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A STUDY OF A STAGE-STRUCTURED MODEL OF TWO
COMPETING SPECIES

by
Jeff Edmunds

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF MATHEMATICS
In Partial Fulfillment of the Requirements
For the Degree of
DOCTOR OF PHILOSOPHY
In the Graduate College
THE UNIVERSITY OF ARIZONA

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I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

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SIGNED:

A handwritten signature in cursive script, appearing to read "Jeff Edmunds", written over a horizontal line.

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TABLE OF CONTENTS

LIST OF FIGURES	6
LIST OF TABLES	7
ABSTRACT	8
CHAPTER 1. INTRODUCTION	9
CHAPTER 2. MODEL AND PRELIMINARIES	16
2.1. The LPA Model	16
2.2. The Competition LPA Model	18
2.3. Preliminaries	19
CHAPTER 3. EQUILIBRIUM ANALYSIS	23
3.1. Axis Equilibria	23
3.2. Positive Equilibria	27
CHAPTER 4. PERSISTENCE	31
4.1. The Origin	31
4.2. Extinction State	33
CHAPTER 5. NON-EQUILIBRIUM DYNAMICS	39
5.1. Coexistence in the Presence of an Unstable Positive Equilibrium	39
5.2. Coexistence in the Presence of Stable Axis Equilibria	44
5.3. Coexistence in the Presence of Non-equilibrium Attractors within the Axes	50
CHAPTER 6. CONCLUDING REMARKS	57
REFERENCES	62

LIST OF FIGURES

FIGURE 5.1.	Orbit Diagram	41
FIGURE 5.2.	Bifurcation Diagrams	42
FIGURE 5.3.	Orbit Diagram	43
FIGURE 5.4.	Bifurcation Diagrams	45
FIGURE 5.5.	Orbit Diagram	47
FIGURE 5.6.	Orbit Diagram	49
FIGURE 5.7.	Bifurcation Diagrams	51
FIGURE 5.8.	3D Orbit Diagrams	52
FIGURE 5.9.	Bifurcation Diagrams	53
FIGURE 5.10.	Orbit Diagrams	54
FIGURE 5.11.	Bifurcation Diagrams	55
FIGURE 5.12.	Orbit Diagrams	56

LIST OF TABLES

TABLE 5.1.	Parameter Values	40
TABLE 5.2.	Parameter Values	42
TABLE 5.3.	Parameter Values	50
TABLE 5.4.	Parameter Values	51

ABSTRACT

The purpose of this dissertation is to develop and study a competition model which, being capable of a wide range of population dynamics, will exhibit phenomena in multi-species interactions not seen in simpler models. We consider a structured, non-linear model of two competing species, each having three life stages. This model is based on a single-species model that has been used to demonstrate many interesting effects in population dynamics and, in particular, has been highly successful in describing and predicting the dynamics of insect populations in controlled laboratory experiments.

A thorough examination of equilibria provides necessary and sufficient conditions for stability of axis equilibria, which corresponds to the extinction of one species. Applying the concept of persistence to the model, we obtain sufficient conditions under which the model is persistent with respect to the extinction states, implying indefinite coexistence of both species. Finally, we give specific examples in which the model contradicts classical (equilibrium) competition theory by showing non-equilibrium coexistence in the presence of unstable positive equilibria, stable axis equilibria, and high levels of inter-specific competition.

Chapter 1

INTRODUCTION

The classical theory of competitive exclusion states that two similar species competing for the same resource cannot coexist indefinitely; one or the other must eventually go extinct [30]. Mathematically, this idea can be examined via the following system of differential equations, commonly referred to as the *Lotka-Volterra competition model*:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right] \\ \frac{dN_2}{dt} &= r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right].\end{aligned}\tag{1.1}$$

In this simple model N_1 and N_2 represent two different populations with respective inherent per capita growth rates $r_1 > 0$ and $r_2 > 0$. Each species has a carrying capacity ($K_1 > 0$ and $K_2 > 0$) which represents an equilibrium state for the population in the *absence* of the other species. The negative effect of competition is measured by the coefficients $b_{12} > 0$ and $b_{21} > 0$.

The dynamics of equation (1.1) can be studied via a dimensionless version:

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1(1 - u_1 - a_{12}u_2) \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_{21}u_1)\end{aligned}\tag{1.2}$$

where

$$u_i = \frac{N_i}{K_i}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \quad \text{and} \quad a_{ij} = b_{ij} \frac{K_j}{K_i}.$$

Note that u_1 and u_2 represent the ratio of each population to its carrying capacity, so that equation (1.2) has equilibria at $(u_1, u_2) = (1, 0)$ and $(0, 1)$, in addition to the

unstable “trivial” equilibrium $(0, 0)$. There is also a non-axis equilibrium at

$$(u_1, u_2) = \left(\frac{1 - a_{12}}{1 - a_{12}a_{21}}, \frac{1 - a_{21}}{1 - a_{12}a_{21}} \right). \quad (1.3)$$

Consider equation (1.2) along with an initial condition (u_1^0, u_2^0) , with both u_1^0 and u_2^0 positive. If $a_{12} < 1$ and $a_{21} > 1$, the equilibrium (1.3) lies outside of the positive quadrant, and the equilibrium $(1, 0)$ is globally attracting in the positive quadrant. Similarly, if $a_{12} > 1$ and $a_{21} < 1$, the equilibrium (1.3) lies outside of the positive quadrant, and the equilibrium $(0, 1)$ is globally attracting in the positive quadrant. In either of these cases, the better competitor drives the other species to extinction, regardless of the initial condition.

The equilibrium (1.3) lies within the positive quadrant if and only if $a_{12} > 1$ and $a_{21} > 1$ or $a_{12} < 1$ and $a_{21} < 1$. In the first case, the positive equilibrium is unstable while both $(1, 0)$ and $(0, 1)$ are stable. The positive quadrant is divided by a *separatrix*, with all initial conditions on one side resulting in the extinction of species one, and all initial conditions on the other side resulting in the extinction of species two. Only initial conditions lying exactly on the one-dimensional separatrix lead to coexistence at the positive equilibrium (1.3).

In the second case, the positive equilibrium is stable and globally attracting in the positive quadrant. This is the only one of the four possibilities that allows for indefinite coexistence of both species, and that is achieved by having sufficiently small values of the coefficients a_{12} and a_{21} . In the other three cases the presence of a strong competitor, as measured by a large coefficient a_{12} or a_{21} , eliminates the stable coexistence state.

It is notable that the question of coexistence versus exclusion can be determined entirely by the stability properties of the axis equilibria. If *either* axis equilibrium is stable, the system predicts exclusion of one species; coexistence is only possible if *both* axis equilibria are unstable. In fact, ecologists often use the presence of stable axis equilibria to predict competitive exclusion.

One major weakness of the above example is the assumption that each population will reach an equilibrium state (its carrying capacity) in the absence of the other. In this model coexistence is only possible in the presence of a stable, positive equilibrium, and in the absence of stable axis equilibria. However, in population dynamics, equilibria represent but one of many possible long-term behaviors of populations. Populations have been shown to undergo periodic, aperiodic, and even chaotic fluctuations over long periods of time; therefore a thorough mathematical study of competition requires models which can generate non-equilibrium dynamics.

One example of such a competition model that has been widely studied is the *chemostat* model. The chemostat is a model of *exploitative* competition, in which the competitors do not affect each other directly, but rather by depleting a shared resource. Mathematically, this means that a species does not appear within the equations of its competitors. The Lotka-Volterra model discussed above is an example of *interference* competition, in which competitors do have a direct effect on one another. The chemostat has been used to model laboratory cultures in which a variety of microorganisms compete for nutrients. This type of setting allows for extremely accurate data collection, and the chemostat model has been shown to predict experimental outcomes very well.

Unlike the Lotka-Volterra model, the chemostat model with self-renewable resource dynamics is capable of non-equilibrium dynamics, and in fact non-equilibrium coexistence. Smith and Waltman [33] give an example of a one-species one-resource limit cycle bifurcating into a two-species one-resource coexistence limit cycle in such a model. Waltman [35] gives a similar example of a coexistence state in an exploitative model of two predators competing for a renewable resource.

The models mentioned so far are all examples of *continuous* dynamical systems. Furthermore, they consider homogeneous species, i.e., species in which all individuals are identical. For most biological populations, however, this assumption is too simplistic. More accurate descriptions of population dynamics require “structured”

models in which individuals are classified into important subclasses (life cycle stage, age, body size, etc.) [2, 17, 29, 36].

Structured population models for competing species have been recently introduced and studied; for example see [2, 7, 8, 9, 32]. In [9] Cushing considers a size-structured version of the chemostat model introduced by Gage *et.al.* [19] and Smith [32]. This discrete, exploitative competition model allows only for equilibrium dynamics and supports the classical competition theory. On the other hand, Cushing [9] also presents an example of a discrete interference competition model, in which both a two-cycle and a chaotic attractor undergo bifurcations from a single-species state into a coexistence state. Crowe [6] provides an example of a discrete interference competition model generating coexistence two-cycles and invariant loops.

In this thesis we study equilibrium and non-equilibrium competitive coexistence by means of a life cycle stage-structured model. This particular model, while rather general and suitable for a large class of biological populations, is particularly important because it is based on the LPA model, a single-species model which has recently been used in a variety of experimental projects in which it has been shown to be capable of accurate description and prediction of insect populations. Specifically, the LPA model has been used extensively to predict the dynamics of flour beetle populations in laboratory experiments [3, 4, 14].

The competition model studied here is a two-species extension of the LPA model, a discrete, stage-structured non-linear population model, representative of insect populations with three life stages [3, 11, 14]. Because of the non-linearities, the model is capable of generating extremely complicated dynamics, from simple equilibria and periodic cycles to aperiodic cycles and chaos. With such rich dynamics present within a single species, the LPA model is ideal for extension to a study of competition between species.

The competition LPA model is an interference competition model. Contacts among individuals reduce survival and fecundity. For example, certain species of flour

beetle exhibit nonlinear interactions in the form of cannibalism among different life stages. Cannibalism within each species can be thought of as a form of intra-specific competition. When two cannibalistic species are put together, their cannibalistic acts extend to members of the other species.

Laboratory experiments involving flour beetles often take place in small environments. The LPA model has been used in conjunction with experiments in which species of the flour beetle *Tribolium* are kept in bottles containing only 20 grams of standard media, with total populations of several hundred individuals. A similar experiment involving two different species in such a confined space would represent an extremely competitive environment, as cannibalism has been shown to result from random encounters [5].

Some very famous and oft cited experiments in support of the classical theory of competition involve different species of flour beetle. Leslie *et.al.* placed adults of *Tribolium castaneum* and *Tribolium confusum* together in vials containing 8 grams of flour [27]. Thirty five trials were run, each with a different initial condition. All but one of the trials resulted in extinction of one or the other species, with the outcome dependent on the initial condition. The outcome of these 34 trials shows a resemblance to the unstable positive equilibrium case of the Lotka-Volterra model, with a separatrix dividing the positive quadrant into initial conditions which result in the extinction of one or the other species. This result is often cited as a laboratory demonstration of the Lotka-Volterra competition theory [26].

However, in one trial, namely the trial begun with 4 *T. castaneum* adults and 32 *T. confusum* adults, both species continued to maintain healthy numbers for 960 days. This trial suggested the possibility of a coexistence state. Leslie *et.al.* found this extended coexistence example quite remarkable, and in fact ran further tests to study it. They came to no explanation for this intriguing case, and none exists to this day.

It is worth noting that experiments have been done to determine the relationship

between intra-specific cannibalism and inter-specific predation among *T. castaneum* and *T. confusum*. Park *et.al.* found strong evidence that adults of each species will develop a preference for pupae of the *other* species over the pupae of their own species when put together [31]. This excess of inter-specific competition likely contributed to the exclusion seen in Leslie's experiment. Differences were also found between consumption rates of eggs by larvae and adults of the different species, though the results did not clearly favor either inter-specific or intra-specific competition. In recent laboratory experiments with *T. castaneum*, rates of adult cannibalism on pupae have been successfully manipulated, and it is reasonable to assume that such manipulation can be accomplished in an experiment involving two species.

The competition LPA model presented in this thesis is worthy of study for a number of reasons. First, the model is capable of generating a wide range of non-equilibrium dynamics, which are essential for a thorough examination of competition. Second, the single-species LPA model on which the competition model is based has been used very successfully in predicting laboratory populations under many different circumstances. Finally, there is an important history of experimental work in the area of competition between specific species which are closely tied to the model, work that is considered fundamental to competition theory in ecology [26].

The main goal of this thesis is to add to the mathematical theory of competition through a thorough examination of the asymptotic dynamics of the competition LPA model. Though the possibilities for analytical results are limited by the complexity of the model, we will see that some useful conclusions can be reached. Furthermore, numerical simulations are easily carried out, and through these new and interesting asymptotic dynamics of species interactions become evident.

This thesis begins with a thorough description of both the single-species and competition LPA models. After a brief introduction to terminology and concepts, equilibria are studied in full detail, with the hope of providing some analytical insight into the asymptotic dynamics of the model. The concept of persistence is then applied

to the model, so as to determine conditions under which one or both species are expected to survive indefinitely. Finally, specific examples of non-equilibrium behavior are given, with a primary goal of showing that coexistence is possible in a number of circumstances in which the classical theory predicts competitive exclusion.

Chapter 2

MODEL AND PRELIMINARIES

The model explored in this work is an extension of a model designed to study single-species dynamics. The first section of this chapter defines the single-species model and discusses some applications. The second section extends the model to include a second species and discusses the competitive interactions. The chapter concludes with a brief introduction to terms and concepts which will be used in later chapters.

2.1 The LPA Model

The *deterministic LPA model*:

$$\begin{aligned}
 l_{t+1} &= ba_t e^{-c_{el}l_t - c_{ea}a_t} \\
 p_{t+1} &= l_t(1 - \mu_l) \\
 a_{t+1} &= p_t e^{-c_{pa}a_t} + a_t(1 - \mu_a)
 \end{aligned}
 \tag{2.1}$$

is a three-stage model representative of insect populations with a complete life cycle stage: larval, pupal, and adult. The model assumes an equal length of time for the larval and pupal stages, as all larvae at time t who survive to time $t + 1$ become pupae, and all pupae at time t who survive to time $t + 1$ become adults. On the other hand, all adults who survive to time $t + 1$ remain in the adult class. Several species of flour beetle have these characteristics, with a time step of two weeks and adult survival on average close to six months. Larval recruitment is described by $b > 0$, the *inherent* number of larvae produced per adult per time unit; that is, the mean number of viable eggs produced per adult in the absence of density effects described by the nonlinear term $e^{-c_{el}l_t - c_{ea}a_t}$. The constants $0 < \mu_l < 1$ and $0 < \mu_a < 1$ are the

death rates of larvae and adults, respectively; the pupal death rate is assumed to be zero. Nonlinear interactions are introduced via $c_{el} > 0$, $c_{ea} > 0$ and $c_{pa} > 0$.

In the case of flour beetles, c_{el} , c_{ea} , and c_{pa} represent cannibalism of eggs by larvae and adults, and of pupae by adults. This cannibalism occurs from random encounters between larvae and eggs, adults and eggs, and adults and pupae. Under the assumption that an encounter between a pupa and an adult is proportional to the elapsed time, the probability of *no* encounter between a_t adults and a pupa during a given time interval Δt is approximately $(1 - c_{pa}\Delta t)^{a_t}$. The probability of no encounter during a *unit* of time is then $(1 - c_{pa}\Delta t)^{a_t/\Delta t}$ whose limit as $\Delta t \rightarrow 0$ is $e^{-c_{pa}a_t}$. Thus the effects of cannibalism are well represented by these exponential nonlinearities.

Model parameters have been estimated using data from laboratory trials under a variety of circumstances [11, 14]. Different species and different circumstances yield different parameters, but reasonable approximations for cultures of flour beetles under normal laboratory protocols are $b \approx 10$, $\mu_l \approx 0.2$, $\mu_a \approx 0.1$, $c_{el} \approx 0.01$, $c_{ea} \approx 0.01$, $c_{pa} \approx 0.005$. Parameters in these ranges generate stable, positive equilibria or two-cycles. Higher values of μ_a and c_{pa} can generate aperiodic and chaotic attractors, which have been documented by laboratory experiments. This model has been very successful at predicting population numbers in actual laboratory cultures of flour beetles, even in the presence of exotic dynamics [11, 15]. Parameter values are simulated in the laboratory through manipulation of adult numbers. The LPA model was used in the ‘‘Hunt for Chaos’’ experiment, which is credited as the first demonstration of chaos in a population [3, 4]. The model has been used to study many nonlinear phenomena, including multiple attractors [21, 22], phase shifts in oscillating behavior [24], and unstable manifolds of saddle equilibria [10, 12, 13]. A modified version of the LPA model has also been used to study population dynamics in periodic habitats [21, 23] and, in particular, an unusual resonance effect.

As non-equilibrium dynamics are essential for a thorough examination of inter-specific competition, the LPA model is therefore ideal for a study of multi-species

interactions.

2.2 The Competition LPA Model

The *deterministic competition LPA model*:

$$\begin{aligned}
 l_{t+1} &= ba_t e^{-c_{el}l_t - c_{ea}a_t - c_{eL}L_t - c_{eA}A_t} \\
 p_{t+1} &= l_t(1 - \mu_l) \\
 a_{t+1} &= p_t e^{-c_{pa}a_t - c_{pA}A_t} + a_t(1 - \mu_a) \\
 L_{t+1} &= BA_t e^{-c_{El}l_t - c_{Ea}a_t - c_{EL}L_t - c_{EA}A_t} \\
 P_{t+1} &= L_t(1 - \mu_L) \\
 A_{t+1} &= P_t e^{-c_{Pa}a_t - c_{PA}A_t} + A_t(1 - \mu_A)
 \end{aligned} \tag{2.2}$$

adds a second species to the LPA model. For notational convenience, “species one” is represented by the lower case letters l, p, a, b and the subscript e , while “species two” is represented by the capital letters L, P, A, B and the subscript E . Each species has its own larval recruitment and death rates, and in addition to the intra-specific nonlinearities there are nonlinear interactions between the two species.

In the case of flour beetles, this means that each species preys on the eggs and pupae of the other species, as well as cannibalizing its own. For example, the coefficient c_{eL} represents the consumption of species one’s eggs by the larvae of species two, c_{El} represents the consumption of species two’s eggs by the larvae of species one, and c_{el} and c_{EL} are the intra-specific cannibalism coefficients. The other c coefficients are defined in similar fashion. The competition model has twelve of these “competition” coefficients in all; six intra-specific coefficients represented by c_{el}, c_{EL} , etc., and six inter-specific coefficients denoted by c_{El}, c_{eL} , etc. The primary goal of this model is to study competition between two similar species, so the parameters values used in this work will in general be reasonably close for each species.

Of particular interest is the competition represented by c_{pa} , c_{PA} , c_{pA} , and c_{Pa} . By developing a preference for pupae of the other species (i.e. $c_{Pa} > c_{pa}$ or $c_{pA} > c_{PA}$), adults can give their species a competitive edge. There is experimental evidence that when two similar species of cannibalistic flour beetles are placed together, the adults of each species do in fact develop a preference for pupae of the other species [31]. In experimental work based on the LPA model, c_{pa} can be easily manipulated, and it is reasonable to assume that these coefficients can also be manipulated in multi-species experiments.

The competition represented by this model is an example of *interference* competition; mathematically, each species appears explicitly in the equations of the other species, implying that each species *directly* affects the other. Note that the effects of competition in this model are purely detrimental; the existence of species one has a negative effect on species two, but the interaction does not *directly* benefit species one in any way. Indirectly, species one benefits by reducing the numbers of species two, which reduces the negative effect of inter-specific competition on species one. In this respect, the coupled LPA model is similar to the classical Lotka-Volterra competition model [28, 34].

2.3 Preliminaries

Let \mathbb{R}_+^n denote the *non-negative cone* of \mathbb{R}^n , the subset of \mathbb{R}^n consisting of all points with all n coordinates non-negative. The coupled LPA model defines a continuous map $f : \mathbb{R}_+^6 \rightarrow \mathbb{R}_+^6$. Given an initial condition $x_0 = (l_0, p_0, a_0, L_0, P_0, A_0)$, successive applications of the map: $f(x_0)$, $f(f(x_0)) = f^2(x_0)$, etc. result in a sequence of points $\{f^n(x_0)\}$ in \mathbb{R}_+^6 called a (*forward*) *orbit*. A *backward orbit* is any sequence of points $\{x_0, x_{-1}, x_{-2}, \dots\}$ such that $x_{-k+1} = f(x_{-k})$, $k = 1, 2, 3, \dots$. The *forward limit set* of an orbit is the set

$$\omega(x_0) = \{x: \text{for all } N, \epsilon \text{ there exists } n > N \text{ such that } |f^n(x_0) - x| < \epsilon\}.$$

The *backward limit set* is defined similarly for negative orbits. An *attractor* is a forward limit set which attracts a set of initial values with nonzero measure [1].

An *equilibrium* is a point $x^* = (l^*, p^*, a^*, L^*, P^*, A^*)$ in \mathbb{R}_+^6 for which $f(x^*) = x^*$. The competition LPA map has an *extinction equilibrium* at the origin $(0, 0, 0, 0, 0, 0)$. An *axis equilibrium* is an equilibrium at which only one species exists, i.e. $(l^*, p^*, a^*, 0, 0, 0)$ with $l^* > 0, p^* > 0, a^* > 0$ or $(0, 0, 0, L^*, P^*, A^*)$ with $L^* > 0, P^* > 0, A^* > 0$. A *positive equilibrium* is an equilibrium for which all six components are positive. An equilibrium is *(locally) stable* if for every $\epsilon > 0$ there exists a $\delta > 0$ such that $|x - x^*| < \delta$ implies $|f^n(x) - x^*| < \epsilon$ for all n . An equilibrium which is not stable is called *unstable*. An equilibrium x^* is called *asymptotically stable* if it is stable and for all points x in some neighborhood of x^* , $f^n(x) \rightarrow x^*$ as $t \rightarrow \infty$. In this work we are concerned only with asymptotically stable equilibria, so for simplicity the term *stable equilibrium* will imply asymptotic stability.

The stability of an equilibrium can be determined through the *linearization* of the system near the equilibrium. An equilibrium is called *hyperbolic* if none of the eigenvalues of the Jacobian evaluated at the equilibrium have absolute value 1. As non-hyperbolic equilibria represent a degenerate case, equilibria will be assumed hyperbolic unless denoted otherwise. The *Jacobian* matrix of f evaluated at the equilibrium, $Df(x^*)$, represents the linear part of f near x^* . If all eigenvalues of the Jacobian evaluated at x^* have magnitude less than 1 (lie within the unit circle), x^* is a stable equilibrium. If any one of the eigenvalues has magnitude greater than 1 (lies outside the unit circle), x^* is unstable. This fact is commonly known as the *Linearization Theorem*.

The *stable manifold* E^s of the linearization is the span of the eigenvectors associated with eigenvalues λ of the Jacobian satisfying $|\lambda| < 1$. The *unstable manifold* E^u of the linearization is the span of the eigenvectors associated with eigenvalues satisfying $|\lambda| > 1$. The *Stable Manifold Theorem* states that there exist stable and unstable manifolds S and U of dimensions $\dim(E^s)$ and $\dim(E^u)$, respectively, tan-

gent to E^s and E^u , such that for all $x \in S$, $\lim_{n \rightarrow \infty} f^n(x) = x^*$, and for all $x \in U$, $\lim_{n \rightarrow -\infty} f^n(x) = x^*$ [20].

The statements of the Linearization and Stable Manifold Theorems generally require that the map f be invertible. This assumption is not necessary, however, as the results hold for non-invertible maps f with sufficient differentiability properties [9]. In particular, the result holds for the competition LPA map.

An initial condition x_p for which $f^k(x_p) = x_p$ for some $k > 1$ and $f^m(x_p) \neq x_p$ for any $m < k$ generates a *periodic cycle of period k* :

$$\{x_p, f(x_p), f^2(x_p), \dots, f^{k-1}(x_p)\}.$$

Note that any point in the sequence is an equilibrium of the map $f^k(x)$. A set Y such that $f(Y) = Y$ is said to be an *invariant set* of f . A set Y is said to be *forward invariant* if $f(Y) \subset Y$, and *backward invariant* if $Y \subset f(Y)$. An *invariant loop* is a one-dimensional closed invariant set C in \mathbb{R}_+^6 . Orbits contained within C may be periodic, or they may be quasi-periodic, moving around C with no repeating pattern.

Denote the union of all forward limit sets in \mathbb{R}_+^6 by $\Omega(f) = \cup\{\omega(x) : x \in \mathbb{R}_+^6\}$, and denote its closure by $\bar{\Omega}(f)$. Let Y be a closed, invariant (under f) subset of \mathbb{R}_+^6 . An *isolated covering* $\Pi = M_1, M_2, \dots, M_k$ of f is a covering of $\bar{\Omega}(f|_Y)$ such that M_1, M_2, \dots, M_k are pairwise disjoint, compact and each is the maximal invariant set of f in a neighborhood of itself. The *stable set* of M_i (under f) is the set consisting of all orbits with forward limit sets contained in M_i . The *unstable set* of M_i (under f) is the set of all negative orbits with backwards limit sets contained in M_i . M_1 is said to be *chained* to M_2 if there exists an $x_0 \notin M_1 \cup M_2$ such that some negative orbit through x_0 is in the unstable set of M_1 and the positive orbit through x_0 is in the stable set of M_2 . A finite sequence M_1, M_2, \dots, M_k is called a *chain* if each M_i is chained to M_{i+1} ; a *cycle* is a chain for which $M_k = M_1$. An isolated covering $\Pi = M_1, M_2, \dots, M_k$ of f is called an *acyclic covering* of $f|_Y$ if no subsets of Π form a cycle for $f|_Y$ in Y [18].

A map f is said to be *dissipative* if there exists a constant $M > 0$ such that for each $x \in \mathbb{R}_+^6$ there is an integer $k \geq 0$ such that $|f^n(x)| \leq M$ for all $n \geq k$. Let Y be a closed subset of a metric space X , $f : X \rightarrow X$ a continuous map such that $f(Y) \subset Y$. A map f is said to be *persistent with respect to Y* if for all $x \in X \setminus Y$, $\liminf_{n \rightarrow \infty} d(f^n(x), Y) > 0$ [18]. In the context of population models, X is typically \mathbb{R}_+^n , and Y a subset which represents an extinction state of one or more species. For instance, persistence with respect to the origin implies the indefinite survival of *at least* one species.

Chapter 3

EQUILIBRIUM ANALYSIS

The single-species LPA map (2.1) has inherent net reproductive number

$$b \frac{1 - \mu_l}{\mu_a}.$$

The trivial equilibrium $(0, 0, 0)$ is stable if this quantity is less than one, and unstable if it is greater than one. If $b \frac{1 - \mu_l}{\mu_a} > 1$, the LPA map has a unique, positive equilibrium (l^*, p^*, a^*) , where l^*, p^*, a^* are all positive. For the competition LPA map (2.2), in addition to the trivial equilibrium $(0, 0, 0, 0, 0, 0)$, there are axis equilibria $(l^*, p^*, a^*, 0, 0, 0)$ and $(0, 0, 0, L^*, P^*, A^*)$, provided that both quantities $b \frac{1 - \mu_l}{\mu_a}$ and $B \frac{1 - \mu_L}{\mu_A}$ are greater than one. Under certain conditions there may also exist positive equilibria $(l^*, p^*, a^*, L^*, P^*, A^*)$. Stable, positive equilibria are of interest since they represent states in which both species coexist indefinitely.

3.1 Axis Equilibria

The competition LPA map clearly has the origin $(0, 0, 0, 0, 0, 0)$ in \mathbb{R}^6 as an equilibrium point for any parameter values. For the single-species LPA map, the equilibrium point $(0, 0, 0)$ is stable if $b \frac{1 - \mu_l}{\mu_a} < 1$ and unstable if $b \frac{1 - \mu_l}{\mu_a} > 1$ [9]. For the competition LPA map, if *either* $b \frac{1 - \mu_l}{\mu_a}$ or $B \frac{1 - \mu_L}{\mu_A}$ is greater than one, then the origin has an unstable manifold and is therefore unstable.

The competition LPA map has an *axis equilibrium* of the form $(l^*, p^*, a^*, 0, 0, 0)$ (l, p, a all positive) provided $b \frac{1 - \mu_l}{\mu_a} > 1$, and also an axis equilibrium of the form $(0, 0, 0, L^*, P^*, A^*)$ (L, P, A all positive) provided $B \frac{1 - \mu_L}{\mu_A} > 1$. To study the stability of the first axis equilibrium, we consider the Jacobian evaluated at $(l^*, p^*, a^*, 0, 0, 0)$:

$$\begin{pmatrix} -c_{el}a^*\beta & 0 & (1 - c_{ea}a^*)\beta & -c_{eL}a^*\beta & 0 & -c_{eA}a^*\beta \\ 1 - \mu_l & 0 & 0 & 0 & 0 & 0 \\ 0 & e^{-c_{pa}a^*} & -c_{pa}p^*e^{-c_{pa}a^*} + (1 - \mu_a) & 0 & 0 & -c_{pAp^*}e^{-c_{pa}a^*} \\ 0 & 0 & 0 & 0 & 0 & Be^{-c_{El}l^* - c_{Ea}a^*} \\ 0 & 0 & 0 & 1 - \mu_L & 0 & 0 \\ 0 & 0 & 0 & 0 & e^{-c_{Pa}a^*} & 1 - \mu_A \end{pmatrix}$$

where $\beta = be^{-c_{el}l^* - c_{ea}a^*}$.

Because of the 3×3 block of zeros in the lower left hand corner, the eigenvalues of this 6×6 matrix are the eigenvalues of the 3×3 block in the upper left corner and the 3×3 block in the lower right corner. Under the assumption that the equilibrium is stable in the absence of a second species, the three eigenvalues of the upper left block all lie within the unit circle. The characteristic polynomial of the lower right block is

$$\lambda^3 - (1 - \mu_A)\lambda^2 - B(1 - \mu_L)e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*}.$$

Let $\alpha = B(1 - \mu_L)e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*}$. To determine the position of the roots of this equation in relation to the unit circle, we consider the *Jury conditions* [25]:

$$\mu_A > \alpha \quad (3.1)$$

$$2 - \mu_A > -\alpha \quad (3.2)$$

$$\alpha < 1 \quad (3.3)$$

$$|1 - \alpha^2| > (1 - \mu_A)\alpha \quad (3.4)$$

$$|1 - \alpha^2 + (1 - \mu_A)\alpha| > 1 - \mu_A. \quad (3.5)$$

Satisfaction of these five inequalities provides a necessary and sufficient condition that all three eigenvalues lie within the unit circle.

Assume that (3.1) is true, so that $0 < \alpha < \mu_A$. Since $\mu_A \leq 1$, (3.2) is trivial and (3.3) follows from (3.1). Since $0 < \alpha < 1$ implies $\alpha^2 < 1$, the absolute values on the left hand sides of (3.4) and (3.5) can be removed. This reduces (3.4) to a quadratic

inequality in α :

$$\alpha^2 + (1 - \mu_A)\alpha - 1 < 0.$$

Since by assumption $0 < \alpha < \mu_A$, the above inequality holds if

$$\mu_A^2 + (1 - \mu_A)\mu_A - 1 < 0,$$

which reduces to $\mu_A < 1$; thus (3.4) follows from (3.1). Inequality (3.5) can be written as

$$\alpha^2 + \mu_A\alpha < \mu_A + 1;$$

this follows if

$$\mu_A^2 + \mu_A^2 < \mu_A + 1,$$

which is true since $0 < \mu_A^2 < \mu_A < 1$.

Thus all five inequalities follow from the first:

$$B \frac{1 - \mu_L}{\mu_A} e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*} < 1.$$

This is a necessary and sufficient condition for stability of the axis equilibrium $(l^*, p^*, a^*, 0, 0, 0)$. A similar argument shows that an axis equilibrium of the form $(0, 0, 0, L^*, P^*, A^*)$ exists if $B \frac{1 - \mu_L}{\mu_A} > 1$, and is stable if and only if

$$b \frac{1 - \mu_l}{\mu_a} e^{-c_{eL}L^* - (c_{eA} + c_{pA})A^*} < 1.$$

Thus, for the competition LPA map, if we define the quantities

$$n = b \frac{1 - \mu_l}{\mu_a} e^{-c_{eL}L^* - (c_{eA} + c_{pA})A^*}$$

$$N = B \frac{1 - \mu_L}{\mu_A} e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*},$$

then the axis equilibrium $(l^*, p^*, a^*, 0, 0, 0)$ (or $(0, 0, 0, L^*, P^*, A^*)$) destabilizes as n (or N) increases through one. Unlike the corresponding stability determining quantities for the single-species LPA map, which consist only of parameters, these quantities

contain the equilibrium values l^*, a^*, L^* , and A^* . This complicates further analysis, as there are not explicit formulas for these values.

One approach to further understanding is a *Lyapunov/Schmidt expansion* [9]. In this approach we introduce a parameter ϵ and parameterize the quantity N and the equilibrium values. We expand l, p , and a about l^*, p^* , and a^* (i.e. $l = l^* + l_1\epsilon + l_2\epsilon^2 + \dots$, etc.) and L, P , and A about 0 ($L = L_1\epsilon + L_2\epsilon^2 + \dots$, etc.) From the expansion of N about one:

$$N = 1 + N_1\epsilon + N_2\epsilon^2 + \dots$$

we can see that the sign of the quantity N_1 then determines the stability of the equilibrium $(l^*, p^*, a^*, 0, 0, 0)$; a negative N_1 makes $N < 1$ which guarantees a stable axis equilibrium, while a positive N_1 makes $N > 1$, and implies that the axis equilibrium is unstable. This latter case represents a situation in which species two can “invade” with small numbers.

A straightforward calculation shows that

$$N_1 = c_{El}l_1 + c_{EL}L_1 + (c_{Ea} + c_{Pa})a_1 + (c_{EA} + c_{PA})A_1, \quad (3.6)$$

and further analysis results in the formula

$$\begin{aligned} N_1 = & c_{EL} \frac{\mu_A}{1-\mu_L} + (c_{EA} + c_{PA})e^{-c_{Pa}a^*} + \\ & (c_{Pa} + c_{Ea}) \frac{c_{eL} \frac{\mu_A}{1-\mu_L} + e^{-c_{Pa}a^*} (c_{eA} - (1+c_{el}l^*)c_{pA})}{c_{pa} + c_{ea} + l^*c_{el}(c_{pa} + \frac{1}{a^*})} + \\ & c_{El} \frac{l^*}{1+c_{el}l^*} \left[\frac{c_{eL} \frac{\mu_A}{1-\mu_L} + e^{-c_{Pa}a^*} (c_{eA} - (1+c_{el}l^*)c_{pA})}{c_{pa} + c_{ea} + l^*c_{el}(c_{pa} + \frac{1}{a^*})} \left(\frac{1}{a^*} - c_{ea} \right) \right. \\ & \left. - c_{eL} \frac{\mu_A}{1-\mu_L} - c_{eA} e^{-c_{Pa}a^*} \right]. \end{aligned} \quad (3.7)$$

(A similar expansion can be obtained for n in order to determine stability of the other axis equilibrium $(0, 0, 0, L^*, P^*, A^*)$.)

The formula (3.7) is complicated and does not provide much in the way of useful information. However, we can garner some information from equation (3.6) about

the basic dynamics of axis equilibria. In the presence of small numbers of species two, L_1 and A_1 must be positive, as L and A are expansions about 0. In this case we expect l_1 and a_1 to be negative, as the introduction of species two has a detrimental effect on the numbers of species one. The coefficients c_{EL} , c_{EA} , and c_{PA} of L_1 and A_1 represent intra-specific competition, and an increase of any of these coefficients will have a tendency to increase N_1 . On the other hand, the coefficients c_{El} , c_{Ea} , and c_{Pa} of l_1 and a_1 represent inter-specific competition, and an increase of any of these quantities will have a tendency to decrease N_1 .

Equation (3.6) shows that the relationship between inter- and intra-specific competition has an effect on the stability of the axis equilibrium; large values of c_{El} , c_{Ea} , and c_{Pa} tend to make N_1 negative and keep the equilibrium stable, while large values of c_{EL} , c_{EA} , and c_{PA} tend to make N_1 positive and destabilize the equilibrium. This is consistent with the classical theory, as an unstable axis equilibrium suggests the existence of a coexistence state.

3.2 Positive Equilibria

Linearization of the competition LPA map about the origin and axis equilibria is reasonably tractable because the resulting Jacobian is block diagonal, and the eigenvalues can be found via the 3×3 corner blocks. The linearization about a positive equilibrium $(l^*, p^*, a^*, L^*, P^*, A^*)$ is not block diagonal, and explicit formulas for the eigenvalues cannot be found because the characteristic polynomial is of degree six. For set numerical parameter values it is, of course, possible to numerically estimate the positive equilibrium and the eigenvalues of the resulting Jacobian.

A positive equilibrium $(l^*, p^*, a^*, L^*, P^*, A^*)$ must satisfy the equations

$$l^* = ba^*e^{-c_{el}l^* - c_{ea}a^* - c_{eL}L^* - c_{eA}A^*} \quad (3.8)$$

$$p^* = l^*(1 - \mu_l) \quad (3.9)$$

$$a^* = p^*e^{-c_{pa}a^* - c_{pA}A^*} + a^*(1 - \mu_a) \quad (3.10)$$

$$L^* = BA^*e^{-c_{El}l^* - c_{Ea}a^* - c_{EL}L^* - c_{EA}A^*} \quad (3.11)$$

$$P^* = L^*(1 - \mu_L) \quad (3.12)$$

$$A^* = P^*e^{-c_{Pa}a^* - c_{PA}A^*} + A^*(1 - \mu_A). \quad (3.13)$$

These six equations can be reduced to two equations as follows.

Solving equation (3.10) for p^* gives

$$p^* = a^*(\mu_a e^{c_{pa}a^* + c_{pA}A^*}). \quad (3.14)$$

Substituting this p^* into equation (3.9) and solving for l^* gives

$$l^* = a^* \left(\frac{\mu_a}{1 - \mu_l} e^{c_{pa}a^* + c_{pA}A^*} \right). \quad (3.15)$$

Substitution of this l^* into equation (3.8) results in the equation

$$\begin{aligned} & \ln \frac{\mu_a}{b(1 - \mu_l)} + (c_{pa} + c_{ea})a^* + (c_{pA} + c_{eA})A^* = \\ & -c_{el}(a^* \frac{\mu_a}{1 - \mu_l} e^{c_{pa}a^* + c_{pA}A^*}) - c_{eL}(A^* \frac{\mu_A}{1 - \mu_L} e^{c_{Pa}a^* + c_{PA}A^*}). \end{aligned} \quad (3.16)$$

A similar calculation involving equations (3.11), (3.12), and (3.13) yields

$$\begin{aligned} & \ln \frac{\mu_A}{B(1 - \mu_L)} + (c_{Pa} + c_{Ea})a^* + (c_{PA} + c_{EA})A^* = \\ & -c_{El}(a^* \frac{\mu_a}{1 - \mu_l} e^{c_{pa}a^* + c_{pA}A^*}) - c_{EL}(A^* \frac{\mu_A}{1 - \mu_L} e^{c_{Pa}a^* + c_{PA}A^*}). \end{aligned} \quad (3.17)$$

These constitute two equations for the two unknowns a^* and A^* . From a positive solution pair we can use (3.14) and (3.15) (and the corresponding equations for P^* and L^*) to calculate a positive equilibrium $(l^*, p^*, a^*, L^*, P^*, A^*)$.

These two nonlinear equations (3.16) and (3.17) cannot be solved explicitly for a^* and A^* . However, we can obtain some conditions sufficient for the existence of non-axis equilibria under the simplifying assumptions

$$c_{El} = c_{el} \quad \text{and} \quad c_{EL} = c_{eL}$$

as follows.

Subtracting (3.17) from (3.16) yields

$$\begin{aligned} & \ln \frac{\mu_a}{b(1-\mu_l)} - \ln \frac{\mu_A}{B(1-\mu_L)} + \\ & (c_{ea} - c_{Ea} + c_{pa} - c_{+a})a^* + (c_{eA} - c_{EA} + c_{pA} - c_{PA})A^* = \\ & (c_{El} - c_{el})\left(a^* \frac{\mu_a}{1-\mu_l} e^{c_{pa}a^* + c_{pA}A^*}\right) + (c_{EL} - c_{eL})\left(A^* \frac{\mu_A}{1-\mu_L} e^{c_{pA}a^* + c_{PA}A^*}\right). \end{aligned}$$

The simplifying assumptions reduce this to a linear relationship between a^* and A^* :

$$A^* = \frac{\ln \frac{\mu_a B(1-\mu_L)}{\mu_A b(1-\mu_l)} + (c_{ea} - c_{Ea} + c_{pa} - c_{PA})a^*}{c_{EA} - c_{eA} + c_{PA} - c_{pA}}. \quad (3.18)$$

We are interested in *positive* equilibria where both a^* and A^* are positive, so we will consider two cases in which the slope of the linear equation (3.18) is positive, namely

$$\text{case 1: } c_{ea} \geq c_{Ea}, \quad c_{EA} \geq c_{eA}, \quad c_{pa} > c_{PA}, \quad c_{PA} > c_{pA}, \quad \text{and}$$

$$\text{case 2: } c_{ea} \leq c_{Ea}, \quad c_{EA} \leq c_{eA}, \quad c_{pa} < c_{PA}, \quad c_{PA} < c_{pA}.$$

In case 1 the inequalities guarantee that both of the quantities $c_{ea} - c_{Ea} + c_{pa} - c_{PA}$ and $c_{EA} - c_{eA} + c_{PA} - c_{pA}$ are positive; in case 2 the inequalities guarantee that both of these quantities are negative. In either case the ratio $\frac{c_{ea} - c_{Ea} + c_{pa} - c_{PA}}{c_{EA} - c_{eA} + c_{PA} - c_{pA}}$ is positive, which implies that A^* is a strictly increasing linear function of a^* . Note that case 1 implies that there is more intra-specific than inter-specific competition, while case 2 implies that there is more inter-specific than intra-specific competition.

Consider now equations (3.16) and (3.17) under the simplifying assumptions above. Since A^* is an increasing linear function of a^* , the left hand sides of both equations are clearly increasing linear functions of a^* . The exponential terms $e^{c_{pa}a^* + c_{pA}A^*}$

and $e^{c_{Pa}a^* + c_{PA}A^*}$ appearing on the right hand sides are both also increasing in a^* . This implies that both of the functions $c_{el}(a^* \frac{\mu_a}{1-\mu_l} e^{c_{pa}a^* + c_{pA}A^*})$ and $c_{eL}(A^* \frac{\mu_A}{1-\mu_L} e^{c_{Pa}a^* + c_{PA}A^*})$ are increasing in a^* , so that the right hand side of (3.16):

$$-c_{el}(a^* \frac{\mu_a}{1-\mu_l} e^{c_{pa}a^* + c_{pA}A^*}) - c_{eL}(A^* \frac{\mu_A}{1-\mu_L} e^{c_{Pa}a^* + c_{PA}A^*}),$$

is a strictly *decreasing* function of a^* . By the assumption that $c_{El} = c_{el}$ and $c_{EL} = c_{eL}$, the right hand side of (3.17) is identical to the right hand side of (3.16), and is therefore also strictly decreasing in a^* .

The above argument shows that under the particular assumptions in case 1 and case 2, each of equations (3.16) and (3.17) has *at most* one solution pair (a^*, A^*) , which proves:

Theorem 3.1 *If $c_{El} = c_{el}$ and $c_{EL} = c_{eL}$, and either of the sets of inequalities*

$$c_{ea} \geq c_{Ea}, \quad c_{EA} \geq c_{eA}, \quad c_{pa} > c_{Pa}, \quad c_{PA} > c_{pA} \quad \text{or}$$

$$c_{ea} \leq c_{Ea}, \quad c_{EA} \leq c_{eA}, \quad c_{pa} < c_{Pa}, \quad c_{PA} < c_{pA}$$

holds, then the competition LPA map has at most one non-axis equilibrium point.

The assumptions of Theorem 3.1 are fairly restrictive. However, the complicated nature of equations (3.16) and (3.17) makes a more general result about the existence of positive equilibria difficult. Nonetheless the restrictive assumptions in Theorem 3.1 have meaningful biological interpretations and represent important cases of competition.

In fact, the conclusion of Theorem 3.1 is not valid in general. It will be shown in Chapter 5 that the competition LPA map can have as many as three non-axis equilibria, and we will explore in depth a case in which two positive equilibria are present. We will also examine a case in which the assumptions of Theorem 3.1 hold.

Chapter 4

PERSISTENCE

Persistence of a discrete map is defined with respect to a closed, invariant subset of a metric space. In population models, the metric space is \mathbb{R}_+^n , and the idea of persistence is often applied to some subset which represents an extinction state of one or more species, such as the origin or some collection of coordinate hyper-planes. Persistence with respect to the origin implies the indefinite survival of at least one species, but not necessarily all. In the first section of this chapter, the competition LPA map is shown to be persistent with respect to the origin provided at least one species has an inherent net reproductive number greater than one. The second section discusses persistence with respect to the subset of \mathbb{R}_+^6 corresponding to extinction of either species. A sufficient condition is given for persistence with respect to this extinction state, which is then a sufficient condition for indefinite coexistence of both species.

4.1 The Origin

The origin $(0, 0, 0, 0, 0, 0)$ is a closed subset of \mathbb{R}_+^6 and is invariant under the action of the competition LPA map. A map f is *persistent with respect to* $(0, 0, 0, 0, 0, 0)$ if

$$\liminf_{n \rightarrow \infty} |f^n(x)| > 0$$

for all $x \in \mathbb{R}_+^6 \setminus (0, 0, 0, 0, 0, 0)$.

The competition LPA map is:

$$\begin{aligned}
 l_{t+1} &= ba_t e^{-c_{el}l_t - c_{ea}a_t - c_{eL}L_t - c_{eA}A_t} \\
 p_{t+1} &= l_t(1 - \mu_l) \\
 a_{t+1} &= p_t e^{-c_{pa}a_t - c_{pA}A_t} + a_t(1 - \mu_a)
 \end{aligned} \tag{4.1}$$

$$\begin{aligned}
 L_{t+1} &= BA_t e^{-c_{El}l_t - c_{Ea}a_t - c_{EL}L_t - c_{EA}A_t} \\
 P_{t+1} &= L_t(1 - \mu_L) \\
 A_{t+1} &= P_t e^{-c_{Pa}a_t - c_{PA}A_t} + A_t(1 - \mu_A).
 \end{aligned}$$

Assume $l_t \geq 0, p_t \geq 0$, and $a_t \geq 0$. Clearly $p_{t+1} = 0$ if and only if $l_t = 0$. If $a_t = 0$, then both quantities $p_t e^{-c_{pa}a_t - c_{pA}A_t}$ and $a_t(1 - \mu_a)$ must be equal to zero, since $1 - \mu_a > 0$. Thus $a_{t+1} = 0$ if and only if $p_t = 0$ and $a_t = 0$. A similar argument shows that L_{t+1} , P_{t+1} , and A_{t+1} are all equal to zero if and only if L_t, P_t , and A_t are all equal to zero. Thus, the only point in \mathbb{R}_+^6 which maps to the origin is the origin itself, and no orbit originating in \mathbb{R}_+^6 can reach the origin in a *finite* number of steps.

The single species LPA map is persistent with respect to the origin provided $\frac{b(1-\mu_l)}{\mu_a} > 1$ [9]. One would then expect the competition LPA map to be persistent with respect to the origin provided that either one of the species' net reproductive numbers $\frac{b(1-\mu_l)}{\mu_a}$ or $\frac{B(1-\mu_L)}{\mu_A}$ is greater than 1. Assume then without loss of generality that $\frac{b(1-\mu_l)}{\mu_a} > 1$.

The Jacobian of the competition LPA map evaluated at the origin is:

$$\begin{pmatrix}
 0 & 0 & b & 0 & 0 & 0 \\
 1 - \mu_l & 0 & 0 & 0 & 0 & 0 \\
 0 & 1 & 1 - \mu_a & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & B \\
 0 & 0 & 0 & 1 - \mu_L & 0 & 0 \\
 0 & 0 & 0 & 0 & 1 & 1 - \mu_A
 \end{pmatrix}$$

This is block-diagonal, so the eigenvalues of the Jacobian are the eigenvalues of the two non-zero 3×3 matrices in the upper left and lower right corners. Each 3×3 is

irreducible and primitive, and thus has a simple, positive, strictly dominant eigenvalue with a corresponding *uniquely* positive eigenvector. The Jacobian thus has at most two non-negative eigenvectors:

$$(l, p, a, 0, 0, 0), \quad l, p, a > 0,$$

and also possibly

$$(0, 0, 0, L, P, A), \quad L, P, A > 0,$$

if $\frac{B(1-\mu_L)}{\mu_A} > 1$.

By the Stable Manifold Theorem [20], the stable manifold at the origin (if it exists; all eigenvalues may lie outside the unit circle) is tangent to the manifold spanned by the eigenvectors with eigenvalues inside the unit circle. But these eigenvectors each must have at least one negative component, so this manifold cannot intersect $\mathbb{R}_+^6 \setminus (0, 0, 0, 0, 0, 0)$. Thus no orbit originating in $\mathbb{R}_+^6 \setminus (0, 0, 0, 0, 0, 0)$ can approach the origin, and we have proved:

Theorem 4.1 *If either $\frac{b(1-\mu_l)}{\mu_a} > 1$ or $\frac{B(1-\mu_L)}{\mu_A} > 1$, the competition LPA map (4.1) is persistent with respect to the origin.*

4.2 Extinction State

The single-species LPA map is persistent with respect to the origin if and only if $\frac{b(1-\mu_l)}{\mu_a} > 1$. As this section deals with persistence of the competition LPA map with respect to the extinction states of *either* species, we will assume that *both* of the quantities $\frac{b(1-\mu_l)}{\mu_a}$ and $\frac{B(1-\mu_L)}{\mu_A}$ are greater than one.

Freedman and So show in [18] that a continuous map f such as the competition LPA map is persistent with respect to a closed, invariant subset Y of a finite-dimensional metric space X if the following four conditions are met:

- (a) $f(X \setminus Y) \subset X \setminus Y$.
- (b) $f|_Y$ is dissipative.
- (c) $f|_Y$ has an acyclic covering.
- (d) No sequence originating in $X \setminus Y$ approaches Y as $t \rightarrow \infty$.

Let Y be the set of all points in our metric space $X = \mathbb{R}_+^6$ of the form: $(l, p, a, 0, 0, 0)$ or $(0, 0, 0, L, P, A)$. This set represents points at which one of the two species is nonexistent. Persistence of the system with respect to Y thus implies indefinite survival of *both* species.

A point in $\mathbb{R}_+^6 \setminus Y$ has the form (l, p, a, L, P, A) where at least one of l, p, a and at least one of L, P, A are positive. As shown in the previous section, l_{t+1}, p_{t+1} , and a_{t+1} are all equal to zero if and only if l_t, p_t , and a_t are all equal to zero, and L_{t+1}, P_{t+1} , and A_{t+1} are all equal to zero if and only if L_t, P_t , and A_t are all equal to zero. This shows that $f(\mathbb{R}_+^6 \setminus Y) \subset \mathbb{R}_+^6 \setminus Y$, so (a) is true for the competition LPA map.

Lemma 4.2.1 *The competition LPA map is dissipative.*

Proof: Each of the six functions defined by the right hand side of (4.1) is bounded below by zero. We will show that there exists a constant $M > 0$ such that each orbit initiating in \mathbb{R}_+^6 satisfies $|(l, p, a, L, P, A)| \leq M$ for t sufficiently large. We can bound l by noting that

$$l_{t+1} = ba_t e^{-c_e l_t - c_{ea} a_t - c_e L_t - c_e A_t} \leq ba_t e^{-c_{ea} a_t};$$

as a function of a_t , the right hand side has a maximum $\frac{b}{c_{ea}e}$ which occurs at $a_t = \frac{1}{c_{ea}}$, so

$$l_t \leq \frac{b}{c_{ea}e} \quad \text{for all } t > 0.$$

Since $p_{t+1} = (1 - \mu_l)l_t$, it follows that

$$p_t \leq \frac{b(1 - \mu_l)}{c_{ea}e} \quad \text{for all } t > 1.$$

The function $a_{t+1} = p_t e^{-c_{pa} a_t - c_{pA} A_t} + a_t(1 - \mu_a)$ contains both p_t and a_t . Clearly $a_{t+1} \leq p_t + a_t(1 - \mu_a)$. Using the upper bound for p_t given above, we have for $t > 2$,

$$a_{t+1} \leq \frac{b(1 - \mu_l)}{c_{ea} e} + a_t(1 - \mu_a),$$

and by induction, for $t > 3$,

$$a_t \leq \sum_{i=3}^t (1 - \mu_a)^i \frac{b(1 - \mu_l)}{c_{ea} e} + \sum_{j=0}^2 (1 - \mu_a)^{t-j} a_j.$$

As $t \rightarrow \infty$, the last term vanishes and is therefore less than 1 for t sufficiently large.

Thus since

$$\sum_{i=0}^{\infty} (1 - \mu_a)^i \frac{b(1 - \mu_l)}{c_{ea} e} = \frac{b(1 - \mu_l)}{\mu_a c_{ea} e},$$

we have for large enough t that

$$a_t \leq \frac{b(1 - \mu_l)}{\mu_a c_{ea} e} + 1.$$

A similar argument gives, for sufficiently large values of t ,

$$L_t \leq \frac{B}{c_{EA} e}, \quad P_t \leq \frac{B(1 - \mu_L)}{c_{EA} e}, \quad \text{and}$$

$$A_t \leq \frac{B(1 - \mu_L)}{\mu_A c_{EA} e} + 1.$$

This shows that the competition LPA map is dissipative. \square

By Lemma 4.2.1, the competition LPA map is dissipative over \mathbb{R}_+^6 , so it is certainly dissipative when restricted to Y . This proves that (b) holds. We now turn our attention to condition (c).

Consider an initial condition $(l_0, p_0, a_0, 0, 0, 0)$, with at least one of l_0, p_0, a_0 positive. As $\frac{b(1 - \mu_l)}{\mu_a}$ is assumed greater than one (and we have persistence with respect to the origin), the orbit resulting from this initial condition has a forward limit set consisting of points of the form $(l, p, a, 0, 0, 0)$, with at least one of l, p, a positive. Similarly, an orbit generated by an initial condition of the form $(0, 0, 0, L_0, P_0, A_0)$ with at

least one of L_0, P_0, A_0 positive has a forward limit set consisting of points of the form $(0, 0, 0, L, P, A)$, with at least one of L, P, A positive. Denote the union of these two forward limit sets by M_1 , and let M_2 consist of the single point $(0, 0, 0, 0, 0, 0)$. These sets are isolated invariant and compact, and they are disjoint, so $\Pi = \{M_1, M_2\}$ forms an isolated covering of $f|_Y$.

As shown in the previous section, the coupled LPA map is persistent with respect to the origin, since we are assuming that both $\frac{b(1-\mu_l)}{\mu_a}$ and $\frac{B(1-\mu_L)}{\mu_A}$ are greater than one. Hence no orbit originating in \mathbb{R}_+^6 can lie in the stable set of the origin, and M_2 cannot be part of any cycle with M_1 . Thus $\Pi = \{M_1, M_2\}$ is an acyclic covering of $f|_Y$, and condition (c) holds.

Conditions (a) – (c) hold in full generality for the coupled LPA map; all that remains is to determine conditions under which (d) holds. As we will see, (d) holds only for certain parameter values. One way of approaching this problem is to consider the stability of axis equilibria discussed in Section 3.1. There it is shown that the axis equilibrium $(l^*, p^*, a^*, 0, 0, 0)$ is unstable if

$$\frac{B(1-\mu_L)}{\mu_A} e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*} > 1, \quad (4.2)$$

and similarly the axis equilibrium $(0, 0, 0, L^*, P^*, A^*)$ is unstable if

$$\frac{b(1-\mu_l)}{\mu_a} e^{-c_{eL}L^* - (c_{eA} + c_{pA})A^*} > 1. \quad (4.3)$$

Satisfaction of both of these inequalities simultaneously guarantees that both axis equilibria are unstable. Furthermore, any stable manifold that may exist under these conditions lies within Y and does not intersect the positive cone of \mathbb{R}^6 , so that no sequence originating in $\mathbb{R}_+^6 \setminus Y$ can approach Y as $t \rightarrow \infty$. We would like to determine necessary and sufficient conditions under which both of the inequalities (4.2) and (4.3) hold, but the presence of the unknown quantities l^*, a^*, L^* , and A^* prevents the construction of inequalities based solely on parameter values. We will obtain *sufficient* conditions, involving only the parameter values, for the satisfaction of inequalities (4.2) and (4.3).

The values a^* , A^* are solutions of the equilibrium equations:

$$\begin{aligned} & \ln \frac{b\mu_a}{1-\mu_l} + (c_{pa} + c_{ea})a^* + (c_{pA} + c_{eA})A^* = \\ & -c_{el}\left(a^* \frac{\mu_a}{1-\mu_l} e^{c_{pa}a^* + c_{pA}A^*}\right) - c_{eL}\left(A^* \frac{\mu_A}{1-\mu_L} e^{c_{pA}a^* + c_{pA}A^*}\right) \end{aligned} \quad (4.4)$$

$$\begin{aligned} & \ln \frac{B\mu_A}{1-\mu_L} + (c_{pA} + c_{eA})a^* - (c_{pA} + c_{eA})A^* = \\ & -c_{El}\left(a^* \frac{\mu_a}{1-\mu_l} e^{c_{pa}a^* + c_{pA}A^*}\right) - c_{EL}\left(A^* \frac{\mu_A}{1-\mu_L} e^{c_{pA}a^* + c_{pA}A^*}\right). \end{aligned} \quad (4.5)$$

These equations do not have explicit solutions for a^* and A^* . However, strict upper bounds on l^* , a^* , L^* and A^* will provide lower bounds for

$$\begin{aligned} & \frac{b(1-\mu_l)}{\mu_a} e^{-c_{eL}L^* - (c_{eA} + c_{pA})A^*} \quad \text{and} \\ & \frac{B(1-\mu_L)}{\mu_A} e^{-c_{El}l^* - (c_{eA} + c_{pA})a^*}, \end{aligned}$$

and thus give sufficient conditions for persistence based on the inequalities (4.2) and (4.3).

From the proof of Lemma 4.2.1 we have upper bounds on l^* , a^* , L^* , and A^* given by:

$$\begin{aligned} l^* & \leq \frac{b}{c_{ea}e}, \quad a^* \leq \frac{b(1-\mu_l)}{\mu_a c_{ea}e} + 1, \\ L^* & \leq \frac{B}{c_{EA}e}, \quad \text{and} \quad A^* \leq \frac{B(1-\mu_L)}{\mu_A c_{EA}e} + 1. \end{aligned}$$

For the reasonable equilibrium parameters given in chapter 2, these give upper bounds for l^* , p^* , L^* , and P^* in the 300 – 400 range, which is acceptable for a sufficient condition. But the upper bounds for a^* and A^* are in the tens of thousands, which is extremely unrealistic, and thus not suitable for this purpose.

Another way of establishing upper bounds for a^* and A^* is to consider the special case: $c_{el} = c_{EL} = 0$. To find an upper bound for a^* , we start by assuming $L = P = A = 0$. The equation for l_{t+1} then reduces to $l_{t+1} = ba_t e^{-c_{el}l_t - c_{ea}a_t} \leq ba_t e^{-c_{ea}a_t}$. As this holds for all t , l_{t+1} is clearly maximized by the condition $c_{el} = 0$ versus $c_{el} > 0$,

as is $p_{t+2} = (1 - \mu_l)l_{t+1}$. Finally, $a_{t+3} = p_{t+2}e^{-c_{pa}a_{t+2}} + (1 - \mu_a)a_{t+2}$ will also be maximized for all t by the condition $c_{el} = 0$. Since l^* , p^* , and a^* represent long term behavior, they will be maximized by the condition $c_{el} = 0$. Thus an upper bound for a^* obtained by setting $c_{el} = 0$ will serve as an upper bound for a^* for any positive value of c_{el} . A similar argument shows that an upper bound for A^* obtained by setting $c_{EL} = 0$ will serve as an upper bound for A^* for any positive value of c_{EL} .

With the assumptions $c_{el} = c_{EL} = 0$ the equilibrium values a^* and A^* can be written explicitly:

$$a^* = (c_{ea} + c_{pa})^{-1} \ln\left(\frac{b(1 - \mu_l)}{\mu_a}\right) \quad (4.6)$$

$$A^* = (c_{EA} + c_{PA})^{-1} \ln\left(\frac{B(1 - \mu_L)}{\mu_A}\right). \quad (4.7)$$

The presence of a positive c_{el} (or c_{EL}) is strictly detrimental to population numbers, so these values provide upper bounds for a^* and A^* for any non-negative values of c_{el} or c_{EL} . When fitted with the same reasonable parameter values noted above, these equations give upper bounds on a^* and A^* which are less than a thousand.

Substituting $l^* = \frac{b}{c_{ea}e}$ and $a^* = (c_{ea} + c_{pa})^{-1} \ln\left(\frac{b(1 - \mu_l)}{\mu_a}\right)$ into (4.2) results in the inequality:

$$(c_{Ea} + c_{Pa}) \frac{\ln\left(\frac{b(1 - \mu_l)}{\mu_a}\right)}{c_{ea} + c_{pa}} + c_{EL} \frac{b}{c_{ea}e} < \ln\left(\frac{B(1 - \mu_L)}{\mu_A}\right). \quad (4.8)$$

This, together with the inequality:

$$(c_{EA} + c_{PA}) \frac{\ln\left(\frac{B(1 - \mu_L)}{\mu_A}\right)}{c_{EA} + c_{PA}} + c_{eL} \frac{B}{c_{EA}e} < \ln\left(\frac{b(1 - \mu_l)}{\mu_a}\right) \quad (4.9)$$

provide *sufficient* conditions for persistence of the system with respect to either extinction state.

Chapter 5

NON-EQUILIBRIUM DYNAMICS

The classical theory of competitive exclusion as exemplified by the Lotka-Volterra model can be viewed in a number of ways. In that model the question of coexistence can be reduced to a simple pair of inequalities involving model coefficients, which essentially represents the ratio of inter-specific to intra-specific competition. Because of the complexity of the competition LPA model it is not possible to reduce the problem to such a simple inequality. There are, however, more general interpretations; the classical theory allows for coexistence only in the presence of a stable, positive equilibrium, which is possible only if the amount of inter-specific competition is small relative to the amount of intra-specific competition. Coexistence should not be possible in the presence of an unstable positive equilibrium, or in the presence of stable axis equilibria representing extinction states. In this chapter we will show by means of example using the competition LPA model that coexistence is possible in both of these scenarios. In the final section we will consider situations in which the underlying single-species dynamics are more complicated than stable equilibria, and see that non-equilibrium attractors can be made to undergo bifurcations into coexistence states.

5.1 Coexistence in the Presence of an Unstable Positive Equilibrium

In the Lotka-Volterra model (1.1) an unstable positive equilibrium exists if and only if the appropriate inequalities hold. All initial conditions in the positive quadrant not on the one-dimensional stable manifold of the positive equilibrium result in the extinction of one species and indefinite survival of the other, as the resulting orbits

head off towards one of the stable axis equilibria. The positive quadrant is thus divided into two regions, each representing all initial conditions for which a given species will go extinct.

With certain parameter values the competition LPA model exhibits the same behavior. We begin by considering examples in which the parameters for both species are identical except for the four c_{pa} components.

$b=10$	$B=10$	$\mu_l=0.2$	$\mu_L=0.2$	$\mu_a=0.02$	$\mu_A=0.02$
$c_{el}=0.01$	$c_{EL}=0.01$	$c_{ea}=0.01$	$c_{EA}=0.01$	$c_{pa}=0.01$	$c_{PA}=0.012$
$c_{eL}=0.01$	$c_{El}=0.01$	$c_{eA}=0.01$	$c_{EA}=0.01$	$c_{pA}=0.02$	$c_{Pa}=0.015$

TABLE 5.1. Parameter Values

The inter-specific parameters c_{pA} and c_{Pa} given in Table 5.1 are set higher than the intra-specific parameters c_{pa} and c_{PA} . With these parameter values the competition LPA map has a unique (by Theorem 3.1) positive equilibrium (59.8, 47.8, 129.6, 37.3, 29.9, 81.0) which is unstable, and two stable axis equilibria, (84.4, 67.5, 257.4, 0, 0, 0) and (0, 0, 0, 91.8, 73.4, 230.6). All initial conditions in the positive quadrant not on the one-dimensional stable manifold of the positive equilibrium generate orbits which approach one of the axes. This is an identical situation to that of the Lotka-Volterra model when both of the competition coefficients are greater than one. Figure 5.1 shows two different orbits, each leading to a different outcome.

In the above example the positive equilibrium is unstable because of the disparity between inter-specific and intra-specific competition. In the following example we will begin with a *stable* positive equilibrium by reversing the disparity. The positive equilibrium will then destabilize upon increasing adult mortality in both species, resulting not in stable axis equilibria, but in a globally attracting, stable two-cycle in the positive cone.

The parameter values in Table 5.2 generate a stable, positive equilibrium at (35.3, 28.2, 122.3, 44.1, 35.3, 152.9). As μ_a and μ_A are raised simultaneously, we see

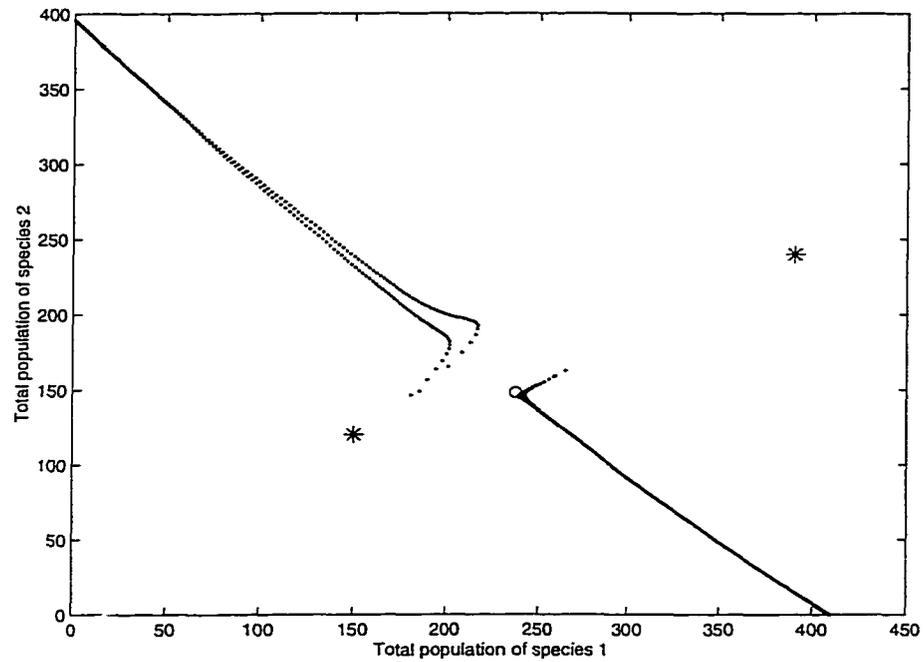


FIGURE 5.1. Two different initial conditions, denoted by asterisks, result in the extinction of different species. The initial condition $(50, 50, 50, 40, 40, 40)$ results in the extinction of species 1. The initial condition $(130, 130, 130, 80, 80, 80)$ results in the extinction of species 2. The unstable positive equilibrium is denoted by a circle. Parameter values are given in Table 5.1.

$b=10$	$B=10$	$\mu_l=0.2$	$\mu_L=0.2$	$\mu_a=0.02$	$\mu_A=0.02$
$c_{el}=0.01$	$c_{EL}=0.01$	$c_{ea}=0.01$	$c_{EA}=0.01$	$c_{pa}=0.01$	$c_{PA}=0.012$
$c_{eL}=0.01$	$c_{El}=0.01$	$c_{eA}=0.01$	$c_{EA}=0.01$	$c_{pA}=0.008$	$c_{PA}=0.005$

TABLE 5.2. Parameter Values

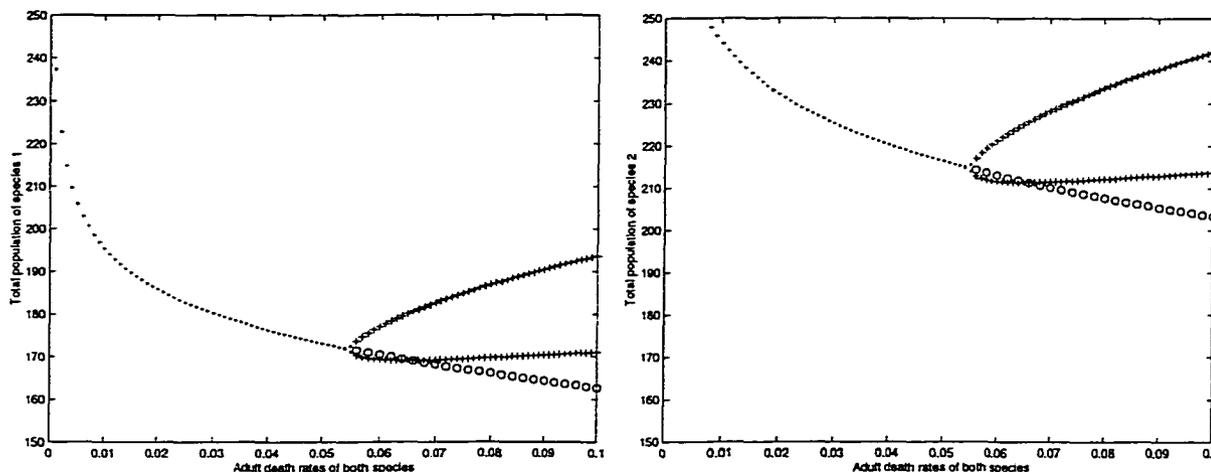


FIGURE 5.2. Bifurcation diagrams for both species as μ_a and μ_A range from 0 to 0.1. The stable equilibrium bifurcates to an unstable equilibrium (circles) and a stable two-cycle (crosses) near $\mu_a = \mu_A = 0.0551$. Other parameter values are given in Table 5.2.

the positive equilibrium destabilize near $\mu_a = \mu_A = .0551$ and a stable two-cycle bifurcation occurs. This bifurcation is a result of the dominant eigenvalue of the Jacobian exiting the unit circle through -1 . Figure 5.2 shows the total population size of each species for $\mu_a = \mu_A$ between 0 and 0.1.

For values of $\mu_a = \mu_A$ slightly greater than this bifurcation point, the competition LPA map has a positive two-cycle which acts as a global attractor in the positive cone, along with an unstable positive equilibrium. (As $\mu_a = \mu_A$ is increased further, the equilibrium eventually restabilizes, near $\mu_a = \mu_A = 0.62$.) For example, when $\mu_a = \mu_A = 0.1$ there is a globally attracting two-cycle at $(14.7, 75.2, 81.1, 18.3, 94.0, 101.3)$ and $(94.0, 11.7, 87.8, 117.5, 14.7, 109.8)$. This is a very robust coexistence state, with both populations maintaining total numbers well over 100 at each time step. The positive equilibrium point $(46.9, 37.5, 78.3, 58.6, 46.9, 97.9)$ is unstable, with a domi-

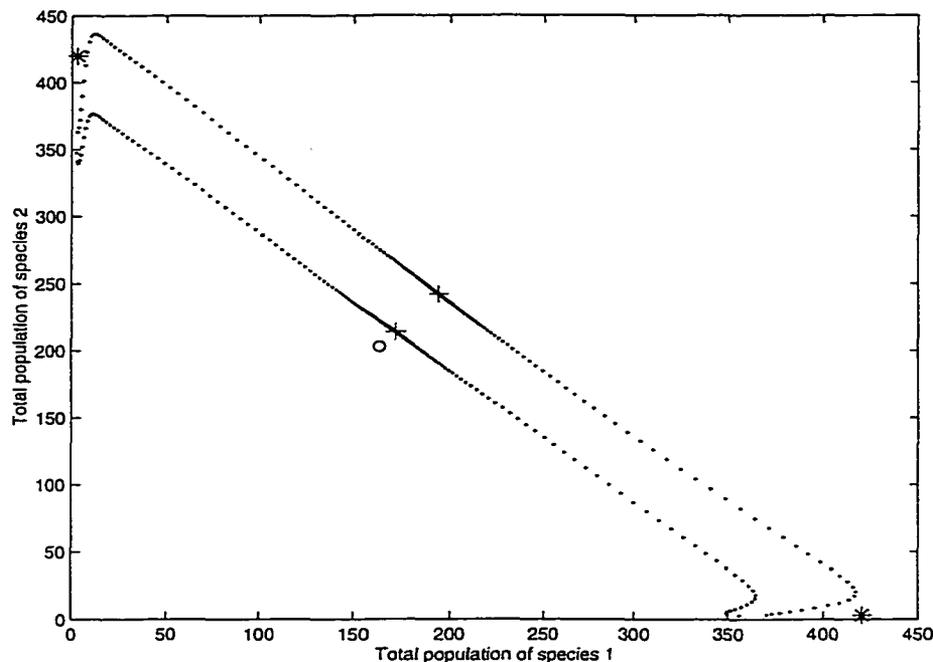


FIGURE 5.3. Two different initial conditions, $(140, 140, 140, 0, 0, 0)$ and $(0, 0, 0, 140, 140, 140)$ (denoted by asterisks), lead to stable two-cycle coexistence. Each orbit moves away from the axis in periodic fashion, oscillating back and forth as it approaches the stable two-cycle. The stable two-cycle is denoted by crosses, the unstable equilibrium by a circle. Parameter values are given in Table 5.2, with the exception that $\mu_a = \mu_A = 0.1$.

nant eigenvalue less than -1.09 . Figure 5.3 shows two orbits with initial conditions very close to each axis; the introduction of small numbers of one species into a large population of the other results in stable coexistence.

Although it has a non-equilibrium coexistence state, the example above is not unlike the classical Lotka-Volterra case in that both axis equilibria are unstable and the stable two-cycle plays the role of the stable equilibrium. While the existence of positive two-cycles is not terribly surprising in the competition LPA model, with this simple example we see that it is capable of generating dynamics beyond the scope of traditional competition theory. In the next section we will examine a similar set of parameters, and see that coexistence is possible even when the amount of inter-specific

competition is greatly increased.

5.2 Coexistence in the Presence of Stable Axis Equilibria

Up until this point we have focused on the c_{pa} coefficients as the main source of competitive asymmetry in the model. In this example we will see that by keeping the inter-specific coefficients c_{pA} and c_{Pa} slightly lower than the intra-specific coefficients c_{pa} and c_{PA} (as in the previous example), coexistence can occur even with large values of the inter-specific coefficients c_{eL} and c_{El} .

We again start with a stable positive equilibrium, using the parameter values given in Table 5.2. With these parameters there exists a stable positive equilibrium (35.3, 28.2, 122.3, 44.1, 35.3, 152.9), and unstable axis equilibria (84.4, 67.5, 257.4, 0, 0, 0) and (0, 0, 0, 91.8, 73.4, 230.6). The quantities

$$n = b \frac{1 - \mu_l}{\mu_a} e^{-c_{eL}L^* - (c_{eA} + c_{pA})A^*} = 2.516$$

$$N = B \frac{1 - \mu_L}{\mu_A} e^{-c_{El}l^* - (c_{Ea} + c_{Pa})a^*} = 3.62$$

are fairly close to one. Increasing c_{eL} and c_{El} will leave the equilibrium values l^* , a^* , L^* , and A^* unaffected, while decreasing n and N exponentially. Solving $n = 1$ for c_{eL} and $N = 1$ for c_{El} shows that the axis equilibria are stable for $c_{El} > 0.02525$ and $c_{eL} > 0.02005$, respectively.

Figure 5.4 shows bifurcation diagrams for both equilibria and two-cycles as c_{El} and c_{eL} are increased simultaneously. The positive equilibrium persists until the axis equilibrium (0, 0, 0, 91.8, 73.4, 230.6) stabilizes at $c_{El} = c_{eL} = 0.02005$. The positive equilibrium is stable through most of this parameter region, but loses stability between roughly $c_{El} = c_{eL} = .01835$ and 0.01902 , where the dominant eigenvalue briefly exits the unit circle and then returns through -1 . In this region there is a stable positive two-cycle very close to the unstable equilibrium.

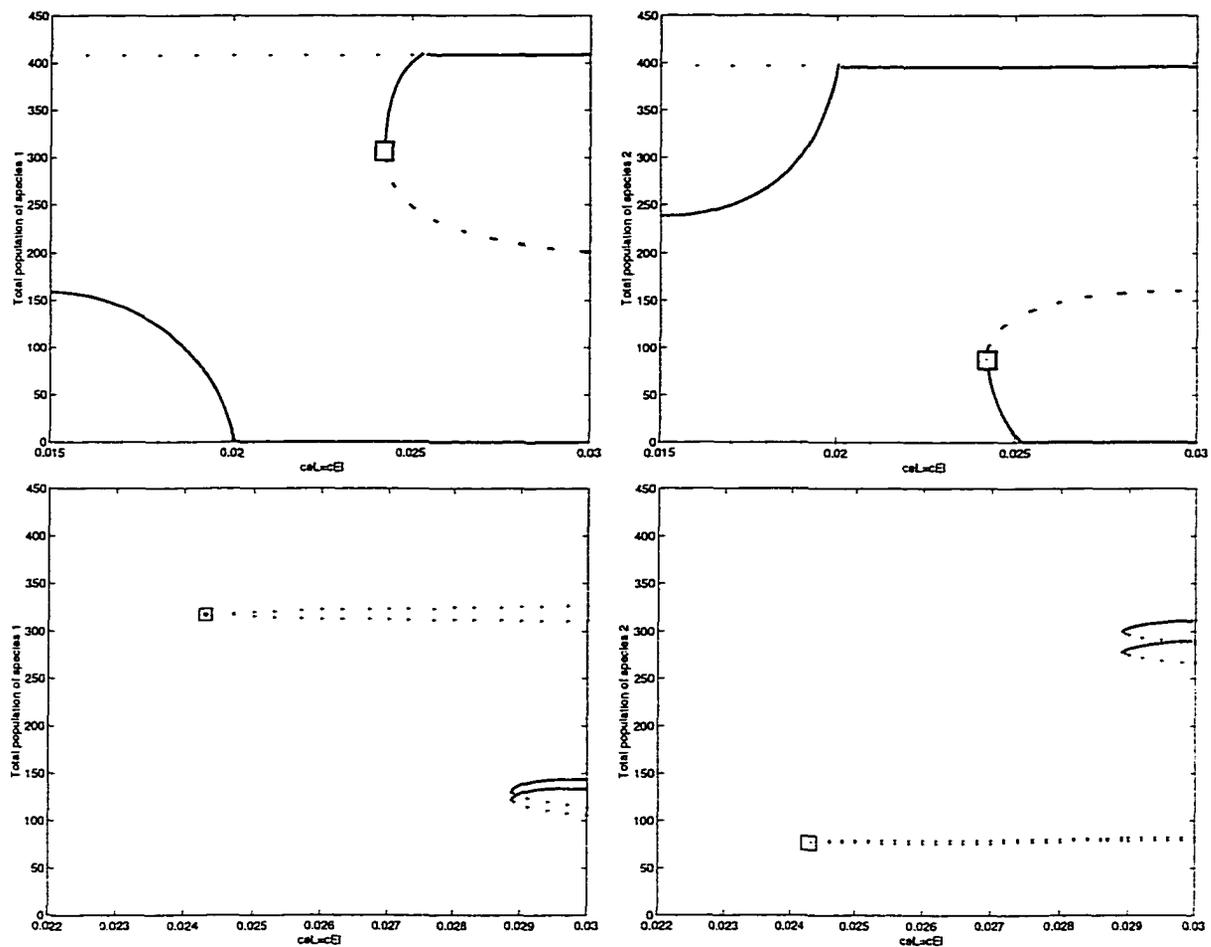


FIGURE 5.4. The top two diagrams show the stable (solid) and unstable (dotted) branches of equilibria for $c_{EI} = c_{eL}$ between 0.015 and 0.03. The initially stable positive equilibrium hits the axis of species 2 near 0.02005. (Not shown is the brief destabilization into a two-cycle near 0.019.) An *unstable* saddle-node bifurcation occurs near 0.02425, and eventually gives rise to a stable positive equilibrium branch, which hits the axis of species 1 near 0.02525. Beyond 0.02525 there is only one *unstable* positive equilibrium. The bottom two figures show the stable (solid) and unstable (dotted) branches of two-cycles for $c_{EI} = c_{eL}$ between 0.022 and 0.03. Near 0.0243, an unstable two-cycle appears, coinciding with the appearance of the *stable* positive equilibrium shown above. (This event is denoted by squares in all four diagrams.) Near 0.0289 a saddle-node bifurcation of the composite map gives rise to both a stable and an unstable branch of two-cycles. The stable branch represents a robust coexistence state, and persists for arbitrarily large values of $c_{EI} = c_{eL}$.

As c_{El} and c_{eL} are increased further through 0.02005, the positive equilibrium collides with the axis equilibrium $(0, 0, 0, 91.8, 73.4, 230.6)$ and exits the positive cone. This axis equilibrium is globally stable for values of $c_{El} = c_{eL}$ between 0.02005 and 0.02425.

Near 0.02425, a saddle-node bifurcation of equilibria occurs in the positive cone at $(60.2, 48.2, 196.7, 10.1, 8.1, 67.3)$. This bifurcation is *unstable*, as the dominant eigenvalue of the equilibrium point is slightly less than -1 . However, one branch of the bifurcation quickly stabilizes (near 0.0243) as it approaches the other axis equilibrium $(84.4, 67.5, 257.4, 0, 0, 0)$, eventually colliding with the axis at 0.02525. The other branch remains in the positive cone and remains unstable with a negative eigenvalue less than -1 and a positive eigenvalue greater than 1.

Thus, in the parameter region between 0.0243 and 0.02525 there exist *four* equilibria of interest. Most notably, there is both a stable positive equilibrium and a stable axis equilibrium, each with non-trivial basins of attraction. In this case species one cannot be driven to extinction by species two, but species two can survive indefinitely under certain initial conditions. This configuration of equilibria cannot occur in the classical Lotka-Volterra model. Figure 5.5 is an illustrative example of this case, in which three orbits are shown, one of which results in the extinction of species one, and two which approach the stable positive equilibrium and lead to coexistence. In this picture $c_{El} = c_{eL} = 0.0245$.

Increasing c_{El} and c_{eL} even further, we turn our attention to two-cycles. The unstable branch of the equilibrium saddle-node bifurcation stabilizes near 0.0243 and as a result gives birth to an unstable positive two-cycle. This occurs because the dominant eigenvalue passes through -1 . The effect of this two-cycle on orbits is visible in Figure 5.5. Between 0.02525 and roughly 0.0289 we have this unstable two-cycle, along with an unstable positive equilibrium and the two stable axis equilibria.

Near 0.0289, a new significant event occurs. As $c_{El} = c_{eL}$ is increased through this value, a saddle-node bifurcation occurs in the *composite* of the competition LPA

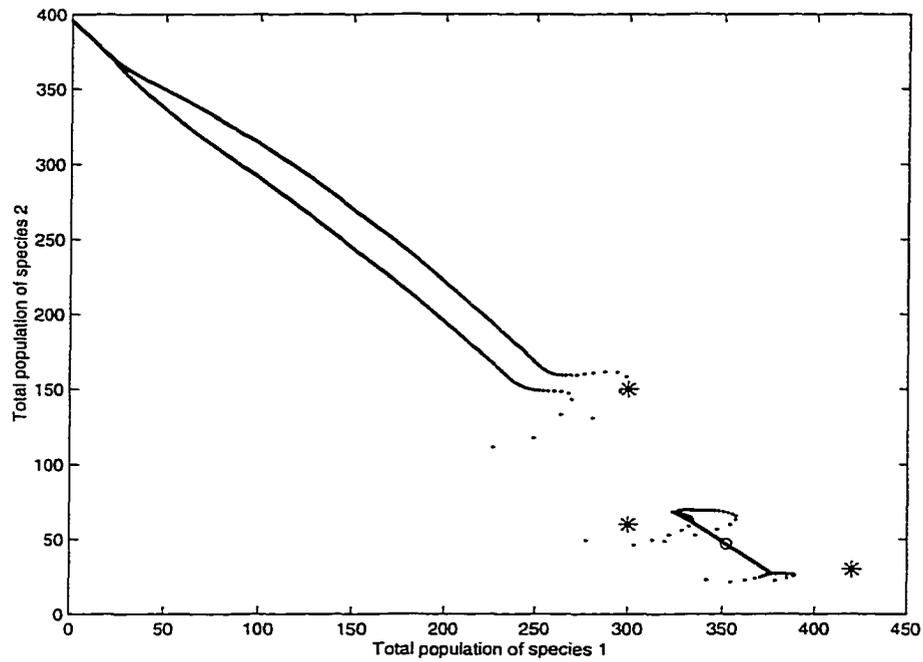


FIGURE 5.5. Three initial conditions are denoted by asterisks. The orbit with initial condition $(100, 100, 100, 50, 50, 50)$ approaches the stable axis equilibrium of species 2, while the orbits with initial conditions $(140, 140, 140, 10, 10, 10)$ and $(100, 100, 100, 20, 20, 20)$ approach the stable positive equilibrium, denoted by a circle. Parameter values are given in Table 5.2, with the exception that $c_{El} = c_{eL} = 0.0245$.

map, giving rise to two new branches of two-cycles. One of these branches is *stable*, and remains stable for very large values of $c_{El} = c_{eL}$. Thus for $c_{El} = c_{eL} > 0.0289$, there are *three* attractors, a positive two-cycle and the two axis equilibria, each with a sizable basin of attraction.

This example is interesting for several reasons. It represents a clear contradiction to the classical theory in the sense that a coexistence state exists *in the presence of stable equilibria on both axes*. Furthermore, this coexistence state is achieved by *raising* the inter-specific competition while leaving the intra-specific competition fixed. This is counter-intuitive because dogma in competition theory asserts that such an increase should result in competitive exclusion. The stable two-cycle in fact persists at approximately $(0, 60.6, 124.4, 0, 75.7, 155.5)$ and $(75.7, 0, 127, 94.6, 0, 158.7)$ for *arbitrarily large* values of $c_{El} = c_{eL}$.

We began with a stable positive equilibrium, and found that a small increase in $c_{El} = c_{eL}$ results in a globally stable axis equilibrium, which is not surprising. Further increase brings about a small parameter region which allows a stable positive equilibrium in the presence of the stable axis equilibrium, and then in a separatrix situation similar to the unstable positive equilibrium case in the classical Lotka-Volterra model; again this is what we expect to see in the presence of a large amount of inter-specific competition. Finally, for large enough values of $c_{El} = c_{eL}$, a very robust coexistence state appears in the presence of *two* stable axis equilibria.

One other feature of note is that the coexistence two-cycle does not indicate a *temporal niche*. It might be expected that in a coexistence two-cycle, the populations would oscillate out of phase, with one population reaching a maximum while the other reaches a minimum, and vice versa. In this example, the populations in fact oscillate in phase; each population reaches its maximum at the same time. Figure 5.6 shows three orbits with $c_{El} = c_{eL} = 0.1$, each approaching a different attractor. Here the stable two-cycle is clearly seen to be in phase.

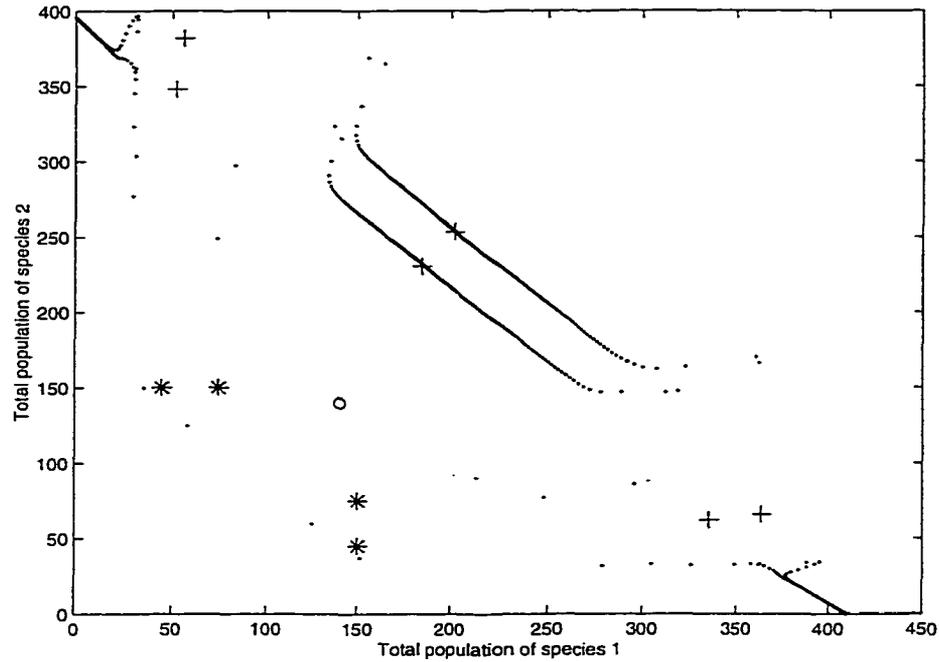


FIGURE 5.6. Four initial conditions are denoted by asterisks. The orbit with initial condition $(15, 15, 15, 50, 50, 50)$ approaches the stable axis equilibrium of species 2. The orbit with initial condition $(50, 50, 50, 15, 15, 15)$ approaches the stable axis equilibrium of species 1. The orbits with initial conditions $(25, 25, 25, 50, 50, 50)$ and $(50, 50, 50, 25, 25, 25)$ approach the *stable* coexistence two-cycle; that and the two unstable two-cycles are denoted by crosses. The unstable positive equilibrium is denoted by a circle. Parameter values are given in Table 5.2, with the exception that $c_{E1} = c_{eL} = 0.1$.

5.3 Coexistence in the Presence of Non-equilibrium Attractors within the Axes

Up to this point we have considered only examples in which the underlying axis dynamics were governed by *stable* equilibria. Perhaps the most compelling fact about the LPA model is the existence of exotic dynamics within populations of a *single* species; thus we should consider the possibility of coexistence states arising from non-equilibrium axis attractors.

The simplest such example involves the bifurcation of a stable two-cycle from the axis into the positive cone. Examples of such bifurcations have been demonstrated in other discrete population maps [6, 9]. One interesting feature of this type of bifurcation is that the positive two-cycle which arises is typically in phase. The two-cycles shown in Figure 5.6 are in phase; each population reaches its maximum at the same time. Thus, the species are not “time-sharing” an ecological niche.

The parameter values given in Table 5.3 are identical to the values in Table 5.1, except for μ_a and μ_A , which have been raised to 0.1, and c_{Pa} , which has been raised to 0.015. This increase in inter-specific competition leads to global extinction of species 2, but the increase in μ_a destabilizes the axis equilibrium, leading to a stable two-cycle on the axis at $(28.6, 184.3, 173, 0, 0, 0)$ and $(230.4, 22.9, 188.4, 0, 0, 0)$.

$b=10$	$B=10$	$\mu_l=0.2$	$\mu_L=0.2$	$\mu_a=0.1$	$\mu_A=0.1$
$c_{el}=0.01$	$c_{EL}=0.01$	$c_{ea}=0.01$	$c_{EA}=0.01$	$c_{pa}=0.01$	$c_{PA}=0.012$
$c_{eL}=0.01$	$c_{El}=0.01$	$c_{eA}=0.01$	$c_{EA}=0.01$	$c_{pA}=0.008$	$c_{PA}=0.015$

TABLE 5.3. Parameter Values

We expect a coexistence state to arise from an increase in intra-specific competition, which is achieved by raising c_{pa} from 0.01. The two-cycle lifts off the axis near $c_{pa} = 0.0146$, leading to a stable, positive two-cycle which is globally attracting, as shown in Figure 5.7.

The competition LPA model is capable of a vast array of complicated dynamics.

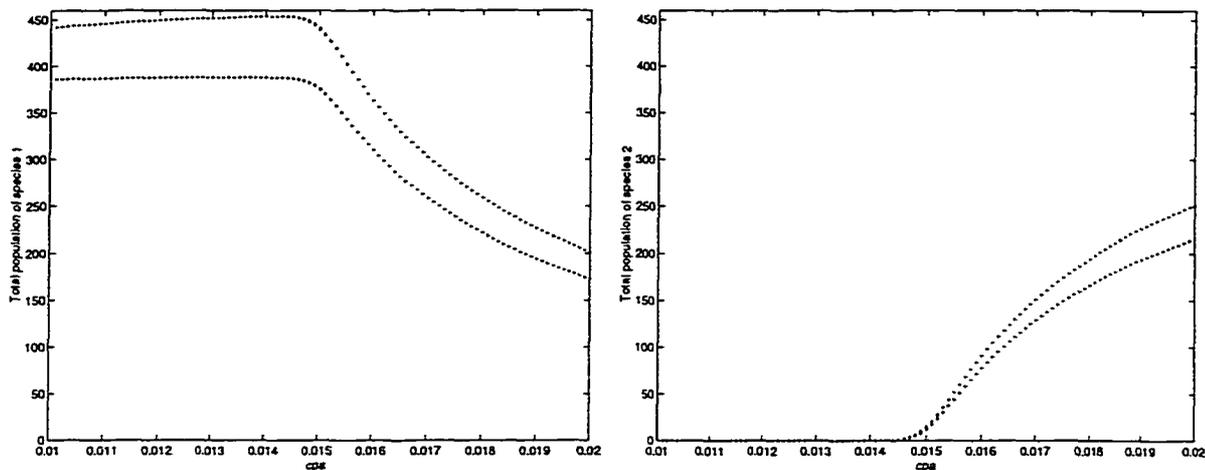


FIGURE 5.7. Bifurcation diagrams for both species as c_{pa} ranges from 0.01 to 0.02. A stable two-cycle on the axis of species 1 bifurcates to a stable positive two-cycle as c_{pa} passes through 0.0146. Other parameter values are given in Table 5.3.

In these final two examples, we will consider parameter values similar to those used in the Hunt for Chaos experiment based on the single-species LPA model [4, 16]. In that experiment, chaos was achieved by raising adult mortality while leaving the other parameters at values fit to laboratory cultures of the species *Tribolium castaneum*. The adult death rate μ_a was raised to 0.96, while the adult-pupal cannibalism coefficient c_{pa} was raised to 0.35.

As shown in Table 5.4, we raise the death rate μ_A of species 2 to 0.98 and the intra-specific competition coefficient c_{PA} to 0.35. In the absence of species 1, these parameter values will cause species 2 to undergo chaotic fluctuations. Species 1 has a considerably smaller death rate $\mu_a = 0.62$ and the same intra-specific competition coefficient $c_{pa} = 0.35$. In the absence of species 2, these parameter values will cause species 1 to undergo aperiodic oscillations. Figure 5.8 shows three-dimensional plots

$b=10$	$B=10$	$\mu_l=0.2$	$\mu_L=0.2$	$\mu_a=0.62$	$\mu_A=0.98$
$c_{el}=0.01$	$c_{EL}=0.01$	$c_{ea}=0.01$	$c_{EA}=0.01$	$c_{pa}=0.35$	$c_{PA}=0.35$
$c_{eL}=0.01$	$c_{El}=0.01$	$c_{eA}=0.01$	$c_{EA}=0.01$	$c_{pA}=0.5$	$c_{PA}=-$

TABLE 5.4. Parameter Values

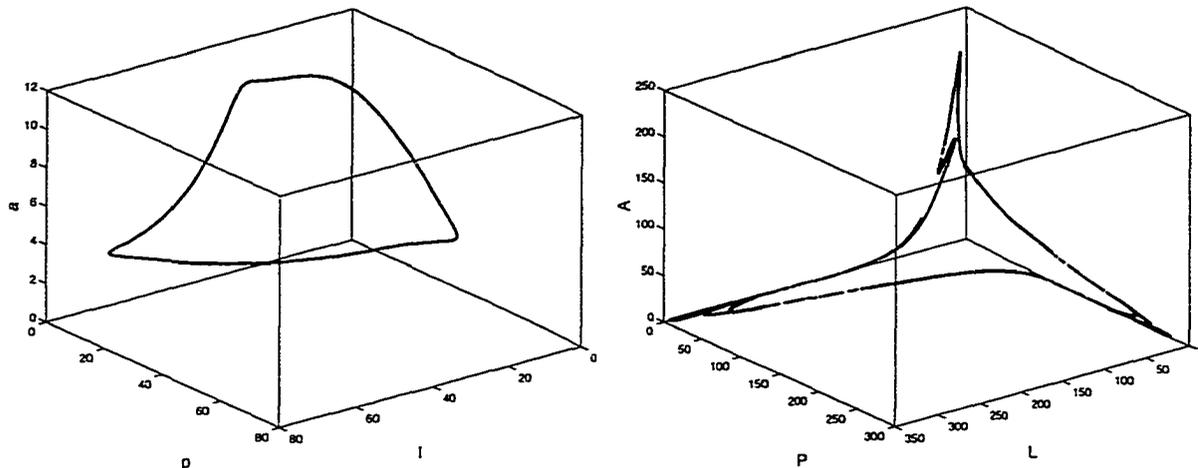


FIGURE 5.8. Attractors within each of the axes, shown in phase space. On the left is an invariant loop within the species 1 axis. On the right is a chaotic attractor within the species 2 axis. Parameter values are given in Table 5.4.

of the attractors on each axis.

To compensate for the higher death rate, species 2 is given a competitive edge by setting $c_{pA} = 0.5$. We will consider values of the other inter-specific competition coefficient c_{Pa} ranging from 0 to 0.25. Figure 5.9 shows bifurcation diagrams for both species.

An invariant loop is seen to bifurcate off the horizontal axis and into the positive cone at the critical value $c_{Pa} = 0.23$. For values of c_{Pa} lower than this, the two species can coexist in non-equilibrium states. Figure 5.10 shows coexistence attractors for four different values of c_{Pa} , including a chaotic coexistence attractor that arises from a complicated bifurcation sequence.

Finally, we consider a bifurcation of a chaotic attractor from the axis into the positive cone. In this final example, we raise μ_a to 0.9 and leave all other parameters values as in Table 5.4. We set $c_{Pa} = 0.3$ and vary c_{pA} from 0.45 to 0.55. The chaotic attractor on the vertical axis remains as in Figure 5.8. Figure 5.11 shows bifurcation diagrams for both species as c_{pA} is varied.

A chaotic attractor is seen to bifurcate into the positive cone as c_{pA} is lowered

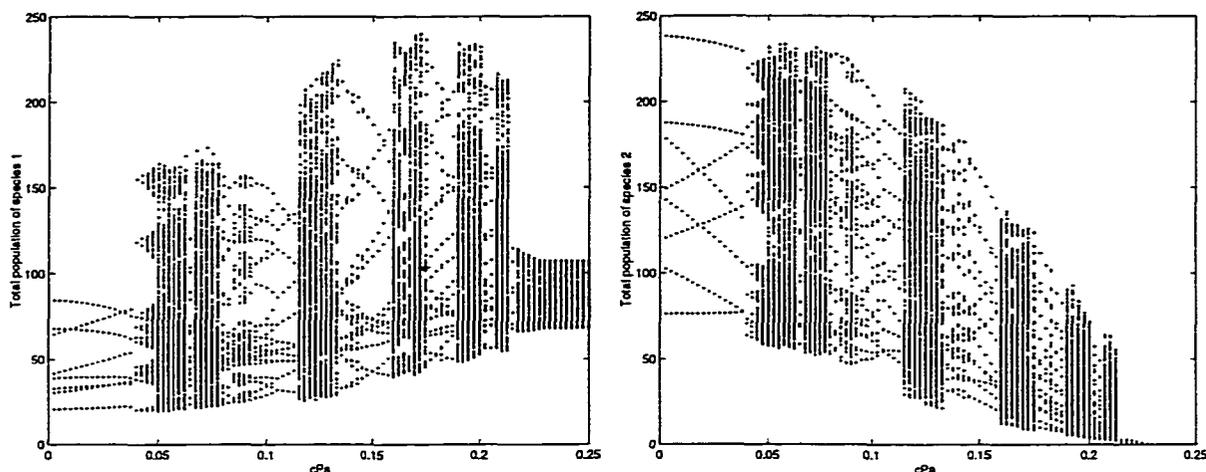


FIGURE 5.9. Bifurcation diagrams for both species as c_{Pa} ranges from 0 to 0.25. A wide range of dynamics are present in this parameter region, including aperiodic cycles and chaos. Species 2 goes extinct for values of c_{Pa} greater than 0.23. Other parameter values are given in Table 5.4.

through 0.54. For values of c_{pA} lower than this, the two species can coexist in non-equilibrium states. Figure 5.12 shows attractors for four different values of c_{pA} .

Periodic cycles are simply equilibria of composites of the underlying map, so bifurcations of periodic cycles can be approached analytically. In fact, general results exist regarding the existence and stability of such bifurcations [6, 9]. Aperiodic cycles and chaotic attractors are much more difficult to study, and there are open questions involving the occurrence of such bifurcations. The examples given in this section may shed some light on this problem.

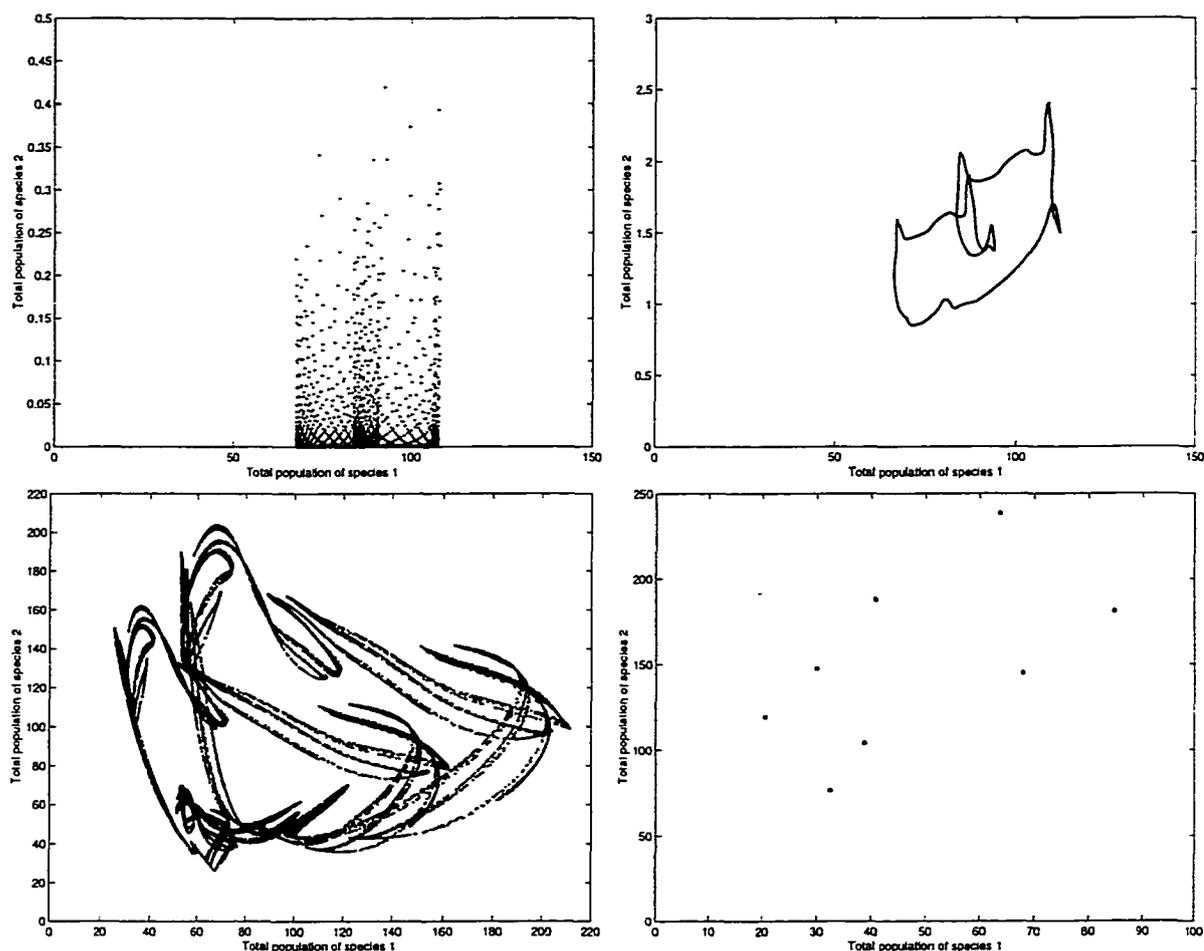


FIGURE 5.10. Orbits for four decreasing values of c_{P_a} . In the upper left, an orbit is seen slowly approaching the attracting invariant loop on the horizontal axis, with $c_{P_a} = .23$. In the upper right, the invariant loop has lifted slightly off of the horizontal axis at $c_{P_a} = .22$. In the lower left is a chaotic coexistence attractor at $c_{P_a} = 0.12$. In the lower right is a coexistence 8-cycle at $c_{P_a} = 0$. Other parameter values are given in Table 5.4.

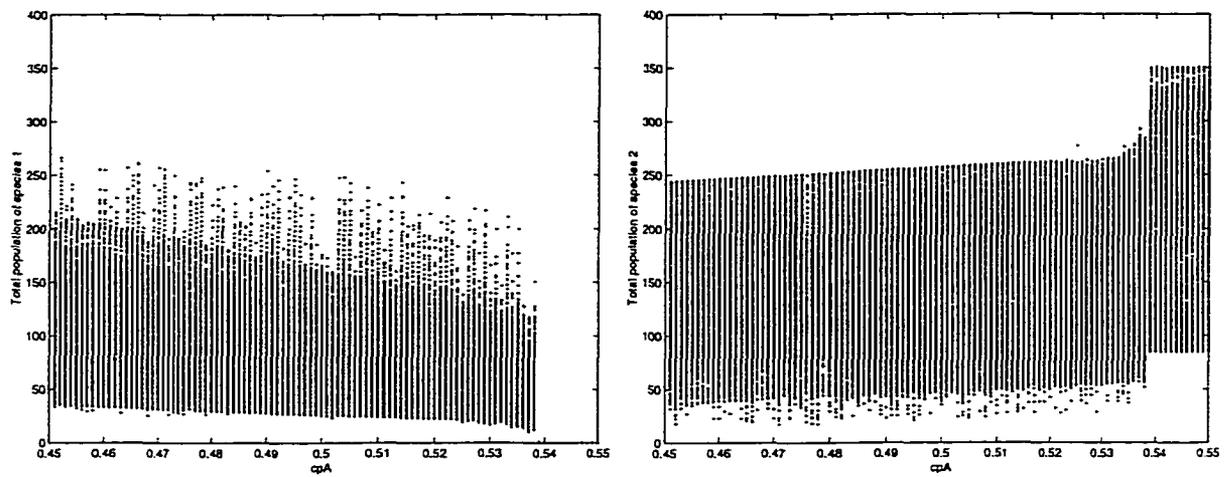


FIGURE 5.11. Bifurcation diagrams for both species as c_{pA} ranges from 0.45 to 0.55. Chaotic dynamics are present throughout this parameter region. Species 1 goes extinct for values of c_{pA} greater than 0.54. Other parameter values are given in Table 5.4, with the exceptions that $\mu_a = 0.9$ and $c_{P_a} = 0.3$.

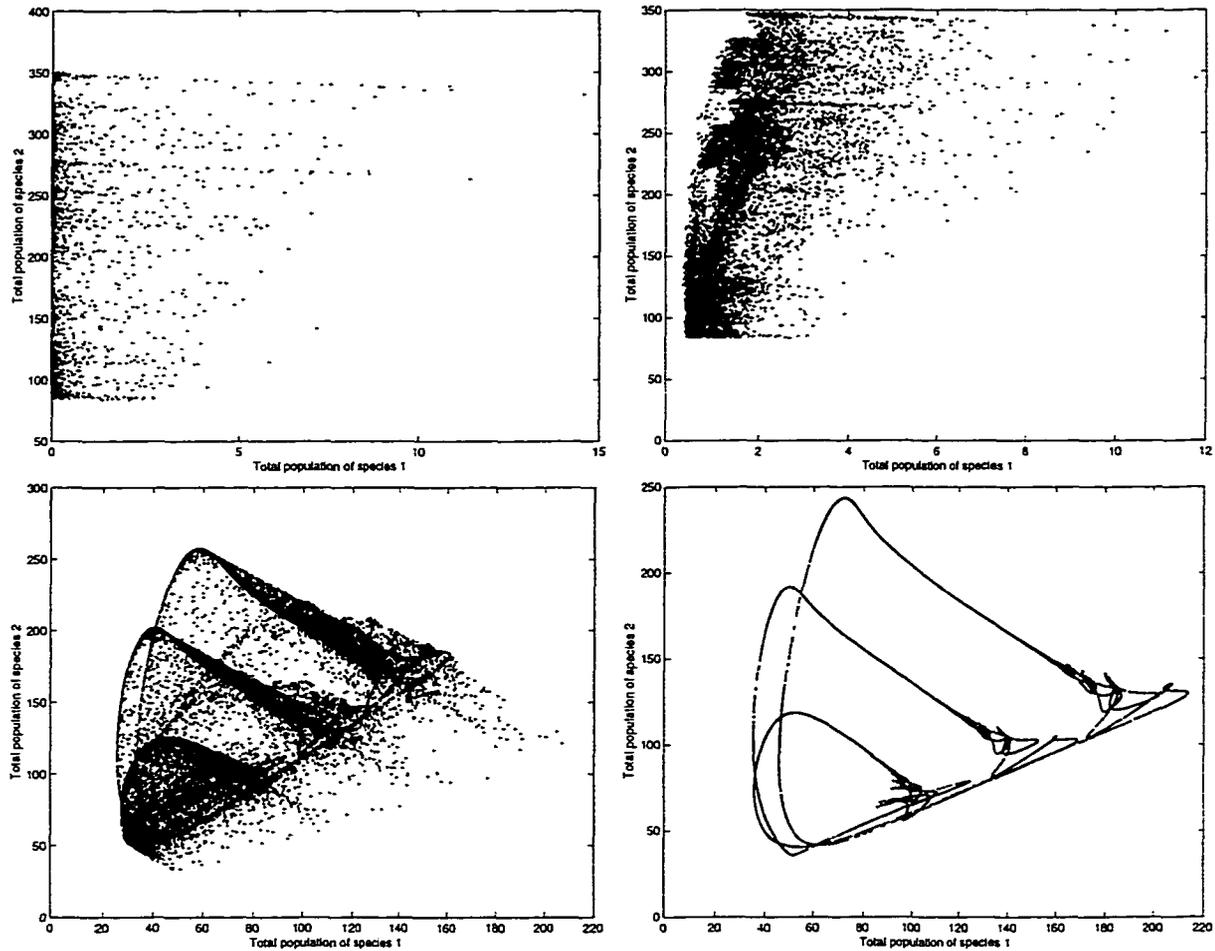


FIGURE 5.12. Orbits for four decreasing values of c_{pA} . In the upper left, an orbit is seen slowly approaching the chaotic attractor on the vertical axis, with $c_{pA} = 0.54$. In the upper right, the attractor has lifted slightly off of the vertical axis at $c_{pA} = 0.532$. In the lower left is a chaotic coexistence attractor with $c_{pA} = 0.5$. In the lower right is an odd coexistence attractor with $c_{pA} = 0.45$. Other parameter values are given in Table 5.4, with the exceptions that $\mu_a = 0.9$ and $c_{Pa} = 0.3$.

Chapter 6

CONCLUDING REMARKS

The question of competition between species is highly complicated, and mathematical models have been used extensively in this area. Simple models such as the Lotka-Volterra model provide answers to basic questions about long-term behavior of interacting species, but lack the necessary biological detail to approach specific problems. Further mathematical study of competition requires models that take into account more than total population numbers. Structured models allow for a breakdown of each species into different subclasses of individuals. Biologically, the interactions among these subclasses may vary considerably, and lead to population dynamics which the unstructured models cannot describe.

In this thesis we have studied a three life-stage model of two competing species. The model is capable of highly complex dynamics, and applies to a wide range of populations, making it ideal for a study of species interactions. Several single-species versions of the model have been used in conjunction with laboratory populations with very successful results, opening the possibility for future experimentation based on the competition model.

After an introduction to the model and associated terminology, chapter 3 examines equilibria in detail. We defined necessary and sufficient conditions for the existence and stability of axis equilibria. The question of positive equilibria is considerably more complicated. We studied bifurcations of axis equilibria by means of a Lyapunov-Schmidt expansion. By studying the equilibrium equations we showed that under certain simplifying assumptions there can exist at most one positive equilibrium. However, as shown in chapter 5, in general there can exist multiple positive equilibria.

Chapter 4 deals with persistence, a concept often applied to population mod-

els to determine conditions under which populations will survive indefinitely. The competition map was shown to be persistent with respect to the origin if either of the corresponding single-species maps is; that is, if either population can survive on its own, then at least one of the species will survive indefinitely, regardless of any competitive interactions. We also studied persistence with respect to the extinction states of either species, with the hope of determining conditions for species coexistence. Sufficient conditions were given for persistence with respect to both extinction states.

In chapter 5 we considered simulations involving specific parameter values, and presented several interesting examples in which the competition LPA model contradicts classical competition theory. The competition LPA map allows for coexistence in the presence of unstable positive equilibria, and also in the presence of stable axis equilibria. An example was given in which a robust coexistence state arises from an increase in inter-specific competition, in direct contradiction to the classical theory. Finally we considered examples involving non-equilibrium single-species dynamics, and showed bifurcations of periodic cycles, aperiodic cycles, and chaotic attractors from the axes into the positive cone.

Though this thesis presents a detailed study of the competition LPA model, there is much more that can be learned from the model. Because of the unusual competition dynamics presented in chapter 5, and also the potential for experimentation based on the model, more thorough study is warranted.

For example, the results presented regarding positive equilibria and persistence with respect to extinction states involve somewhat restrictive assumptions, and can possibly be extended to more general situations. The examples presented in chapter 5 cover but a tiny fraction of possible parameter values. In particular, larval recruitment and death rates were unchanged throughout chapter 5, and were assumed equal for both species. Further simulations will certainly uncover more unusual dynamics.

The examples given in section 5.3 exhibit bifurcations of invariant loops and

chaotic attractors from the axes into the positive cone. There are open questions involving the existence and stability of these types of bifurcations. While there are only specific examples presented here, they show that such bifurcations are commonplace in structured nonlinear models, and may shed some light on the problem.

In addition to further study of the competition LPA model specifically, work can be done on various extensions of the model. The single-species LPA model has been amended to study topics such as periodic habitat fluctuations and genetic variation; the competition model can be as well. Experiments involving flour beetles have shown that periodic flour volume can lead to highly unusual dynamics, including total population sizes much larger than those seen in constant habitats; this fact is predicted by the LPA model. The introduction of periodic habitat to the competition model may generate interesting results.

More importantly, the LPA model used in conjunction with experiments is a stochastic model; as the competition model considers questions of extinction and survival, stochasticity plays a crucial role. Any experimental work based on the competition model will therefore require a stochastic version. The coexistence states examined in sections 5.1 and 5.2 are quite robust, and should persist even in the presence of random fluctuations. However, the more exotic coexistence states exhibited in section 5.3 involve total populations as small as a few dozen, so that stochastic effects may cause extinction. A stochastic model will provide more information about the possibility of long-term coexistence in these situations.

The potential for experimentation based on the competition LPA model is strong. Costantino *et.al.* have conducted experiments based on the single-species LPA model for over a decade, using the flour beetle *Tribolium* [3, 4, 11, 14, 16]. Leslie *et.al.* used two species of *Tribolium*, *castaneum* and *confusum*, in their classic competition experiments [27, 31]. Single-species experiments have typically involved the manipulation of only *adult* numbers, and various strains of these species are available for which adults and pupae of different species are easily distinguishable. Such strains could be

used in a competition experiment involving manipulation of adult mortality.

For example, parameter values similar to those given in Table 5.2 could be easily simulated in a laboratory, with only small manipulation of adult numbers. The values given in Table 5.2 are very close to those that occur naturally in laboratory populations of flour beetles (rounded off for convenience). One notable assumption is the difference between inter-specific and intra-specific competition, represented by the inequalities $c_{Pa} < c_{pA} < c_{pa} < c_{PA}$. There is clearly a skew in favor of intra-specific competition. The competition model with these parameter values predicts coexistence; however, coexistence within laboratory populations of flour beetles has rarely been seen under any circumstances. Other experiments have shown that in reality the above inequalities are reversed, putting more weight on inter-specific competition; that is, adults of one species tend to develop a preference for pupae of the other species over their own. An experiment along those lines will provide insight into why flour beetles cannot generally coexist in a small habitat.

One final obvious model extension would include more than two species. With just *two* species, analytical results were difficult to obtain; a search for general conclusions involving an arbitrary number of species may not be worthwhile. However, simulations involving any number of species will be simple to carry out. As the simulations presented in chapter 5 show fascinating dynamics, simulations involving more species are certainly worth examination.

In conclusion, we have seen that the competition LPA model raises interesting challenges to classical competition theory and is therefore worthy of further detailed study. The inclusion of multiple life stages in competition models like the competition LPA model leads to dynamics far more complicated than those seen in simpler, classical models, and therefore much more remains to be learned from further examination of the model and its extended versions. Coupled with biological experiments, insights provided by the competition LPA model will lead to a deeper understanding of competition among species and the structure of biological communities and

ecosystems.

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