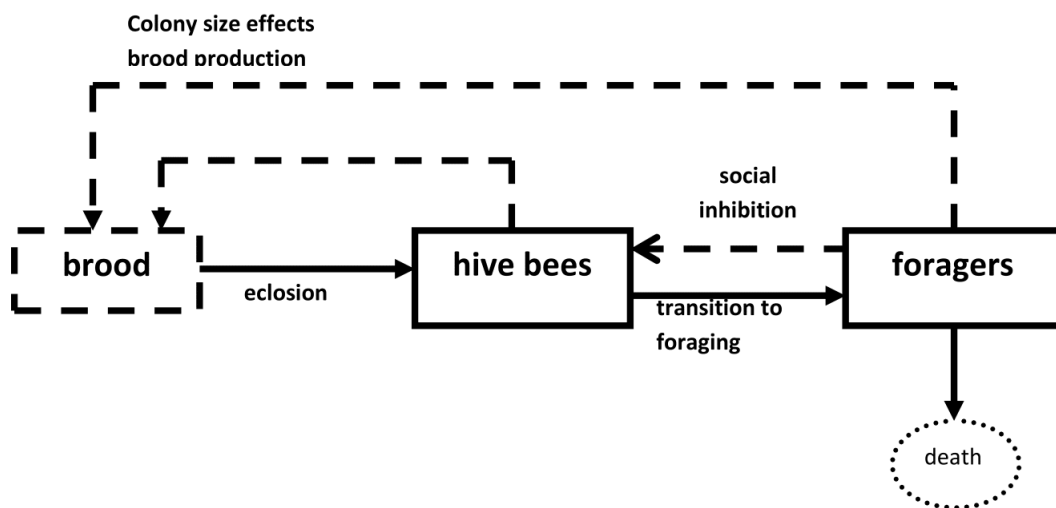


Figure 3.4: Social dynamics of a honey bee population model modified from [43].

**Remark 3.2.2.** *Based on Assumption 9, if new workers become foragers in a minimum of 4 days in the absence of foragers, it makes sense to take  $\alpha = 0.25$ . As a result of this and Assumption 10 whereby less than  $\frac{0.25}{\sigma}N$  of the total population are foragers, we can choose  $\sigma = 0.75$  so that  $\frac{1}{3}$  of the total population are foragers. Indeed,*

$$R(H, F) = \left(\alpha - \sigma \frac{F}{H+F}\right)H = 0 \quad \text{iff} \quad \alpha = \sigma \frac{F}{H+F}$$

or

$$\frac{\sigma}{3} = \alpha.$$

*This is precisely the choice made in [43]. We extend this assumption by assuming that*

$$0.25 \leq \alpha < \frac{\sigma}{2}. \quad (3.2.5)$$

Throughout this work, we further assume that

$$\alpha - \frac{L}{\omega} > 0, \quad (3.2.6)$$

in order to have the only condition (3.3.14) below instead of double condition used in [43].

### 3.3 Analysis of the model

For the well-posedness of the KMB model (3.2.3), we assume for simplicity that we are in the normal situation where social inhibition works. In this case the recruitment rate is positive. More precisely, we assume that there exists a constant  $\Gamma > 0$  such that

$$R \equiv R(H, F) = \alpha - \sigma \frac{F}{H + F} \geq \Gamma > 0. \quad (3.3.1)$$

We use the three facts below:

- a. The existence of unique local solution of (3.2.3), which is trivial;
- b. The positivity of any solution corresponding to positive initial conditions, which follows from the intermediate value theorem,
- c. The boundedness of any solution, which is established by Gronwall's inequality.

Then the following result can be proved (see [50]):

**Theorem 3.3.1.** *The model (3.2.3) is a dynamical system in the biological feasible region*

$$\Omega = \left\{ (H, F) \in \mathbb{R}_+^2 : H \leq \frac{L}{\Gamma} \quad \text{and} \quad F \leq \frac{L}{m\Gamma} \right\}.$$

*In other words, for  $(H_0, F_0) \in \Omega$ , there exists one and only one solution  $(H(t), F(t))$  of the System (3.2.3) such that  $(H(t), F(t)) \in \Omega$  for any time  $t \geq 0$ .*

**Remark 3.3.2.** *Adding the equations in (3.2.3), we have the following conservation law:*

$$\frac{dN}{dt} = \frac{LN}{N + \omega} - mF. \quad (3.3.2)$$

Let  $(H(t), F(t)) \in \Omega$  be a solution of the model (3.2.3) corresponding to the initial condition  $(H_0, F_0) \in \Omega$ . From (3.3.2) it follows, using the relations

$$F = N - H, \quad H \leq \frac{L}{\Gamma} \quad \text{and} \quad 0 < \Gamma \leq 1 \quad \text{that}$$

$$\frac{dN}{dt} \leq \frac{L}{\Gamma} + m\frac{L}{\Gamma} - mN. \quad (3.3.3)$$

By Lemma 2.1.8, we have from (3.3.3)

$$N(t) \leq N_0 e^{-mt} + \left( \frac{L}{m\Gamma} + \frac{L}{\Gamma} \right) (1 - e^{-mt}). \quad (3.3.4)$$

**Remark 3.3.3.** Assume that  $(H(t), F(t))$  is a solution of the model (3.2.3) that satisfies the relation (3.3.3) such that

$$N(t) > \frac{L}{m\Gamma} + \frac{L}{\Gamma} \quad \text{for all } t \geq 0. \quad (3.3.5)$$

Then, it follows from (3.3.3) and (3.3.5) that

$$\frac{dN}{dt} < 0.$$

Thus,  $N(t)$  is a decreasing function that converges to  $\frac{L}{m\Gamma} + \frac{L}{\Gamma}$  as  $t \rightarrow \infty$ , in view of (3.3.4) and (3.3.5). This means that the region  $\Omega$  is attracting [89]. This explains why we will study the KMB model (3.2.3) in the compact invariant set  $\Omega$ .

With regard to the qualitative analysis of the KMB model (3.2.3), we note that the defining equations of an equilibrium point  $(\bar{H}, \bar{F})$  are

$$\frac{L(H+F)}{H+F+\omega} - \left( \alpha - \sigma \frac{F}{H+F} \right) H = 0 \quad (3.3.6)$$

$$\left( \alpha - \sigma \frac{F}{H+F} \right) H - mF = 0.$$

It is obvious from (3.3.6) that the origin,  $(0,0)$ , is an equilibrium point of the system. It is equally clear that the system does not have boundary equilibrium points  $(\bar{H}, 0)$  and  $(0, \bar{F})$  for  $\bar{H} > 0$  and  $\bar{F} > 0$ . For a potential interior equilibrium point  $(\bar{H}, \bar{F})$ , we follow [16, 43, 51] and set

$$H = \frac{1}{J}F. \quad (3.3.7)$$

Substituting (3.3.7) in first equation in (3.3.6) we have

$$\frac{L(H+JH)}{(H+JH+\omega)} - mJH = 0. \quad (3.3.8)$$

Multiplying both sides of (3.3.8) by  $(H + JH + \omega)$  we get:

$$\begin{aligned} 0 &= L(H + JH) - mJH(H + JH + \omega) \\ &= LH + LHJ - mJH^2 - mJ^2H^2 - mJH\omega. \end{aligned}$$

Thus

$$L + LJ - mJH - mJ^2H - mJ\omega = 0 \quad \text{after dividing by } H.$$

Solving for  $H$  we obtain

$$\bar{H} = \frac{L}{Jm} - \frac{\omega}{1+J}, \quad (3.3.9)$$

which in view of (3.3.7) gives

$$\bar{F} = \frac{L}{m} - \frac{\omega J}{1+J}. \quad (3.3.10)$$

In order to determine the expression for  $J$ , we substitute (3.3.7) in the second equation in (3.3.6) and obtain

$$\left(\alpha - \sigma \frac{JH}{H + JH}\right)H - mJH = 0,$$

which is equivalent to

$$J^2 - \left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right)J - \frac{\alpha}{m} = 0. \quad (3.3.11)$$

Thus, the unique positive root of (3.3.11) is

$$J = \frac{1}{2} \left[ \left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right) + \sqrt{\left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right)^2 + 4\frac{\alpha}{m}} \right] \quad (3.3.12)$$

**Lemma 3.3.4.** *Under the second condition in Inequality (3.2.5), the root in (3.3.12) of (3.3.11) is such that  $J < 1$ .*

*Proof.* It should be noted that  $\left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right) < 0$  whenever  $\alpha < \frac{\sigma}{2}$ , for any  $m > 0$ . Now, assume by contradiction that  $J \geq 1$ . Then, we will have

$$\left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right) + \sqrt{\left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right)^2 + 4\frac{\alpha}{m}} \geq 2,$$

which implies that

$$\sqrt{\left(\frac{\alpha}{m} - \frac{\sigma}{m} - 1\right)^2 + 4\frac{\alpha}{m}} \geq \left(1 + \frac{\sigma - \alpha}{m}\right) + 2. \quad (3.3.13)$$



Squaring on both sides of (3.3.13) we obtain

$$\left(1 + \frac{\sigma - \alpha}{m}\right)^2 + 4\frac{\alpha}{m} \geq \left(1 + \frac{\sigma - \alpha}{m}\right)^2 + 4\left(1 + \frac{\sigma - \alpha}{m}\right) + 4,$$

which simplifies to

$$\frac{2\alpha}{m} \geq \frac{\sigma}{m} + 2,$$

or equivalently

$$\frac{\alpha}{m} \geq \frac{\sigma}{2m} + 1.$$

This is impossible since

$$\frac{2\alpha}{m} < \frac{\sigma}{m} \quad \text{because} \quad 2\alpha < \sigma \quad \text{by relation (3.2.5).}$$

Thus,  $J < 1$ . □

**Theorem 3.3.5.**

1. If the foragers' death rate,  $m$ , is smaller than a critical value  $m_c$  in the sense that

$$m < \frac{L}{2\omega} \left( \frac{(\alpha + \sigma) + \sqrt{(\alpha - \sigma)^2 + 4\frac{L\sigma}{\omega}}}{\alpha - \frac{L}{\omega}} \right) =: m_c, \quad (3.3.14)$$

then KMB model (3.2.3) has a unique interior equilibrium point, which is globally asymptotically stable (GAS), while the trivial equilibrium point is unstable.

2. If the condition (3.3.14) is not satisfied, then the trivial equilibrium point  $(0,0)$  is GAS.

Theorem 3.3.5 is stated in [43] without a proof. We provide its proof in different steps consisting of Propositions 3.3.6 to 3.3.10 below.

**Proposition 3.3.6.** *The positivity of the forager component of the equilibrium point,  $(\bar{H}, \bar{F})$ , given in Equation (3.3.10) is equivalent to the condition (3.3.14).*

*Proof.* The condition

$$\bar{F} = \frac{L}{m} - \frac{\omega J}{1 + J} > 0 \quad \text{or equivalently} \quad m < \frac{L(1 + J)}{\omega J} \quad (3.3.15)$$

is, in view of (3.3.12), equivalent to

$$m < \frac{L}{\omega} \frac{\left[ \left( \frac{\alpha}{m} - \frac{\sigma}{m} + 1 \right) + \sqrt{\left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right)^2 + 4 \frac{\alpha}{m}} \right]}{\left[ \left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right) + \sqrt{\left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right)^2 + 4 \frac{\alpha}{m}} \right]}.$$

Rationalizing the denominator, we get

$$m < \frac{L}{2\omega} \frac{\left[ \left( \frac{\alpha}{m} + \frac{\sigma}{m} + 1 \right) + \sqrt{\left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right)^2 + 4 \frac{\alpha}{m}} \right]}{\frac{\alpha}{m}},$$

which is equivalent to

$$m\alpha - \frac{L}{2\omega}(\alpha + \sigma + m) < \frac{Lm}{2\omega} \sqrt{\left( \frac{\alpha}{m} - \frac{\sigma}{m} - 1 \right)^2 + 4 \frac{\alpha}{m}}. \quad (3.3.16)$$

From (3.3.16) we deal, separately, with cases when

$$m\alpha - \frac{L}{2\omega}(\alpha + \sigma + m) > 0 \quad (3.3.17)$$

and

$$m\alpha - \frac{L}{2\omega}(\alpha + \sigma + m) \leq 0. \quad (3.3.18)$$

Assuming that case (3.3.17) holds true, by squaring on both sides of (3.3.16) we obtain

$$m^2\alpha^2 - 2m\alpha \frac{L}{2\omega}(\alpha + \sigma + m) + \frac{L^2}{4\omega^2}(\alpha + \sigma + m)^2 < \frac{L^2}{4\omega^2}(\alpha - \sigma - m)^2 + 4 \frac{\alpha}{m}.$$

Expanding bracket and simplifying we have

$$m^2\alpha \left( \alpha - \frac{L}{\omega} \right) - m\alpha \frac{L}{\omega}(\alpha + \sigma) < \frac{L^2}{4\omega^2}(-4\alpha\sigma),$$

which (after dividing by  $\alpha$ ) is equivalent to

$$m^2 \left( \alpha - \frac{L}{\omega} \right) - m \frac{L}{\omega}(\alpha + \sigma) < \frac{-L^2}{\omega^2}\sigma.$$

We are therefore led to the following quadratic inequality in  $m$ :

$$m^2 \left( \alpha - \frac{L}{\omega} \right) - m \frac{L}{\omega}(\alpha + \sigma) + \frac{L^2}{\omega^2}\sigma < 0. \quad (3.3.19)$$

Thus solving for  $m$  we get

$$m < \frac{\frac{L}{\omega}(\alpha + \sigma) + \sqrt{\frac{L^2}{\omega^2}(\alpha + \sigma)^2 - 4\left(\alpha - \frac{L}{\omega}\right)\frac{L^2\sigma}{\omega^2}}}{2\left(\alpha - \frac{L}{\omega}\right)}$$

or equivalently

$$m < \frac{\frac{L}{\omega} \left[ (\alpha + \sigma) + \sqrt{\alpha^2 - 2\alpha\sigma + \sigma^2 + 4\sigma\frac{L}{\omega}} \right]}{2\left(\alpha - \frac{L}{\omega}\right)}.$$

Simplifying the expression under the square root we obtain condition (3.3.14). Now, assuming Condition (3.3.18) is satisfied, we have

$$m\alpha - \frac{L}{2\omega}(\alpha + \sigma + m) \leq 0$$

or

$$m\alpha \leq \frac{L}{2\omega}(\alpha + \sigma + m).$$

Re-arrangement gives

$$m\left(\alpha - \frac{L}{2\omega}\right) \leq \frac{L}{2\omega}(\alpha + \sigma). \quad (3.3.20)$$

For any positive real numbers,  $L$  and  $\omega$ , the following equality is always true:

$$\frac{L}{2\omega} < \frac{L}{\omega}.$$

That is

$$-\frac{L}{2\omega} > -\frac{L}{\omega}.$$

Addition of  $\alpha$  yields

$$\alpha - \frac{L}{2\omega} > \alpha - \frac{L}{\omega} > 0 \quad \text{by (3.2.6).}$$

Solving for  $m$  from (3.3.20) we get:

$$\begin{aligned} m &\leq \frac{\frac{L}{2\omega}(\alpha + \sigma)}{\alpha - \frac{L}{2\omega}} \\ &< \frac{\frac{L}{2\omega}(\alpha + \sigma)}{\alpha - \frac{L}{\omega}} \end{aligned}$$

Addition of the positive quantity

$$\frac{L}{2\omega} \left( \frac{\sqrt{(\alpha - \sigma)^2 + 4\frac{L\sigma}{\omega}}}{\alpha - \frac{L}{w}} \right)$$

does not affect the inequality sign. So

$$m < \frac{L}{2\omega} \left( \frac{(\alpha + \sigma) + \sqrt{(\alpha - \sigma)^2 + 4\frac{L\sigma}{\omega}}}{\alpha - \frac{L}{w}} \right).$$

Thus, the positivity of (3.3.15) is equivalent to condition (3.3.14).  $\square$

**Proposition 3.3.7.** *Under the condition (3.3.14), the interior equilibrium point,  $(\bar{H}, \bar{F})$ , is locally asymptotically stable.*

*Proof.* We use Hartman-Grobman [15] linearization process as stated in Theorem 2.2.2, Remark 2.2.3 and Corollary 2.2.4. The Jacobian matrix,  $J_c := J_c(H, F)$ , of the right hand side of the model (3.2.3) is

$$J_c = \begin{pmatrix} \frac{\omega L}{(H + F + \omega)^2} - \alpha + \sigma \frac{F^2}{(H + F)^2} & \frac{\omega L}{(H + F + \omega)^2} + \sigma \frac{H^2}{(H + F)^2} \\ \alpha - \sigma \frac{F^2}{(H + F)^2} & -\sigma \frac{H^2}{(H + F)^2} - m \end{pmatrix}. \quad (3.3.21)$$

At the interior equilibrium point  $(\bar{H}, \bar{F})$  that is given by Equations (3.3.9) and (3.3.10), the matrix (3.3.21) becomes

$$J_c(\bar{H}, \bar{F}) = \begin{pmatrix} \frac{\omega m^2 J^2}{L(1 + J)^2} - \alpha + \frac{\sigma J^2}{(1 + J)^2} & \frac{\omega m^2 J^2}{L(1 + J)^2} + \frac{\sigma}{(1 + J)^2} \\ \alpha - \frac{\sigma J^2}{(1 + J)^2} & -\frac{\sigma}{(1 + J)^2} - m \end{pmatrix}, \quad (3.3.22)$$

which has trace

$$\text{tr} J_c(\bar{H}, \bar{F}) = m \left( \frac{\omega m J^2}{L(1 + J)^2} - 1 \right) - \alpha + \sigma \frac{J - 1}{1 + J} \quad (3.3.23)$$

and determinant

$$\det J_c(\bar{H}, \bar{F}) = \frac{\omega m^2 \sigma J^2}{L(1 + J)^3} (J - 1) - \frac{\omega m^3 J^2}{L(1 + J)^2} + \alpha m - \frac{\sigma m J^2}{(1 + J)^2} - \frac{\omega \alpha m^2 J^2}{L(1 + J)^2}. \quad (3.3.24)$$

We show that  $\text{tr}J_c(\overline{H}, \overline{F}) < 0$ . Since  $J < 1$  as proved in Lemma 3.3.4, it is enough to show that

$$\frac{\omega m J^2}{L(1+J)^2} - 1 < 0.$$

Now,

$$\begin{aligned} \left( \frac{\omega J^2 m}{L(1+J)^2} - 1 \right) &< \left( \frac{\omega J^2 L(1+J)}{\omega J L(1+J)^2} - 1 \right) \quad \text{using (3.3.15) i.e } m < \frac{L(1+J)}{\omega J} \\ &= \left( \frac{J}{1+J} - 1 \right) \\ &< 0. \end{aligned}$$

Next, we show that  $\det J_c(\overline{H}, \overline{F}) > 0$ . From the second equation in (3.3.6) and (3.3.7), we have

$$\sigma = \left( \alpha - mJ \right) \frac{1+J}{J}. \quad (3.3.25)$$

With the equation (3.3.25) in mind, the expression (3.3.24) of  $\det J_c(\overline{H}, \overline{F})$  simplifies to

$$\det J_c(\overline{H}, \overline{F}) = \alpha m \left[ 1 - \frac{\omega m J}{L(1+J)^2} - \frac{J}{1+J} \right] + \frac{m^2 J^2}{1+J} \left[ 1 - \frac{\omega m J}{L(1+J)} \right].$$

Thus,

$$\begin{aligned} \det J_c(\overline{H}, \overline{F}) &> \alpha m \left[ 1 - \frac{1}{1+J} - \frac{J}{1+J} \right] + \frac{m^2 J^2}{1+J} [1 - 1] \quad \text{using } m < \frac{L(1+J)}{\omega J} \\ &= 0. \end{aligned}$$

Therefore, the local asymptotic stability of  $(\overline{H}, \overline{F})$  follows directly from Theorem 2.2.2 and Corollary 2.2.4.  $\square$

**Proposition 3.3.8.** *When Condition (3.3.14) is satisfied, the trivial equilibrium point  $(0,0)$  is unstable and not attractive.*

*Proof.* Using the fact that  $m < m_c$ , we have, from Remark 3.3.2 and the definition of  $\Omega$  that

$$\begin{aligned} \frac{dN}{dt} &= \frac{LN}{N+\omega} - mF \\ &\geq \frac{LN}{\frac{L}{\Gamma} + \frac{L}{m\Gamma} + \omega} - m_c \frac{L}{m\Gamma}. \end{aligned}$$

By comparison theorem (Gronwall's inequality) in Lemma 2.1.8, we obtain

$$N(t) \geq N_0 e^{-at} + \frac{b}{a}(1 - e^{-at}) \quad \text{where} \quad a = \frac{L}{\frac{L}{\Gamma} + \frac{L}{m\Gamma} + \omega}, \quad b = m_c \frac{L}{m\Gamma}.$$

Thus,  $N(t)$  cannot tend to zero. □

**Proposition 3.3.9.** *The system (3.2.3) does not have periodic orbits.*

*Proof.* By Dulac criterion [15], Theorem 2.3.4, using the function

$$\beta(H, F) = \frac{1}{HF},$$

we have

$$\begin{aligned} \nabla \cdot \left\langle \frac{\partial(\beta f_1)}{\partial H}, \frac{\partial(\beta f_2)}{\partial F} \right\rangle &= - \frac{L(H^2 F + 2HF^2 + F^3 + \omega F^3)}{(H^2 F + HF^2 + \omega HF)^2} \\ &= - \frac{L(H^2 F + 2HF^2 + F^3 + \omega F^3)}{(H^2 F + HF^2 + \omega HF)^2} - \frac{\alpha}{F^2} \\ &< 0 \quad \text{for} \quad H > 0 \quad \text{and} \quad F > 0. \end{aligned}$$

Therefore, from Theorem 2.3.4, the model (3.2.3) does not have periodic solutions. □

Combining Propositions 3.3.6 to 3.3.9, part 1 of Theorem 3.3.5 is proved. Regarding the second part we have the following result:

**Proposition 3.3.10.** *When Condition (3.3.14) is violated so that there is no interior equilibrium point, the trivial equilibrium point  $(0,0)$  is globally asymptotically stable.*

*Proof.* Here, we use a Lyapunov argument as in [29]. The candidate Lyapunov function  $V : \mathbb{R}_+^2 \rightarrow \mathbb{R}$  is the  $C^1$  function defined by

$$V \equiv V(H, F) := H + F.$$

For any  $H$  and  $F$ , we have  $V(H, F) > 0$  for all  $H, F \in \Omega \setminus \{(0,0)\}$  and  $V(0,0) = 0$ .

This shows that  $V$  is positive definite. Now, the derivative  $\dot{V}$  along the trajectories

is

$$\begin{aligned}
\dot{V}(H, F) &= \nabla V \cdot \overrightarrow{(f_1, f_2)} \\
&= \frac{\partial V}{\partial H} f_1 + \frac{\partial V}{\partial F} f_2 \\
&= 1 \times f_1 + 1 \times f_2 \\
&= \frac{L(H + F)}{H + F + \omega} - mF,
\end{aligned}$$

which is the right hand side of the conservation law (3.3.2). We observe that

$$\frac{\partial \dot{V}}{\partial F}(H, 0) = \frac{L\omega}{(H + \omega)^2} - m$$

$$\leq \frac{L}{\omega} - m$$

< 0 by (3.2.6) since the death rate is large, i.e.  $m > \alpha$ .

Therefore, there exists  $r > 0$  such that  $\dot{V}(H, F) < 0$  for  $0 < H \leq r$  and  $0 < F \leq r$ . This shows that  $V$  is indeed a positive definite Lyapunov function, in  $\Omega$ , by Definition 2.4.1. Furthermore, Theorem 2.4.2 guarantees that the equilibrium point  $(0,0)$  is locally asymptotically stable. Combining this result with Proposition 3.3.9, we obtain the global asymptotic stability of the trivial equilibrium point  $(0,0)$  based on Theorem 2.3.2.  $\square$

**Remark 3.3.11.** *Note that Poincaré-Bendixson Theorem 2.3.2 on which the proof of Proposition 3.3.10 is based is not valid for dynamical systems of more than two space dimension. For the sake of completeness, let us reprove Proposition 3.3.10 by using the LaSalle Invariance Principle in Theorem 2.4.4, which applies to any space dimension.*

*Knowing that the KMB model is dissipative, we want to show that the largest invariant set,  $\mathcal{M}$ , contained in the set  $\mathcal{E} = \{(H, F) \in \Omega \ ; \ \dot{V} = 0\}$  is reduced to the singleton set  $\{(0, 0)\}$  where  $V$  is the Lyapunov function defined by  $V(H, F) = H + F$ . The global asymptotic stability of the equilibrium point  $(0,0)$  will then follow from Theorem 2.4.4.*

*Let  $\mathcal{A}$  be an invariant set such that  $\mathcal{A} \subset \mathcal{E}$ . For any initial condition  $(H_0, F_0) \in \mathcal{A}$ ,*

the corresponding solutions  $(H(t), F(t)) = \phi(t)(H_0, F_0)$  of the KMB model (3.2.3) is such that  $(H(t), F(t)) \in \mathcal{A} \subset \mathcal{E}$ . Thus, with  $V(t) = H(t) + F(t)$ ,

$$\frac{dV}{dt} \equiv \dot{V} = \frac{LV}{V + \omega} - m(V - H) = 0. \quad (3.3.26)$$

Consequently,  $V$  is a constant:  $V(t) \equiv \bar{V}$ . By Definition 2.3.1, the  $\omega$ -limit set of the point  $(H_0, F_0)$  is the singleton  $(0, 0)$  in view of the violation of the condition (3.3.14). Therefore  $\bar{H} = 0$ ,  $\bar{F} = 0$ , and  $\mathcal{A} \subset \{(0, 0)\}$ . Thus,  $\mathcal{M} = \{(0, 0)\}$ .

### 3.4 Some models for colony population declines

Possible extensions of our work which we intend to carry out elsewhere includes focusing on other factors that contribute to declines of honey bee populations. This section is dedicated to introduce some of mathematical models, in the literature, that explore such factors. In all the models, the impact of these factors (that contribute to the declines) is the high foragers' death rate, which in turn remains the underlying reason for the colony declines.

- **Mathematical models of honey bee populations: rapid population declines [16].**

This is a direct extension of the model formulated in [43]. In this model, author [16] has included death rate of hive bees. Apart from  $\mu$  that represents the death rate of hive bees, the other parameters and variables have the same meaning as those the KMB model (3.2.3). The model reads as follows:

$$\begin{cases} \frac{dH}{dt} = \frac{L(H + F)}{(H + F + \omega)} - \left(\alpha - \sigma \frac{F}{H + F}\right)H - \mu H \\ \frac{dF}{dt} = \left(\alpha - \sigma \frac{F}{H + F}\right)H - mF \end{cases}. \quad (3.4.1)$$

It is discovered that there exists critical values of hive bees death rate and that of foragers above which the colony declines.

- **Modeling Colony Collapse Disorder in honey bees as a contagion [47].**



This model is also an extension of the KMB model [43] where an additional compartment of the infected population ( $I$ ) of bees due to CCD is incorporated. Authors found that the survival of the colony can be attained if the queen's laying rate is greater than the maximum recruitment rate from hive class to foraging class at the egg-laying half-saturation threshold. The model reads as follows:

$$\begin{cases} \frac{dH}{dt} = L \frac{H}{H + \Omega} - \gamma H - \alpha H \frac{\Phi}{F + I + \Phi} \\ \frac{dF}{dt} = \gamma H + \alpha H \frac{\Phi}{F + I + \Phi} - \mu_1 F - \beta F \frac{I}{I + \mathcal{K}} \\ \frac{dI}{dt} = \beta F \frac{I}{I + \mathcal{K}} - \mu_2 I \end{cases} \quad (3.4.2)$$

The parameters and variables of the model are tabulated in Table 3.2 below.

Table 3.2: The parameters and variables of the model (3.4.2).

Parameter	Description
H	hives populations
F	foragers population
$L$	queen's laying rate
$\Omega$	number of hives needed for the emergence rate to reach $\frac{L}{2}$
$\gamma$	recruitment rate from hives class to foragers class
$\alpha$	the maximum additional maturation rate when there is a need to accelerate transition from hive to foragers class
$\Phi$	number of foragers at which additional maturation rate is $\frac{\alpha}{2}$
$\mu_1$	death rate of foragers
$\mu_2$	death rate of infected bees
$I$	population of infected bees
$\beta$	rate at which bees are infected
$\mathcal{K}$	half-saturation constant

- Dynamic modeling of honey bee (*Apis mellifera*) colony growth and failure [80].

This model explores how interaction between internal demographic process within honey bee colony and the availability of food and brood rearing impact on the growth of the hive. The model is formulated based also on the KMB model [43]. It is discovered that the growth of the honey bee colony is influenced mainly by death rate of foragers, availability of food and other factors influencing the age at which workers transit to foraging class. The model parameters and variables are listed in Table 3.3 below.

Table 3.3: The parameters of the model (3.4.3).

<b>Parameter</b>	<b>Description</b>
H	hives populations
F	foragers population
$L_{max}$	maximum effective laying rate of the queen
$L_s$	proportion of the maximum laying rate approximated to particular season
$\alpha_{min}$	minimum possible transition rate from hives to foragers when there is plenty of food but no foragers
$\alpha_{max}$	maximum additional rate of transition when food stores are low
$b$	constant that determines the steepness of the function governing the rate that the food dependent term decreases as food stores increases.
$f$	variable describing the amount of food in the colony
$m_l$	maximum death rate of foragers in summer
$m_s$	death rate seasonality term
$\gamma_B, \gamma_H, \gamma_F$	food consumption rate of brood, hives and foragers respectively
$B_L$	number of brood in the larval stage
$C_{max}$	highest rate at which foragers can collect food
$C_s$	seasonality factor representing food collection rate

The model reads as:

$$\left\{ \begin{array}{l} \frac{dH}{dt} = \frac{L(H+F)}{H+F+\Omega} - \left( \frac{\alpha_t - \sigma F}{H+F} \right) H \\ \frac{dF}{dt} = \left( \frac{\alpha_t - \sigma F}{H+F} \right) H - m_F F \\ \frac{df}{dt} = CF(\gamma_B B_L + \gamma_H + \gamma_F F) \end{array} \right. , \quad (3.4.3)$$

where

$$\begin{aligned} L &= L_{max} \times L_s \\ \alpha_t &= \alpha_{max} \times \left( \frac{b^2}{b^2 + f^2} \right) + \alpha_{min} \\ m_F &= m_s \times m_t, \\ C &= C_{max} \times C_s. \end{aligned}$$

- **Importance of brood maintenance terms in simple models of the honey bee-varroa destructor acute bee paralysis virus complex [29].**

This is the mathematical model that focuses on the infestation of honey bee population as a result of the Acute paralysis virus. The outcome of the study shows that colonies contaminated with the virus can still function like any other healthy colonies for some years before declining provided they (virus-contaminated colonies) have the required number of workers to care for the brood at the end of winter seasons. The model reads as follows:

$$\left\{ \begin{array}{l} \frac{dm}{dt} = \beta_1(M-m)\frac{y}{x+y} - \beta_2 m \frac{x}{x+y} \\ \frac{dx}{dt} = \mu g(x)h(m) - \beta_3 m \frac{x}{x+y} - d_1 x \\ \frac{dy}{dt} = \beta_3 m \frac{x}{x+y} - d_2 x \end{array} \right. . \quad (3.4.4)$$

The parameters and variables of the model are presented in Table 3.4.

Table 3.4: The parameters and variables of the model (3.4.4).

Parameter	Description
$m$	number of the mites carrying the virus
$x$	number of virus-free bees
$y$	number of infected bees
$M$	mites population in the colony
$\mu$	maximum birth rate of workers per day
$d_1, d_2$	death rate of uninfected and infected bees respectively
$\beta_1$	rate at which mites do not carry the virus acquire it
$\beta_2$	rate at which mites lose virus to an uninfected host
$\beta_3$	rate at which bees are infected
$h(m)$	the function that shows that the birth rate is affected by the presence of mites that carry the virus
$g(x)$	the function that represents the relation that sufficiently large number of healthy workers is needed to care for the brood

- **A mathematical model of the honey bee-*varroa destructor*- acute bee paralysis virus system with seasonal effect [77].**

This is an extension of the mathematical model formulated in [29], in which an additional compartment,  $M$  (governed by logistic equation), for the number of mites that infest the colony is included. The findings of the study show that the use of varroacide treatment is important in that it reduces the rate at which colonies might collapse as a result of the virus. Additional parameters and variables to the model (3.4.4) are listed in Table 3.5 below.

Table 3.5: Additional parameters to the model .

Parameter	Description
$r(t)$	maximum birthrate of mites
$\alpha(t)$	carrying capacity for the mites
$x + y$	the total population of the host bees
$\delta_1, \delta_3$	the mortality rates of uninfected and infected bees due to varroacide respectively
$\delta_2$	shows that the effect of varroacide on mites that carry the virus and on the total mite is the same.
$\gamma_1, \gamma_2$	rates at which mites kill healthy bees and infected bees respectively

The model reads as follows:

$$\left\{ \begin{array}{l} \frac{dm}{dt} = \beta_1(M - m)\frac{y}{x + y} - \beta_2m\frac{x}{x + y} - \delta_2m \\ \frac{dx}{dt} = \mu g(x)h(m) - \beta_3m\frac{x}{x + y} - d_1x - \gamma_1Mx - \delta_1x \\ \frac{dy}{dt} = \beta_3m\frac{x}{x + y} - d_2y - \gamma_2My - \delta_3y. \\ \frac{dM}{dt} = rM\left(1 - \frac{M}{\alpha(x + y)}\right) - \delta_2M \end{array} \right. \quad (3.4.5)$$

- **A mathematical model of *Varroa* mite (*Varroa destructor* Anderson and Trueman and honey bee (*Apis mellifera* L.) population dynamics [25].**

This is a mathematical model that describes the interactions between *Varroa destructor* and a honey bee colony. This model shows, through numerical simulations, how the growth of the colony population and that of mites are affected by weather conditions, seasonal brood rearing and mite infestation rates for both worker and drone cells. It is discovered that the survival of thresholds for miticides depend on climate and yearly brood rearing cycle in a colony.

# Chapter 4

## The presence of a social parasite

### 4.1 The social parasite scenario

We started describing social parasitic scenario in the honors project [50]. In this section, we provide more details on the biology of honey bee races found in South Africa including their geographical location, their morphology, reproduction biology as well as the history and symptoms of the *capensis calamity* (cc).

Social parasitism in social insects is a situation whereby insects benefit from brood care or managed resources (such as food stores) of the host colony [26]. Our main references in this section are [23, 26, 35]. It has been confirmed that honey bee workers can function as social parasites in social bees [26, 65]. The host-parasites relationships in honey bees is composed of sharing the nest, enslavement of the host workers and elimination of the host queen from the colony [26].

South Africa is home to two races of honey bees that occur naturally, namely *A.m. scutellata* Lepeletier and *A.m. capensis* Escholtz [52]. These two sub-species are separated by a region of introgression or a buffer zone where hybrids exist [23]. Figure 4.1 shows geographical distribution of these two races of *A. mellifera* across South Africa together with the hybrid zone. *A.m. capensis* are found in the winter rainfall region of the Cape such as the Bokkeveld (1), Cedarberg (2), Swartberg (3) and Suurberg (4) mountains while *A.m. scutellata* occurs in the summer rainfall region north of the Roggenveldberg (5), Nuweveldberg (6), Sneeuwberg (7), Kikvorsberg (8),

Stormberg (9) and Drakensberg (10) mountains [52].

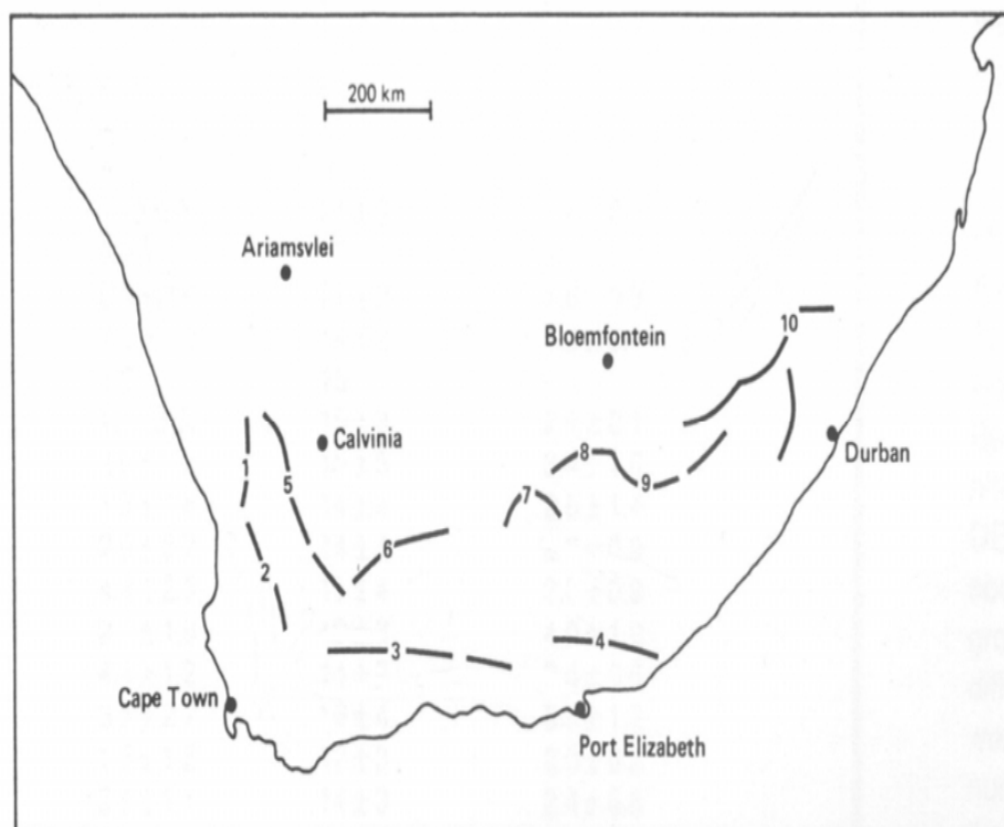


Figure 4.1: Geographical distribution of *Apis mellifera capensis* (South of mountain ranges 1 - 4), *Apis mellifera scutellata* (North of mountain ranges 5 - 10) and the hybrid zone between mountain ranges 1 - 4 and 5 - 10 [52]. The numbers correspond to towns described above [52].



(a) *A.m. scutellata*. (b) *A.m. capensis*.

Figure 4.2: Morphology of honey bee races found in South Africa

The difference between these races is that *A.m. capensis* have dark abdomen and well developed spermatheca whereas *A.m. scutellata* have orange/yellow abdomen and do not have a well developed spermatheca [23]. Worker reproduction in honey bee races, including *A.m. scutellata*, result in male offspring through the process called arrhenotokous parthenogenesis [10] (See Fig 4.3 (A)). This is not the case with *A.m. capensis* as workers are capable of laying unfertilized eggs which develop into female offspring through thelytokous parthenogenesis [23] (see Fig 4.3 (B)).

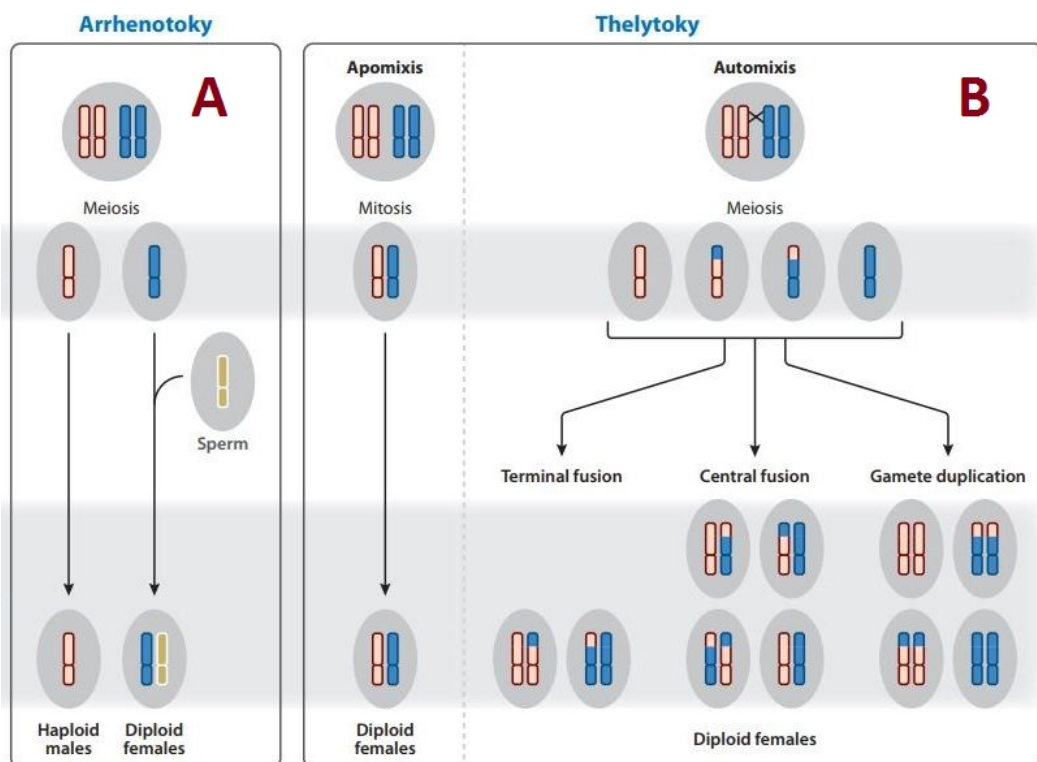
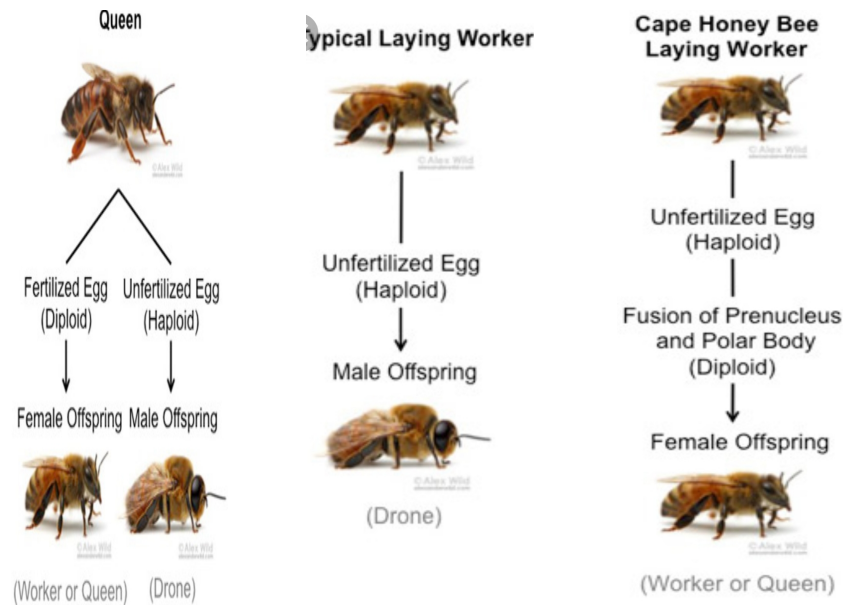


Figure 4.3: Reproduction methods in insects, edited from [34]

To produce female offspring, *A.m. capensis* workers produce gametes that fuse their pronuclei with one of their polar bodies in the absence of meiosis and produce female offspring [35]. *A.m. capensis* thelytokous workers then mimic the pheromone of the host queen and start to lay eggs undetected by the host queen [3]. The actively reproductive pseudo-queens may suppress the development of the ovaries of their clones which will result in dominance hierarchies of these clones [35]. These clones do not contribute to activities of the hive mainly because they activate their ovaries, which make it liable for them to reproduce rather than to care for the



brood. As a result of this, foraging becomes a problem for them as their pollen combs and baskets on their hind legs are suppressed [2, 35, 67]. When these clones enter the host colony of other races, they immediately activate their ovaries and start reproducing [24, 52, 62, 66]. It has been discovered that if the host colony has its own queen, then about 10% of the clones activate their ovaries whereas in a queen-less host colonies all the clones activate their ovaries and start producing females [62]. In comparison with the *A.m. capensis*, *A.m. scutellata* workers only activate their ovaries in the absence of the queen and her pheromonal controls to reproduce only haploid eggs that lead to male offspring [10, 101]. Figure 4.4 shows how queens, typical *Apis mellifera* workers and *A.m. capensis* workers reproduce.



(a) Queen. (b) Typical worker. (c) *A.m. capensis*.

Figure 4.4: How queen, typical *A.m.* worker and *A.m. capensis* worker produce offspring edited from [30].

## Background of the recent *capensis* calamity

There were two major movements of honey bees that involved large number of colonies of *A.m. capensis* into the region of *A.m. scutellata* [52]. The first one was in 1990, where about 400 colonies of *A.m. capensis* were moved from Lamberts Bay region in the Cape to the Rust-der-Winter region in Limpopo province [2, 52]. The

second recorded movement was in 1991, where colonies from high flats in Natal were moved to the Langkloof in the Cape and returned to Natal and subsequently moved to Douglas in the Northern Cape [52]. The main reason for these migrations was for pollination services [2, 4, 52]. It is reported that one of these movement caused the so called “capensis problem bee” [52] or *capensis calamity* (cc).

In what follows, we describe the *capensis calamity*. As mentioned earlier, under normal circumstances, honey bee workers do not reproduce diploid offspring but can do so under queenless conditions [66]. *A.m. capensis* workers are an exception to this rule as they parthenogenetically produce female offspring that normally develop into workers and occasionally queens [2, 24, 66]. Some of the workers produced by *A.m. capensis* workers can develop into pseudoqueens, which are characterized by high ovarial development and queenlike pheromone bouquet [24, 52, 66]. These workers then act as parasites when placed in foreign colonies [24, 52, 62, 66]. As a result of one of the above mentioned movements that took place in the 1990s, it is assumed that *A.m. capensis* workers (parasites) gained access to *A.m. scutellata* colonies (host) and established themselves as pseudo-queens taking over the roles of the host queen [24, 52, 62, 66].

The offspring of these parasites are cared for by the workers of the *A.m. scutellata* [66] as they themselves do not participate in hive activities as mentioned previously [2, 67]. As a result, the infected colonies end up with large number of these idle clones and few host workers to sustain their colony [2, 24, 35, 51, 67]. As time goes on, these infested colonies dwindles down and dies out [2, 6, 35, 35] with the cycle continuing as clones seek new host colonies. The parasites of the *A.m. capensis* workers have infested and are continuing to infest the colonies of the *A.m. scutellata* colonies resulting in the so-called *capensis calamity* for South African bee keeping enterprises [2, 3]. Due to *capensis calamity*, an estimated number of 100,000 *A.m. scutellata* colonies die every year [2]. Figure 4.5 (b) shows how the *A.m. capensis* parasites are being nursed or tendered for by the *A.m. scutellata* workers just like a typical queen being nursed by workers (Fig 4.5(a)).



(a) Workers nursing the queen (green dot). (b) Parasites (circled) [35].

Figure 4.5: The queen and parasites being attended by nurse bees.

According to Johannsmeier, the following are the signs or symptoms of *capensis calamity* (cc) [39]:

1. Outside the hive:

- reduced foraging activities
- a lot of dead bees
- bees engaged in fighting

2. Inside the hive:

- absence of the queen
- mixture of dark abdomen bees (*A.m. capensis* clones) and yellow abdomen bees (*A.m. scutellata* workers)
- multiple eggs inside the cells of workers and queen
- matured queen cells ripped open on the sides.
- scattered non-diseased brood with all larval stages next to each other

Due to the social parasitism by the *A.m. capensis*, we propose a mathematical model basing ourselves with the model developed in [43], so as to capture the impact of social parasitism by the *A.m. capensis* clones on the population of the *A.m. scutellata*. Our main focus is on the transition from hive compartment to the foragers' compartment.

## 4.2 Model formulation

The compartmental model that we propose for the social parasite by the *A.m. capensis* clones is in line with the KMB model (3.2.3) studied in Chapter 3. It is based on the following assumptions, as well as explanations made, apart from those made for the normal scenario. We shall call this model Social Parasite (SP) model throughout this dissertation.

### Assumptions:

1. Brood diseases on clones is not considered.
2. The rate at which hive bees leave their compartments is  $\alpha + \tilde{m}$ .
3. Death rate of clones in the hive is negligible.

From the above assumptions and the flow chart in Figure 4.6, we have the following model:

$$\left\{ \begin{array}{l} \frac{dH}{dt} = \frac{L(H+F)}{(H+F+\omega)} - (\alpha + \tilde{m})H \\ \frac{dF}{dt} = \alpha H - mF \end{array} \right. \quad (4.2.1)$$

$$H(0) = H_0 \quad \text{and} \quad F(0) = F_0 \quad (4.2.2)$$

It should be noted that:

- The quantity  $\tilde{m}H$  in the first equation in (4.2.1) is the number of clones/parasites leaving the hive compartment and not becoming foragers, while  $\alpha H$  is the number of *A.m. scutellata* workers/hosts which are recruited to the foraging class.
- The number of the *A.m. scutellata* workers/hosts which are dying is represented in the second equation in (4.2.1) by  $mF$ .
- In [50], the death rate  $m$  of foragers was assumed to be equal to the rate  $\tilde{m}$  of parasites that leave the hive compartment. Note that the parasites  $\tilde{m}H$  that abscond the hive class due to shortage of resources (food and care) proceed to invade other colonies [5].

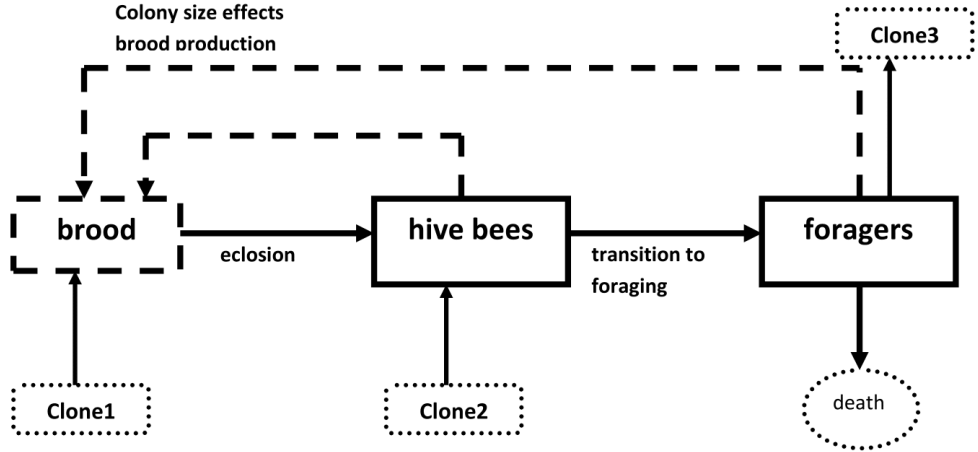


Figure 4.6: The flow diagram of honey bees (*A.m. scutellata*) in the presence of social parasite (*A.m. capensis* clones). Clone 1 = clone brood, clone 2 = hive bees that are hatched from clone brood and clone 3 = effect of clones on foragers.

### 4.3 Analysis of the model

The analysis carried out in the previous chapter for the KMB model (3.2.3) applies to the model (4.2.1). Thus, we just state the main results without repeating the arguments for all the proofs, observing that the condition (3.2.6) implies that

$$\alpha + \tilde{m} - \frac{L}{\omega} > 0, \quad (4.3.1)$$

which is used here and after.

The analysis of the model reads as follows:

**Theorem 4.3.1.** *The model (4.2.1) is a dynamical system on the biologically feasible region*

$$\Omega = \left\{ (H, F) \in \mathbb{R}_+^2 : H \leq \frac{L}{\alpha + \tilde{m}} \quad \text{and} \quad F \leq \frac{L}{m(\alpha + \tilde{m})} \right\}.$$

*That is, for any  $(H_0, F_0) \in \Omega$ , there exists one and only one solution  $(H(t), F(t))$  of the system (4.2.1) such that  $(H(t), F(t)) \in \Omega$  for any  $t \geq 0$ .*

The equilibrium points of the model are described in the next results.

**Theorem 4.3.2.** *1. The system (4.2.1) has trivial equilibrium point  $(0, 0)$  and does not have boundary equilibrium points.*

2. Under the condition

$$m < \frac{\alpha L}{\omega \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right]}, \quad (4.3.2)$$

there exists a unique interior equilibrium point,  $(H^I, F^I)$  given by

$$H^I = \frac{L}{\alpha + \tilde{m}} - \frac{\omega m}{\alpha + m}$$

and

$$F^I = \frac{\alpha}{m} \left( \frac{L}{\alpha + \tilde{m}} - \frac{\omega m}{\alpha + m} \right).$$

For the stability analysis of the equilibrium points of the model (4.2.1), we denote the Jacobian matrix of the right hand side of (4.2.1) by  $J(H, F)$ , and obtain

$$J(H, F) = \begin{pmatrix} \frac{\omega L}{(H + F + \omega)^2} - (\alpha + \tilde{m}) & \frac{\omega L}{(H + F + \omega)^2} \\ \alpha & -m \end{pmatrix}. \quad (4.3.3)$$

When evaluated at the trivial equilibrium point,  $(0,0)$ , (4.3.3) simplifies to

$$J(0, 0) = \begin{pmatrix} \frac{L}{\omega} - (\alpha + \tilde{m}) & \frac{L}{\omega} \\ \alpha & -m \end{pmatrix}. \quad (4.3.4)$$

At the interior equilibrium point

$$J(H^I, F^I) = \begin{pmatrix} \frac{\omega m^2 (\alpha + \tilde{m})^2}{L(\alpha + m)^2} - (\alpha + \tilde{m}) & \frac{\omega m^2 (\alpha + \tilde{m})^2}{L(\alpha + m)^2} \\ \alpha & -m \end{pmatrix}. \quad (4.3.5)$$

Thus, from (4.3.4),

$$\text{tr}J(0, 0) = \left( \frac{L}{\omega} - (\alpha + \tilde{m}) \right) - m, \quad (4.3.6)$$

and

$$\begin{aligned} \det J(0, 0) &= m(\alpha + \tilde{m}) - m \frac{L}{\omega} - \alpha \frac{L}{\omega} \\ &= m \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right] - \alpha \frac{L}{\omega}. \end{aligned} \quad (4.3.7)$$

From (4.3.5)

$$\begin{aligned}
\text{tr}J(H^I, F^I) &= \frac{\omega m^2(\alpha + \tilde{m})^2}{L(\alpha + m)^2} - (\alpha + \tilde{m}) - m \\
&= \frac{\omega m(\alpha + \tilde{m})^2}{L(\alpha + m)^2} \left( m - \frac{L(\alpha + m)^2}{\omega(\alpha + \tilde{m})^2} \right) - (\alpha + \tilde{m}) \quad (4.3.8)
\end{aligned}$$

and

$$\begin{aligned}
\det J(H^I, F^I) &= m(\alpha + \tilde{m}) - \frac{\omega m^3(\alpha + \tilde{m})^2}{L(\alpha + m)^2} - \frac{\alpha \omega m^2(\alpha + \tilde{m})^2}{L(\alpha + m)^2} \\
&= m(\alpha + \tilde{m}) - \frac{\omega m^2(\alpha + \tilde{m})}{L(m + \alpha)} \\
&= \frac{\omega m(\alpha + \tilde{m})^2}{L(\alpha + m)} \left( \frac{L(\alpha + m)}{\omega(\alpha + \tilde{m})} - m \right). \quad (4.3.9)
\end{aligned}$$

From Equations (4.3.6)-(4.3.7), we derive the following results for the model (4.2.1) regarding the stability of the equilibrium points:

**Theorem 4.3.3.**

1. When Condition (4.3.2) is satisfied, the trivial equilibrium point  $(0,0)$  is unstable and the interior equilibrium point  $(H^I, F^I)$  is locally asymptotically stable.
2. Otherwise if (4.3.2) is violated, the system (4.2.1) does not have an interior equilibrium point  $(H^I, F^I)$  and the trivial equilibrium point  $(0,0)$  is locally asymptotically stable.

*Proof.* Given the importance of this result, we give the proof in detail.

1. From (4.3.7) we have

$$\begin{aligned}
\det J(0,0) &= m \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right] - \alpha \frac{L}{\omega} \\
&< \frac{\alpha L}{\omega \left( (\alpha + \tilde{m}) - \frac{L}{\omega} \right)} \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right] - \alpha \frac{L}{\omega} \quad \text{by (4.3.2)} \\
&= \alpha \frac{L}{\omega} - \alpha \frac{L}{\omega} \\
&= 0.
\end{aligned}$$

Thus,  $(0,0)$  is unstable. For the local asymptotic stability of the interior equilibrium point, we have, from (4.3.8)

$$\begin{aligned} \text{tr}J(H^I, F^I) &< \frac{\omega m(\alpha + \tilde{m})^2}{L(\alpha + m)^2} \left( \frac{\alpha L}{\omega((\alpha + \tilde{m}) - \frac{L}{\omega})} - \frac{L(\alpha + m)^2}{\omega(\alpha + \tilde{m})^2} \right) - (\alpha + \tilde{m}) \\ &< \frac{m(\alpha + \tilde{m})^2}{(\alpha + m)^2} \left( \frac{(\alpha + m)^2}{((\alpha + \tilde{m}) - \frac{L}{\omega})} - \frac{(\alpha + m)^2}{(\alpha + \tilde{m})^2} \right) - (\alpha + \tilde{m}) \\ &< 0. \end{aligned}$$

From (4.3.9) we have

$$\begin{aligned} \det J(H^I, F^I) &> \frac{\omega m(\alpha + \tilde{m})^2}{L(\alpha + m)} \left( \frac{L(\alpha + m)}{\omega(\alpha + \tilde{m})} - \frac{\alpha L}{\omega[(\alpha + \tilde{m}) - \frac{L}{\omega}]} \right) \\ &> \frac{m(\alpha + \tilde{m})^2}{(\alpha + m)} \left( \frac{\alpha + m}{\alpha + \tilde{m}} - \frac{\alpha}{\alpha + \tilde{m}} \right) \\ &= \frac{m(\alpha + \tilde{m})^2}{(\alpha + m)} \left( \frac{m}{\alpha + \tilde{m}} \right) \\ &> 0. \end{aligned}$$

Therefore, the local asymptotic stability of  $(H^I, F^I)$  follows directly from Theorem 2.2.2 and Corollary 2.2.4.

2. Based on Condition (4.3.1), the trace of  $J(0,0)$  in (4.3.6) is always negative regardless of the condition (4.3.2). It only remains to show that  $\det J(0,0)$  is positive. Now, from (4.3.7) we have

$$\begin{aligned} \det J(0,0) &= m \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right] - \alpha \frac{L}{\omega} \\ &> \frac{\alpha L}{\omega \left( (\alpha + \tilde{m}) - \frac{L}{\omega} \right)} \left[ (\alpha + \tilde{m}) - \frac{L}{\omega} \right] - \alpha \frac{L}{\omega} \quad \text{violating (4.3.2)} \\ &= 0. \end{aligned}$$

Therefore  $(0,0)$  is locally asymptotically stable by Theorem 2.2.2 and Corollary 2.2.4. □



Furthermore, Dulac criterion (Theorem 2.3.4) applies to the model (4.2.1) and rules out the existence of periodic orbits. Thus, Theorem 4.3.3 can be improved as follows:

**Theorem 4.3.4.** *If Condition (4.3.2) is satisfied, then the interior equilibrium point  $(H^I, F^I)$  is globally asymptotically stable, otherwise the “trivial” equilibrium point  $(0,0)$  is globally asymptotically stable.*

The conclusion of Theorem 4.3.4 does not as such take into consideration the social parasite nature of the *Apis mellifera capensis* because the theorem is simply based on the analogues of the conditions in Theorem 3.3.5 for the KMB model (3.2.3). In order to obtain a more relevant conclusion, we have to refer to the biology of honey bees in the social parasite scenario as described in Section 4.1.

In the social parasite scenario, the impact of the ability of parasites to mimic pheromones of the host brood and queen [24] is that the rate  $\omega$ , at which the maximum eclosion is approached, is large. On the other hand, the number of clones who do not contribute to foraging but leave the hive class at the rate  $\tilde{m}$  after benefiting from the host workers resources is large. Also, the mortality rate of host workers who are recruited to foragers class is large (since there are many bees in the hive to feed) [5]. It has been shown biologically that *A.m. capensis* parasites lay multiple eggs resulting in an increased number of parasitic offspring [54, 66] and rapid spread in an apiary [17]. Also *A.m. capensis* workers need more (at least five) *A.m. scutellata* workers to tender their needs within the colony [82]. These facts can mathematically be reflected by the following condition:

$$\frac{L}{\omega} < \min\{m, \tilde{m}\}, \quad (4.3.10)$$

which is stronger than Condition (4.3.1). Now, adding equations in (4.2.1) yields the conservation law

$$\begin{aligned} \frac{dN}{dt} &= \frac{LN}{N + \omega} - \tilde{m}H - mF \\ &\leq \frac{LN}{N + \omega} - \min\{m, \tilde{m}\}N \\ &\leq \left(\frac{L}{\omega} - \min\{m, \tilde{m}\}\right)N. \end{aligned}$$

By Lemma 2.1.8, we have

$$N(t) \leq N_0 e^{\left(\frac{L}{\omega} - \min\{m, \tilde{m}\}\right)t}.$$

We have thus proved the following result which explains how fast colonies of the *A.m. scutellata* are lost as a result of social parasitism by the *A.m. capensis* clones:

**Theorem 4.3.5.** *If Condition (4.3.2) is violated, the total population decays to zero under the condition (4.3.10)*

# Chapter 5

## Nonstandard finite difference schemes for honey bee models

In this chapter, we propose reliable numerical methods which are dynamically consistent with the continuous, KMB and SP, models considered in Chapter 3 and Chapter 4, respectively. We use the nonstandard finite difference approach [55] as explained in Section 2.9. This chapter is a detailed version of our results published in [51].

### 5.1 The KMB discretization

To construct NSFD schemes, we apply Mickens' method of sub-equations [7, 55]. That is, we divide the full equation into simpler equations for which exact schemes are known or available useful qualitative information can be incorporated into the derived schemes.

From the model (3.2.3), in the absence of hive bees, the foragers are governed by the decay equation

$$\frac{dF}{dt} = -mF. \quad (5.1.1)$$

The exact scheme of the decay equation was given in Proposition 2.9.7 and reads as follows:

$$\frac{F_{n+1} - F_n}{(e^{m\Delta t} - 1)/m} = -mF_{n+1}. \quad (5.1.2)$$

In the absence of foragers, hive bees are governed by the equation

$$\frac{dH}{dt} = \frac{LH}{H + \omega} - \alpha H, \quad (5.1.3)$$

which has both the decay equation

$$\frac{dH}{dt} = -\alpha H \quad (5.1.4)$$

and the Michaelis-Menten, M-M, equation

$$\frac{dH}{dt} = \frac{LH}{H + \omega}. \quad (5.1.5)$$

Once again the exact scheme of (5.1.4) is

$$\frac{H_{n+1} - H_n}{(e^{\alpha \Delta t} - 1)/\alpha} = -\alpha H_{n+1}. \quad (5.1.6)$$

For the NSFD approximation of (5.1.5), we use the scheme (2.9.21) which by Proposition 2.9.13 is elementary stable. It reads

$$\frac{H_{n+1} - H_n}{\phi} = \frac{LH_n}{H_n + \omega}, \quad (5.1.7)$$

where  $\phi$  is specified in (5.1.11), (5.1.15) and (5.1.17) below. In order to preserve unconditional positivity, we propose the following NSFD scheme for Eq (5.1.3), based on (5.1.6) and (5.1.7):

$$\frac{H_{n+1} - H_n}{\phi} = \frac{LH_n}{H_n + \omega} - \alpha H_{n+1}. \quad (5.1.8)$$

Furthermore, using Definition 2.9.9, the nonlinear term  $\frac{HF}{H + F}$  in (3.2.3) is approximated in a nonlocal manner by

$$\frac{F_n H_{n+1}}{H_{n+1} + F_n}. \quad (5.1.9)$$

Combining the partial schemes in equations (5.1.2), (5.1.8) and (5.1.9) we propose the following NSFD scheme for the KMB model (3.2.3):

$$\left\{ \begin{array}{l} \frac{H_{n+1} - H_n}{\phi} = \frac{L(H_n + F_n)}{H_n + F_n + \omega} - \alpha H_{n+1} + \sigma \frac{F_n H_{n+1}}{H_{n+1} + F_n} \\ \frac{F_{n+1} - F_n}{\phi} = \alpha H_{n+1} - \sigma \frac{F_n H_{n+1}}{H_{n+1} + F_n} - m F_{n+1}. \end{array} \right. \quad (5.1.10)$$

Here and after

$$\phi \equiv \phi(\Delta t) = \frac{1 - e^{-\Delta t Q}}{Q} \quad (5.1.11)$$

is a complex denominator function where the number  $Q > 0$  to be determined shortly in different situations is supposed to capture the features of the model. It should be noted that  $\phi$  satisfies the asymptotic relation (2.9.16) in Definition 2.9.9.

We now address the issue of implementation of the NSFD scheme (5.1.10) and the choice of  $Q$ . The first equation in (5.1.10) is quadratic in  $H_{n+1}$ . That is,

$$AH_{n+1}^2 + B_n H_{n+1} - C_n = 0, \quad (5.1.12)$$

where

$$\begin{aligned} A &= 1 + \phi\alpha > 0 \\ B_n &= (1 + \phi\alpha - \phi\sigma)F_n - H_n - \phi \frac{LN_n}{N_n + \omega} \\ C_n &= H_n F_n + \phi \frac{LN_n F_n}{N_n + \omega}. \end{aligned}$$

Assuming that  $H_n$  and  $F_n$  are nonnegative, so that  $C_n > 0$ , there is a unique nonnegative root of (5.1.12), given by

$$H_{n+1} = \frac{-B_n + \sqrt{B_n^2 + 4AC_n}}{2A}. \quad (5.1.13)$$

Once  $H_{n+1}$  has been computed from (5.1.13), we continue in the Gauss-Seidel type process to compute  $F_{n+1}$  as follows:

$$F_{n+1} = \frac{\left[ \phi\alpha H_{n+1} + F_n \left( 1 - \phi\sigma \frac{H_{n+1}}{F_n + H_{n+1}} \right) \right]}{\left( 1 + m\phi \right)}. \quad (5.1.14)$$

In order for  $F_{n+1}$  in (5.1.14) to be positive, we assume that

$$Q \geq \sigma \quad \text{so that} \quad 0 < \phi < \frac{1}{\sigma}, \quad (5.1.15)$$

in view of equation (5.1.11). The root in (5.1.13) can also be written in the following

implicit equivalent form:

$$H_{n+1} = \frac{\left[ H_n + \phi \frac{L(H_n + F_n)}{H_n + F_n + \omega} \right]}{\left( 1 + \phi\alpha - \phi\sigma \frac{F_n}{H_{n+1} + F_n} \right)}. \quad (5.1.16)$$

In view of (5.1.15) and in order to incorporate essential parameters  $m$  and  $\alpha$  that appear in the sub-equations (5.1.1)-(5.1.2), (5.1.4) and (5.1.6), we choose the denominator function  $\phi$  in (5.1.11) such that

$$Q \geq m + \alpha + \sigma. \quad (5.1.17)$$

**Theorem 5.1.1.**

1. *The NSFD scheme (5.1.10) is dynamically consistent with respect to positivity.*
2. *Under the condition (3.3.1), the NSFD scheme (5.1.10) is a dynamical system on the same biologically feasible region  $\Omega$  just as for the continuous KMB system (3.2.3) in Theorem 3.3.1.*

*Proof.*

1. The positivity is obtained by construction of the NSFD scheme (5.1.10).
2. From Equation (3.3.1) and the first equation of (5.1.10), we have

$$\frac{H_{n+1} - H_n}{\phi} \leq L - \Gamma H_{n+1}.$$

Solving for  $H_{n+1}$ , assuming that  $H_n \leq \frac{L}{\Gamma}$ , we get

$$H_{n+1} \leq \frac{L}{\Gamma}. \quad (5.1.18)$$

The second equation of (5.1.10) and Equation (5.1.18) yield

$$\frac{F_{n+1} - F_n}{\phi} \leq \alpha H_{n+1} - m F_{n+1} \leq \frac{L}{\Gamma} - m F_{n+1}, \quad \text{since } 0 < \alpha \leq 1,$$

which implies that

$$F_{n+1} \leq \frac{L}{m\Gamma} \quad \text{if } F_n \leq \frac{L}{m\Gamma}. \quad (5.1.19)$$

Therefore the NSFD scheme (5.1.10) is a dynamical system on  $\Omega$ .

□

**Theorem 5.1.2.** *The NSFD scheme (5.1.10) is elementary stable (Definition 2.9.12). That is:*

1. *The fixed-points of the NSFD scheme (5.1.10) are the equilibrium points of the continuous model (3.2.3).*
2. *The fixed-points of the NSFD scheme (5.1.10) have the same local stability properties as the equilibrium points of the KMB model (3.2.3). More precisely, whenever for  $J_c$ , representing the Jacobian matrix associated with KMB model (3.2.3) at the equilibrium point,  $Q$  is chosen such that*

$$Q \geq \frac{\|J_c\|^2}{|\text{trace}J_c|}$$

*apart from satisfying the relation (5.1.17), we have the following:*

- (a) *Under the condition (3.3.14), the unique interior fixed-point  $(\bar{H}, \bar{F})$  is locally asymptotically stable (LAS) and the trivial fixed-point  $(0,0)$  unstable.*
- (b) *If (3.3.14) is violated, then  $(0,0)$  is GAS.*

*Proof.* We prove Theorem 5.1.2 in different steps.

- A. A point  $(\bar{H}, \bar{F})$  is a fixed point of the NSFD scheme (5.1.10) if, and only, if it satisfies the defining equations (3.3.6) of the equilibria of the continuous KMB model (3.2.3).
- B. We prove the local asymptotic stability of the interior fixed-point  $(\bar{H}, \bar{F})$ .  
Putting

$$U = H - \bar{H} \quad \text{and} \quad V = F - \bar{F},$$

the linearized continuous equation (3.3.21) about the equilibrium point  $(\bar{H}, \bar{F})$  in terms of the eclosion function  $E(H, F)$  and the recruitment function  $R(H, F)$  can be re-written as

$$\begin{pmatrix} \frac{dU}{dt} \\ \frac{dV}{dt} \end{pmatrix} = J_c \begin{pmatrix} U \\ V \end{pmatrix}$$

where

$$J_c = \begin{pmatrix} E_H - R_H & E_F - R_F \\ R_H & R_F - m \end{pmatrix} = \begin{pmatrix} E_H & E_F - R_F \\ 0 & R_F \end{pmatrix} - \begin{pmatrix} R_H & 0 \\ -R_H & m \end{pmatrix} \quad (5.1.20)$$

is the Jacobian matrix at the interior equilibrium point  $(\bar{H}, \bar{F})$ . Here and after,  $E_H$ ,  $R_H$ ,  $E_F$  and  $R_F$  denote the partial derivatives of the functions  $E(H, F)$  and  $R(H, F)$  at the point  $(\bar{H}, \bar{F})$ .

The NSFD scheme (5.1.10) can be re-written in the form

$$\begin{cases} \frac{H_{n+1} - H_n}{\phi} = E(H_n, F_n) - R(H_{n+1}, F_n) \\ \frac{F_{n+1} - F_n}{\phi} = R(H_{n+1}, F_n) - mF_{n+1}. \end{cases} \quad (5.1.21)$$

The linearized equation about the interior fixed-point  $(\bar{H}, \bar{F})$  is

$$\begin{cases} (1 + \phi R_H)U_{n+1} & = (1 + \phi E_H)U_n + \phi(E_F - R_F)V_n \\ \phi R_H U_{n+1} + (1 + \phi m)V_{n+1} & = (1 + \phi R_F)V_n. \end{cases} \quad (5.1.22)$$

Solving the algebraic system (5.1.22) in  $(U_{n+1}, V_{n+1})$ , the linearized NSFD scheme reads

$$\begin{pmatrix} U_{n+1} \\ V_{n+1} \end{pmatrix} = J_d \begin{pmatrix} U_n \\ V_n \end{pmatrix} \quad (5.1.23)$$

where

$$\begin{aligned} J_d &= \begin{pmatrix} 1 + \phi R_H & 0 \\ -\phi R_H & 1 + \phi m \end{pmatrix}^{-1} \begin{pmatrix} 1 + \phi E_H & \phi(E_F - R_F) \\ 0 & 1 + \phi R_F \end{pmatrix} \\ &= T \begin{pmatrix} 1 + \phi E_H & \phi(E_F - R_F) \\ 0 & 1 + \phi R_F \end{pmatrix}, \end{aligned}$$



for

$$T = \begin{pmatrix} \frac{1}{1 + \phi R_H} & 0 \\ \frac{\phi R_H}{(1 + \phi R_H)(1 + \phi m)} & \frac{1}{1 + \phi m} \end{pmatrix}.$$

From the expression of  $J_c$  in (5.1.20) we have

$$J_d = I + \phi T J_c. \quad (5.1.24)$$

With  $R_H(\bar{H}, \bar{F})$  being positive, the spectral radius of the matrix  $(T - I)$  is less than 1. Therefore, the sequence  $(T - I)^n$  of the matrices converges to the null matrix. Consequently, the difference system (5.1.23) has the same qualitative behavior as the system

$$\begin{pmatrix} \tilde{U}_{n+1} \\ \tilde{V}_{n+1} \end{pmatrix} = \tilde{J}_d \begin{pmatrix} \tilde{U}_n \\ \tilde{V}_n \end{pmatrix} \quad (5.1.25)$$

where

$$\tilde{J}_d = I + \phi J_c. \quad (5.1.26)$$

It is easy to check that  $\mu$  is an eigenvalue of the matrix  $\tilde{J}_d$  if, and only, if  $\lambda = \frac{\mu - 1}{\phi}$  is an eigenvalue of  $J_c$ . That is

$$\mu = \phi\lambda + 1 = (1 + \phi\lambda_1) + i\phi\lambda_2.$$

Furthermore,

$$|\mu|^2 = \begin{cases} 1 - 2\phi|\lambda_1| + \phi^2|\lambda|^2 & \text{if } \lambda_1 < 0 \\ 1 + 2\phi|\lambda_1| + \phi^2|\lambda|^2 & \text{if } \lambda_1 > 0. \end{cases}$$

Thus, whenever

$$\phi < \frac{2|\lambda_1|}{|\lambda|^2}, \quad (5.1.27)$$

we have, for  $\lambda_1 < 0$ ,

$$\begin{aligned} |\mu|^2 &< 1 - 2\phi|\lambda_1| + \frac{2\phi|\lambda_1|}{|\lambda|^2}|\lambda|^2 \\ &= 1. \end{aligned}$$

Therefore  $|\mu| < 1$  if  $\lambda_1 < 0$ . In a similar manner,  $|\mu| > 1$  if  $\lambda_1 > 0$ . The function  $\phi$  in (5.1.11) with  $Q$  as specified in the statement of Theorem 5.1.2 satisfies the condition (5.1.27) because

$$\phi < \frac{1}{Q} \quad \text{and} \quad Q \geq \frac{|\lambda|^2}{2|\lambda_1|}$$

for each eigenvalue of  $J_c$ , given that  $|\lambda| \leq \|J_c\|$  and  $\lambda_1 = 2\text{trace}J_c$  for the 2x2 matrix  $J_c$ . This proves the local asymptotic stability of the fixed-point  $(\bar{H}, \bar{F})$ , based on Theorem 2.7.8, whenever the interior equilibrium point is locally asymptotically stable.

- C. We deal with the stability of the trivial fixed-point  $(0,0)$  with the assumption that Condition (3.3.14) holds true. We proceed as follows:

Adding the two equations in (5.1.10), we obtain the discrete conservation law

$$\frac{N_{n+1} - N_n}{\phi} = \frac{LN_n}{N_n + \omega} - mF_{n+1}. \quad (5.1.28)$$

Under the condition (3.3.14), and using the definition of  $\Omega$ , we have

$$\frac{N_{n+1} - N_n}{\phi} \geq \frac{LN_n}{\frac{L}{\Gamma} + \frac{L}{m\Gamma} + \omega} - m_c \frac{L}{m\Gamma}.$$

Hence

$$N_{n+1} \geq \left(1 + \phi \frac{L}{\frac{L}{\Gamma} + \frac{L}{m\Gamma} + \omega}\right) N_n - m_c \frac{L}{m\Gamma}.$$

By Gronwall inequality (Lemma 2.6.3), the sequence  $(N_n)_n$  cannot tend to zero. Thus  $(0,0)$  is unstable and not attractive.

- D. We prove part 2 of Theorem 5.1.2 regarding the stability of the fixed-point  $(0,0)$  when Condition (3.3.14) is not satisfied.

Since the NSFD scheme (5.1.10) is convergent, the discrete conservation law (5.1.28) has the same behavior as the difference equation

$$N_{n+1} - N_n = \phi \frac{LN_n}{N_n + \omega} - \phi m F_n \quad (5.1.29)$$

for  $n$  large enough. Consequently, when Condition (3.3.14) is violated it follows from the Lyapunov argument used in the continuous setting for the proof of Proposition 3.3.10 that

$$N_{n+1} - N_n < 0 \quad \text{for} \quad 0 < H_n \leq r \quad \text{and} \quad 0 < F_n \leq r.$$

This shows that the trivial fixed point  $(0,0)$  is locally asymptotically stable.

E. For the global asymptotic stability of the trivial fixed-point  $(0,0)$ , we are going to apply Theorem 2.8.4. In this regard, it suffices to show that the largest invariant set  $\mathcal{M}$  contained in the set  $\mathcal{E}$  can be reduced to the singleton set  $\mathcal{M} = \{(0,0)\}$ . That is;

$$\begin{aligned}\mathcal{E} &= \left\{ (H, F) \in \Omega : V(G(H, F)) = V(H, F) \right\} \\ &= \left\{ (H, F) \in \Omega : \phi \frac{L(H+F)}{H+F+\omega} - mF = H+F \right\} \\ &= \{(0,0)\}\end{aligned}$$

We shall prove by contradiction. Assume that there are  $H > 0$  and  $F > 0$  such that

$$\phi \frac{L(H+F)}{H+F+\omega} - \phi mF = H+F.$$

Or equivalently

$$\phi \frac{LV}{V+\omega} - \phi mF = V.$$

This implies that

$$\begin{aligned}\phi mF &= \phi \frac{LV}{V+\omega} - V \\ &= \left( \frac{\phi L}{V+\omega} - 1 \right) V \\ &< \left( \frac{\phi L}{\omega} - 1 \right) V \\ &< 0 \quad \text{since} \quad \phi \frac{L}{\omega} - 1 < \phi \left( \frac{L}{\omega} - 1 \right) \quad \text{by (3.2.6), (5.1.15) and Remark 3.2.2.}\end{aligned}$$

But it is impossible to have  $\phi mF < 0$  for  $F > 0$ . So  $F = 0$ . Which implies that  $H = F = 0$  from the definition of  $V(H, F)$ . Thus,  $\mathcal{E} = \{(0,0)\}$ .

□

**Remark 5.1.3.** *We conjecture that the interior fixed-point of the NSFD scheme (5.1.10) is GAS. This conjecture which is supported by numerical simulations in Section 5.3 could probably be proven by using an appropriate Lyapunov function.*

## 5.2 The SP discretization

We now construct a NSFD scheme for the SP model (4.2.1). Using the method of sub-equations that led to the scheme (5.1.10), we propose, for the SP model, the NSFD scheme

$$\begin{cases} \frac{H_{n+1} - H_n}{\phi} = \frac{L(H_n + F_n)}{H_n + F_n + \omega} - (\alpha + \tilde{m})H_{n+1} \\ \frac{F_{n+1} - F_n}{\phi} = \alpha H_{n+1} - mF_{n+1}, \end{cases} \quad (5.2.1)$$

which is equivalent to

$$\begin{cases} H_{n+1} = \frac{\left(\frac{\phi L(H_n + F_n)}{H_n + F_n + \omega} + F_n\right)}{1 + \alpha + \tilde{m}} \\ F_{n+1} = \frac{\alpha \phi H_{n+1} + F_n}{1 + \phi m}, \end{cases} \quad (5.2.2)$$

where  $\phi$  is defined in (5.1.11) with  $Q = \alpha + \tilde{m} + m$ .

The analysis carried out for the NSFD scheme (5.1.10) does apply to the NSFD scheme (5.2.1). Therefore, we are going to mention main results without giving their proofs.

In a similar manner to the proof of Theorem 4.3.1, we obtain the result below.

**Theorem 5.2.1.** *The NSFD scheme (5.2.1) is a dynamical system in the biological feasible region  $\Omega$  defined in Theorem 4.3.1.*

Adding the equations in (5.2.1), we have the conservation law

$$\frac{N_{n+1} - N_n}{\phi} = \frac{LN_n}{N_n + \omega} - \tilde{m}H_{n+1} - mF_{n+1},$$

from which it follows that

$$-(m + \tilde{m})N_{n+1} \leq \frac{N_{n+1} - N_n}{\phi} \leq \frac{LN_n}{\omega} - \min\{m, \tilde{m}\}N_{n+1}. \quad (5.2.3)$$

From the left inequality in (5.2.3) we have

$$\begin{aligned} -(m + \tilde{m})N_{n+1} &\leq \frac{N_{n+1} - N_n}{\phi} \\ \frac{N_n}{1 + \phi(m + \tilde{m})} &\leq N_{n+1}. \end{aligned} \quad (5.2.4)$$

On the other hand, the second inequality in (5.2.3) gives

$$\begin{aligned} \frac{N_{n+1} - N_n}{\phi} &\leq \frac{LN_n}{\omega} - \min\{m, \tilde{m}\}N_{n+1} \\ N_{n+1} &\leq \left( \frac{1 + \phi \frac{L}{\omega}}{1 + \phi \min\{m, \tilde{m}\}} \right) N_n. \end{aligned} \quad (5.2.5)$$

Combining (5.2.4) and (5.2.5) we obtain

$$\frac{N_n}{1 + \phi(m + \tilde{m})} \leq N_{n+1} \leq \left( \frac{1 + \phi \frac{L}{\omega}}{1 + \phi \min\{m, \tilde{m}\}} \right) N_n. \quad (5.2.6)$$

When we proceed by mathematical induction from (5.2.6) we obtain

$$\left( \frac{1}{1 + \phi(m + \tilde{m})} \right)^{n+1} N_0 \leq N_{n+1} \leq \left( \frac{1 + \phi \frac{L}{\omega}}{1 + \phi \min\{m, \tilde{m}\}} \right)^{n+1} N_0. \quad (5.2.7)$$

We, therefore, have established the following result, which shows the GAS of the trivial fixed point,  $(0,0)$ , in the more specific way below.

**Theorem 5.2.2.** *Under the condition (4.3.10), the colony declines to zero in a contractive manner.*

### 5.3 Numerical simulations

For numerical simulations for the discrete KMB-NSFD scheme (5.1.10), we use the parameters in Table 5.1 below, which are taken from [43].

Table 5.1: Basic parameters for simulations

Parameter	$L$	$\alpha$	$\sigma$	$\omega$
Value	2000	0.25	0.75	27000

The choice of the values  $\alpha = 0.25$  and  $\sigma = 0.75$  is motivated by the fact that, in the absence of foragers, new workers become foragers in a minimum of four days, and there is reversion (social inhibition) from foragers class to hive class if more than one third of the total population are foragers [43]. To Table 5.1, we add the critical value,  $m_c$ , of the foragers death rate obtained from Equation (3.3.14) as  $m_c = 0.355$ . We will therefore use the quantities below and above the critical value  $m_c$  namely  $m = 0.24$  and  $m = 0.4$ , as in [43]. Finally, we take  $\Delta t = 2$ , a large value of step size which shows the power of the nonstandard approach as this is not permissible in classical numerical schemes [55].

In the KMB setting, Figure 5.1 illustrates through both the phase plane and the population-time axes the GAS of the interior equilibrium or fixed point when  $m = 0.24$  in accordance with Theorem 3.3.5(1) and Theorem 5.1.2(a). Furthermore, when  $m = 0.4$ , the CCD phenomenon or the GAS of the trivial equilibrium or fixed point occurs according to Theorem 3.3.5(2) and Theorem 5.1.2(b), as displayed in Figure 5.2.

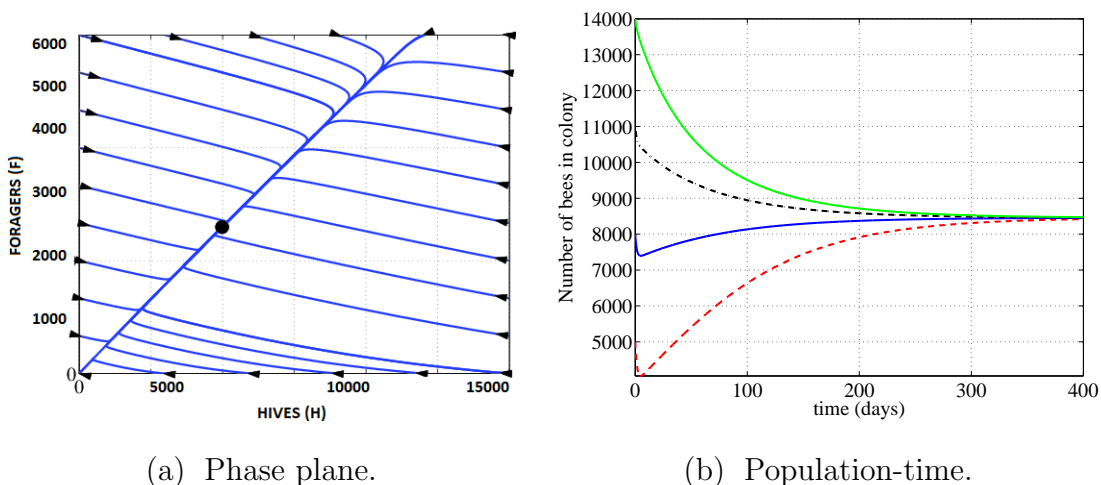


Figure 5.1: GAS of the interior fixed-point for the KMB-NSFD scheme (5.1.10).

The shift between the global asymptotic stability of the trivial fixed point and the interior fixed point is addressed in the following bifurcation diagram where foragers' death rate,  $m$ , is a bifurcation parameter. Moreover,  $m = 0.355$  is a forward/transcritical bifurcation of the model (3.2.3) in the sense that for  $m > 0.355$ , the model has only one equilibrium point  $(0,0)$  which is globally asymptotically sta-

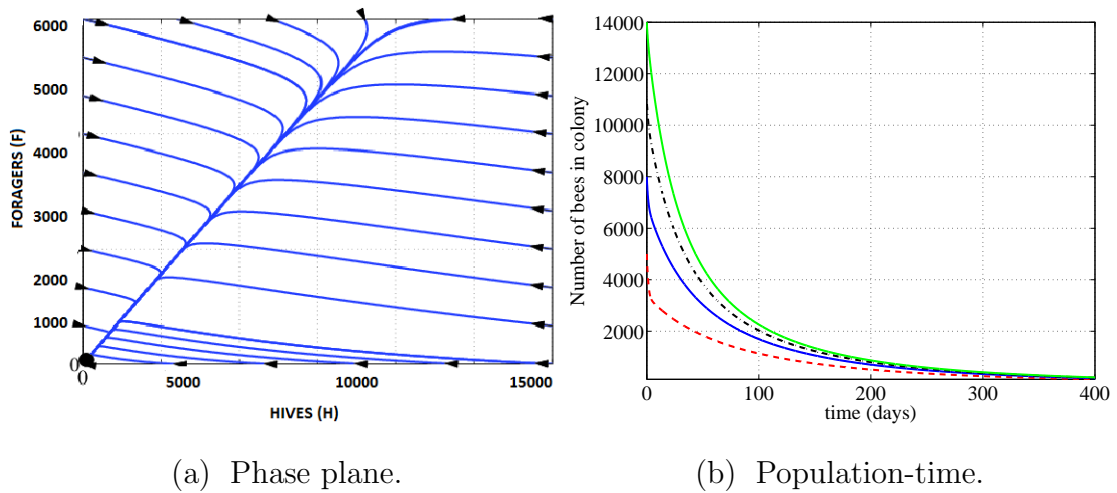


Figure 5.2: CCD in the KMB-NSFD scheme (5.1.10).

ble. But for  $m < 0.355$ , the stability nature of the trivial equilibrium point changes to unstable and an additional interior equilibrium point is born and is globally asymptotically stable. By Definition 2.5.2, the model (3.2.3) undergoes transcritical bifurcation at the point  $m = m_c$ . The NSFD scheme (5.1.10) is dynamically consistent with respect to all these properties as illustrated in Figure 5.1 and 5.2 (see Figure 5.3).

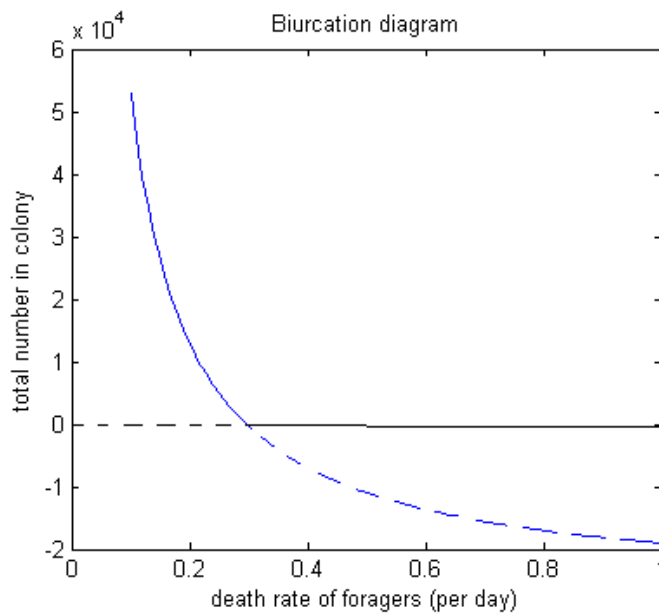


Figure 5.3: The bifurcation diagram of KMB-NSFD scheme (5.1.10)

Regarding the SP setting, we still use the values in Table 1 because we assume that

the laying rate of the queen remains the same. The rate,  $\tilde{m}$ , at which parasites leave the hive class is, for simplicity, taken to be equal to the death rate  $m = 0.24$  of foragers. As predicted by Theorem 4.3.5 and Theorem 5.2.2, Figure 5.4 exhibits faster decay to zero of the total population, which once again justifies the terminology *capensis calamity*

- The colony collapses in 100 days for the SP model when  $m = 0.24$  (Figure 5.4(b)), while there is no CCD for the KMB model in this case (see Figure 5.1(b));
- The colony collapses in 400 days for the KMB model when  $m = 0.4$  (Figure 5.2(b)).

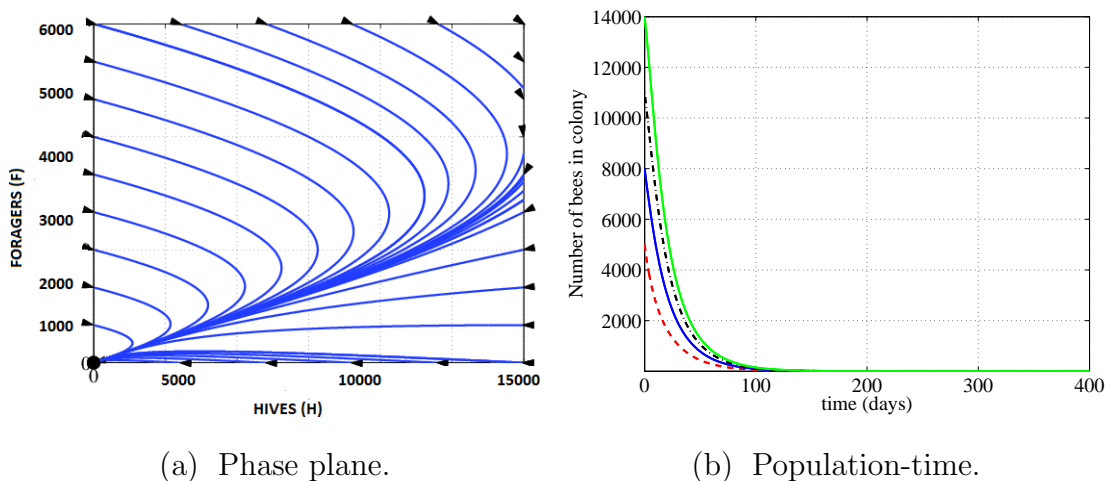


Figure 5.4: Faster decline of the colony for SP-NSFD scheme (5.2.1)



# Chapter 6

## Conclusion

This dissertation is motivated by the work [43], which provides a fundamental mathematical model for the decline of the honey bee populations within the colony. The alarming declines of the colony population of honey bees constitute a serious threat to ecosystem services and honey bee products which would have great consequences. The situation is worsen nowadays by an increase in colony losses world-wide through Colony Collapse Disorder (CCD) and particularly the *capensis calamity(cc)* in South Africa. Both phenomena are characterized by imminent losses of managed honey bee colonies, thus resulting in the decline of these important pollinators.

In this dissertation, we build on the honors project [50], which in turn is based on [43], to investigate some mathematical models of honey bee population dynamics. The starting point is therefore the KMB model [43] consisting of the hive compartment,  $H$ , and the foragers compartment,  $F$ , with positive recruitment rate,  $R = R(H, F)$ . We have provided mathematical details and rigorous analysis of the model. With the assumption that the rate  $\omega$ , at which the maximum eclosion is approached is large enough, the following results have been theoretically established: There exists a critical value,  $m_c$ , of the parameter  $m$  (foragers' death rate) which is a transcritical bifurcation. That is, the trivial equilibrium point  $(0,0)$  is globally attractive whenever  $m > m_c$ , which means that the CCD phenomenon occurs, whereas it is not attractive when  $m < m_c$ , and an additional interior equilibrium point which is globally asymptotically stable (GAS) is born.

We have addressed one of the research questions that was identified in [50] by constructing a nonstandard finite difference (NSFD) scheme for the KMB model that is dynamically consistent with respect to the decline property. More specifically, we have theoretically established that the fixed-points of the KMB-NSFD schemes are exactly the equilibrium points of the KMB model and, they have the same stability properties in the sense that: for  $m > m_c$ , the trivial fixed-point  $(0, 0)$  is GAS while for  $m < m_c$ , there exists a unique interior fixed-point which is LAS.

In addition to the model formulated in [43], we improved the social parasite, SP, model in a way that the rate,  $\tilde{m}$ , at which clones leave the hive compartment is different from the rate  $m$  at which foragers die. This model is motivated by the *capensis calamity* that arises when some *A.m. capensis* clones (parasites) gain access into the colonies of *A.m. scutellata* (hosts). We have described the social parasite scenario by a low positive and constant recruitment rate due to the presence of parasites which do not contribute to foraging but leave the hive compartment at a constant rate after benefiting from the resources produced by the hosts. We have proved that the total population declines rapidly in this parasitic scenario.

We have constructed a NSFD scheme for the SP model (SP-NSFD scheme) and proved theoretically the *capensis calamity* phenomenon. We have provided numerical simulations that confirm the theory for both KMB and SP nonstandard discretizations. In the SP-NSFD scheme, we observed a rapid decline in the total population of the host colony, (Figure 5.4). This means that the SP setting indeed represents abandoned brood as a diagnostic of CCD colonies [43]. In our simulations, it takes about 100 days for *A.m. scutellata* population to reach zero, regardless of the foragers' death rate, after *A.m. capensis* have entered their colony and started producing (Figure 5.4(b)), whereas it takes about 400 days for a normal honey bee population, as in the KMB model, to reach zero when the death rate of foragers is above a certain critical point (Figure 5.2(b)).

Apart from the construction of the NSFD schemes, the following natural question that was raised in [50] remains.

1. Regarding the colony population declines, which measures and strategies are

needed to avoid or at least to reduce honey bee colony declines? Since the model proposed in [43] suggests that the colony growth is attained when the death rate,  $m$ , of the foragers is below a critical value, a possible strategy is to make  $m_c$  small. Given the fact that  $m_c$  is a function of the parameters  $L$ ,  $\alpha$ ,  $\sigma$ , and  $\omega$ , it can be seen from (3.3.14) how  $m_c$  can be reduced by appropriate choice of some of these parameters. From the biological point of view, growth of honey bee colonies can be achieved by providing enough resources to honey bees, either through planting many different flowering plants (bee plants) closer to the colonies as this would prevent foragers from undertaking long and risky travel [96] as it is confirmed that they (foragers) die due to exhaustion [11]. Enactment of legislation that will reduce or ban indiscriminate use of pesticides in agriculture could also help in this regard [85] like the recent ban on the use of neonicotinoid pesticides in Europe.

2. Regarding the model with social parasites, what strategies could be taken to reduce the spread of parasites. Measures that could be taken to reduce the spread of the social parasites in honey bees includes stopping migration of honey bees of different races between regions [92] in South Africa as enshrined by the law. This is important since clones rely heavily on anthropogenic factors to move from one region. Obeying enacted laws that restrict migratory beekeeping and enforcement of same would help in stopping the spread. In the event that migration is unavoidable, hives should be inspected regularly after migration for the presence of the parasites and infested hives placed in quarantine and destroyed accordingly [52].

A further extension, not mentioned in [50], but outlined in Section 3.4 of this dissertation, is to improve the KMB and SP models in a more realistic manner. To this end, one way could be to consider in the models, numerous factors responsible for colony declines. These include:

3. Death rate of hive bees and brood [16,27], pests and diseases [25] and climate change [27].
4. Other compartments can be incorporated that will model colony failure as

contagious by viruses and other pathogens [29, 47, 77].

5. To investigate the interactions of suitable strategies (e.g food and climate) and forager mortality on colony fate [44, 80].
6. Since studies have shown that secreted pheromones, either by queen or workers, play a big role in assigning different tasks in the colony [11], it is of interest to consider the part that drones and drone-produced chemicals play on mediating social interaction with themselves and their importance in communicating with other individuals [14, 97]. It is of interest to see how drones can be considered in the formulation of mathematical models for the honey bee population dynamics since *Varroa* mites prefer drone brood over worker brood to complete their life cycle [11].

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