

Mathematical modeling of plant-herbivore interactions: Stability analysis
and period-doubling bifurcation in a modified Nicholson-Bailey model

by

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AN ABSTRACT OF A DISSERTATION

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Abstract

A Nicholson-Bailey model was initially created with the purpose of examining the dynamics of the population between a parasite and its host. In 1935, Nicholson and Bailey proposed a model for predicting the interactions between *Encarsia Formosa* parasites and *Trialeurodes Vaporariorum* hosts that focused on the interaction between parasites and hosts¹. In the study of biological systems, these types of models, such as discrete-time equations, can be considered invaluable tools for studying the interactions between two species. This dissertation presents a refined iteration of the Nicholson-Bailey discrete host-parasite model in the first Chapter 1. The research unfolds in several chapters. The initial chapter provides a comprehensive background and reviews pertinent literature. Subsequently, fundamental definitions of ordinary differential equations are expounded upon, elucidating key concepts in dynamical systems such as stability analysis, manifold theory and bifurcations. Moreover, essential results and theorems pertinent to the study are delineated. In the second chapter, an investigation scrutinizes the dynamics of the newly formulated host-parasite model, featuring three essential parameters confined to the first quadrant. A rescaling technique is employed to condense the model into a two-parameter format, capturing its dynamics. Notably, the model consistently manifests two boundary steady states, with the potential emergence of a third interior steady state under specific parameter conditions. Utilizing linearized stability analysis, thresholds for system stability are identified, distinguishing between stable and unstable regimes. Further exploration delves into the long-term stability of steady states and center manifold theory, particularly focusing on non-hyperbolic steady states and transitions from stable to unstable regions. The analysis explores bifurcation scenarios, including two-parameter bifurcations, by varying parameter ranges. It highlights period-doubling bifurcations that lead to chaotic behavior as eigenvalues cross critical thresholds. Numerical simulations support the theoretical results, confirming the conclusions.

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PREVIEW

Abstract

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PREVIEW

Dedication

To my beloved husband, Dr. Hadi Mufti,

To my children, Yazan and Maysaa,

With deepest love and gratitude

I dedicate this dissertation to you. Thank you for all the love, support, and encouragement you have given me. I cherish and love you more than anything.

PREVIEW

Chapter 1

Introduction

Mathematical modeling entails the formulation of a system of equations, which extends to various types of equations such as differential, integral, or functional, collectively termed as models. Mathematical models are designed to encapsulate and portray phenomena such as biological or physiological events, whether observable directly or not. Leveraging mathematical principles, modeling enables researchers to delve into complex systems, predict outcomes, and examine scenarios that might prove arduous or impractical to investigate experimentally. Through rigorous scrutiny and validation, mathematical models serve as indispensable instruments for comprehending and unraveling the underlying mechanisms of natural phenomena². This endeavor aids researchers in grasping real life challenges and is particularly pivotal in ecological research, facilitating the exploration of myriad variables such as plant defenses and the complexities of herbivore interactions impacting plant communities^{3;4}.

Furthermore, mathematical models in particular in terms of discrete-time dynamics, find widespread applications in physics, engineering, and mathematical biology. Continuous-time models exhibit distinct dynamical behaviors compared to discrete-time models with the latter often showcasing numerous complex dynamics⁵⁻⁷.

Researchers and agricultural ecologists are keenly interested in discrete models describing interacting populations governed by differential equations. Discrete-time models are suitable for organisms with non-overlapping generations, such as annual plants and insect populations

with an annual life cycle. In contrast, continuous-time models are useful for organisms with overlapping generations dwelling in non-seasonal environments or seasonal environments with overlapping generations, such as perennial plants. Discrete-time models, in contrast to their continuous counterparts, can exhibit more complex or chaotic dynamical behavior. For instance, tropical insects with discrete generation periods, like Sugar-cane hoppers, exhibit rapid population growth, whereas those with overlapping generations, such as stylopids, affect host population dynamics through castration, thereby inducing discrete generations^{8;9}.

The fundamental interaction between plants and herbivores, steeped in predator-prey dynamics, has been a focal point in ecological discourse since antiquity. However, mathematical modeling of this interaction gained traction only in recent decades. Pioneering efforts by Lotka and Volterra laid the groundwork for modeling predator-prey relations, subsequently shaping modern approaches to modeling plant-herbivore interactions. These models, expanding upon the Lotka-Volterra framework, incorporate continuous and discrete-time dynamics, accounting for a spectrum of dynamics within plant-herbivore systems. This intricate relationship fosters a complex negative feedback loop critical for understanding ecosystem dynamics¹⁰⁻¹³.

Caughley's delineation of plant-herbivore dynamics into non-interactive and interactive models underscores the complexity of these interactions. In non-interactive models, herbivores do not impede plant growth, implying minimal impact on vegetation growth rates or size. Consequently, biologists and agricultural ecologists favor difference equations, especially for species with non-overlapping generations, as they offer robust applications in discrete form^{12;14}.

For instance, the populations with short life cycles portray mostly non-overlapping generations; hence, the models are of the discrete nature. These include the recent past new mathematical approaches in the dynamical system, ranging from continuous to partial to discrete, all focusing on interactive systems¹⁵. According to McKendrick-von Foerster equation, Gutierrez et al. use a model based on partial differential equations for the effects of herbivores on different segments of plants^{16;17}. In another strand of development, Leah Edelstein-Keshet proposed a model for a plant-herbivore system where the main variables are

plant quality and herbivore density¹⁸. Her study was based on the following mathematical model

$$\begin{aligned}\frac{dq}{dt} &= f(q, h), \\ \frac{dh}{dt} &= g(q, h)\end{aligned}$$

where plant quality and herbivore population can be represented by the functional responses f and g , respectively. In accordance with the form of q and h , both functions were determined or conjectured using biological information for a particular system of plants and herbivores. Since q can be understood as the rate of change in plant quality and h can be understood as the rate of change in herbivore population density, both these changes are significant; considered to be in a time-dependent fashion to understand a change associated with plant quality and herbivore population density. The specific forms of these functions, denoted as q and etc. are determined or hypothesized, respectively, based on biological information that is quite system-specific to the plant and herbivore under study¹⁹. Biological information may pertain to plants' nutritive value, herbivore reproduction rates, and the efficiency of the plant being fed. It may also pertain to other ecological interactions. Such functional responses are incorporated into the mathematical model to be used in simulating and assessing plant-herbivore dynamics under a plethora of conditions and scenarios. This would provide in-depth knowledge of plant quality and herbivore population size, and how the two may be intertwined to impact dynamics overall within an ecosystem²⁰.

An interesting difference equation model was presented by Allen et al. in their paper that described the plant-herbivore system in order to uncover the dynamics and strategies of control in such ecological systems²¹. This model was developed considering two different control strategies, which remained independent: cane removal and pesticide application. The analysis pointed out the two steady-states within the system: one characterized by the fact of pest presence (disease state) and another one where the pest was absent (disease-free state)^{22;23}. They have outlined, in the parameter space, different regions of global stability

of these steady-states. In addition, they showed that periodic solutions are present where global stability is absent. The periodic solutions bear the dynamics with chaotic areas. In the following system, you will find an overview of their analysis²⁴:

$$F_{n+1} = \frac{F_n f(G_n)}{\alpha_1 + \alpha_2 F_n f(G_n)},$$

$$G_{n+1} = \alpha_3 (F_n + 1) G_n$$

here, F_0 and G_0 represent positive initial conditions, and the function f can take two forms f_1 or f_2 as follows:

$$f_1(G) = \frac{1}{1 + G^2},$$

$$f_2(G) = \exp(-G).$$

Powell et al. undertook comprehensive research that extended mechanistic models from strategic population models of beetle outbreaks to those detailing the tactical behavior of beetles in selecting their host trees. Their analysis included both heuristic methods and empirical observations conducted in the field²⁵.

For instance, their qualitative heuristic comparison aligned Powell et al.'s representation of mountain pine beetle nesting population behavior more closely with observations made in 1980 by Geiszler et al. While Geiszler et al. focused on the cumulative number of successful mountain pine beetle attacks on a single focal tree, Powell et al. provided insights into the relative number of mountain pine beetles nesting in a focal tree per hour of flight²⁶. Remarkably, the numbers depicted in Powell et al.'s diagram closely resembled those observed by Geiszler et al²⁷.

This represented an initial attempt to synthesize three distinct mathematical methodologies into a spatial framework for evaluating the risk of mountain pine beetle attack on individ-

ual hosts. Preliminary results from their study illustrate that stand microclimate—climatic factors measured at specific locations near Earth’s surface—plays a central role in influencing attack risk, surpassing even host immunity and stand age²⁸.

Powell et al. also investigated deeply into the quantitative modeling and analysis of direct temperature control, exploring how these models exhibited dynamic seasonality in oviposition dates for succeeding generations. According to this analysis, the developmental circle map shows a stable steady state. It is related to univoltinism, which can result in high reproductive success in temperate climates by producing a single offspring throughout the season. Univoltine steady-states remained stable over wide temperature bands, but their edges were less stable due to disrupted maladaptive cycles, underscoring the intricate interplay between temperature and reproductive strategies.

Efforts to model the effects of periodic forcing on discrete-time have led to mathematical ecosystem models. These models are characterized by their dynamics defined through mathematical equations. It is worth noting that the specific equations employed may differ across ecosystems. As a result, a general form of such equation can be outlined²⁹:

$$X_{n+1} = f(X_n) + F(t).$$

Here, X_n denotes the state of the ecosystem at time n , $f(X_n)$ describes the intrinsic dynamics of the ecosystem without external forcing, and $F(t)$ represents the periodic forcing function applied at time t .

For instance, in a basic Lotka-Volterra predator-prey model, the equations could be expressed as³⁰:

$$P_{n+1} = P_n + rP_n(1 - P_n) - aP_nH_n + F(t),$$

$$H_{n+1} = H_n + bP_nH_n - dH_n + F(t),$$

where, P_n and H_n denote the number of prey (e.g., herbivores) and predators (e.g., car-

nivores) at time n , respectively. Parameters r , a , b , and d represent growth rates and interaction strengths, while $F(t)$ is the periodically applied forcing function over time t .

Summers et al. analyzed the effects of periodic forcing on four discrete-time ecosystem models³¹. Through their investigation, they demonstrated that such external stimuli could induce a property known as sensitive dependence on initial conditions, distinct from those identified in chaos theory. This property has the potential to alter the stability and dynamics of ecosystems, potentially leading to chaotic behavior. A periodic force is one that repeats itself at regular intervals and can be applied as a feedback stimulus. Their findings suggested that periodic forcing might indeed induce chaotic behavior. In a study by Summers, Danny, Justin G. Cranford, and Brian P. Healey, they examined four typical discrete-time ecosystem models under the effects of periodic forcing. They observed that periodic forcing can lead to dynamic chaos³¹. Moreover, Agiza et al³² found chaotic dynamics in a discrete prey-predator model with Holling's Type II response function. In this study, natural death rates for predators were not taken into account. This discrete model exhibits a greater degree of dynamics than the continuous model, indicating that it is chaotic and complex. The model they presented was as follows:

$$\begin{aligned}x_{n+1} &= ax_n(1 - x_n) - \frac{bx_ny_n}{1 + \alpha x_n}, \\y_{n+1} &= \frac{cx_ny_n}{1 + \alpha x_n}\end{aligned}$$

where a , b and c are positive parameters. The parameter a represents a prey's natural growth rate, similar to the growth rate found in the logistic equation. This models limited growth as the population approaches carrying capacity. parameters b and c govern the interactions between prey and predators: b illustrates the impact of predation on prey populations, while c illustrates the benefit predators gain from consuming prey. The variables x_n , and y_n represent prey and predator population densities respectively and vary as time changes based on the rules defined by model equations. The parameter α modified the inter-

action terms, restricting the growth rate of the predator population as the prey population increases.

Kartal analyzed the dynamics of a plant-herbivore model using both differential and difference equations³³. This model can be represented by the following equations:

$$\begin{aligned}x_{n+1} &= x_n(r - \alpha y_n)e^{-(r - \alpha y_n - rkx_n)}, \\y_{n+1} &= y_n e^{\beta x_n - s}.\end{aligned}$$

In Kartal's model, all parameters are positive, and he focuses on the behavior of the system within a specific sub-interval, which leads to difference equations that describe the system. As a result of his study, he discovered that the system was bounded, periodic, and had local and global stability conditions. Moreover, in certain regions of the parameter space, he identified Neimark-Sacker bifurcation.

In another study, Din et al. introduced a model of plant-herbivore interactions³⁴. He performed bifurcation analysis and investigated chaos control in a plant-herbivore model with weak predator functional responses. In their study, they primarily examined topological classifications of steady-states. They demonstrated that the boundary steady state underwent transcritical bifurcation. In contrast, the positive steady state in the discrete-time plant-herbivore model experienced a Neimark-Sacker bifurcation. Based on the following equations, the model is defined as follows:

$$\begin{aligned}x_{n+1} &= \frac{x_n}{a(1 + y_n^2) + bx_n}, \\y_{n+1} &= cy_n(1 + x_n),\end{aligned}$$

where x_n and y_n refer to the population densities of the plant (Grapevine) and the herbivore (Apple Twig Borer) respectively. The population dynamics in the model are influenced by

the parameters a , b and c , which all have positive values.

Predator and prey, parasite and host, mutualism, and competition between two species in nature can be classically modeled as follows:

$$P_{n+1} = f(P_n, H_n), \tag{1.1}$$

$$H_{n+1} = g(P_n, H_n).$$

By modeling both species' growth in the absence of the other, and by knowing the affect of their interaction on each other, the system in (1.1) is capable of describing the simultaneous population change. In its most basic form, such modelling can be described as follows:

$$P_{n+1} = aP_n + bP_nH_n,$$

$$H_{n+1} = cH_n + dP_nH_n.$$

Note that:

- (i) If we choose $a > 1$, $b < 0$, $0 < c < 1$, and $d > 0$, then this will produce a predator-prey model in which growth and decline are exponential in the absence of the other species, where P_n represent the prey population.
- (ii) If $a, c > 1$ and $b, d > 0$, then this will results in mutualism, where both species benefit from living together.
- (iii) The terms P_nH_n refer to mass-actions in which species encounter randomly with significant outcomes, infecting or eating each other, for example.

In plant-herbivore interactions, Kang, Yun, Dieter Armbruster, and Yang Kuang¹⁶ found quasiperiodicity, period-doubling, and chaos using a host-parasite model. According to observation, such a continuous model exhibits global stability at an interior steady state point.

Here is the typical methodology for discrete-generation host-parasite models

$$P_{n+1} = \lambda P_n f(P_n, H_n), \quad (1.2)$$

$$H_{n+1} = c\lambda P_n (1 - f(P_n, H_n)). \quad (1.3)$$

These models simulate the interaction between a host (a plant) and a parasite (a herbivore). In such models, P_n and H_n represent the biomass of the hosts (plants) and parasites (herbivores) in successive generations n and $n + 1$ respectively. Here $\lambda = e^r$ represent the host's inherent rate of increase in the absence of the parasites where r indicate the intrinsic rate of increase, c is the biomass conversion constant and the function f indicates the fraction of hosts that survive parasitism each generation. As an alternative, f can indicate the probability of each host escaping parasites. Therefore, the complementary expression $1 - f$ indicates the probability of being parasitized in the second equation. As will be shown in the rest of this paper, n takes positive integer values. Among the simplest versions of this model are those of Nicholson³⁵ and Nicholson and Bailey¹ which investigated in depth a model in which the zero-term of one's Poisson distribution determines the proportion of hosts that escape parasitism, in particular,

$$f(P_n, H_n) = e^{-aH_n}. \quad (1.4)$$

In this case, a represents the mean number of encounters per host. As a result, $1 - e^{-aH_n}$ represents the probability of an attack on a host where $f = e^{-aH_n}$ represent Poisson distribution that describes the proportion of hosts escaping parasitism. In Equations (1.2) and (1.3), Equation (1.4) gives:

$$P_{n+1} = \lambda P_n e^{-aH_n}, \quad (1.5)$$

$$H_{n+1} = c\lambda P_n (1 - e^{-aH_n}). \quad (1.6)$$

Beddington et al.³⁶ propose the following modified Nicholson-Bailey model:

$$P_{n+1} = \lambda P_n e^{r\left(\frac{1-P_n}{P_{max}}\right) - aH_n}, \quad (1.7)$$

$$H_{n+1} = c\lambda P_n (1 - e^{-aH_n}). \quad (1.8)$$

Essentially, P_{max} is the so-called environment-imposed 'carrying capacity' for the host for carrying parasites without parasites in its environment. A host density dependence can be expressed as follows:

$$e^{r\left(\frac{1-P_n}{P_{max}}\right)}.$$

For a wide range of parameter values, what was an unstable positive steady state becomes locally stable, when no density-dependent relationship exists for host population growth³⁶. In the case of other parameter values, there is a possibility that the model will generate attractors of different levels of complexity. These attractors can range from a set of regular limit cycles to weird and chaotic patterns. The structure of equations (1.7) and (1.8) illustrates that host density-dependence occurs at a particular stage of their life cycle according to the stage at which the parasites attack. The H_n herbivores hunt for P_n hosts before density-dependent growth regulation takes place. As a result, new herbivore generations are dependent on P_n , the original host population antecedent to parasitism.

A more realistic model could be created by using the following system