Defensive Strategies May Stabilize Unstable Competitive Systems: A Model of “Rock-Paper-Scissors-Lizard-Spock” in the Chemostat

Braselton JP* and Iacob IE
Department of Mathematical Sciences, Georgia Southern University, USA

Abstract

“Rock-paper-scissors” is a game played by two players to determine a single winner. In this paper, we state a continuous model of “rock-paper-scissors” in the chemostat and then generalize the model of “rock-paper-scissors” to a model of “rock-paper-scissors-lizard-Spock” in the chemostat that coincides with the biology of such relationships. The model we develop is based on a well-studied system of nonlinear differential equations that model these types of competitive relationships, which we then extend to give each organism a defense against its competitors in a “rock-paper-scissors-lizard-Spock” relationship. In a “rock-paper-scissors” relationship, it is rare to observe chaos/strange attractors. On the other hand, in a “rock-paper-scissors-lizard-Spock” relationship, chaos/strange attractors are typical. But, by giving a defense to a competitor, we numerically see that chaos/strange attractors can be eliminated from the system.

Keywords: Defensive strategies; Chemostat; Unstable competitive systems

Introduction

Traditionally, “rock-paper-scissors” is a children’s game in which rock attains paper (rock wins), paper covers rock (paper wins), and scissors cut paper (scissors win). When two individuals play the game with their hands, rock is represented by a fist, scissors by two fingers extended to represent a pair of scissors, and paper by a bitten hand. At the count of three, the two players extend their hands into one of the forms described. Rock breaks scissors so defeats scissors, scissors cut paper so scissors defeat paper, and paper covers rock so paper defeats rock. Viewing the relationship between the rock, paper, and scissors, each has an advantage over the other. Although “rock-paper-scissors” may be an amusing way to settle simple disagreements between two friends, “rock-paper-scissors” occurs in meaningful and interesting biological situations as well.

Kerr et al. [1], describe an interesting relationship between three populations of Escherichia coli that produce toxins against each other resulting in a biological “rock-paper-scissors” relationship. Their experiments in a chemostat environment showed that coexistence of all three populations could occur or that one or two of the populations might “win” and eliminate one or both other competitors. Generally, they saw that one population evolved (mutated) and dominated the mixture after one week. Roelke and Eldridge [2], expanded on these results in their article.

Another interesting study is by Karolyi et al. [3], who examine a similar problem and demonstrate that the competition is affected by the distribution of the competitors. They further show that by chaotic mixing of the nutrient (with density S(t)) in what follows) that there are oscillations in the population densities, which in this paper we interpret as limit cycles.

Competing species problems have been extensively studied theoretically and experimentally. We will not list an exhaustive reference of such studies but rather mention a few that seem particularly interesting in the context of the model we develop here. In a general sense, competing species in the chemostat are studied in Smith and Waltman [4]. Many variations of the basic model of competing species in the chemostat have been studied. For example, Li [5] studies a competition model with three competing species competing for three nutrients. His study is based on the experimental results seen by Husiman and Weissing [6], which shows that cyclic competition, such as in a “rock-paper-scissors” relationship, can result in periodic oscillations (or limit cycles). More recently, Cameron et al. [7], examine a “rock-paper-scissors” relationship involving a parasitic plant and experimentally show that coexistence of the three competitors occurs and confirm the conclusion with biological observations. Reichenbach et al. [8], obtain similar results. More recently, in Hsu and Roeger [9], use the May-Leonard competition models to study more complex competition relationships in the chemostat.

Unlike these previously studied models, we give each competitor in a “rock-paper-scissors-lizard-Spock” relationship a defense by giving it the ability to produce a toxin against its enemies (or competitors). The production of anti-competitor toxins is of interest when the weaker competitor can devote some of its resources to the production of a toxin (or inhibitor) against its competitors at some expense to its own growth. In Hsu and Waltman [6], this was modelled as a constant proportion of the resources. Biologically, this makes sense. For example, in Majeed et al. [10], it is documented that mixing strains of Escherichia coli, some of which produce bacteriocins, which are poisons that have a negative effect on competing organisms, the end result can lead to coexistence of all competitors. Inhibitors (including those added to the environment as well as those produced by the organisms) in the chemostat have been studied in Chao and Levin [11], Levin [12], Hsu and Waltman [13],

*Corresponding author: Jim Braselton, Department of Mathematical Sciences, Georgia Southern University, Statesboro, GA, USA, Tel: +19124781966; Fax: 9124780654; E-mail: jbraselton2@gmail.com

Received January 25, 2017; Accepted February 10, 2017; Published March 17, 2017

Citation: Braselton JP, Iacob IE (2017) Defensive Strategies May Stabilize Unstable Competitive Systems: A Model of “Rock-Paper-Scissors-Lizard-Spock” in the Chemostat. J Comput Sci Syst Biol 10: 019-027. doi:10.4172/jcsb.1000244

Copyright: © 2017 Braselton JP, et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.
Background of competition models in the chemostat

The chemostat is a basic model for competition in an open system and a model for the laboratory bioreactor. Such models have applications in ecology like modeling a simple lake or in biotechnology to model the commercial bioreactor. See Frederickson and Stephanopoulos [19], or Smith [20], for a general discussion of competition and Hsu et al. [14], Hsu and Luo [15], Hsu and Waltman [16], Lenski and Hattingh [17], and Braselton et al. [18].

Background of a model of “rock-paper-scissors” in the chemostat

To formulate a continuous model of a biological “rock-paper-scissors-lizard-Spock” relationship in the chemostat, we start with the basic models introduced by Smith and Waltman [4], that are summarized next and then the competition models and, specifically, the model when one competitor produces a toxin studied by Hsu and Waltman in [13]. The model state here is developed and analyzed analytically in [22]. We restate the model and our approach here is strictly numerical to help motivate the development of the model of “rock-paper-scissors-lizard-Spock” in the subsequent sections [22].

We restate these models of competition and then of “rock-paper-scissors” in the chemostat that are developed in [22] to motivate the model of a “rock-paper-scissors-lizard-Spock” in the chemostat where the competitors are given a mechanism (such as a toxin) to defend themselves against their competitors.

We begin with the standard model for two competing organisms in the chemostat. Let \( S(t) \) denote the concentration of a nutrient at time \( t \), and \( x_i(t) \) and \( x_j(t) \) denote the concentration of the two competing microorganisms. The basic model for competition in the chemostat between two competitors takes the form (note that \( \frac{d}{dt} = d \) ).

\[
S' = S(0) - S - D - \frac{m_i S}{a_i + S} - \frac{m_j S}{a_j + S} x_i \\
x_i' = x_i \left( \frac{m_S}{a_i + S} - D \right) \\
x_j' = x_j \left( \frac{m_S}{a_j + S} - D \right)
\]

where \( S(0) \) is the input concentration of the nutrient \( j \), \( D \) is the washout rate, \( m_i \), the maximal growth rates, \( a_i \), the Michaelis-Menten constants and \( n_i \), the yield constants. This is usually called the Monod Model or the model with Michaelis-Menten dynamics. Refer to Smith and Waltman [4], for extensive details.

When scaled, Equation 1 for two competitors in the chemostat as stated in [4] becomes

\[
S' = 1 - \frac{m_i S}{a_i + S} x_i - \frac{m_j S}{a_j + S} x_j \\
x_i' = x_i \left( \frac{m_S}{a_i + S} - 1 \right) \\
x_j' = x_j \left( \frac{m_S}{a_j + S} - 1 \right)
\]

The scaled competition models in the chemostat for when one competitor produces a toxin at a constant rate are studied in by Hsu and Waltman in [13]

\[
S' = 1 - \frac{m_i S}{a_i + S} x_i - \frac{m_j S}{a_j + S} x_j \\
x_i' = x_i \left( \frac{m_S}{a_i + S} - 1 - \gamma P \right) \\
x_j' = x_j \left( 1 - k \right) \frac{m_S}{a_j + S} - 1 \\
P' = k \frac{m_S}{a_j + S} x_j - \rho
\]

In Equations 2 and 3, \( k \) represents the fraction of nutrient compensation of the \( x_j \) organism allocated to the production of the toxin. \( P(t) \) represents the concentration of the toxin present. We assume that that interaction between the toxin and the affected microorganism is of mass-action form, \( -\gamma P x_i \). In both equations, \( \mu(t) \) denotes the concentration of the nutrient in the chemostat. In the first equation, \( x_i(t) \) and \( x_j(t) \) denote the concentration (or density) of the competitors. In the second equation, \( x_i(t) \) denotes the density of the toxin sensitive organism and \( x_j(t) \) denotes the density of the toxin producing organism. \( P(t) \) denotes the density of the concentration of the toxin in the chemostat.

Using the same notation as used with Equation 3, the model studied by Li [5], for three species competing for three essential (or complementary) nutrients in the chemostat is

\[
S'_i = D(S_0 - S_i(t)) - \sum_{j=1}^{3} \epsilon_{ij} \mu_i(S_i, S_j, S_k) x_i , \quad i, j, k = 1, 2, 3
\]

In Equation 4, \( D \) represents the ow rate of the chemostat, \( S_0 \) is the initial concentration of nutrient \( i \), \( \epsilon_{ij} \) is the content of nutrient \( j \) in species \( i \). Because we are assuming that all three nutrients are essential, the growth rate of species \( i \) is determined by the nutrient that is most limiting:

\[
\mu_i(S_i, S_j, S_k) = \min(f_i(S_i), f_j(S_j), f_k(S_k))
\]
where $f_i(S)$ is the growth rate of the species $i$ when nutrient with density $S_i$ is limiting. As described previously, we take

$$f_i(S) = \frac{m_i S_i}{a_i + S_i}$$

(6)

where the $m_i$ are the maximal growth rates and $a_i$ are the Michaelis-Menten constants, as in Hsu and Waltman [13], in Equations 2 and 3 that were described earlier.

**Stabilizing an Unstable System with Three Competitors Competing for Three Essential Nutrients**

Li’s [5] primary result essentially says that Equation 4 has limit cycles that result when competitor $x_i$ is the better competitor for nutrient $S_i$ and the weaker competitor for nutrient $S_j$ but if $x_i$ becomes limited by $S_i$, $x_i$ is the better competitor for nutrient $S_i$ and the weaker competitor for nutrient $S_j$ but becomes limited by $S_j$, and $x_j$ is the better competitor for nutrient $S_j$ and the weaker competitor for nutrient $S_i$ but becomes limited by $S_i$. Hulsman and Weissing [6], numerically illustrate the theorem in [6].

To be consistent with notation with [22] and [23], let $S(t)$, $1 \leq i \leq 3$, denote the concentration of the three nutrients at time $t$, $x_i(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_i(t)$, $x_j(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_j(t)$, $x_3(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_3(t)$. The concentrations of the toxin producing organisms are given by $P_j(t)$ (for $j$). An underlying assumption is that the chemostat is well-stirred so the nutrient is equally available to all competitors.

After incorporating toxin production in the same way as Hsu and Waltman in [13], Equation 4 becomes

$$S_j(t) = D(S_j^{(0)} - S_j(t)) \sum c_{ij} \mu_i (S_i, S_j, S_3) x_i, \quad j = 1, 2, 3$$

$$x_i(t) = x_i(t)(1 - k_i) \mu_i (S_i, S_j, S_3) - D - \gamma_i P_i$$

$$x_j(t) = x_j(t)(1 - k_i) \mu_i (S_i, S_j, S_3) - D - \gamma_i P_i$$

$$x_3(t) = x_3(t)(1 - k_i) \mu_i (S_i, S_j, S_3) - D - \gamma_i P_i$$

$$P_j(t) = k_i \mu_i (S_i, S_j, S_3) x_j - D P_j, \quad j = 1, 2, 3$$

In Equation 7, $S^{(0)}$ is the input concentration of the nutrient, $D$ is the washout rate and, as before $c_{ij}$ is the content of nutrient $j$ in species $i$, $S_j^{(0)}$ and $D$ are usually controlled by the experimenter although in real life situations such as studying how Escherichia coli interact in a (human) digestive system might not be controllable by the individual involved. The Equations 7 are usually called the Monod Model or the model with Michaelis-Menten dynamics as mentioned previously [4]. For the purposes, here $k_i$ represents the fraction of potential growth devoted to producing the toxin. If one had chosen to not start with a standard chemostat model, another sensible choice would have been starting with the May-Leonard competition equations as in Hsu and Roeger [9].

The interaction between the allelopathic agent (toxin producing organism) and the sensitive organism have been taken to be of mass action form, $\gamma P x_i$. This is common in modeling when an interaction depends on the concentrations.

**The case for non-constant $k$**

Both Karolyi et al. [3], and Reichenbach et al. [8] mention that interaction between the organisms was considered or observed. In particular, this would imply that the organisms have some ability to sense those around them. Through mechanisms known as “quorum sensing” bacteria are able to control the expression of their genes in response to density of other bacteria in their environment. Quorum sensing mechanisms have been demonstrated to play a role in the control of gene expression associated with diverse activities like bioluminescence, in massing to form biofilms, and the expression of the gene code for characters responsible for the pathogenicity of these organisms. For example, Sandoz et al. [24], describe a situation in which mutations of the bacteria Pseudomonas aeruginosa use quorum sensing to “cheat” and coexist with non-mutated strains of the bacteria. In a review on quorum sensing, Bassler [25] provides a large bibliography and reading list on this fascinating subject. In her review, she states that “Recent studies show that quorum sensing modulates both intra- and inter-species cell-cell communication.” In discussing a particular case she notes that “the capacity to respond to both intra- and inter-species signals could allow Harvey to know not only its own cell density, but also the relative frequency of bacteria of its type in mixed populations.”

Thus, if a bacterium has the ability to sense the current state of its habitat and the presence of other bacteria, we believe that it is reasonable to conclude that $k_i$ is not constant but rather $k_i = k_i(x_1, x_2, x_j)$ is a function of $x_i$. The problem is magnified so that little rigorous analytical results can be obtained for a general $k_i(x_1, x_2, x_j)$ and so it is necessary to consider special cases. We note first that there are two undesirable cases. If $k_i = 0$, no agent (toxin producing competitor) is produced and the weaker competitor becomes extinct. Similarly, if $k_i = 1$, all uptake is devoted to toxin production and none to growth, so again the competing organism cannot survive. $k_i(x_1, x_2, x_j)$ must fall between these extremes of 0 (no toxin produced) and 1 (the growth rate of the organism is then 0 and the organism faces extinction).

**My enemy’s enemy is my friend**

In a rock-paper-scissors relationship, a given organism is affected by both the organism affected by its toxin as well as by the organism that produces a toxin against the organism. For this choice of $k_i$ we consider “my enemy’s enemy is my friend” to be a natural strategy to consider. However, a given organism might want to detect the densities of both competitors. To take this into consideration in the competition model, the toxin producing organism, say $x_2$, might produce its toxin against the $x_3$ organism at a rate inversely proportional to the density of the $x_3$ organism because the (enemy of $x_3$) $x_1$ organism produces a toxin against the $x_3$ organism. Thus, when the $x_3$ organism decreases its toxin production against the $x_1$ organism, the $x_1$ organism (friend of $x_3$) is allowed to devote more of its resources to producing its toxin against the $x_3$ organism. For this choice of $x_i$ which then benefits the $x_3$ organism by lowering the $x_3$ population and less toxin is produced against the $x_1$ organism. On the other hand, when the $x_3$ population (density) is high but the $x_1$ population (density) is low, $x_3$ devotes more of its resources to producing its toxin against (its enemy) the $x_1$ organism. We illustrate the enemy/friend relationship in Table 1. We then continue a

| $x_i$ | Friends | Enemies |
|------|---------|---------|
| $x_1$ | $x_2$   | $x_3$   |
| $x_2$ | $x_3$   | $x_1$   |
| $x_3$ | $x_1$   | $x_2$   |

Table 1: Relationships between $x_1$, $x_2$, and $x_3$ in the context of a ”rock-paper-scissors” relationship. Observe that in a ”rock-paper-scissors” relationship, if $x_i$ is $x_j$’s ‘friend’ then $x_i$ is $x_j$’s ‘enemy’. Friendship is not transitive in the “rock-paper-scissors” relationship.
similar process for the other organisms. Paradoxically, $x_j$ is a friend of $x_i$ because $x_j$ produces a toxin against $x_i$, enemy $x_h$ who produces a toxin against $x_j$, even though $x_j$ produces a toxin against $x_i$. The same analogy carries over for $x_i$ and $x_j$.

We try to choose simple choices of $k_i (x_i, x_j, x_k)$ that take this into consideration. In our discussion, we choose

$$k_i (x_i, x_j, x_k) = \frac{a_i x_j}{x_i + x_j + x_k}$$

With $k_i (x_i, x_j, x_k, x_l)$ given by Equation 8, Equation 7 becomes,

$$x_1 (t) = x_1 (t) \left[ (1 - k_i (x_i, x_j, x_k)) x_i (S_i + S_j + S_k) - D \right]$$

Equation 9 looks the same as Equation 7 but we keep in mind that the $k_i (x_i, x_j, x_k)$ now are given by Equation 8.

**Stabilizing an Unstable System with Five Competitors Competing for Five Essential Nutrients**

**Rock-Paper-Scissors-Lizard-Spock**

Some believe that the game of “rock-paper-scissors” has biases that might determine the winner of the game. A generalization of the game is “rock-paper-scissors-lizard-Spock”, with rules that follow next. In the following, let $x_i$ denote the density of rock, $x_j$ the density of paper, $x_k$ the density of scissors, $x_l$ the density of Spock. Also, let $P_j$ denote the toxin (or inhibitor) by organism $x_i$. Refer to Figure 1 in the explanations that follow.

The rules of rock-paper-scissors-lizard-Spock are listed as follows. The corresponding toxin production effects are listed in the context of our notation as well (Table 2).

1. Scissors ($x_j$) cut paper ($x_i$). ($x_i$’s toxin, $P_j$, has a negative effect on the growth rate of $x_j$).
2. Paper ($x_j$) covers rock ($x_i$). ($x_i$’s toxin, $P_j$, has a negative effect on the growth rate of $x_j$).
3. Rock ($x_i$) crushes lizard ($x_k$). ($x_k$’s toxin, $P_i$, has a negative effect on the growth rate of $x_i$).
4. Lizard ($x_k$) poisons Spock ($x_i$). ($x_i$’s toxin, $P_i$, has a negative effect on the growth rate of $x_k$).
5. Spock ($x_i$) smashes (or melts) scissors ($x_j$). ($x_j$’s toxin, $P_j$, has a negative effect on the growth rate of $x_i$).
6. Scissors ($x_j$) decapitate lizard ($x_k$). ($x_k$’s toxin, $P_j$, has a negative effect on the growth rate of $x_k$).
7. Lizard ($x_k$) eats paper ($x_j$). ($x_j$’s toxin, $P_j$, has a negative effect on the growth rate of $x_j$).
8. Paper ($x_j$) disproves Spock ($x_i$). ($x_i$’s toxin, $P_i$, has a negative effect on the growth rate of $x_j$).

When you examine the rules of “rock-paper-scissors-lizard-Spock” carefully, some will say that it has some of the same flaws as “rock-paper-scissors” because the hand sign used in the game for “Spock” is difficult for many to implement quickly. The rules of rock-paper-scissors-lizard-Spock are summarized by Sheldon Cooper (played by Jim Parsons) on the popular American television show The Big Bang Theory [26]. Refer to Figure 2 and direct your browser to “https://www.youtube.com/watch?v=_PUEoDYpUyQ” to see the complete YouTube video.

Using Figure 1, we adjust Table 1 to mirror the “rock-paper-scissors-lizard-Spock” relationship. Observe that in a “rock-paper-scissors-lizard-Spock” relationship, if $x_j$ is $x_i$’s “friend” then $x_i$ is $x_j$’s “enemy”. Friendship is not transitive in the “rock-paper-scissors-lizard-Spock” relationship.

| $x_i$ | Friends | Enemies |
|------|---------|---------|
| $x_j$ | $x_j$, $x_k$ | $x_i$, $x_k$ |
| $x_j$ | $x_j$, $x_k$ | $x_i$, $x_k$ |
| $x_j$ | $x_j$, $x_k$ | $x_i$, $x_k$ |
| $x_j$ | $x_j$, $x_k$ | $x_i$, $x_k$ |
| $x_j$ | $x_j$, $x_k$ | $x_i$, $x_k$ |

Table 2: Relationships between $x_i$, $x_j$, $x_k$, $x_l$, and $x_m$ in the context of a “rock-paper-scissors-lizard-Spock” relationship. Observe that in a “rock-paper-scissors-lizard-Spock” relationship, if $x_j$ is $x_i$’s “friend” then $x_i$ is $x_j$’s “enemy”. Friendship is not transitive in the “rock-paper-scissors-lizard-Spock” relationship.

effect on the growth rate of $x_i$.

(9) Spock ($x_i$) vaporizes rock ($x_j$). ($x_j$’s toxin, $P_j$, has a negative effect on the growth rate of $x_i$).

(10) Rock ($x_j$) crushes scissors ($x_k$). ($x_k$’s toxin, $P_j$, has a negative effect on the growth rate of $x_j$).

When you examine the rules of “rock-paper-scissors-lizard-Spock” carefully, some will say that it has some of the same flaws as “rock-paper-scissors” because the hand sign used in the game for “Spock” is difficult for many to implement quickly. The rules of rock-paper-scissors-lizard-Spock are summarized by Sheldon Cooper (played by Jim Parsons) on the popular American television show The Big Bang Theory [26]. Refer to Figure 2 and direct your browser to “https://www.youtube.com/watch?v=_PUEoDYpUyQ” to see the complete YouTube video.

Using Figure 1, we adjust Table 1 to mirror the “rock-paper-scissors-lizard-Spock” relationship. Observe that “rock-paper-scissors-lizard-Spock” has the same friend paradox as “rock-paper-scissors” in that a given organisms’ “friends” are those who it produces a toxin against. That is, if $x_i$ is organism $x_j$’s friend, then $x_j$ is organism $x_i$’s enemy.

For five species competing for five essential nutrients, system (4) is adjusted to

$$S_i (t) = D (S_i - S_i (0)) + \sum c_i x_i (S_j (S_j + S_k + S_l + S_m)) x_i$$

$S_i (t) = x_i (0) [\mu_i (S_i) + S_j + S_k + S_l + S_m]$
The constants have the same interpretation as in system (4); \( \mu_i (S_1, S_2, S_3, S_4, S_5) = \min \{f_1(S_i), f_2(S_i), f_3(S_i), f_4(S_i), f_5(S_i)\} \)

In the absence of toxin production, Figure 3 shows that Equation 10 can exhibit chaotic behavior. In Figure 3, the values of the parameters used are \( D = .25, S_i(0) = 6, S_2(0) = 10, S_3(0) = 14, S_4(0) = 4, S_5(0) = 9, \mu_i = 1, \)

\[
C_v = \begin{pmatrix}
0.04 & 0.04 & 0.07 & 0.04 \\
0.08 & 0.08 & 0.1 & 0.08 \\
0.05 & 0.03 & 0.03 & 0.03 \\
0.07 & 0.09 & 0.07 & 0.07 \\
\end{pmatrix}
\]

and

\[
a_v = \begin{pmatrix}
0.39 & 0.34 & 0.24 & 0.23 \\
0.39 & 0.34 & 0.27 & 0.22 \\
0.39 & 0.34 & 0.27 & 0.22 \\
0.39 & 0.34 & 0.24 & 0.22 \\
0.39 & 0.34 & 0.22 & 0.20 \\
\end{pmatrix}
\]

We incorporate a constant toxin production into Equation 10 in the same way as Hsu and Waltman in [13]. Assuming constant toxin production, Equation 10 is adjusted to

\[
x_i(t) = x_i(0)(1 - k_i)\mu_i(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{12}P_2 - \gamma_{15}P_5
\]

\[
x_i(t) = x_i(0)(1 - k_i)\mu_i(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{23}P_3 - \gamma_{24}P_4
\]

\[
x_i(t) = x_i(0)(1 - k_i)\mu_i(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{31}P_1 - \gamma_{35}P_5
\]

\[
x_i(t) = x_i(0)(1 - k_i)\mu_i(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{41}P_1 - \gamma_{43}P_3
\]

\[
x_i(t) = x_i(0)(1 - k_i)\mu_i(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{52}P_2 - \gamma_{54}P_4
\]

where the \( k_i \) are constants.

Our computations indicate that Equation 14 can exhibit a wide range of behavior even assuming constant toxin production. For example, using the same parameter values as used in Figure 3, in Figure 4 we use constant toxin production as given in Equation 15.

\[
k_1 = .05, k_2 = .05, k_3 = .05, k_4 = .05, k_5 = .05
\]

\[
k_1 = .2, k_2 = .1, k_3 = .1, k_4 = .1, k_5 = .1
\]

\[
k_1 = .05, k_2 = .1, k_3 = .05, k_4 = .1, k_5 = .2
\]

\[
k_1 = .2, k_2 = .1, k_3 = .1, k_4 = .1, k_5 = .1
\]

and the \( \gamma_{ij} \) values are given by Equation 16.

\[
\gamma_{12} = .2, \gamma_{15} = .2, \gamma_{23} = .2, \gamma_{24} = .2, \gamma_{31} = .2, \gamma_{35} = .2, \gamma_{41} = .2, \gamma_{43} = .2, \gamma_{52} = .2, \gamma_{54} = .2
\]

\[
\gamma_{12} = .1, \gamma_{15} = .1, \gamma_{23} = .1, \gamma_{24} = .1, \gamma_{31} = .1, \gamma_{35} = .1, \gamma_{41} = .1, \gamma_{43} = .1, \gamma_{52} = .1, \gamma_{54} = .1
\]
Figure 3: The simulations indicate that a "rock-paper-scissors-lizard-Spock" relationship can result in chaos (or complex limit cycles) where all species coexist.

Figure 4: The figure illustrates typical results we obtained with our simulations. In (a), observe that two species coexist and the remaining become extinct. In (b), all species exist in the form of an apparent "small" limit cycle. (c) Two different species coexist and the remaining become extinct but different species than in (a). (d) The species coexist in the form of an apparent limit cycle.
In this paper, we have numerically analyzed a fifteen-dimensional nonlinear system of differential equations that models a "rock-paper-scissors-lizard-Spock" relationship. In previous models with fewer competitors or different assumptions, a reduction process was able to be carried out to reduce the dimension of the system. In the cases studied here, reducing the dimension of the studied systems is not possible because of the interpretation of the toxin producing agent, \( k = k_2 \), that is allowed to produce a toxin (inhibitor) against its competitors.

We have considered several extreme cases of the "cost" of the metabolic load of producing a toxin against a competitor. We examined the case when \( k = k_2 \) is constant and then two cases when \( k = k_2 \) was constant. To see the coexistence that is biologically documented, we used a non-constant \( k \), which indicates that when coexistence occurs in such situations, quorum sensing is involved in the biological relationship.

Our main results indicate that giving a competitor a defense might help stabilize an unstable system. It would be interesting if one could logically extend this result to other unstable competitive systems, such as social or societal ones. Of course, our assumptions are not exhaustive, but might indicate that in a real biological "rocks-papers-scissors" or "rocks-papers-scissors-lizard-Spock" situation the actual metabolic cost of producing a toxin is quite minimal. An interesting biological analysis might study the value of \( k = k_2 \), which we theorize is quite small, and examine the impact of the \( k = k_2 \) value, if there is any tangible impact on such biological relationships.

Next interesting steps might be to investigate the results seen by Kerr et al. [1], where they observed multiple mutations after several generations. Although incorporating genetics and non-constant \( k \) into the equations developed here would probably only result in numerical results, such results could have meaningful biological significance. Another interesting study would be to adjust the May-Leonard competition equations as in Hsu and Roeger [9], repeat the analysis, and analyze any unexpected results. The authors of this paper think that studying the situation when there are multiple nutrients that the competitors are competing for would be particularly interesting, especially if the availability of the nutrients was dependent on seasons.
Figure 5: With variable toxin production, typical simulations indicated that one species survives (dominates) and the remaining become extinct. (a) $x_2$ dominates. (b) $x_1$ dominates. (c) $x_4$ dominates. (d) $x_3$ dominates.

Figure 6: Stable coexistence can occur with variable toxin production in a “rock-paper-scissors-lizard-Spock” competitive relationship. In this case, $x_2$ and $x_4$ coexist.
or possibly even random. Perhaps, in those situations the models would show the complexity described by other authors.

Computational Notes

In our calculations, we used Mathematica Version 10 (www.wolfram.com) [27]. Primarily, we used Mathematica’s graphing capabilities and its numerical methods for solving systems of ordinary differential equations. Mathematica’s primary function for numerically solving (systems of) differential equations is NDSolve. Detailed information regarding NDSolve can be obtained from the Wolfram website. Alternatively, if you have access to Mathematica, enter the command ?NDSolve. In a broad sense, NDSolve uses a variety of numerical methods to attempt to solve (systems of) differential equations. Because our simulations are over “large” intervals,

We increased the accuracy goal and adjusted other NDSolve options to help assure that the results we illustrate here are (numerically) meaningful.

Our approach is quite general so other choices of the coefficient functions could be investigated with relative small changes in the Mathematica notebooks used in the calculations and plots here. Finally, we note that the positive constant in the denominator keeps the function differentiable at the origin. A smaller constant mimics stricter ratio dependence. In our cases $k_i(0,0,0)=0$: We also chose $q_i$ so that $0<\kappa_i<1$.

References

1. Kerr B, Riley MA, Feldman MW, Bohannan BJM (2002) Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418: 171-174.
2. Roelke DL, Eldridge PM (2010) Losers in the “rock-paper-scissor” game: The role of non-hierarchical competition and chaos as biodiversity sustaining agents in aquatic systems. Ecol Model. 221: 1017-1027.
3. Karolyi G, Neufeld Z, Scheuring I (2005) Rock-scissors-paper game in a chaotic ow: The effect of dispersion on the cyclic competition of microorganisms. J Theor Biol. 236: 12-20.
4. Smith HL, Waltman P (1995) The Theory of the Chemostat: Dynamics of Microbial Competition. Cambridge Studies in Mathematical Biology. Cambridge University Press, USA.
5. Li B (2001) Periodic coexistence in the chemostat with three species competing for three essential resources. Math Biosci. 174: 27-40.
6. Huisman J, Wiessing F (1999) Biodiversity of plankton by species oscillation and chaos. Nature. 402: 407-410.
7. Cameron DD, White A, Antonovics J (2009) Parasite-grass-forb interactions and rock-paper-scissor dynamics: predicting the effects of the parasitic plant Rhinanthus minor on host plant communities. J Ecol. 97: 1311-1319.
8. Reichenbach T, Mobilia M, Frey E (2007) Mobility promotes and jeopardizes biodiversity in rock-paper-scissors games. Nature. 448: 1046-1049.
9. Hsu SB, Roeger LI (2009) Heteroclinic cycles in the chemostat models and the winner-less competition principle. J Math Anal App. 360: 599-608.
10. Majeed H, Gillor O, Kerr B, Riley MA (2011) Competitive interactions in Escherichia coli populations: the role of bacteriocins. SMM Journal. 5: 71-81.
11. Chao L, Levin BR (1981) Structured habitats and the evolution of anti-competitor toxins in bacteria. Proc Nat Acad Sci. 75: 6324-6328.
12. Levin BR (1988) Frequency-dependent selection in bacterial populations. Philos Trans B Soc London. 319: 459-472.
13. Hsu SB, Waltman P (1998) Competition in the chemostat when one competitor produces a toxin. Japan J Indust Appl Math. 15: 471-490.
14. Hsu SB, Luo TK, Waltman P (1995) Competition between plasmid-bearing and plasmid-free organisms in a chemostat with an inhibitor. J Math Biol. 34: 225-238.
15. Luo TK, Hsu SB (1995) Global analysis of a model of plasmid-bearing, plasmid-free competition in a chemostat with inhibitors. J Math Biol. 34: 41-76.
16. Hsu SB, Waltman P (1997) Competition between plasmid-bearing and plasmid-free organisms in selective media. Chem Eng Sci. 52: 23-35.
17. Lenski RE, Hattingh SE (1988) Coexistence of two competitors on one resource and one inhibitor: a chemostat model based on bacteria and antibiotics. J Theor Biol. 122: 83-93.
18. Braselton JP, Abell ML, Braselton LM (2006) A model of allelepoy in the context of bacteriocin production. Appl Math Comput. 183: 916-931.
19. Fredericson AG, Stephanopoulos G (1981) Microbial competition. Science 213: 972-979.
20. Smith HL (1995) Monotone dynamical systems: an introduction to the theory of competitive and cooperative systems. Math Surv Monog, USA.
21. Hansen SR, Hubbell SP (1980) Single nutrient microbial competition: agreement between experimental and theoretical forecast outcomes. Science 20: 1491-1493.
22. Braselton JP, Abell ML, Braselton LM (2013) Rock-paper-scissors in the chemostat. J Comput Sci Syst Biol. 6: 118-131.
23. Braselton JP, Waltman P (2001) A competition model with dynamically allocated inhibitor production. Math Biosci. 173: 55-84.
24. Sando KM, Mitzimberg SM, Schuster M (2007) Social cheating in Pseudomonas aeruginosa quorum sensing. Proc Nat Acad Sci USA. 104: 15876-15881.
25. Bassler BL (1999) How bacteria talk to each other: regulation of gene expression by quorum sensing. Curr Op Microbiol. 2: 582-587.
26. https://www.youtube.com/watch?v=_PUEoDYpUyQ
27. Wolfram Research (2016) Mathematica 10.0.