GLOBAL STABILITY OF CYCLES: LOTKA-VOLTERRA COMPETITION MODEL WITH STOCKING

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Abstract: In this article, we prove that in connected metric spaces k-cycles are not globally attracting (where $k \geq 2$). We apply this result to a two species discrete-time Lotka-Volterra competition model with stocking. In particular, we show that an k-cycle cannot be the ultimate life-history of evolution of all population sizes. This solves Yakubu's conjecture but the question on the structure of the boundary of the basins of attraction of the locally stable n-cycles is still open.

Keywords: global attractivity, cycles, Lotka Volterra, competition model, stocking.

1 INTRODUCTION

Mathematical models have provided important insights into the general conditions that permit the coexistence of competing species and the circumstances that lead to competitive exclusion [1, 2, 4, 6-18, 20-29]. The following mathematical model, System (1), describes the growth dynamics of two species (Species 1 and 2) in competition, where both species are governed by Ricker's model and Species 1 is being stocked at the constant per capita stocking rate α per generation [28, 29]:

$$\begin{array}{rcl} x_1(t+1) & = & x_1(t) \exp(p_1 - q_1(x_1(t) + x_2(t))) + \alpha x_1(t), \\ x_2(t+1) & = & x_2(t) \exp(p_2 - q_2(x_1(t) + x_2(t))). \end{array} \right\} (1)$$

For each Species $i \in \{1, 2\}$, $x_i(t)$ is its population size at generation t and p_i , q_i and α are positive constants. The effects of population density on the survival and growth of each individual species are modeled in System (1), by assuming that each per-capita growth rate, $g_i(x_1+x_2) = \exp(p_i-q_i(x_1+x_2))$, is a function of the total density of the two competitors. For species with closely spaced generations, System (1) without stocking reduces to the Lotka-Volterra differential equations [16]. Notice that System (1) has no isolated positive fixed points.

If the carrying capacity of Species 1, $\frac{p_1}{q_1}$, is less than that of Species 2, $\frac{p_2}{q_2}$, then Species 1 goes extinct whenever there is no stocking ($\alpha = 0$) [10]. Consequently, $\frac{p_1}{q_1} < \frac{p_2}{q_2}$ implies that the endangered Species 1 is the only species being stocked. Very small values of the constant per capita stocking rate α do not save the endangered species from extinction. However, it is possible for the endangered species without stocking to become the dominant species with stocking [28]. This reverse exclusion principle occurs whenever the constant per capita rate of stocking α is sufficiently large. Intermediate values of α promote the stable coexistence of the two competitors via the emergence of stable k-cycles. The boundary of

the basin of attraction of the k-cycles can be fractal in nature [28, 29].

Yakubu obtained parameter regimes for the occurrence of an attracting 2-cycle in System (1) and conjectured on the existence of globally stable 2-cycles [20, 21, 28, 29]. In this paper, we solve Yakubu's problem and we prove that in connected metric spaces, k - cycles are not globally attracting. Therefore, in System (1), an k - cycle cannot be the ultimate life-history of evolution of all population sizes.

2 NOTATIONS AND PRELIMINARIES

To write the reproduction function of System (1), we denote the vector of population densities $x(t) = (x_1(t), x_2(t))$ by $x = (x_1, x_2)$ and define the map

$$F:[0,\infty)\times[0,\infty)\to[0,\infty)\times[0,\infty)$$

by

$$F(x_1, x_2) = (x_1g_1(x_1 + x_2) + \alpha x_1, x_2g_2(x_1 + x_2))$$

where the variable planting coefficient α is positive and where $g_i(x_i) = \exp(p_i - q_i x_i)$ for each $i \in \{1, 2\}$. F^t is the map F composed with itself t times, and $F_j^t(x)$ is the j^{th} component of F^t evaluated at the point $x = (x_1, x_2)$ in \mathbb{R}^2_+ . Therefore, F^t gives the population densities in generation t. The set of iterates of the map F is equivalent to the set of all density sequences generated by System (1).

Define the single species, 1-dimensional maps $f_1: \mathbb{R}_+ \to \mathbb{R}_+$ and $f_2: \mathbb{R}_+ \to \mathbb{R}_+$ by $f_1(x_1) = x_1 \exp(p_1 - q_1 x_1) + \alpha x_1$ and $f_2(x_2) = x_2 \exp(p_2 - q_2 x_2)$, respectively. If Species j is missing in System (1), then F reduces to f_i , where $i \neq j \in \{1, 2\}$. The *only* positive fixed point of f_1 is $X_1 \equiv \frac{p_1 - \ln(1 - \alpha)}{q_1}$ while that of f_2 is $X_2 \equiv \frac{p_2}{q_2}$. Consequently, $(\frac{p_1 - \ln(1 - \alpha)}{q_1}, 0)$ and $(0, \frac{p_2}{q_2})$ are the non-zero boundary fixed points of F.

Since g_i is a strictly decreasing continuous function, $f_i(x_i) > x_i$ whenever $0 < x_i < X_i$ and $f_i(x_i) < x_i$ whenever $x_i > X_i$. Consequently, under f_i iterations,

 $I_i \equiv f_i([0, X_i])$ is a compact invariant interval in \mathbb{R}_+ . Every point either eventually enters I_i and stays or just reaches a limit in it. Thus, $I_i \equiv f_i([0, X_i])$ is a global attractor under f_i iterations. In fact, under f_i iterations, I_i is the dual attractor to infinity. Notice that the fixed point zero in I_i is a repellor. The largest attractor in the open interval $(0, \infty)$, denoted by T_i , is the dual attractor to the pair of repellors zero and infinity (under f_i iterations) [9]. In [28], Yakubu showed that when

$$p_1 < \frac{2}{(1-\alpha)} + \ln(1-\alpha) \tag{1}$$

then

$$T_1 = \{ \frac{p_1 - \ln(1 - \alpha)}{q_1} \},\,$$

and, when

$$p_2 \in (0,2),$$
 (2)

then

$$T_2 = \{ \frac{p_2}{q_2} \}.$$

Large values of p_1 and p_2 give rise to complex (chaotic) dynamics on the attractors T_1 and T_2 , respectively. We will use the following dominance criteria of Franke and Yakubu [9]:

Species 1 dominates $2whenever \max T_1 < \min T_2$,

and,

Species 2 dominates $1 whenever \max T_2 < \min T_1$.

A general result of Franke and Yakubu implies that the dominant species drives the dominated species to extinction in System (1) [9]. In fact, using this result we obtain the following:

Theorem 1: $X_2 \equiv \frac{p_2}{q_2}$ is a global attractor on the 2 – axis and Species 2 drives 1 to extinction whenever inequalities (1) and (2) hold and $X_1 < X_2$.

Theorem 2: $X_1 \equiv \frac{p_1 - \ln(1-\alpha)}{q_1}$ is a global attractor on the 1-axis and Species 1 drives 2 to extinction whenever inequalities (1) and (2) hold and $X_1 > X_2$.

Theorem 1 and Theorem 2 complement Theorem 5 in [28]. In Theorem 5, cited above, it is assumed that $q_1 = q_2$ and $e^{p_2} - e^{p_1} < \alpha$. Then from Theorem 1 we have $p_1 - \ln(1 - \alpha) < p_2$. Exponentiating both sides yields, $e^{p_1} < (1 - \alpha)e^{p_2} < (1 - \alpha)(\alpha + e^{p_1})$. Hence, $p_1 < \ln(1 - \alpha) < 0$ a contradiction.

In [28], Yakubu proved that there is no population explosion in System (1). Hence no point has an unbounded orbit. To understand the properties of System (1), we describe regions in $[0, \infty) \times [0, \infty)$ where each species increases or decreases in abundance.

If $x_1 + x_2 < X_i$ then $F_i(x_1, x_2) > x_i$, and, if $x_1 + x_2 > X_i$ then $F_i(x_1, x_2) < x_i$. That is, after one generation the population size of Species i increases [respectively, decreases] whenever the total population is smaller [respectively, bigger] than its carrying capacity. Consequently, we divide the first quadrant into three regions based on whether the first coordinate increases or decreases under F iterations.

Whenever $X_1 < X_2$, we let $A \equiv \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid x_1 + x_2 > X_2\}$, $B \equiv \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid x_1 + x_2 < X_1\}$ and $M \equiv \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid X_1 < x_1 + x_2 < X_2\}$. In region A [respectively, B], both coordinates of points decrease [respectively, increase] under F iteration and population sizes of Species 1 and 2 decrease [respectively, increase]. On the line segment $L \equiv \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid x_1 + x_2 = X_1\}$, after one generation, the first coordinate remains the same while the second coordinate increases under F iteration. That is, if a population size is on L, after one generation, the population size of Species 2 increases while that of Species 1 remains the same. In region M, after one generation, the first coordinate decreases while the second coordinate increases under F iteration, that is, the population size of Species 1 decreases

3 Boundary Fixed Points

The one-hump single species models, f_1 and f_2 , describe the dynamics on the axes and are capable of supporting period-doubling bifurcations including complex (chaotic) dynamics. In this section, we use f_1 and f_2 to study the ultimate life-history evolution of populations under F iterations.

We need the following result on the (local) stability of the boundary fixed points and periodic points.

Lemma 1: The boundary fixed points are (0,0), X_1 and X_2 .

- 1. The unstable fixed point (0,0) has unstable manifolds on the 1-axis and 2-axis.
- 2. If $X_1 < X_2$ then X_2 has a stable manifold in the interior of R_+^2 while X_1 has an unstable manifold in the interior of R_+^2 .
- 3. If $X_1 > X_2$ then X_1 has a stable manifold in the interior of R^2_+ while X_2 has an unstable manifold in the interior of R^2_+ .
- 4. If p₂ < 2, then X₂ has a stable manifold on the 2 − axis. As p₂ increases past 2, a period-doubling bifurcation occurs resulting in the birth of a stable 2 − cycle with stable manifold on the 2 − axis. Further increases in p₂ values with all other parameters fixed generate stable 2ⁿ − cycles (where n ∈ {2, 3, ...}) with stable manifold on the 2 − axis.
- 5. If $p_1 < \frac{2}{(1-\alpha)} + \ln(1-\alpha)$, then X_1 has a stable manifold on the 1-axis.

 As p_1 increases past $\frac{2}{(1-\alpha)} + \ln(1-\alpha)$, a period-doubling bifurcation occurs resulting in the birth of a stable 2-cycle with stable manifold on the 1-axis.

 Further increases in p_1 values with all other parameters fixed generate stable $2^n cycles$ (where $n \in \{2, 3, ...\}$) with stable manifold on the 1-axis.

To prove (1), (2) and (3) we compute the Jacobian matrix

$$DF(x_1, x_2) = \begin{pmatrix} (1 - q_1 x_1) \exp(p_1 - q_1 (x_1 + x_2)) + \alpha & -q_1 x_1 \exp(p_1 - q_1 (x_1 + x_2)) \\ -q_2 x_2 \exp(p_2 - q_2 (x_1 + x_2)) & (1 - q_2 x_2) \exp(p_2 - q_2 (x_1 + x_2)) \end{pmatrix}.$$

Hence,

$$DF(0,0) = \begin{pmatrix} \exp(p_1) + \alpha & 0 \\ 0 & \exp(p_2) \end{pmatrix},$$

$$DF(X_1) = \begin{pmatrix} 1 - (p_1 - \ln(1 - \alpha))(1 - \alpha) & -(p_1 - \ln(1 - \alpha))(1 - \alpha) \\ 0 & \exp(p_2 - q_2 \frac{(p_1 - \ln(1 - \alpha))}{q_1}) \end{pmatrix},$$

and,

$$DF(X_2) = \begin{pmatrix} \exp(p_1 - q_1 \frac{p_2}{q_2}) + \alpha & 0 \\ -p_2 & 1 - p_2 \end{pmatrix},$$

DF(0,0) has eigenvalues $\lambda_1 = \exp(p_1) + \alpha > 1$ and $\lambda_2 = \exp(p_2) > 1$ with corresponding eigenvectors $v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$ and $v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$, and this proves (1). $DF(X_1)$ has eigenvalues $\lambda_1 = 1 - (p_1 - \ln(1 - \alpha))(1 - \alpha)$ and $\lambda_2 = \exp(q_2(X_2 - X_1))$ with corresponding eigenvectors

$$v_1 = \begin{pmatrix} 1 \\ 0 \end{pmatrix}$$

and

$$v_2 = \begin{pmatrix} (p_1 - \ln(1 - \alpha))(1 - \alpha) \\ 1 - (p_1 - \ln(1 - \alpha))(1 - \alpha) - \exp(p_2 - q_2 \frac{(p_1 - \ln(1 - \alpha))}{q_1}) \end{pmatrix}$$

while $DF(X_2)$ has eigenvalues $\lambda_1 = 1 - p_2$ and $\lambda_2 = \exp(p_1 - q_1 X_2) + \alpha$ with corresponding eigenvectors $v_1 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$ and $v_2 = \begin{pmatrix} 1 - p_2 - (\exp(p_1 - q_1 \frac{p_2}{q_2}) + \alpha) \\ p_2 \end{pmatrix}$. $X_1 < X_2$ implies that the external eigenvalue of $DF(X_1)$, $\lambda_2 = \exp(q_2(X_2 - X_1)) > 1$ while that of $DF(X_2)$, $\lambda_2 = \exp(p_1 - q_1 X_2) + \alpha < 1$, this establishes (2). The proof of (3) is similar and is omitted. In System (1), each axis is F - invariant and on each i - axis the map F is f_i , a one hump map. In [22 - 24], R. May proved that f_2 undergoes period-doubling bifurcations. Proceeding exactly as in [22 - 24] one obtains that the map f_1 undergoes similar period-doubling bifurcations. This completes the proof.

Now, we consider System (1) where both species have the same carrying capacity $(X_1=X_2)$.

Lemma 2: In System (1), let $X_1 = X_2$.

- 1. F has a line of fixed points at L.
- 2. If $p_1 < \frac{2}{(1-\alpha)} + \ln(1-\alpha)$ and $p_2 < 2$, then $x_1 > 0$ or $x_2 > 0$ at the point (x_1, x_2) in R^2_+ implies that $\omega((x_1, x_2)) \subset L$.

Proof: Clearly, $X_1 = X_2$ implies System (1) has a line of fixed points at L. Consider the nonzero point (x_1, x_2) in \mathbb{R}^2_+ . On the i - axis, X_i is locally stable implies it is globally stable in $(0, \infty)$ [9]. Consequently, $p_1 < \frac{2}{(1-\alpha)} + \ln(1-\alpha)$ implies $\omega((x_1, 0)) = X_1 \subset L$ while $p_2 < 2$ implies $\omega((0, x_2)) = X_2 \subset L$. Now, we consider the interior point (x_1, x_2) with its entire orbit in the region below the line L, $B = \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid x_1 + x_2 < X_1\}$. Then for each $i \in \{1, 2\}$, $\{F_i^t(x_1, x_2)\}$ is an increasing sequence bounded above by the line segment L in \mathbb{R}^2_+ , and, $F^t(x_1, x_2)$ converges to a fixed point of F on the line L. Also, if the entire orbit of (x_1, x_2) is in the region above the line L, $A = \{(x_1, x_2) \in [0, \infty) \times [0, \infty) \mid x_1 + x_2 > X_1\}$, then $\{F_i^t(x_1, x_2)\}$, a decreasing sequence bounded below by the line segment L in \mathbb{R}^2_+ , converges to a fixed point of F on the line L.

Now we consider a positive point (x_1, x_2) with some iterate in both regions A and B. If there exists a positive integer T such that $F^t(x_1, x_2)$ remains in A (or B) for all $t \geq T$ —then proceeding exactly as before, we obtain convergence to the line segment L. If the positive point (x_1, x_2) is mapped in and out of region A (or B) indefinitely, then there exists a subsequence $\{t_i\}$ with $t_1 < t_2 < t_3 < \ldots$ such that each $F^{t_i}(x_1, x_2) \in B$. In [9], Franke and Yakubu proved that $F_2^{t_1}(x_1, x_2) < F_2^{t_2}(x_1, x_2) < F_2^{t_3}(x_1, x_2) < \ldots$ Consequently, the continuity of F and the boundedness of orbits force convergence to the line segment L.

Lemma 3: If a point (x_1, x_2) in \mathbb{R}^2_+ is not in the basin of attraction of any fixed point, then there exist nonnegative integers t_1, t_2 and T such that $F^{t_1}(x_1, x_2) \in A$ and $F^{t_2}(x_1, x_2) \in B$, where $t_1, t_2 > T$.

Proof: We will prove the result for region B. The proof for A is similar and is omitted. Recall that the first quadrant is F invariant. Suppose there exists a nonnegative integer T such that the orbit of $F^T(x_1, x_2)$ does not intersect region B.

Then the sequence of first coordinates, $F_1^T(x_1, x_2)$, $F_1(F^T(x_1, x_2))$, $F_1^2(F^T(x_1, x_2))$, ..., is a nonincreasing sequence bounded below by zero and hence has a limit denoted by \overline{x}_1 . Therefore, $F_1^t(x_1, x_2) - F_1^{t+1}(x_1, x_2) \to 0$ as $t \to \infty$. Hence, $F_1^t(x_1, x_2) + F_2^t(x_1, x_2) \to X_1$ as $t \to \infty$. This implies that $F_2^t(x_1, x_2) \to X_1 - \overline{x}_1$ as $t \to \infty$ and $F^t(x_1, x_2)$ is in the basin of attraction of a fixed point, a contradiction.

The following result (Corollary 1) is an immediate consequence of Lemma 3.

Corollary 1:

- 1. n-cycles of F in \mathbb{R}^2_+ have some points in region A and some in B where $n \geq 2$.
- 2. 2-cycles of F in R^2_+ have one point in region A and the other point in B.

4 2-Cycles of F (Yakubu's conjecture)

System (1) has no isolated positive fixed points. However, on solving the system of two equations $x_1(t+2) = x_1(t)$ and $x_2(t+2) = x_2(t)$ simultaneously where $x_1(t), x_2(t) \neq 0$ we obtain that System (1) has a 2-cycle at

$$\begin{pmatrix} \frac{2p_2 - \gamma q_2(1 + \exp(p_2 - \gamma q_2))}{q_2(\alpha + \exp(p_1 - \gamma q_1) + \exp(p_2 - \gamma q_2))} \\ \gamma - (\frac{2p_2 - \gamma q_2(1 + \exp(p_2 - \gamma q_2))}{q_2(\alpha + \exp(p_1 - \gamma q_1) + \exp(p_2 - \gamma q_2))}) \end{pmatrix}$$

where $\gamma = \frac{1}{q_1} \ln(\frac{-\beta \pm \sqrt{(\beta^2 - 4\delta c)}}{2\delta})$, $\beta = \alpha^2 - 1 + \exp(2(p_1 - p_2 \frac{q_1}{q_2}))$, $\delta = \alpha \exp(p_1 - 2p_2 \frac{q_1}{q_2})$ and $c = \alpha \exp(p_1)$ [28, 29]. Yakubu conjectured, in [29], that if $p_1 = \frac{3}{2}$, $q_1 = 1$, $q_2 = 1$ and $\alpha = \frac{1}{2}$ then System (1) has a globally stable positive 2-cycle in $(0, \infty) \times (0, \infty)$ whenever $X_1 \leq p_2 \leq 3.411822071$. Here, we use a very general result to show that in connected metric spaces, n - cycles of continuous maps are not globally stable whenever $n \geq 2$. Consequently, in Yakubu's conjecture, the positive 2 - cycle is locally asymptotically stable and not globally stable.

First, we introduce additional notation and definitions. Let $f: \mathbb{X} \to \mathbb{X}$ be a continuous map on a metric space \mathbb{X} and $x^* \in \mathbb{X}$ is a locally asymptotically stable fixed point of f. The basin of attraction of x^* , $W_f^S(x^*)$, is $\{x \in \mathbb{X} \mid \lim_{n \to \infty} f^n(x) = x^*\}$. If $y^* \in \mathbb{X}$ is a locally asymptotically stable k-periodic point of f then it is a fixed point of $g = f^k$ and its basin of attraction under g is $W_g^S(y^*)$. The basin of attraction of the cycle $O(y^*) = (y^*, f(y^*), ..., f^(k-1)(y^*)$ is given by $W^S(O(y^*)) = \bigcup_{j=0}^{k-1} W_g^S(f^j(y^*))$.

 $W_f^S(x^*)$ is an open f invariant set [6]. Furthermore, the complement of $W_f^S(x^*)$ in \mathbb{X} and the boundary of $W_f^S(x^*)$ in \mathbb{X} are f invariant sets [6. Next, we prove that stable period k-cycles are not globally stable in connected metric spaces.

Theorem 3. If $f: X \to X$ is a continuous map on a connected metric space X and $y^* \in X$ is a locally asymptotically stable k-cycle of f with $k \ge 2$, then $W^S(O(y^*)) \subsetneq X$.

Proof: For each $j \in \{0, 1, 2, ..., k-1\}$, $W_g^S(f^j(y^*))$ is a nonempty subset of \mathbb{X} and contains $f^j(y^*)$, since $g(f^j(y^*)) = f^j(y^*)$. Furthermore, the sets $W_g^S(y^*)$, $W_g^S(f(y^*)), ..., W_g^S(f^{k-1}(y^*))$ are disjoint. If $W^S(O(y^*)) = \mathbb{X}$, then \mathbb{X} is a disjoint union of nonempty open sets. This is impossible as \mathbb{X} is a connected metric space.

4.1 Example

In Yakubu's example with $p_1 = \frac{3}{2}$, $q_1 = 1$, $q_2 = 1$, $\alpha = \frac{1}{2}$ and $p_2 = 2.2$, System (1) has a locally asymptotically stable positive 2 - cycle at

$$\left\{ \left(\begin{array}{c} 0.4063\\ 1.9592 \end{array} \right), \left(\begin{array}{c} 0.3741\\ 1.6604 \end{array} \right) \right\}.$$

The positive 2-cycle is locally asymptotically stable and not globally stable in $(0,\infty)\times(0,\infty)$ (Theorem 3). In fact, X_2 is a saddle fixed-point and $X_1=1.5+\ln 2 < X_2=2.2$ implies that the stable manifold of X_2 is in the interior of R_+^2 (Lemma 1) while the unstable manifold is on the vertical axis. Figure 1 shows the stable manifold of X_2 (black region in $(0,\infty)\times(0,\infty)$) and the basin

of attraction of the positive 2-cycle (white region in $(0,\infty)\times(0,\infty)$). A lot of positive population sizes are in the stable manifold of the saddle fixed-point, $X_2=2.8$, and a lot more are in the basin of attraction of the positive 2-cycle (see Figure 1). FIG. 1: Stable manifold of X_2 (black region) and basin of attraction of the positive 2-cycle (white region). Horizontal axis is x_1 and vertical axis is x_2 . The parameter p_2 measures the level of intraspecific competition in Species 2. To study the changes in the basin of attraction of the positive 2-cycle as we increase the level of intraspecific competition, we keep the parameters p_1, q_1, q_2 , and α fixed at $p_1 = \frac{3}{2}, q_1 = 1, q_2 = 1$ and $\alpha = \frac{1}{2}$ and increase p_2 . At $p_2 = 3$, the system has a locally asymptotically stable positive 2-cycle at

$$\left\{ \left(\begin{array}{c} 0.5793 \\ 0.6103 \end{array} \right), \left(\begin{array}{c} 1.0799 \\ 3.7305 \end{array} \right) \right\}$$

coexisting with the saddle fixed-point at $X_2=3$. Figure 2 shows the stable manifold of X_2 (black region in $(0,\infty)\times(0,\infty)$) and the basin of attraction of the positive 2-cycle (white region in $(0,\infty)\times(0,\infty)$). Our numerical simulations show an increase in fragmentation of the basin of attraction of the 2-cycle as we increase p_2 . Constructing the geometric structure of the basin of attraction of the 2-cycle and deciding if it is a connected set are open questions that we are working on FIG. 2: Stable manifold of X_2 (black region) and basin of attraction of the positive 2-cycle (white region). Horizontal axis is x_1 and vertical axis is x_2 .

5 References

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