Braselton and Iacob, J Comput Sci Syst Biol 2017, 10:2
DOI: 10.4172/jcsb.1000244

Journal of
Computer Science & Systems Biology

Research Article Open Access

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

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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 attens 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 attened 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 Eldrige [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. Reichenback 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],

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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

Hsu et al. [14], Hsu and Luo [15], Hsu and Waltman [16], Lenski and Hattingh [17], and Braselton et al. [18].

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 bio-reactor. See Frederickson and Stephanopoulos [19], or Smith [20], for a general discussion of competition and Hsu et al. [14], or Smith and Waltman [4], for a mathematical description of competition in the chemostat and detailed analysis of Equations 2 and 3 that follow. Refer to Hansen and Hubbell [21], for experimental verification of the match between theory and experiment in the chemostat.

In this paper, we consider a basic, resource-based model of competition of which the chemostat is the standard example. Such models have applications in ecology to model a simple lake, a simple digestive system, or in biotechnology to model the commercial bio-reactor. Experimental verification of the match between theory and experiment can be found in Hanson and Hubbel's study [21]. For a general discussion of competition models in the chemostat see Frederickson and Stephanopoulos [19], or Smith [20].

First, we revisit a model of three competitors competing for three nutrients and give each competitor a defense by giving it the ability to produce a toxin against its enemy (or enemies) in a "rock-paper-scissors" relationship. Next, we form a model of five competitors competing for five nutrients and give each competitor a defense by giving each competitor the ability to produce a toxin against its enemy (or enemies) resulting in a "rock-paper-scissors-lizard-Spock" relationship. The simulations we obtained for five competitors mirror those obtained for three competitors and indicate that giving competitors a defense may stabilize some unstable biological relationships.

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 we 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 $x_1(t)$ and $x_2(t)$ denote the concentration of the two competing microorganisms. The basic model for competition in the chemostat between two competitors takes the form (note that $' = d = dt$).

$$\begin{aligned} S' &= \left(S^{(0)} - S\right)D - \frac{m_1 S}{\alpha_1 + S}\frac{x_1}{\eta_1} - \frac{m_2 S}{\alpha_2 + S}\frac{x_2}{\eta_2} \\ x_1' &= x_1\left(\frac{m_1 S}{\alpha_1 + S} - D\right) \\ x_2' &= x_2\left(\frac{m_2 S}{\alpha_2 + S} - D\right) \end{aligned} \tag{1}$$

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, i=1, 2, 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

$$\begin{aligned} S' &= 1 - \frac{m_1 S}{\alpha_1 + S}x_1 - \frac{m_2 S}{\alpha_2 + S}x_2 \\ x_1' &= x_1\left(\frac{m_1 S}{\alpha_1 + S} - 1\right) \\ x_2' &= x_2\left(\frac{m_2 S}{\alpha_2 + S} - 1\right) \end{aligned} \tag{2}$$

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]

$$\begin{aligned} S' &= 1 - \frac{m_1 S}{\alpha_1 + S}x_1 - \frac{m_2 S}{\alpha_2 + S}x_2 \\ x_1' &= x_1\left(\frac{m_1 S}{\alpha_1 + S} - 1 - \chi P\right) \\ x_2' &= x_2\left((1-k)\frac{m_2 S}{\alpha_2 + S} - 1\right) \\ P' &= k\frac{m_2 S}{\alpha_2 + S}x_2 - P \end{aligned} \tag{3}$$

In Equations 2 and 3, k represents the fraction of nutrient compensation of the x_2 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, $-\gamma P x_1$. In both equations, $S(t)$ denotes the concentration of the nutrient in the chemostat. In the first equation, $x_1(t)$ and $x_2(t)$ denote the concentration (or density) of the competitors. In the second equation, $x_1(t)$ denotes the density of the toxin sensitive organism and $x_2(t)$ 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

$$\begin{aligned} S_j'(t) &= \mathrm{D}\left(S_j^{(0)} - S_j(t)\right) - \sum_{i=1}^{3} c_{ji}\mu_i\left(S_1, S_2, S_3\right)x_i, \quad j = 1,2,3 \\ x_i'(t) &= x_i(t)\left[\mu_i\left(S_1, S_2, S_3\right) - D\right], \qquad i = 1,2,3 \\ x_i(0) &> 0, \quad S_i(0) \geq 0, \qquad i, j = 1,2,3 \end{aligned} \tag{4}$$

In Equation 4, D represents the ow rate of the chemostat, $S_j^{(0)}$ is the initial concentration of nutrient j, c_{ji} 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:

$$\mu_i(S_1,S_2,S_3) = min\left(f_{1i}(S_1), f_{2i}(S_2), f_{3i}(S_3)\right) \tag{5}$$

where $f_{ji}(S_j)$ is the growth rate of the species i when nutrient with density S_j is limiting. As described previously, we take

$$f_{ji}(S_j) = \frac{m_{ji} S_j}{a_{ji} + S_j} \tag{6}$$

where the m_{ji} are the maximal growth rates and a_{ji} 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_1 is the better competitor for nutrient S_2 and the weaker competitor for nutrient S_1 but if x_1 becomes limited by S_3, x_2 is the better competitor for nutrient S_3 and the weaker competitor for nutrient S_2 but becomes limited by S_1, and x_3 is the better competitor for nutrient S_1 and the weaker competitor for nutrient S_3 but becomes limited by S_2. Hulsman and Weissing [6], numerically illustrate the theorem in [6].

To be consistent with notation with [22] and [23], let $S_i(t)$, $1 \le i \le 3$, denote the concentration of the three nutrients at time t, $x_1(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_3(t)$, $x_2(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_1(t)$, $x_3(t)$ the concentration of the organism susceptible to the toxin secreted by the organism with concentration $x_2(t)$. The concentrations of the toxin producing organisms are given by $P_i(t)$ (for x_i). 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

$$\begin{aligned}
S_j'(t) &= D\,(S_j^{(0)} - S_j(t)) - \sum_{i=1}^{3} c_{ji}\mu_i(S_1, S_2, S_3)x_i, \quad j = 1,2,3\\
x_1'(t) &= x_1(t)[(1-k_1)\mu_1(S_1, S_2, S_3) - D - \gamma_3 P_3]\\
x_3'(t) &= x_3(t)[(1-k_3)\mu_3(S_1, S_2, S_3) - D - \gamma_3 P_3]\\
x_3'(t) &= x_3(t)[(1-k_3)\mu_3(S_1, S_2, S_3) - D - \gamma_3 P_3]\\
P_j'(t) &= k_j\mu_j(S_1, S_2, S_3)x_j - DP_j, \qquad j = 1,2,3
\end{aligned} \tag{7}$$

In Equation 7, $S_j^{(0)}$ is the input concentration of the nutrient, D is the washout rate and, as before c_{ji} 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, $\gamma_i P_i x_j$. 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 Harveyi 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 $k_i = k_i(x_1, x_2, x_3)$ is a function of x_i. The problem is magnified so that little rigorous analytical results can be obtained for a general $k_i(x_1, x_2, x_3)$ 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. $k_i(x_1, x_2, x_3)$ 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_1, might produce its toxin against the x_2 organism at a rate inversely proportional to the density of the x_3 organism because the (enemy of x_1) x_3 organism produces a toxin against the x_1 organism. Thus, when the x_1 organism decreases its toxin production against the x_2 organism, the x_2 organism (friend of x_1) is allowed to devote more of its resources to producing its toxin against the x_3 organism (enemy of x_1), which then benefits the x_1 organism by lowering the x_3 population and less toxin is produced against the x_1 organism. On the other hand, when the x_2 population (density) is high but the x_3 population (density) is low, x_1 devotes more of its resources to producing its toxin against (its enemy) the x_2 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_j is x_i's "enemy". Friendship is not transitive in the "rock-paper scissors" relationship.

similar process for the other organisms. Paradoxically, x_2 is a friend of x_1 because x_2 produces a toxin against x_1 enemy x_3 who produces a toxin against x_1, even though x_1 produces a toxin against x_2. The same analogy carries over for x_2 and x_3.

We try to choose simple choices of k_i (x_1, x_2, x_3) that take this into consideration. In our discussion, we choose

$$k_1(x_1,x_2,x_3)=\frac{\alpha_1 x_2}{\beta_1+x_2+x_3}$$
$$k_3(x_1,x_2,x_3)=\frac{\alpha_3 x_1}{\beta_3+x_1+x_2} \quad (8)$$
$$k_3(x_1,x_2,x_3)=\frac{\alpha_3 x_1}{\beta_3+x_1+x_2}$$

With $k_i=k_i$ (x_1, x_2, x_3) given by Equation 8, Equation 7 becomes,

$$\begin{aligned}
&S_j'(t)=D(S_j^{(0)}-S_j(t))-\sum_{i=1}^{3}c_{ji}\mu_i(S_1,S_2,S_3)x_i, \quad j=1,2,3\\
&x_1'(t)=x_1(t)[(1-k_1(x_1,x_2,x_3))\mu_1(S_1,S_2,S_3)-D-\gamma_3P_3]\\
&x_2'(t)=x_2(t)[(1-k_2(x_1,x_2,x_3))\mu_2(S_1,S_2,S_3)-D-\gamma_1P_1] \quad (9)\\
&x_3'(t)=x_3(t)[(1-k_3(x_1,x_2,x_3))\mu_3(S_1,S_2,S_3)-D-\gamma_2P_2]\\
&P_j'(t)=k_j\mu_j(S_1,S_2,S_3)x_j-DP_j, \quad j=1,2,3\\
&x_i(0)>0, S_i(0)\geq 0, P_i(0)\geq 0, i=1,2,3
\end{aligned}$$

Equation 9 looks the same as Equation 7 but we keep in mind that the k_i (x_1, x_2, x_3) 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_1 denote the density of rock, x_2 the density of paper, x_3 the density of scissors, x_4 the density of lizard, and x_5 the density of Spock. Also, let P_i denote the toxin (or inhibitor) by organism xi. 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_3) cut paper (x_2). (x_3's toxin, P_3, has a negative effect on the growth rate of x_2.)

(2) Paper (x_2) covers rock (x_1). (x_2's toxin, P_2, has a negative effect on the growth rate of x_1.)

(3) Rock (x_1) crushes lizard (x_4). (x_1's toxin, P_1, has a negative effect on the growth rate of x_4.)

(4) Lizard (x_4) poisons Spock (x_5). (x_4's toxin, P_4, has a negative effect on the growth rate of x_5.)

(5) Spock (x_5) smashes (or melts) scissors (x_3). (x_5's toxin, P_5, has a negative effect on the growth rate of x_3.)

(6) Scissors (x_3) decapitate lizard (x_4). (x_3's toxin, P_3, has a negative effect on the growth rate of x_4.)

(7) Lizard (x_4) eats paper (x_2). (x_4's toxin, P_4, has a negative effect on the growth rate of x_2.)

(8) Paper (x_2) disproves Spock (x_5). (x_2's toxin, P_2, has a negative effect on the growth rate of x_5.)

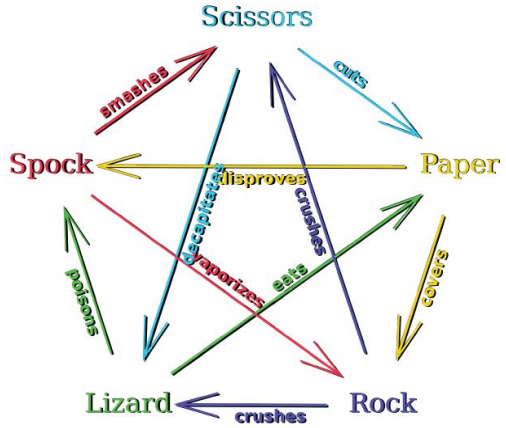

Figure 1: The figure illustrates the relationships between the competitors in "rock-paper-scissors-lizard-Spock.

x_i	Friends	Enemies
x_1	x_3, x_4	x_2, x_5
x_2	x_1, x_5	x_3, x_4
x_3	x_2, x_4	x_1, x_5
x_4	x_2, x_5	x_1, x_3
x_5	x_1, x_3	x_2, x_4

Table 2: Relationships between x_1, x_2, x_3, x_4, and x_5 in the context of a "rock-paper-scissors-lizard-Spock" relationship. Observe that in a "rock-paper-scissors-lizard-Spock" relationship, if x_i is x_j's "friend" then x_j is x_j's "enemy". Friendship is not transitive in the "rock-paper scissors-lizard-Spock" relationship.

(9) Spock (x_5) vaporizes rock (x_1). (x_5's toxin, P_5, has a negative effect on the growth rate of x_1.)

(10) Rock (x_1) crushes scissors (x_3). (x_1's toxin, P_1, has a negative effect on the growth rate of x_3.)

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_j is organism x_i's friend, then x_i is organism x_j's enemy.

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

$$\begin{aligned}
&S_j'(t)=D(S_j^{(0)}-S_j(t))-\sum_{i=1}^{5}c_{ji}\mu_i(S_1,S_2,S_3,S_4,S_5)x_i, \quad j=1,2,3,4,5\\
&x_i'(t)=x_1(t)[(\mu_i(S_1,S_2,S_3,S_4,S_5)-D], \quad i=1,2,3,4,5
\end{aligned}$$

$$x_i(0) > 0, S_i(0) \geq 0, \quad i, j = 1,2,3,4,5 \tag{10}$$

The constants have the same interpretation as in system (4); $\mu_i(S_1, S_2, S_3, S_4, S_5)$ is

$$\mu_i(S_1, S_2, S_3, S_4, S_5) = \min(f_{1i}(S_1), f_{2i}(S_2), f_{3i}(S_3), f_{4i}(S_4), f_{5i}(S_5))$$

In the absence of toxin production, Figure 3 show that Equation 10 can exhibit chaotic behaviour. In Figure 3, the values of the parameters used are D= .25,

$S_1^{(0)}=6$, $S_2^{(0)}=10$, $S_3^{(0)}=14$, $S_4^{(0)}=4$, $S_5^{(0)}=9$, $m_{ij}=1$,

$$C_{ij} = \begin{pmatrix} .04 & .04 & .07 & .04 & .04 \\ .08 & .08 & .08 & .1 & .08 \\ .1 & .1 & .1 & .1 & .14 \\ .05 & .03 & .03 & .03 & .03 \\ .07 & .09 & .07 & .07 & .07 \end{pmatrix} \tag{12}$$

and

$$a_{ij} = \begin{pmatrix} .39 & .34 & .3 & .24 & .23 \\ .39 & .34 & .3 & .27 & .22 \\ .39 & .34 & .3 & .27 & .22 \\ .39 & .34 & .3 & .24 & .22 \\ .39 & .34 & .3 & .22 & .20 \end{pmatrix} \tag{13}$$

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

$$S_j'(t) = D(S_j^{(0)} - S_j(t)) - \sum_{i=1}^{3} c_{ji}\mu_i(S_1, S_2, S_3, S_4, S_5)x_i, \quad j = 1,2,3,4,5$$

$$\begin{aligned}
x_1'(t) &= x_1(t)[(1-k_1)\mu_1(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{12}P_2 - \gamma_{15}P_5] \\
x_3'(t) &= x_3(t)[(1-k_3)\mu_3(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{31}P_1 - \gamma_{35}P_5] \\
x_3'(t) &= x_3(t)[(1-k_3)\mu_3(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{31}P_1 - \gamma_{35}P_5] \\
x_5'(t) &= x_5(t)[(1-k_5)\mu_5(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{52}P_2 - \gamma_{54}P_4] \\
x_5'(t) &= x_5(t)[(1-k_5)\mu_5(S_1, S_2, S_3, S_4, S_5) - D - \gamma_{52}P_2 - \gamma_{54}P_4] \\
x_i(0) &> 0, S_i(0) \geq 0, P_i(0) \geq 0, \qquad i = 1,2,3,4,5 \\
x_i(0) &> 0, S_i(0) \geq 0, P_i(0) \geq 0, \qquad i = 1,2,3,4,5
\end{aligned} \tag{14}$$

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	k_2	k_3	k_4	k_5
(a)	.05	.05	.05	.05	.05
(b)	.2	.1	.1	.1	.1
(c)	.05	.1	.05	.1	.2
(d)	.2	.1	.1	.1	.1

(15)

and the γ_{ij} values are given by Equation 16

	γ_{12}, γ_{15}	γ_{23}, γ_{24}	γ_{31}, γ_{35}	γ_{41}, γ_{43}	γ_{52}, γ_{54}
(a)	.2, .1	.1, .2	.2, .1	.1, .2	.2, .1
(b)	.1, .1	.1, .1	.1, .1	.1, .1	.1, .1

Figure 2: Sheldon (played by Jim Parsons) explains "rock-paper-scissors-lizard-Spock" on The Big Bang Theory.

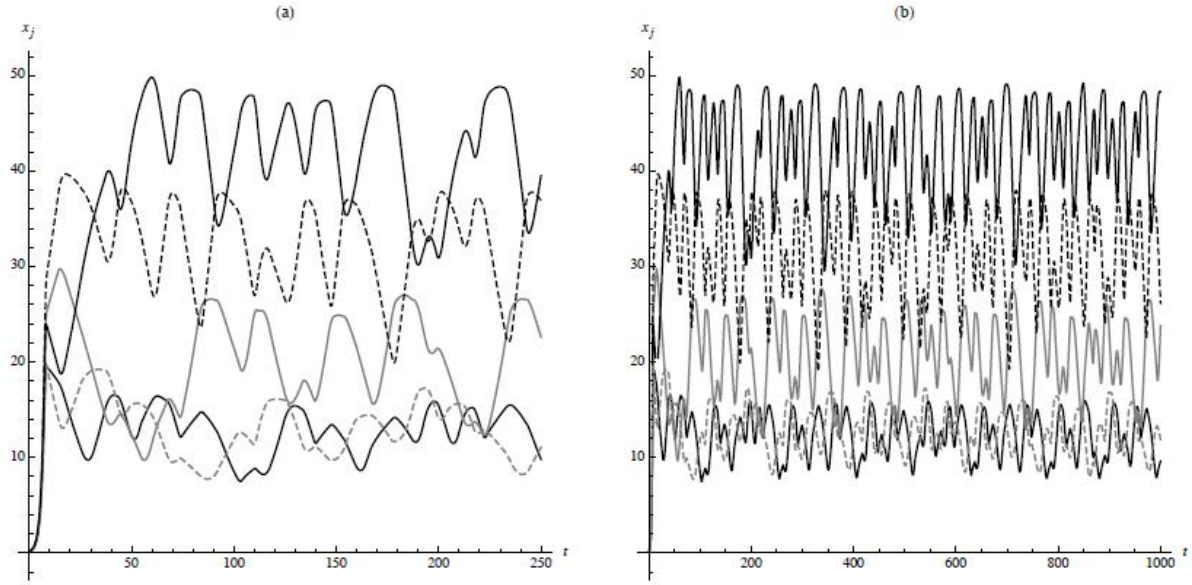

Figure 3: The simulations indicate that a "rock-paper-scissors-lizard-Spock" relationship can result in chaos (or complex limit cycles) where all species coexist.

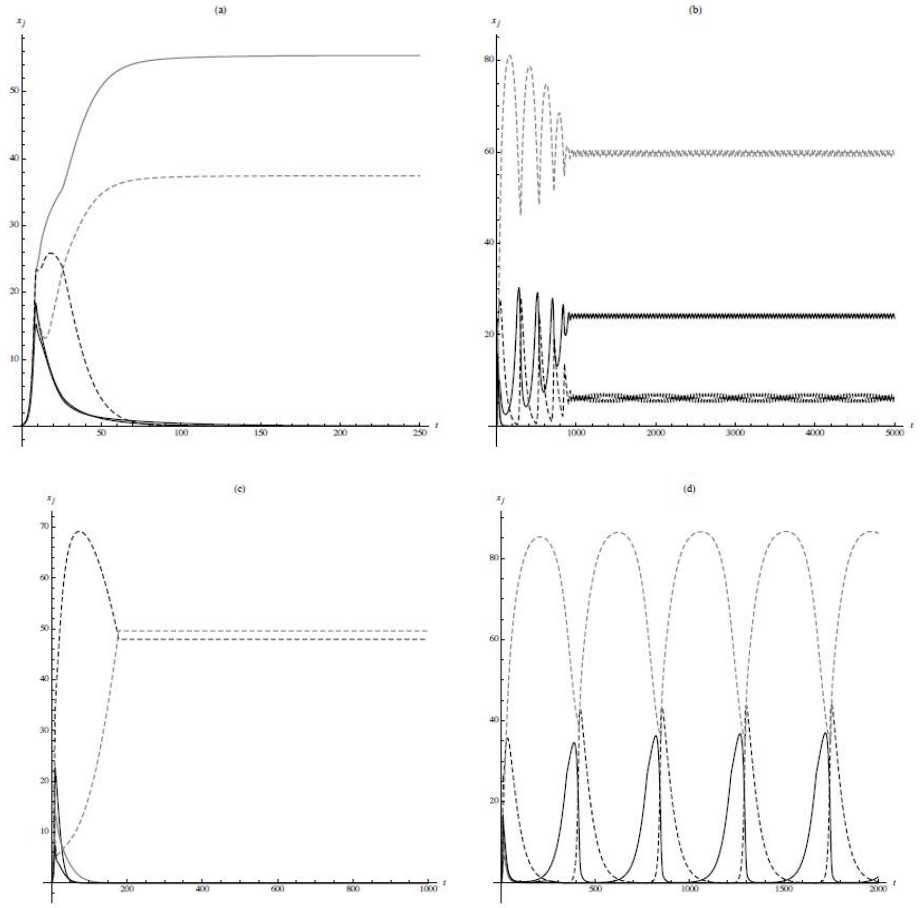

Figure 4: The figure illustrates typical results we obtained with our simulations. In (a), observe that two species coexist and the remaining become extinct. In (b), all species exist in the form of an apparent "small" limit cycle. (c) Two different species coexist and the remaining become extinct but different species than in (a). (d) The species coexist in the form of an apparent limit cycle.

(c)	.1, .1	.2, .2	.1, .1	.2, .2	.1, .1
(d)	.1, .1	.2, .2	.1, .1	.1, .1	.1, .1

(16)

In Figure 4, observe that constant toxin production can eliminate the chaotic behavior observed in Figure 3.

Non-constant *k*

For non-constant *k*, in the same manner as before, we try to choose simple choices of $k_i=k_i(x_1, x_2, x_3, x_4, x_5)$. Following the same approach as with Equation 8, we choose

$$k_1=\frac{\alpha_{13}x_3+\alpha_{14}x_4}{\beta_1+x_2+x_3+x_4+x_5}$$
$$k_2=\frac{\alpha_{21}x_1+\alpha_{25}x_5}{\beta_2+x_1+x_3+x_4+x_5} \quad (17)$$
$$k_3=\frac{\alpha_{32}x_2+\alpha_{34}x_4}{\beta_3+x_1+x_2+x_4+x_5}$$
$$k_4=\frac{\alpha_{42}x_2+\alpha_{45}x_5}{\beta_4+x_1+x_2+x_3+x_5}$$
$$k_5=\frac{\alpha_{51}x_1+\alpha_{53}x_3}{\beta_5+x_1+x_2+x_3+x_4}$$

With k_i given by 8, Equation 14 becomes

$$\begin{aligned}
&S_j'(t)=D(S_j^{(0)}-S_j(t))-\sum_{i=1}^{3}c_{ji}\mu_i(S_1,S_2,S_3,S_4,S_5)x_i, \quad j=1,2,3,4,5\\
&x_2'(t)=x_2(t)[(1-k_2)\mu_2(S_1,S_2,S_3,S_4,S_5)-D-\gamma_{23}P_3-\gamma_{24}P_4]\\
&x_2'(t)=x_2(t)[(1-k_2)\mu_2(S_1,S_2,S_3,S_4,S_5)-D-\gamma_{23}P_3-\gamma_{24}P_4] \quad (18)\\
&x_3'(t)=x_3(t)[(1-k_3)\mu_3(S_1,S_2,S_3,S_4,S_5)-D-\gamma_{31}P_1-\gamma_{35}P_5]\\
&x_4'(t)=x_4(t)[(1-k_4)\mu_4(S_1,S_2,S_3,S_4,S_5)-D-\gamma_{41}P_1-\gamma_{43}P_3]\\
&x_5'(t)=x_5(t)[(1-k_5)\mu_5(S_1,S_2,S_3,S_4,S_5)-D-\gamma_{52}P_2-\gamma_{54}P_4]\\
&P_j'(t)=k_j\mu_j(S_1,S_2,S_3,S_4,S_5)x_j-DP_j, \quad j=1,2,3,4,5\\
&x_i(0)>0, S_i(0)\geq 0, P_i(0)\geq 0, \quad i=1,2,3,4,5
\end{aligned}$$

where we keep in mind that $k_i=k_i(x_1, x_2, x_3, x_4, x_5)$. The choice of non-constant *k* results in significantly more complicated algebra and calculus computations.

An example

For our second model of quorum sensing and using Equations 18, we choose parameter values that are identical to those used in the first two examples to observe the similarities and differences between the three models. First, we set

$(D, S_1^{(0)}, S_2^{(0)}, S_3^{(0)}, S_4^{(0)}, S_5^{(0)})=(.25, 6, 10, 14, 4, 9)$ and $m_{ij}=1$. The c_{ij} values are given by Equation 12 and the a_{ik} values are given by Equation 13.

For our basic model of variable toxin production, the α_{ij} and β_i values used to create Figures 5 and 6 are given in Equation 19.

	$\alpha_{13}, \alpha_{14}, \beta_1$	$\alpha_{21}, \alpha_{25}, \beta_2$	$\alpha_{21}, \alpha_{25}, \beta_2$	$\alpha_{21}, \alpha_{25}, \beta_2$	$\alpha_{21}, \alpha_{25}, \beta_2$
(a)	.025, .025, .005	.075, .025, .005	.1, .25, .005	.05, .05, .005	.25, .1, .005
(b)	.04, .01, .005	.4, .6, .005	.025, .025, .005	.03, .02, .05	.02, .03, .005
(c)	.09, .01, .005	.04, .06, .005	.05, .05, .005	.03, .02, .005	.02, .03, .005
(d)	.05, .05, .005	.25, .05, .005	.05, .05, .005	.05, .05, .005	.05, .05, .005
	.25, .05, .005	.25, .05, .005	.25, .05, .005	.25, .05, .005	.25, .05, .005

A More General Choice for k_i

Of course, one can conceive of many other strategies that could be investigated. For example, Equations 8 and 17 are specific cases of a more general strategy that takes the form

$$k_1(x_1,x_2,x_3)=\frac{\alpha_{11}x_1+\alpha_{12}x_2+\alpha_{13}x_3}{\beta_1+\beta_{11}x_1+\beta_{12}x_2+\beta_{13}x_3}$$
$$k_2(x_1,x_2,x_3)=\frac{\alpha_{21}x_1+\alpha_{22}x_2+\alpha_{23}x_3}{\beta_2+\beta_{21}x_1+\beta_{22}x_2+\beta_{23}x_3} \quad (20)$$
$$k_3(x_1,x_2,x_3)=\frac{\alpha_{31}x_1+\alpha_{32}x_2+\alpha_{33}x_3}{\beta_3+\beta_{31}x_1+\beta_{32}x_2+\beta_{33}x_3}$$

that will be discussed in a future study. Incorporating Equation 20 into Equation 18 and examining various combinations and interpretations of the parameter values might result in an interesting study. For example, if the density of one of the organisms xi is large, a competitor with density x_j may increase its toxin production because it is already losing the competition and facing extinction.

Conclusion

In this paper, we have numerically analyzed a fiffteen-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, $k=k_i$, 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 $k=k_i$ is constant and then two cases when $k=k_i$ was not 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=ki, which we theorize is quite small, and examine the impact of the k=ki 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

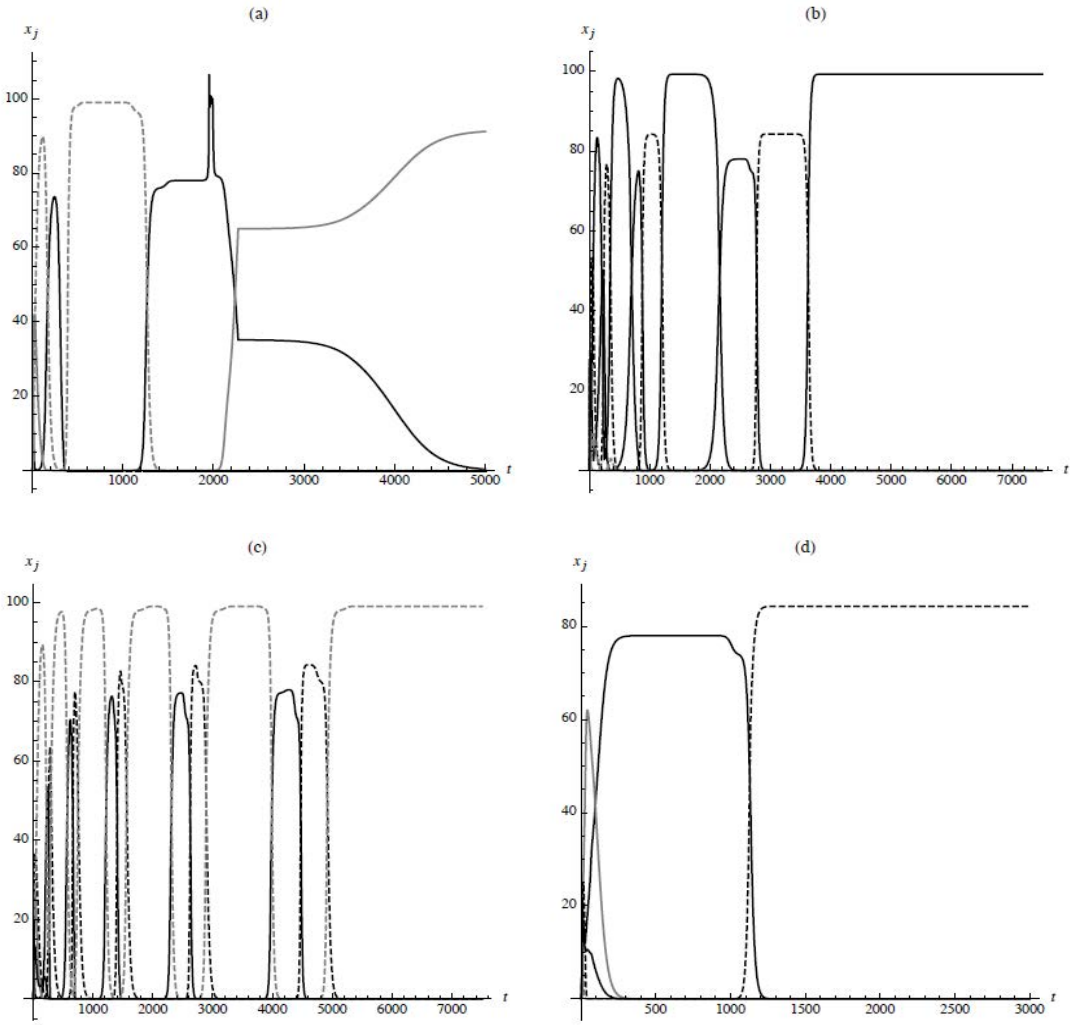

Figure 5: With variable toxin production, typical simulations indicated that one species survives (dominates) and the remaining become extinct. (a) x2 dominates. (b) x1 dominates. (c) x4 dominates. (d) x3 dominates.

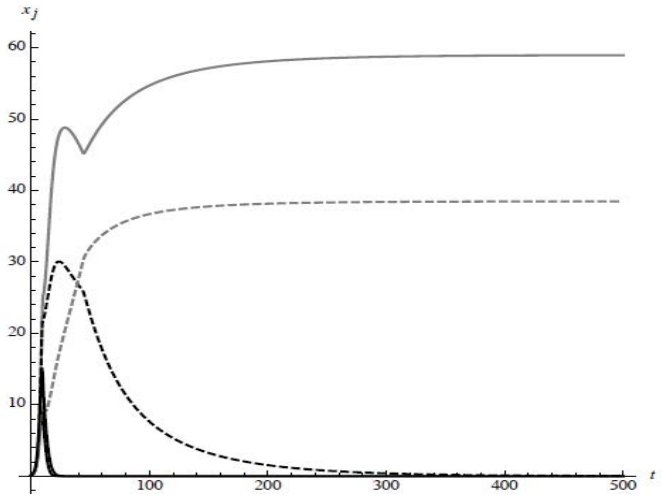

Figure 6: Stable coexistence can occur with variable toxin production in a "rock-paper-scissors-lizard-Spock" competitive relationship. In this case, x2 and x4 coexist.

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_{ij} (0, 0, 0)=0: We also chose α_j so that $0<k_{ij}<1$.

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