**A MATHEMATICAL MODEL OF INTER-COLONY SPREAD OF AMERICAN FOULBROOD IN EUROPEAN HONEYBEES (APIS MELLIFERA L.)**

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**A MATHEMATICAL MODEL OF INTER-COLONY SPREAD OF AMERICAN FOULBROOD IN EUROPEAN HONEYBEES (APIS MELLIFERA L.)**

by

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**BIOGRAPHICAL SKETCH**

Born on August 30, 2001, in Makati City, Kieffer P. Santos is the eldest child of Antonio P. Santos and Ruth P. Santos, and sibling to Seymour P. Santos, Calahan P. Santos, and Austein P. Santos. Growing up, he received his primary education at Golden Lampstand Grade School in San Pedro, Laguna, followed by his secondary education at Immaculate Heart of Mary School, also in San Pedro. In September 2020, Kieffer embarked on his academic journey at the University of the Philippines Los Baños (UPLB), where he pursued a degree in BS Applied Mathematics. With a keen interest in mathematical applications, Kieffer is committed to leveraging his education to contribute meaningfully to his field and beyond.

KIEFFER P. SANTOS

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**ABSTRACT**

KIEFFER P. SANTOS, University of the Philippines Los Baños, June 2023

**A MATHEMATICAL MODEL OF INTER-COLONY SPREAD OF AMERICAN FOULBROOD IN EUROPEAN HONEYBEES (APIS MELLIFERA L.)**

**Major Professor: Eduardo O. Jatulan**

American Foulbrood (AFB) remains a critical concern for European honeybee colonies globally, exerting profound impacts on bee health and apiary productivity. This study endeavors to deepen our comprehension of the inter-colony transmission dynamics of AFB among European honeybee colonies by developing a comprehensive mathematical model. The model incorporates influential factors such as bee drifting, providing a nuanced exploration of disease ecology in honeybee communities. This study contributes to the advancement of our understanding of disease ecology in honeybee populations and represents a significant step forward in the quest for sustainable beekeeping practices and the preservation of honeybee populations.

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**Keywords:** American Foulbrood (AFB), European honeybees (Apis mellifera L.), epidemiology, population dynamics

**Chapter 1**

**INTRODUCTION**

Chapter 1 provides a comprehensive overview of key aspects related to honeybee health and disease management. It begins with a discussion on American Foulbrood (AFB) in Section 1.1, followed by an exploration of the honeybee lifecycle in Section 1.2. Section 1.3 delves into factors influencing colony survival and disease dynamics, while Section 1.4 focuses on inter-colony behavior and disease spread. Section 1.5 examines pathogen infectivity, colony density, AFB eradication, spore carriage, and control methods, offering insights into effective management strategies. Finally, Section 1.6 presents a comparison between environmental hazards and infectious diseases, providing context for understanding broader challenges in honeybee health management.

**1.1 Description and Characteristics of American Foulbrood (AFB)**

American Foulbrood (AFB) is a highly contagious and devastating disease that poses a significant threat to honeybee colonies [1]. It is caused by the bacterium Paenibacillus larvae and primarily affects honeybee brood at the pre-pupal and pupal stages of development [1, 5]. Infected colonies display characteristic symptoms, including sunken and punctured cappings on brood cells, along with a distinctive "ropy" condition of infected larvae and a sulfur-like foul smell [1, 5]. AFB spreads through various means, including infected colonies, robbing, drifting bees, and beekeepers, making it challenging to contain and manage effectively [1, 5]. Moreover, natural behaviors of honeybees, such as robbing infected hives or drifting between colonies, also contribute to the spread of AFB [5]. Preventive measures and prompt action are crucial to contain outbreaks, given the resilience of AFB spores, which can remain viable for over 50 years [5]. The transmission of American Foulbrood (AFB) among bee colonies occurs through multiple routes, including extracted honey supers, transfer of brood and honey frames, and other contaminated hive parts [13]. Additionally, factors such as robbing, drift, and the introduction of infected queens and package bees can facilitate the spread of AFB within and between apiaries [13]. It is noteworthy that AFB infections do not arise from a single bacterial spore; rather, millions of spores are typically required to infect larvae in a colony [13]. Thus, understanding the diverse transmission pathways and implementing rigorous preventive measures are essential for effective AFB management and the preservation of honeybee populations [13].

**1.2 Honey Bee Lifecycle**

The lifecycle of honeybees, specifically the European honey bee, progresses through four distinct stages: egg, larva, pupa, and adult [12]. Eggs laid by the queen bee develop into larvae, which are fed royal jelly by nurse bees, facilitating their growth and development [12]. After undergoing metamorphosis in capped cells, the larvae transition to the pupal stage, during which their wings, head, thorax, and abdomen develop [12]. Upon emerging as adults, honey bees initially have their wings hardening and require feeding by other workers until they are fully integrated into the colony [12]. The survival and productivity of honeybee colonies depend on various factors, including foraging behavior and resource availability [6, 15]. Foraging bees collect nectar and pollen from flowers, with foraging flights typically restricted to less than one kilometer from the hive [15]. Communication through dances and trophallaxis guides foragers to food sources, with bees exhibiting flower and location constancy during trips [15]. Additionally, honeybee colonies require ample food resources, with colonies needing approximately 50 pounds of pollen and 100 pounds of honey to survive for 12 months [6]. During peak seasons, colonies can consist of 40,000 to 50,000 foragers, highlighting the significant foraging activity required to sustain hive populations [6]. The pre-foraging stage significantly influences honeybee lifespan, with a notable proportion of bees perishing during this period [10]. Mortality rates during foraging remain constant, with individuals facing risks of 9% and 36% per hour and per day, respectively [10]. These findings underscore the importance of understanding natural mortality patterns and drivers in honeybee workers to assess the impact of various stressors on bee populations [10]. Moreover, drifting among honeybee colonies can contribute to the spread of diseases like AFB [18]. Although AFB symptoms slightly elevate drifting levels, the infection does not significantly affect drifting frequency, particularly among young bees during orientation flights [18]. However, colonies with AFB symptoms exhibit higher levels of P. larvae spores in pollen and honey compared to healthy colonies, suggesting drifting's potential role in AFB transmission, especially during young bee orientation flights [18].

**1.3 Factors Influencing Colony Survival and Disease Dynamics**

Factors influencing colony survival and disease dynamics in honeybee populations are multifaceted and encompass various aspects of disease transmission and colony management [2, 4, 9, 10]. The rate of transmission (b) and disease-induced death rates (dH and dF) are critical factors affecting colony survival, with higher disease-induced death rates paradoxically aiding colony survival in certain scenarios [2]. Infections occurring approximately 20 days before winter onset significantly impact colony survival due to insufficient bee numbers surviving winter [2]. Additionally, disease spread through robbing occurs when drifting is rare, emphasizing the importance of reducing drift for disease mitigation [3]. The model developed in one study provides insights into the mechanisms underlying colony survival or collapse in the face of infection, highlighting the critical role of disease dynamics and timing of infection [9]. Moreover, distance and ownership significantly contribute to the spread of AFB, suggesting the importance of location and management practices in disease control [4]. The study emphasizes the significance of preventing infection through good colony management practices, such as regular inspections for AFB signs and minimizing hive material interchange [3]. Recommendations for beekeepers include avoiding locations with known AFB outbreaks and focusing on strengthening larval immunity to spore infection through measures like probiotics and pollen feeding [8]. Additionally, treatment strategies focusing on preventing precocious foraging and boosting brood production are suggested to restore failing colonies [9]. Furthermore, insights into honeybee lifespan and foraging behavior provide valuable understanding of colony dynamics and underscore the importance of the pre-foraging stage in honeybee survival [10]. The pre-foraging stage facilitates learning of the environment and development of flight physiology, while also exposing bees to extrinsic mortality risks, ultimately influencing forager lifespan and colony dynamics [10].

**1.4 Inter-colony Behavior and Disease Spread**

Inter-colony behavior, including drifting among honeybee colonies, plays a crucial role in disease spread within apiaries [2, 3, 16]. Drifting can facilitate the transmission of diseases between colonies, especially in dense apiaries where the likelihood of drifting is higher [2, 16]. Interestingly, while drifting can contribute to disease transmission, it may also reduce the severity of diseases in affected colonies, potentially aiding colony survival against infection [3, 16]. This phenomenon underscores the complexity of disease dynamics within bee populations and highlights the importance of efficient guarding behavior to mitigate disease spread [2, 16]. Mite immigration among honeybee colonies, particularly during late summer and fall, has been observed to contribute to spikes in varroa mite infestations [11, 18]. Factors such as worker bee behavior, drone activity, and the role of guard bees influence mite drift, with potential implications for disease transmission [11, 18]. The study of mite immigration dynamics sheds light on factors contributing to late-season varroa spikes and offers insights for beekeepers to better manage varroa infestations [11, 18]. Bee drifting, where forager bees inadvertently enter the wrong colony, can lead to population imbalances and potential disease spread within apiaries [14, 16]. Beekeepers employ strategies such as hive placement and hive color differentiation to prevent drifting [14, 16]. Additionally, robbing behavior among colonies, especially during nectar dearths, can escalate rapidly and contribute to disease transmission [16, 17]. Beekeepers can recognize and mitigate robbing behavior by removing stimuli attracting bees and implementing preventative measures [16, 17].

**1.5 Pathogen Infectivity, Colony Density, Eradication, Spore Carriage, and Control Methods for AFB**

Control and treatment methods for American Foulbrood (AFB) vary in effectiveness and feasibility [1, 5, 8]. Antibiotics can be used to prevent and treat active AFB infections, but they don't kill spores, which can persist for decades [1]. The most effective control method involves sealing and burning infected colonies and equipment [1]. Additionally, good colony management practices, such as regular inspections for AFB signs, comb replacement, and minimizing hive material interchange, are crucial for prevention [5]. Implementing strategies like secondary radial checks and earlier inspections can effectively reduce epidemic size and increase disease extinction likelihood [4]. However, the cost and manpower required for certain strategies may be prohibitive [4]. To prevent AFB spread, beekeepers can implement a barrier management system to separate infected materials between hives and apiaries [5]. While antibiotics like Oxytetracycline (OTC) are not recommended for AFB control due to their limited efficacy and potential negative impacts, early detection through regular inspections is key for timely intervention [5]. Monitoring the number of infected cell combs (C) is also crucial, as rapid decline in other state variables occurs as C approaches its maximum value [8]. Beekeeping management practices, such as moving extracted honey supers between hives and transferring brood or honey frames between colonies, are common causes of AFB spread [13]. Robbing and drift can also contribute to AFB transmission, although the latter is less significant in lightly infected colonies [13]. Contrary to common belief, certain beekeeping equipment and items like hive tools, smokers, gloves, and queen bees have little consequence as sources of AFB spread [13]. Instead, the focus should be on improving beekeeping practices to minimize the risk of AFB transmission [13]. Understanding these transmission routes and emphasizing proper hive management are crucial for controlling the spread of AFB and maintaining healthy bee colonies [5, 13].

**1.6 Comparison between Environmental Hazards and Infectious Diseases**

The comparison between environmental hazards and infectious diseases in honeybee colonies highlights distinct outcomes [2]. Exposure to infectious diseases is more likely to result in colony collapse, whereas colonies generally have a better chance of survival under environmental hazards like pesticides [2]. This suggests differing impacts on colony health and resilience between these two types of stressors. Furthermore, drifting and the tendency for colonies to be located closer together may have evolved as mechanisms to reduce overall stress within the honeybee meta-population, possibly influenced by environmental changes [3]. Additionally, robbing behavior observed in honeybee colonies may be an adaptation to human influence, potentially warranting further evolutionary studies [3]. These observations underscore the complex interplay between environmental factors, evolutionary adaptations, and honeybee colony dynamics. Moreover, the infectivity of pathogens and colony density play crucial roles in disease transmission within honeybee colonies [3]. Extremely infectious pathogens or dense colonies can lead to rapid transmission between colonies, regardless of other parameters [3]. Additionally, when almost all cell combs within a colony are infected, colony eradication becomes imminent, resulting in widespread carriage of spores among adult bees [8]. This highlights the severity of colony-level infections and underscores the potential for rapid transmission of pathogens within and between colonies.

Chapter 2

**Chapter 3**

**REVIEW OF RELATED LITERATURE**

**Chapter 4**

**STATEMENT OF THE PROBLEM**

**4.1 Objectives**

The main objective of this study is to develop a mathematical model (SI model) to investigate the dynamics of inter-colony spread of American Foulbrood (AFB) in European honeybee (Apis mellifera L.) populations. Specifically, the study aims to:

1. Incorporate key factors such as drifting rate, effectiveness of drifting bees in integrating into other colonies, and return rate of unsuccessful drifting bees into the model to comprehensively capture AFB transmission dynamics between honeybee colonies.
2. Analyze the model to identify factors influencing the spread of AFB between honeybee colonies.
3. Utilize numerical simulations to assess the accuracy and effectiveness of the model.
4. Provide insights and recommendations for beekeepers and policymakers to develop targeted disease management protocols aimed at controlling AFB outbreaks and preserving honeybee populations.

**4.2 Methodology**

**4.2.1 Model**

This mathematical model builds upon the model presented in Jatulan et al.’s paper by incorporating an inter-colony interaction. Specifically, it focuses on modeling two colonies, designated as Colony 1 and Colony 2, to illustrate how different behaviors impact disease transmission between colonies. The mathematical model for Colony 1 is given by the following system:

|  |  |
| --- | --- |
|  | (1) |
|  | (2) |
|  | (3) |
|  | (4) |
|  | (5) |
|  | (6) |

The dynamics of Colony 2 exhibit similarities to Colony 1, albeit with distinct subscripts of the state variables and parameters , , , , , and . The dynamics of Colony 2 are governed by the following system:

|  |  |
| --- | --- |
|  | (7) |
|  | (8) |
|  | (9) |
|  | (10) |
|  | (11) |
|  | (12) |

The drifting component's dynamics are governed through the following system:

|  |  |
| --- | --- |
|  | (13) |
|  | (14) |
|  | (15) |
|  | (16) |

From the equations, the following terms , , , and . The parameters that have been introduced include and , representing the drifting rate of forager honey bees; and , indicating the rejection rate of drifting honey bees not accepted by the other colony; and finally and , signifying the return rate of drifting adult bees to their original colony upon failure to integrate into the other colony.

**4.3 Significance**

This study is significant for its comprehensive analysis of the dynamics of American Foulbrood (AFB) transmission between honeybee colonies. By developing a mathematical model, the study sheds light on the mechanisms driving AFB spread, offering insights crucial for devising effective disease management strategies and safeguarding the economic viability of beekeeping operations. Furthermore, the study's implications extend to biodiversity conservation, public health, and scientific research, highlighting its importance in addressing a pressing threat to honeybee populations and the ecosystems they support.

**4.4 Scope and Limitation**

The study focuses on developing a mathematical model to simulate the inter-colony spread of American Foulbrood (AFB) in European honeybee populations, aiming to understand the influence of factors like colony density, bee movement, behavior, and health on AFB transmission dynamics. While offering insights into long-term AFB exposure effects and identifying critical control points for mitigating epidemics, the study acknowledges limitations inherent in mathematical modeling, including simplifications and data availability constraints, which may affect the accuracy and generalizability of findings to real-world scenarios. Thus, caution is warranted when applying the study's results to practical beekeeping and disease management practices.

**REFERENCES**

|  |  |  |
| --- | --- | --- |
| **Parameters** | **Description** | **Value** |
|  | The queen’s maximum laying rate per day | , |
|  | A coefficient that influences the rate at which the term approaches as the number of adult bees in a colony gets large [11]. |  |
|  | The rate at which broods are infected by colony spore-carrying adult bees | , |
|  | The rate at which adult bees become infected by the infected cell | , |
|  | The rate at which adult bees become infected upon contact with spore-carrier adult bees | , |
|  | The rate at which broods become immune with the spores |  |
|  | The rate at which immune broods become adult bees |  |
|  | The death rate of infected broods | variable, |
|  | The rate at which a diseased dead brood is cleaned by adult bees | variable, |
|  | The maximum number of cells in the colony |  |
|  | The percentage of clean cell combs that will be contaminated by AFB spores |  |
|  | The death rate of adult bees (both spore-carrier and spore-free) |  |
|  | The rate at which honeybees drift multiplied by the percentage of foraging honeybees | , , \* |
|  | The rejection rate of drifting honeybees that are not accepted by the receiving colony. |  |
|  | The rate at which drifting adult bees return to their original colony after failing to integrate into the other colony. | , |